FLUCTUATIONS IN GROWTH AND YEAR-CLASS STRENGTH OF THE WALLEYE IN SAGINAW BAY

BY RALPH HILE

FISHERY BULLETIN 91

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The annual commercial take of Saginaw Bay walleyes averaged 1,149,000 pounds in 1891–1919, 652,000 pounds in 1920–31, 1,466,000 pounds in 1932–43, and only 396,000 pounds in 1944–51. The catch was under 100,000 pounds in each of the years 1949–51. Overfishing does not appear to have been a significant factor in the collapse of the fishery; many fishermen attribute the decline to pollution.

Age was determined for 3,652 fish and growth calculated for 2,427 specimens collected in 1926–30 and 1943. The average age (number of annuli) and the dominant age group at various seasons in 1926–30 were as follows: Spawning season—7.60 years, VII group; late spring—3.90 years, IV group; fall—1.28 years, I group. The percentage of legal fish (minimum total length, 15½ inches) in the catch of commercial impounding nets ranged from as high as 100 in the 1929 spawning season to as low as 1 in the fall in 1926 and 1928. The late-spawning-run sample of 1943 averaged 4.06 years old, was dominated by the III group, and included 96 percent legal-sized walleyes.

The strength of the year classes was well above average in 1919, 1925, 1937, and 1940, and weaker than average in 1917, 1924, 1928, 1938, and 1941.

Females were larger than males in all but the first 2 years of life, and walleyes of the 1943 collection had grown much more rapidly than fish captured in 1926–30. Times of attainment of legal length of 15½ inches (corresponding weight 1.12 pounds) were as follows: 1926–30 fish—males, early in fifth growing season and females in latter part of fourth; 1943 fish—males near the end and females past the middle of the third season. Calculated lengths and weights for latest years of life for which data were available were for 1926–30 males—14 years, 21.3 inches, 3.05 pounds; 1926–30 females—15 years, 25.0 inches, 4.91 pounds; 1943 males—10 years, 23.3 inches, 4.00 pounds; 1943 females—13 years, 29.5 inches, 8.14 pounds. Annual fluctuations in growth showed an irregular but pronounced downward trend in 1916–29. The growth advantage of the 1943 over the 1926–30 specimens was established in the early and middle 1930's.

The weight of walleyes in the combined samples from Saginaw Bay increased as the 2.989 power of the length. Walleyes taken in the fall were heavier than fish taken in late spring. Pronounced short-term fluctuations in weight during the late spring indicated heterogeneity of the stock with respect to the length-weight relation at that season. Sound walleyes were from 5½ to 6½ percent heavier than fish infected with *Lymphocystis*.

The percentage of males was higher in the younger than in the older age groups and during the spawning run than in late spring. A higher rate of exploitation for males than for females was suggested as a major cause of the change of the sex ratio with increase in age. Lengths at which 50 percent of the walleyes had reached maturity were about 15½ inches for males and 17 inches for females.

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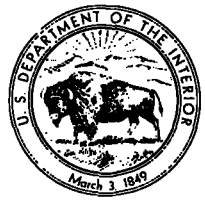

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STUDIES OF GEORGES BANK HADDOCK
Part II: Prediction of the Catch

By WILLIAM F. ROYCE and HOWARD A. SCHUCK

FISHERY BULLETIN 90

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

A prediction of the catch of the Georges Bank haddock, *Melanogrammus aeglefinus*, is possible because haddock have rather regular habits and because there are statistics on the haddock stocks. Analysis of the relation between catch and amount of fishing provides a statement of a relation that explains 83 percent of the variation in the catch of haddock over a period of 20 years. The catch depends primarily on the number of fish in year classes when they first enter the fishery, and on the amount of fishing. By use of formulas developed, predictions of catch were made for 1951 and 1952 that deviated 2.1 percent and 1.3 percent from actual landings in those years. These predictions are closer than can be expected in the long run. With a coefficient of variation of 8 percent, predictions should be within 8 percent of the actual catch about two-thirds of the time, and within twice that about 19 times out of 20.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

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STUDIES OF GEORGES BANK HADDOCK

Part II: Prediction of the Catch

By WILLIAM F. ROYCE, and HOWARD A. SCHUCK, *Fishery Research Biologists*

The Georges Bank haddock, *Melanogrammus aeglefinus*, has been the most important stock of fish available to New England fishermen for about 25 years. During this time it has produced annually as much as 223 million pounds (in 1929) and as little as 50 million pounds (in 1934); since its low point it has fluctuated from 78 million pounds to 122 million pounds. In addition to this fluctuation, there was a steady trend from 1942 through 1949 toward smaller catches per day's fishing. In 1950 the catch per unit of effort increased somewhat, but this was due to an especially large run of small scrod haddock and the market category of large haddock was scarcer than in any previously recorded year.

Such fluctuations in production have always been a cause of concern and have contributed to crises in the fishing industry. Some degree of correction of these fluctuations through proper methods of conservation may be possible. Meanwhile, a reliable prediction of the possible catch is of use to all branches of the fishing industry concerned with haddock.

GEORGES BANK HADDOCK POPULATION

A prediction of the catch of the Georges Bank haddock is possible because haddock have rather regular habits and because there are available accurate statistics on the haddock stocks. These statistics, developed as part of an intensive study of the population, include the total catch and the catch per day's fishing, in terms of pounds, numbers, numbers of each size, and pounds and numbers of each age group from each fishing area.[1]

Part of the regularity that makes a prediction possible is to be seen in table 1, which shows the weight of each age group landed in each year from 1931 to 1950. It may be noted that large catches of 2-year-olds in one year are usually followed by large catches of 3-year-olds in the next year and of 4-year-olds in the second year. For example, the 1939 year class appeared as 2-year-olds in the landings of 1941 and continued to rank high in the catches as 3-year-olds in 1942, as 4-year-olds in 1943, and so on. A small year class contributes consistently small catches. The 1942 year class, for instance, which made the smallest recorded contribution of only 1.2 million pounds as 2-year-olds in 1944, continued to contribute relatively little in succeeding years.

This tendency to consistently high or low catches, from year to year, from a given year class, is due to the facts that (1) the haddock on Georges Bank do not mix appreciably with haddock on the Nova Scotian banks (Schuck and Arnold, 1951), and (2) they remain the year round on Georges Bank or in the nearby Gulf of Maine, where they are available to the New England otter-trawl fleet all year (even though there are seasonal movements within this area and a seasonal cycle in the landings).

Some irregularities in the landings from a year class of haddock are due to changes in the amount of fishing from year to year. Such changes have occurred not only as vessels have been added to or removed from the fleet, but also as fishing for other species and on other banks has been more or less attractive than the Georges Bank fishery. We have obtained a measure of this amount of haddock fishing by calculating the catch per day's fishing for haddock on Georges Bank by a selected group of large otter trawlers fishing out of Boston. This measure provides an index of availability of the haddock that we believe to be independent of changes in the size or relative efficiency of vessels in the complete fleet. We then divided the year's landings by the average catch per day during the year. This has produced an estimate (table 2) of the amount of fishing in terms of standard days fished by these selected large trawlers.

[1] Some of these basic statistics have been published by Herrington (1948) and Schuck (1951); the rest are scheduled for publication.

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Method of analysis

Our approach is empirical. We have analyzed what has happened in the Georges Bank haddock population during a period of 20 years, and we assume that this analysis forms a reliable basis for what may be expected to happen. We have determined the relation of the catch of an age group to the previous year's catch from the same year class, and the amount of fishing in the two years. In statistical terms we have made a multiple-regression analysis of the catch in year $n+1$ (Y) as related to the amount of fishing in year n (X_1), the catch in year n (X_2), and the amount of fishing in year $n+1$ (X_3). We have followed Snedecor (1946, ch. 13) in our use of symbols and computational techniques.

TABLE 1.—*Landings of Georges Bank haddock, by age groups, 1931–50*

[In millions of pounds. Bold-face figures denote landings from the "large" 1930 year class, and italic figures denote landings from the "small" 1942 year class, which are mentioned in the text]

Year [1]	Landings in age group—									Total [2]
	1	2	3	4	5	6	7	8	9+	
1931	2.6	13.2	4.6	15.2	29.0	23.4	15.1	8.8	3.3	115.0
1932	.2	3.4	54.4	8.5	13.5	12.3	7.0	3.8	2.4	105.4
1933	.3	12.0	15.8	27.6	7.0	7.3	5.8	2.7	3.2	81.6
1934	.3	6.3	11.9	10.9	10.8	4.3	3.1	1.4	1.0	49.9
1935	1.1	20.3	20.9	11.5	10.3	9.5	2.5	2.4	.7	79.2
1936	.9	19.4	26.4	16.4	7.1	5.6	6.2	1.3	.8	84.0
1937	1.2	18.5	26.1	16.6	15.5	7.9	5.2	2.9	1.5	95.5
1938	1.1	34.2	20.5	12.8	8.8	7.1	4.9	1.7	1.2	92.4
1939	.7	22.1	44.8	16.4	8.2	4.6	4.3	1.9	1.6	104.5
1940	**2.2**	12.5	30.1	25.4	9.1	6.7	4.2	1.3	1.0	92.7
1941	.8	**36.0**	22.7	24.3	20.8	8.0	4.9	1.7	2.6	121.7
1942	.3	22.0	**36.2**	18.5	13.2	9.1	5.3	1.4	1.2	107.1
1943	.0	5.9	33.8	**23.1**	10.2	9.9	3.6	1.9	1.2	89.6
1944	.1	*1.2*	17.8	40.1	**20.6**	10.2	2.5	2.8	.8	96.0
1945	.1	13.9	*4.9*	19.4	21.6	**10.6**	4.8	1.7	1.3	78.3
1946	.2	11.3	35.3	*8.6*	20.5	16.5	**9.6**	1.7	.2	103.9
1947	.1	23.6	23.0	22.4	*8.3*	12.5	8.1	**4.4**	2.9	105.3
1948	.1	14.7	38.6	15.3	10.3	*5.5*	4.1	2.8	**2.5**	93.5
1949	.3	9.2	23.6	26.6	8.8	4.9	*5.3*	2.5	2.5	81.7
1950 [3]	.1	38.4	8.6	11.1	11.7	4.9	2.6	*1.4*	1.7	80.5
Total	13.4	337.8	500.0	370.5	265.3	180.7	106.8	50.5	33.7	1,857.8
Average	.6	16.9	25.0	18.5	13.3	9.0	5.3	2.5	1.7	92.9

[1] Because of habits of haddock, the years include 12 months beginning February 1 and ending January 31.
[2] Slight discrepancies in totals are caused by "rounding off."
[3] Partly estimated.

TABLE 2.—*Average daily catch and days fished for haddock on Georges Bank, 1931–50*

[Calculated on basis of fishing by a selected group of large otter trawlers]

Year	Average catch (pounds) per day	Days fished
1931	8,880	12,955
1932	11,572	9,110
1933	9,708	8,410
1934	10,308	4,839
1935	12,275	6,451
1936	13,500	6,224
1937	11,650	8,194
1938	11,733	7,874
1939	13,040	8,016
1940	12,836	7,218
1941	16,615	7,326
1942	18,682	5,732
1943	18,351	4,882
1944	16,973	5,656
1945	16,000	4,892
1946	14,264	7,283
1947	12,801	8,223
1948	12,123	7,714
1949	11,444	7,140
1950 [1]	14,074	5,721

[1] Partly estimated

Because haddock become increasingly available to the fishery until their third year, and then decline in abundance at a fairly constant rate (as indicated in table 1 by the average catch of each age group), it appeared necessary to make separate computations for relations involving the first three age groups. Accordingly we have related the catch of 2-year-olds to the previous year's catch of yearlings, of 3-year-olds to 2-year-olds, of 4-year-olds to 3-year-olds, and of 5-year-olds and older to the previous year's catch of 4-year-olds and older. We assume that the amount of fishing is the same for all groups.

The relations that we have found are expressed in the formulas and parameters listed in table 3. The closeness of the relations is indicated by the standard errors of estimate, the coefficients of variation, and the multiple-correlation coefficients. It is apparent immediately that the fluctuations in the catch of older fish are accounted for more accurately than those of the younger. The

formulas derived for the 3-year-olds, 4-year-olds, and 5-year-olds and older may each be judged statistically highly significant according to the value of the multiple-correlation coefficient. The value for 2-year-olds is not statistically significant, and the high value of the standard error of estimate in relation to the mean catch indicates that this formula does not account for much of the variation.

Particularly noteworthy is the close agreement between the actual and estimated total landings (fig. 1). The standard error of estimate is only 8 percent of the mean, and the correlation coefficient (r) is 0.912. The square of this (0.832) indicates that 83 percent of the variation in catch is associated with the previous year's catch and the amount of fishing in the previous and current years. It is noteworthy also that the standard error of estimate for the total (7.34) is far less than the standard error of estimate expected from a sum of the parts (15.03) if we assume that the parts are independent. Clearly, some relation among the catch of the different age groups is indicated and this is supported by general knowledge of the habits of the fish and the fishing fleet. It is well known that the young haddock tend to school more than the older individuals which are found more widely distributed over the Bank. Therefore, when there is a run of small haddock the fleet tends to concentrate on them at the expense of other areas. Thus, even though the regression for 2-year-olds is not a good one, it does not unduly diminish the accuracy of the total.

Some inconsistencies appear in the regression coefficients and in the intercept values in table 3. For example, the coefficients of X_1 vary from -4.2581 to $+1.0629$ and the coefficients of X_3 vary from -0.4715 to $+3.7930$, and in neither case do they change in relation to the age of the fish. This is not explainable with the data at hand, but it is believed that most of the variation arises because, as was indicated in the preceding paragraph, the assumption of equal distribution of the fishing effort is not a fact.

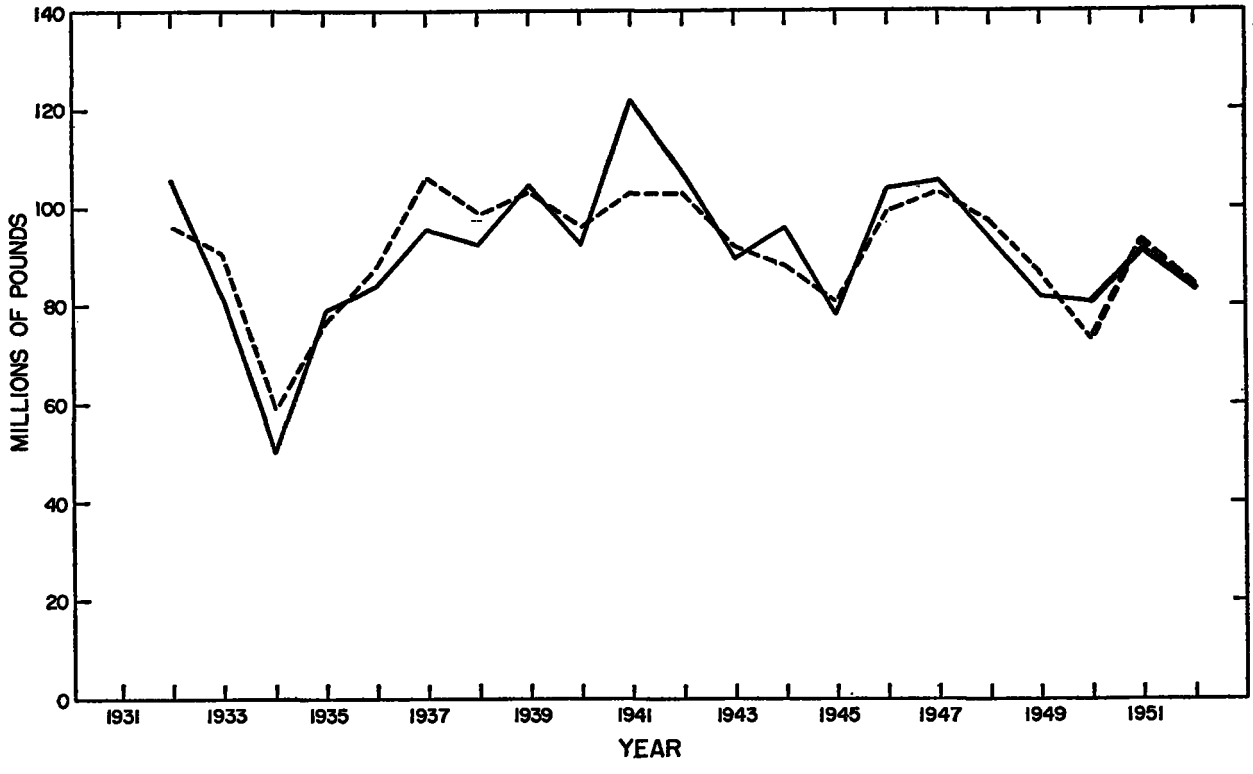

FIGURE 1.—Comparison of actual and estimated landings from Georges Bank.

TABLE 3.—*Multiple-regression equations and other statistics*

$\hat{Y}$=estimated catch in year $n+1$ (in hundreds of thousands of pounds).
X_1=amount of fishing in year n (in hundreds of days by standard trawlers).
X_2=catch in year n (in hundreds of thousands of pounds).
X_3=amount of fishing in year $n+1$ (in hundreds of days by standard trawlers).

Age group	Regression equation	Mean catch [1]	Standard error of estimate	Coefficient of variation (percent)	Multiple-correlation coefficient
2-year-olds	$\hat{Y}_2=209.8764-2.3987X_1+6.5582X_2+1.3446X_3$	17.09	10.84	63.4	0.375
3-year-olds	$\hat{Y}_3=-169.6105+1.0629X_1+0.7924X_2+3.3146X_3$	26.07	8.19	31.4	**.799
4-year-olds	$\hat{Y}_4=154.1039-0.8123X_1+0.4810X_2-0.4715X_3$	18.70	5.21	27.9	**.803
5-year-olds and older	$\hat{Y}_5=62.9507-4.2581X_1+0.5440X_2+3.7930X_3$	29.34	3.77	12.8	**.909
All ages	$\hat{Y}_T=0.5+\hat{Y}_2+\hat{Y}_3+\hat{Y}_4+\hat{Y}_5$	91.72	†7.34	8.0	**†.912

[1] Mean values (in millions of pounds) do not include the year 1931 and hence differ slightly from table 1.
**Statistically highly significant, that is, expected less than once in 100 times owing to chance.
† Standard error of estimate and simple correlation coefficient (r) have been computed from actual total catches and derived estimates.

Because of the great amount of labor required to determine the catch by age groups, it is worth while to consider the direct relation of total catch to the current findings of fishing and to the previous year's total catch and amount of fishing. This is readily computed, using the total figures from table 1 and the same data on the amount of fishing. The regression formula is

$$\hat{Y}=16.043-0.55200X_1+0.58078X_2+0.89318X_3$$

However, the standard of error of estimate becomes 11.24 or 12.25 percent of the mean, and the multiple-correlation coefficient (R) becomes 0.754. This value is statistically highly significant, but R^2 is 0.568, indicating that only about 57 percent of the variation in catch is accounted for by this shortcut method as contrasted with 83 percent when using the catch by age groups. We have therefore not further considered this method.

THE PREDICTION

The preceding formulas relate the catch to the amount of fishing in the same year, and to the catch and the amount of fishing in the preceding year. If the formulas are practicable, they can be used to predict the catch of a forthcoming year. But the proposed amount of fishing is best known by the people interested in haddock—the fishermen themselves, the vessel owners, and the primary dealers.

These men are in the best position to know about boats entering or leaving the fishery, whether the price of cod will be higher than the price of haddock (inducing some boats to fish cod instead of haddock), or whether there is an expanding market for haddock fillets (which will increase the demand and the price). From our observations the number of boats is usually the most important factor in determining the amount of fishing, and their number is fairly well known at the beginning of the year. Though in the absence of data on price trends, retirement of old vessels, and other factors pertaining to the fishery, any estimate of the amount of fishing one year hence is problematical.

A multiple prediction is needed that may be based on the best guess of the probable amount of fishing as well as greater and lesser amounts. For instance, in 1951 on the basis of some new vessels joining the fleet we guess that about 10 percent more fishing is expected than was done in 1950, and make an estimate accordingly. At the same time, we estimate the catch with 10 percent less fishing, with the same amount, with 20 percent more, and with 30 percent more. These amounts of catch are readily computed from the formulas by substituting the values for landings and amount of fishing in 1950 and the various amounts of fishing in 1951 (table 4). The result is a prediction of 93.4 million pounds with an increase of 10 percent in fishing, 88.8 million pounds with the same amount of fishing, 97.9 million pounds with an increase of 20 percent, and so on.

With 10 percent more fishing expected, the average catch per day will be slightly more (15,481 pounds) than in 1950 (14,074 pounds). Comparison of any column in table 4 with the average year-class catch in table 1 indicates also that there will be a much larger than usual proportion of 3-year-old haddock. These will average about 2 pounds each at the beginning of the year

and increase in weight about three-quarters of a pound during the year. Since scrod haddock are defined as those weighing from 1½ to 2½ pounds, this means a high proportion of fish in this market category.

TABLE 4.—*Predicted catch for 1951*

[In millions of pounds]

Age group	Predicted catch, assuming a change in fishing from 1950 of—				
	−10 percent	No change	+10 percent	+20 percent	+30 percent
1-year-olds	0.5	0.5	0.5	0.5	0.5
2-year-olds	14.9	15.6	16.4	17.2	18.0
3-year-olds	36.6	38.5	40.4	42.3	44.2
4-year-olds	12.5	12.2	12.0	11.7	11.4
5-year-olds and older	19.8	22.8	24.1	26.3	28.4
Total [1]	84.3	88.8	93.4	97.9	102.5
Average catch per day in thousands of pounds	16.4	15.5	15.9	14.3	13.8

[1] Slight discrepancies occur because of rounding off.

DISCUSSION AND SUMMARY

In our analysis we have considered only the matters having to do with the relation between catch and amount of fishing, or with the prediction of the catch. We have avoided many complications that go beyond the scope of this paper: these include an explanation of why a 10-percent change in the amount of fishing changes the total catch only about 5 percent, and why the catch of 4-years-olds decreases with an increase in the amount of fishing. Furthermore, our empirical approach omits any separate consideration of the interacting factors of growth, recruitment, and mortality. Better knowledge of these matters is desirable and will be sought in our continuing analysis of the haddock population.

Despite these qualifications we have a statement of a relation that explains 83 percent of the variation in the catch of haddock over a period of 20 years. It shows that the catch depends primarily on the number of fish in the year classes when they first enter the fishery, and on the amount of fishing. Even so, there is room for improvement in the prediction. The largest unexplained variation is associated with the estimates of the catch of the young year classes while they are entering the fishery. This estimate could be improved with special gear from research vessels to obtain an adequate estimate of the abundance of a year class before it is fully available to the fishery.

Any prediction based on an average, such as this, may be invalidated by long-term trends or unusual conditions not encountered during the study period. The effect of trends can be negligible if the latest data are included each year in the computation of the regression formulas. But nothing can be done about the unexpected. Catastrophic changes in environment, like the one that caused the mass mortality of the tilefish in 1882, have been known to occur in the vicinity of the New England banks. Such changes might cause unusual mortality among haddock, or change the migratory pattern and induce haddock to migrate between the Nova Scotian banks and Georges Bank in greater numbers; haddock might be subject to an epidemic of disease; there might be a recurrence of predators on the large haddock. Since things of this nature have not occurred in 20 years, the odds are against their occurrence.

ACCURACY OF PREDICTIONS FOR 1951 AND 1952

Because of delay in the appearance of this paper, it is possible to compare the results of predictions for 1951 and 1952 with the actual catches. It was predicted that in 1951, if a 10 percent increase in the amount of fishing occurred, the total catch of Georges Bank haddock would be 93.4 million pounds.

There was actually a 9.7 percent increase in the amount of fishing (Schuck 1952a), and a total catch of 91.3 million pounds, caught at a rate of 14,500 pounds per day. Approximately 43 percent of the landings were 2- to 2½-pound fish. With this amount of fishing the expected catch had been 93.2 million pounds,[2] caught at a rate of 14,800 pounds per day. And with any amount of fishing the 3-year-old fish (averaging 2 to 3¾ pounds each) were expected to predominate.

The prediction for 1952 was for less fishing on Georges Bank, owing to more abundant fish on the Nova Scotian Banks and fewer haddock on Georges (Schuck 1952b). The predicted catch was 79 million pounds with 20-percent less fishing, 84 million pounds with 10-percent less fishing, and 89 million pounds with the same amount of fishing. The prediction also stated that in 1952 a larger-than-usual proportion would be in the 2½- to 3½-pound size, and the ratio of market categories, "large" and "scrod" would return to near normal

[2] Recomputation has slightly changed Schuck's figures.

after the predominance of "scrod" in 1950 and 1951.

The exact prediction for 1952 was 84.5 pounds, allowing for a 9-percent decrease in effort. Pounds landed in 1952 were actually 83.4 million. Thus actual landings deviated from predicted landings by about 1.3 percent. The expected large proportion of 2½- to 3½-pound fish did not appear. A large run of 2-year-old scrod (many less than 1½ pounds) occurred, and the proportion of scrod haddock is perhaps larger than in any previous year of the fishery. This run of small haddock did not increase the total catch over the predicted catch because the fleet apparently fished for the small haddock in locations where the larger haddock are not found, and the catch of the larger haddock was less than expected.

These two predictions, off 2.1 percent from the actual landings in 1951 and off 1.3 percent in 1952, are gratifyingly close. They are closer than can be expected in the long run. With a coefficient of variation of 8.0 percent, predictions should be within 8.0 percent of the actual catch about two-thirds of the time, and within twice this about 19 times out of 20.

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FLUCTUATIONS IN GROWTH AND YEAR-CLASS STRENGTH OF THE WALLEYE IN SAGINAW BAY

By RALPH HILE, *Fishery Research Biologist*

Saginaw Bay normally stands second only to western Lake Erie in the commercial production of the walleye, *Stizostedion v. vitreum* (Mitchill), in the Great Lakes; and among the fishes of the bay, the walleye customarily ranks first in economic importance. Despite its importance, no previous major investigation of the Saginaw Bay walleye has been undertaken. Available information has been limited largely to that given in Hile's (1937) study of the relation between plantings of fry and the later abundance and production of walleyes, in Krumholz's (1945) investigation of the loss of weight on filleting, and in the account by Van Oosten, Hile, and Jobes (1946) of bathymetric distribution and vertical movements of walleyes in late spring, summer, and early autumn.

This report presents additional information on the Saginaw Bay walleye in such matters as age, growth, the length-weight relation, maturity, sex ratio, ... The 1926–30 collections which form the basic material for this study, were mostly made as opportunity presented itself during the course of experimental studies of pound-net meshes carried on cooperatively by the United States Bureau of Fisheries (since incorporated in the Fish and Wildlife Service) and the Michigan State Department of Conservation. It was the generous financial support of the latter agency that made the project possible.

In many respects the data leave much to be desired and the conclusions based on them are correspondingly restricted. It is believed, nevertheless, that the results presented here may provide reasonably sound, fundamental information on certain phases of the natural history of the walleye in Saginaw Bay, and offer a basis for the planning of continuing studies of population changes.

For the principal purpose of this publication—the presentation of basic information on the life history of the walleye—the 1926–30 samples would suffice. Data on the 1943 samples are included primarily to bring out the pronounced change in growth rate that occurred between 1929 and 1943.

I am much indebted to the following persons for the collection of materials and recording of field data: Dr. T. H. Langlois, the late Dr. Jan Metzelaar, Edward W. Ross, and Russell Robertson of the Michigan Department of Conservation, and Dr. Frank W. Jobes. Dr. L. A. Krumholz, Michigan Institute for Fisheries Research, assisted in the collection of the 1943 samples.

Dr. Hilary J. Deason determined ages for most of the fish collected in 1926 and prepared the original tabulations of relationships among total, fork, and standard lengths. He also had derived the body-scale equation used in this study from his earlier work with the Lake Erie walleye. Dr. John Van Oosten gave valuable advice during the course of this study. Dr. James W. Moffett and Dr. Paul H. Eschmeyer read the original manuscript.

Field operations were greatly facilitated by the cooperation of the Bay Port Fish Co., the R. L. Gillingham Fishing Co., and conservation officer A. J. Neering.

MATERIALS AND METHODS

COLLECTION OF MATERIALS

Investigation of age and growth rates of the Saginaw Bay walleye was based on the determination of the age of 3,652 fish and the computation of individual growth histories (from scale measurements) of 2,427 specimens collected in 1926–30 and 1943 as recorded in table 1.

A lack of sex data is principally responsible for the lower number of fish employed in the growth studies than in age studies. In the collections of May 15 to June 18, 1929, sex was determined only for the larger, mature walleyes; in these samples, therefore, only fish older than the VI group (at which age nearly all or all fish are mature) could be used for the investigation of growth. Sex was determined for fewer than half the fish collected in 1928, but there was no selection on the basis of maturity; hence, no blocks of age groups were excluded.

TABLE 1.—*Ports and dates of collection of Saginaw Bay walleyes used in age and growth studies*

Dates of collection	Port	Number of fish used for study of—	
		Age composition	Rate of growth
Nov. 11–20, 1926	Bay City	305	304
Mar. 30–Apr. 16, 1927	Bay Port	127	113
Nov. 5–12, 1928	Bay City	119	52
Apr. 4–23, 1929	Bay Port	570	548
May 15–June 18, 1929	Bay Port	1,183	64
Apr. 30–June 20, 1930	Bay Port	1,060	1,060
May 4, 1943	Bay Port	288	286
Total		3,652	2,427

In the spawning-run samples of 1927 and April 4–23, 1929, all walleyes younger than the VI group were excluded from the growth materials as probably not representative by reason of selection on the basis of maturity (spawning runs are made up almost entirely of mature fish). The 1943 collection, although taken at a time when numbers of fish had not yet spawned, could not be considered a true spawning-run sample since the catch included a considerable number of immature fish. In this collection all fish were used in the study of growth except the II-group individuals which were held to be of uncertain status because of their small number.

The numbers of walleyes employed in the study of other phases of the life history—length-weight relation, ratios of the various length measurements, sex ratio, maturity—varied according to the materials available or required.

All samples were captured by experimental or commercial impounding nets (pound nets and shallow trap nets) of 2- to 3-inch mesh, extension measure, as manufactured.[1]

RECORDS FOR INDIVIDUAL FISH

The following procedures were used in compiling length, weight, and maturity records for individual fish.

Length

The method of measurement differed from sample to sample. In the periods of most extensive sampling—in 1929 after the spawning season had ended and in 1930—both the total length (from tip of the head to tip of the tail, with the lobes compressed to give the maximum measurement) and the standard length (tip of the head to base of the caudal peduncle) were measured for almost all the fish. In addition to these measurements, fork length (tip of the head to fork of the tail) was recorded for a majority of the walleyes collected in the fall of 1928. Only standard lengths were recorded in the fall of 1926. Total lengths alone were measured in the spawning-run samples of 1927 and 1929, in the fall of 1929, in 1943, and for a few fish in the fall of 1928.

Walleyes of the 1926–30 collections were measured with a steel tape. The tape is held with its 0-graduation at the tip of the head, follows the curve of the body to the point of greatest thickness, and then runs parallel to the surface on which the fish is lying. A measuring board was used in 1943. The tape length exceeds the board length by about 2.5 percent.

Lengths of the bulk of the samples were recorded to the nearest millimeter. Measurements were to the nearest 0.5 centimeter for most of the 1929 spawning-run collection and to the nearest quarter inch for the remainder of the 1929 spawning-run fish and for the samples of 1927 and 1943.

The diversity of procedure necessitated a large number of conversions to attain the uniformity required. The original compilations and analyses were carried on in terms of standard lengths in millimeters (tape measurement), and where conversions were necessary, they were made for the individual fish by means of factors given in table 2.

TABLE 2.—*Factors for conversions between standard and total lengths of Saginaw Bay walleyes, with and without change of unit*

[S. L. = standard length; T. L. = total length]

Interval of standard length	Number of fish	Conversion factor			
		S. L. to T. L. (no change of unit)	T. L. to S. L. (no change of unit)	S. L. (millimeters) to T. L. (inches)	T. L. (inches) to S. L. (millimeters)
<225 mm	447	1.179	0.848	0.0464	21.54
225–447 mm	4,190	1.159	.863	.0456	21.92
>447 mm	162	1.136	.880	.0447	22.35

Since the relative size of the tail of the Saginaw Bay walleye decreases with increase in the length of the fish, different factors were determined for each of three intervals of length. Good argument could be offered for the establishment of more than three intervals or for the use of a continuous curve, since the differences between the factors for the successive intervals are sufficiently great to introduce irregularities into the converted data, and thus call for certain arbitrary adjustments. In table 18, for example, the total lengths corresponding to the standard lengths of 219 and 229 millimeters were computed as 10.2 and 10.4 inches, respectively. In order that the sequence of total lengths might proceed more regularly, however, they were written as 10.1 and 10.5 inches, respectively. At the second change of factor the required adjustments were larger. The total lengths equivalent to

[1] The mesh sizes of the nets as actually fished were smaller than those given here, since their treatment with a preservative produces a certain amount of shrinkage. See Van Oosten, Hile, and Jobes (1946) for data on extent of shrinkage.

standard lengths of 434, 443, and 453 millimeters, respectively, were computed as 19.8, 20.2, and 20.2(5) inches but entered in the table as 19.7, 20.0, and 20.3 inches. Similar adjustments, never exceeding 0.2 inch for any particular length, were made for other tables of length-weight relation and length-frequency distributions and also for the tables showing the calculated growth in length of the year classes.

Comparisons of group averages were affected little by the irregularities resulting from the changes in conversion factors since the conversions were made for individual fish and hence underestimates on the one side of the point of change were compensated by overestimates on the other. Furthermore, both standard and total lengths were at hand for the large majority of the specimens.

From the measurements of both fork and total lengths of 550 fish, a fork-length/total-length ratio of 0.944 was determined. No change in the ratio with increase in length could be detected; the length range was small, however—most of the fish falling in the second of the three intervals of table 2.

Following completion of the original tabulations, tape lengths were converted to board lengths by means of the factor 0.9756. Only board lengths are presented in this paper, and the conversions to board lengths account for the fact that in certain tables the differences between the midpoints of successive length intervals, set up originally as 10 millimeters (tape length) are occasionally only 9 millimeters.[2]

Weight

Weights were recorded in the field to the nearest quarter ounce or 0.1 ounce. For purposes of compilation and analysis, conversions were made to decimal fractions of pounds or to grams, as desired.

Records of weight were not made in the fall collections of 1926 or for the spawning-run samples of 1927 and 1929. This reduced enormously information on the average weights of the older age groups. Fortunately, a considerable number of weights was at hand for large fish not in the scale collections. It was accordingly possible to derive a general length-weight equation that could be applied to the calculated lengths for the later years of life, and provide a good estimate of the growth in weight in those years.

Maturity

No records of maturity were made in the fall of 1926 or in the spawning-run collections of 1927 and 1929. This deficiency was not particularly damaging for the last two collections, since immature fish are taken rarely at the time of the spawning run. Maturity was recorded in the fall of 1928, but records of sex were not taken for a majority of the immature fish. In 1929 (late spring), sex was determined for only a small percentage of the immature individuals, but in 1930 and 1943 both sex and maturity were recorded.

[2] The long hours spent converting lengths of Saginaw Bay walleye provided much of the stimulus for the preparation of my 1948 article on standardization of methods of expressing lengths and weights of fish (Hile 1948).

DETERMINATION OF AGE

Age, as determined from the scales,[3] has been expressed in Roman numerals corresponding to the number of annuli, or year-marks. Thus, a fish in the first year of life belongs to age-group 0, one in its second year to age-group I, ... As a convention, each fish was held to pass into the next higher age group on January 1. This usage required in turn that a "virtual" annulus be credited at the edge of the scale from that date until such time as the current season's year-mark was completed. For practically all Saginaw Bay walleyes captured in the spring and early summer the outermost annulus was virtual, since only a negligible number of the scales exhibited marginal growth even as late as mid-June. The season's growth appears to begin later in Saginaw Bay (in 1929 and 1930, at least) than in Lake of the Woods where Carlander (ms. 1942) found annulus formation to take place "during the latter part of May or early June."

Carlander (op. cit.) demonstrated that the annulus is a true year-mark in the Lake of the Woods walleye. Data for the Saginaw Bay stock also support strongly the belief that annuli are valid indicators of age. An extended consideration of this matter does not seem to be desirable here; nor are all of the supporting data presented, but certain points may be listed as follows:

1. Agreement between the modal length of the youngest fish (those that had completed 2 growing seasons) as determined from scales and from modes in certain length-frequency distribution of all ages combined.
2. Systematic increase of mean size with increase in number of annuli.
3. Generally good agreement of calculated lengths at the end of various years of life as computed from the scales of fish of the same or different age groups and year classes.
4. Better agreement between calculated growth histories of different age groups of the same year class than between the growth histories of the same or different age groups of different year classes.
5. Agreement between year classes as to good or poor growth in certain calendar years.
6. Close correlation between data for the sexes on annual fluctuations in growth rate.
7. Numerical strength or weakness of certain year classes in different calendar years.[4]

The agreement among year classes and between the sexes with respect to annual fluctuations in growth rate is especially significant because of the

[3] Scales were mounted on glass slides in a glycerin-gelatin medium and examined by means of a microprojection apparatus.

[4] The bearing of certain of these points on the validity of the annulus as a year-mark may not be immediately obvious. To avoid repetition here, reference is made to Hile (1941).

evidence it affords that scales of the Saginaw Bay walleye can be read with a high degree of accuracy up to relatively advanced ages. Males that had completed as many as 11 years of life and females that had completed as many as 13 were employed in those analyses.

Difficulties encountered in the reading of scales were the usual type: annuli that could not be determined as true or false; annuli crowded together from slow growth; semiopacity and pronounced light and dark markings; pitting of the scale surface; peripheral resorption. Scales that gave evidence of earlier resorption along the anterior edge were discarded since they could not yield reliable measurements for the computing of past growth.

Age determinations were more difficult for older fish, especially those more than 7 or 8 years of age. The scales of all older fish were read twice. At the first examination an age was assigned, if possible. At the second examination, the earlier reading was confirmed or corrected, a decision made whether to retain the fish, and if usable, the scale was measured.

Rate of growth also affected ease of reading the scales. The scales of females were considerably easier to interpret than those of the more slowly growing males, despite the generally higher average age of the females. Fish of the 1943 sample, which had grown more rapidly than the walleyes captured in 1926–30, had the clearest scales collected at any time. Whereas, 5.5 percent of the scales were discarded from the spawning run of 1929, an age was assigned to every one of the 288 fish taken in 1943.

A third factor bearing on ease of interpretation is the size and shape of the individual scales. Comparisons of extremely small scales with larger ones from the same individual suggested that annuli in undersized scales might be overlooked as the result of faint marking or closeness to neighboring annuli. In extremely large scales the transmission of light often is inadequate and the shading (light and dark bands that bear no fixed relation to annuli) may be accentuated. The largest scales are often extremely wide (dorso-ventral axis) in relation to their length (antero-posterior axis). In such scales, annuli readily visible in the lateral field can be most difficult to trace through the anterior field. Highly elongate scales likewise are undesirable since on them the cutting over in the lateral fields, a most helpful criterion of the annulus, is much reduced.

The scales best suited to age determination in the walleye, then, are those of medium size and ordinary shape (reasonably nearly symmetrical about the antero-posterior axis [5] and neither excessively long nor broad). Scales from the middle of the body of walleyes and just above the lateral line meet these specifications most satisfactorily.

CALCULATION OF GROWTH

Measurements of the magnified ($\times$ 40.7) scales for the calculation of individual growth histories were made along the anterior radius most nearly collinear with the focus. The distances from the focus to each annulus and to the edge of the scale were recorded to the nearest millimeter.

Since materials were not available for investigation of the body-scale relation of the Saginaw Bay walleye, use has been made of Deason's unpublished work with the Lake Erie population. Deason determined that the body-scale relation of the Lake Erie walleye was described satisfactorily by a straight line intersecting the length axis at a standard length of 50 millimeters.

The body-scale relation as derived for the Lake Erie walleye and applied here to the Saginaw Bay stock differs notably from the one determined for the Lake of the Woods walleye by Carlander (1945) who made use of an equation of the type:

$$L = a + b\,S + c\,S^2 + d\,S^3,$$

where a, b, c, and d = constants. The values of the constants were such that the graph of the equation followed a distinctly sigmoid course. It is obvious from Carlander's figure 1 that the theoretical curve fitted his empirical data extremely well. Eschmeyer (1950) also obtained a sigmoid curve (from key scales). He fitted the curve by inspection and calculated lengths from scale measurements by means of a nomograph of the type described by Hile (1950).

Differences in the location on the body of the fish from which the scales were taken may account for the dissimilar body-scale relation as determined by Deason, by Carlander, and by Eschmeyer. Deason used scales from the middle of the body and above the lateral line, Carlander took his samples near the lateral line immediately above

[5] Curvature of the radii in asymmetrical scales makes measurement more difficult and less accurate.

the posterior edge of the pectoral fin, and Eschmeyer's key scales came from the third row below the lateral line. That the body-scale relation can vary considerably according to the location from which the scales are taken is indicated in the works of Hile (1941) and Beckman (1941) on the rock bass (*Ambloplites rupestris*). Hile found that the mathematical relation between the length (anterior radius) of "key scales" from the second row above the lateral line and the length of fish of the Nebish Lake (Wis.) population was described satisfactorily by the general parabola, $L = cS^n$, in which n had a value of approximately 0.7. Using essentially the same procedures but taking his scales from the third row below the lateral line (actual position not stated in paper but communicated privately by author), Beckman obtained an equally satisfactory fit for the Standard Lake (Mich.) stock with a straight line that intersected the length axis at a standard length of 15 millimeters.

COMMERCIAL PRODUCTION IN SAGINAW BAY, 1885–1951

Records of the production of walleyes in Saginaw Bay (table 3) through 1940 were adapted from Gallagher and Van Oosten (1943). Figures for later years were compiled in the Great Lakes offices of the United States Fish and Wildlife Service from commercial fishing reports turned over to the Service by the Michigan Department of Conservation. These reports are submitted each month by commercial fishermen licensed to operate in State of Michigan waters of the Great Lakes.

In 1885, the first year for which we have statistics, the take amounted to 673,000 pounds. The level of production was much higher (1,558,000 pounds) in 1891, the next year for which there is a record. This year was the first in a relatively extended period (1891–1919) in which the catch varied widely (and gave some indication of cyclic fluctuations) but was without a long-term trend (fig. 1). Of the 22 years within this period for which there are statistics, the take exceeded 1½ million pounds in 5 (maximum catch, 1,885,000 pounds in 1894), fell between 1 and 1½ million pounds in 9, and was less than a million pounds in 8 (minimum of 654,000 pounds in 1916). The 1891–1919 average was 1,149,000 pounds.

TABLE 3.—*Commercial production of walleyes in Saginaw Bay, 1885, 1891–1908, and 1916–51*

[In thousands of pounds]

Year	Production	Year	Production	Year	Production
1885	673	1908	801	1933	1,455
1891	1,558	1916	654	1934	1,349
1892	1,035	1917	1,002	1935	1,293
1893	686	1918	1,803	1936	1,401
1894	1,885	1919	1,246	1937	1,529
1895	878	1920	758	1938	1,179
1896	723	1921	546	1939	1,492
1897	1,217	1922	1,098	1940	1,443
1898	1,242	1923	622	1941	1,463
1899	1,167	1924	314	1942	2,050
1900	800	1925	335	1943	1,559
1901	716	1926	589	1944	988
1902	1,003	1927	621	1945	560
1903	1,771	1928	630	1946	909
1904	1,652	1929	632	1947	366
1905	1,415	1930	1,004	1948	142
1906	1,044	1931	681	1949	78
1907	980	1932	1,375	1950	62
				1951	65

The 12-year period, 1920–31, was one of rather consistently low yield. Production was above a million pounds in only 2 years (maximum of 1,098,000 pounds in 1922) and fell below 500,000 pounds twice (minimum of 314,000 pounds in 1924). The mean for 1920–31 was 652,000 pounds—43 percent below the 1891–1919 level. The statistics suggest a general downward trend during the early years and an upward trend during the later years of the period.

The irregular upward trend that started in 1925 carried the take to 1,375,000 pounds in 1932. This year was the first of a 12-year period during which the catch did not fall below 1,179,000 pounds (the figure for 1938) and reached the record high of 2,050,000 pounds in 1942. The 1932–43 average of 1,466,000 pounds was 2.25 times the mean for 1920–31 and 1.28 times the 1891–1919 average.

The decline from the record high of 2,050,000 pounds in 1942 was both rapid and disastrous. The catch dropped to less than a million pounds (988,000) in 1944 and almost to a half million (560,000) in 1945. A recovery to 909,000 pounds in 1946 was followed by a further decrease to only 62,000 pounds in 1950. The catches of 1948, 1949, and 1950 set new record lows, and the 1951 take of 65,000 pounds represented insignificant improvement over the preceding year. The average output in 1944–51 was only 396,000 pounds. Many commercial fishermen of Saginaw Bay believe that industrial pollution brought about the collapse of the walleye fishery.

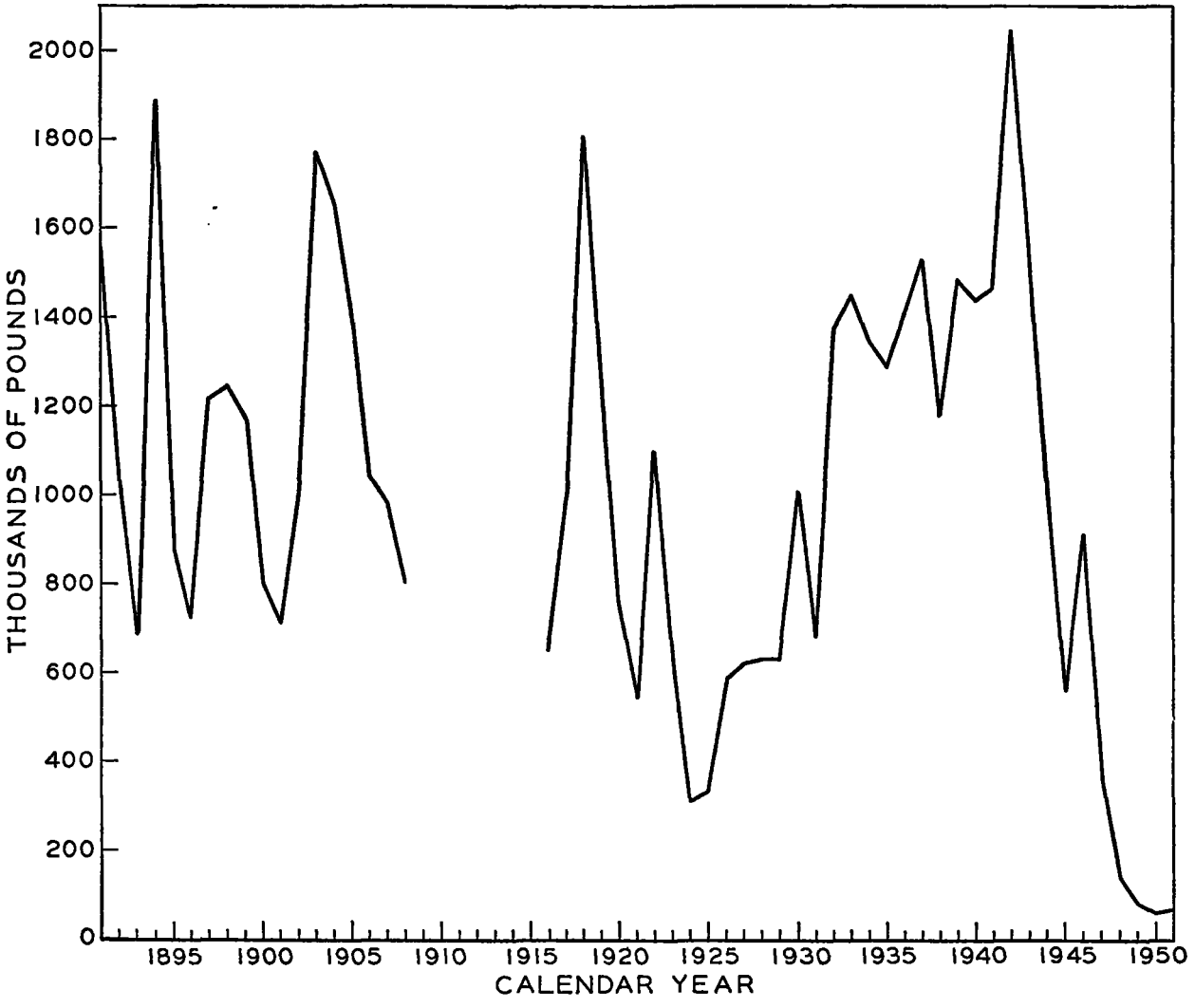

FIGURE 1.—Commercial production of walleyes in Saginaw Bay, 1891–1908 and 1916–51.

An earlier publication (Hile 1937) discussed fluctuations in the production and abundance of walleyes in Saginaw Bay in 1929–35. Similar information, and also statistics on fishing intensity, now available through 1951, give no evidence that overfishing was a significant factor in the recent collapse of the walleye fishery in Saginaw Bay.

AGE COMPOSITION AND YEAR-CLASS STRENGTH

AGE COMPOSITION OF 1926–30 COLLECTIONS

Seasonal differences

The records of age composition of the several collections made from 1926 to 1930 (table 4) indicate that greatly different age segments of the walleye population of Saginaw Bay are available at various periods of the year.

Both of the fall samples were made up of extremely young fish. Age-group I was overwhelmingly dominant in both years (95.5 percent in 1926; 73.1 percent in 1928) and only 4 individuals older than the IV group were present in the combined total of 424 specimens. Even though the number of annuli be increased by 1 to give ages in terms of completed growing seasons each collection has an average age of less than 2.5 and the unweighted mean for the two is 2.28.

The spawning-run samples of 1927 and April 4–23, 1929, on the other hand, were composed of old fish. Age-group VII was dominant in both

years (27.6 percent in 1927; 29.3 percent in 1929), fish younger than the VI group were scarce (11.0 percent in 1927; 3.9 percent in 1929) and no walleyes younger than the IV group were captured. Fish more than 8 years old, however, made up 16.5 percent of the 1927 and 31.9 percent of the 1929 collection. The average age of spawning-run fish was between 7 and 8 years in both collections (unweighted mean of 7.60).

The late-spring collections of 1929 and 1930 were of intermediate age. Age-group IV was dominant in both years (38.5 percent in 1929; 38.7 percent in 1930) and fish of this age and younger made up 85.7 and 70.5 percent, respectively, of the total in the 2 years. No age group older than the VII group in 1929 or the VIII group in 1930 had a representation as great as 1 percent. The unweighted mean age for the two collections was 3.90.

Fluctuations within a collecting period

In three collections (spawning-run, 1929; late-spring, 1929 and 1930) sufficiently large samples were taken on different dates to permit inquiry into the variation of age composition during the collecting period.

The variation in the mean age of spawning-run walleyes captured on different dates in April 1929 (table 5) exhibited no clear-cut trends. For the males, the average number of annuli ranged from 6.66 on April 23 to 8.31 on April 13, a maximum difference of 1.65. The variation of average age was less for the females (from 7.84 on April 7 to 8.89 on April 4—difference, 1.05) and still smaller for the combined sexes (7.75 on April 23 to 8.28 on April 13—difference of 0.53; 7.68 on April 6 to 8.28 on April 13—difference of 0.60, if we include the former collection which contained no females). The lesser range of age for the combined sexes can be traced to the fact that the ages of males and females varied more or less independently.

Age-group VII was dominant [6] both in the combined samples and in 5 of the 6 individual collections from the 1929 spawning run. The exception, sample of April 6, not only contained relatively few fish (53) but was abnormal in that females were entirely lacking. There is little evidence that had fewer samples been available time of collection would have affected greatly the conclusions relative to the age composition of the 1929 spawning run.

The mean age, sexes combined, of late-spring samples in 1929 varied from 3.12 on May 17 to 4.32 on June 3—a difference of 1.20. This maximum

[6] Statements in this section relative to dominance are based on the combined numbers of males and females.

TABLE 4.—*Age and year-class composition of the 1926–30 collections of Saginaw Bay walleyes*

[A "virtual" annulus at the edge of the scale was credited to fish captured in the spring before the onset of the current season's growth]

Date of capture [1]	Year class—															Total or average [2]
	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	
Nov. 11–20, 1926:																
Age group		XI		IX				V	IV	III	II	I				1.13
Number of fish		1		1				1	3	1	7	291				305
Percentage		(0.3)		(0.3)				(0.3)	(1.0)	(0.3)	(2.3)	(95.5)				
Mar. 30–Apr. 16, 1927:																
Age group	XIII	XII	XI	X	IX	VIII	VII	VI	V	IV						7.24
Number of fish	2	2	4	5	8	24	35	33	13	1						127
Percentage	(1.6)	(1.6)	(3.1)	(3.9)	(6.3)	(18.9)	(27.6)	(26.0)	(10.2)	(0.8)						
Nov. 5–12, 1928:																
Age group				XI							IV	III	II	I		1.43
Number of fish				1							1	8	22	87		119
Percentage				(0.8)							(0.8)	(6.8)	(18.5)	(73.1)		
Apr. 4–23, 1929: [3]																
Age group		XIV	XIII	XII	XI	X	IX	VIII	VII	VI	V	IV				7.96
Number of fish		3	9	14	31	61	64	109	167	90	16	6				570
Percentage		(0.5)	(1.6)	(2.5)	(5.4)	(10.7)	(11.2)	(19.1)	(29.3)	(15.8)	(2.8)	(1.1)				
May 15–June 18, 1929:																
Age group	XV		XIII	XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	I	3.67
Number of fish	1		1	1	3	5	7	10	41	41	59	456	308	348	2	1,183
Percentage	(0.1)		(0.1)	(0.1)	(0.2)	(0.4)	(0.6)	(0.8)	(3.5)	(3.5)	(5.0)	(38.5)	(26.0)	(21.0)	(0.2)	
Apr. 30–June 20, 1930:																
Age group					XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	4.14
Number of fish					4	2	4	10	15	23	25	230	410	297	40	1,060
Percentage					(0.4)	(0.2)	(0.4)	(0.9)	(1.4)	(2.2)	(2.3)	(21.7)	(38.7)	(28.0)	(3.8)	

[1] Extreme dates of the collecting period.
[2] Average number of annuli; the averages for the fall collections should be increased by 1 to obtain the mean number of completed growing seasons.
[3] From spawning run.

TABLE 5.—*Age composition and mean age of Saginaw Bay walleyes in 1929*

[Sex data lacking for the bulk of fish collected in May and June]

Date of collection, and sex	Number in age group—															Total	Average age [1]	
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV		By sex	Both sexes [2]
April 4:																		
Males				1	2	7	19	9	9	2						49	7.39	8.05
Females					1	1	9	7	5	6	6	2	1			38	8.89	(87)
April 6: Males [3]				1	2	7	12	19	7	3	2					53	7.68	
April 7:																		
Males					2	10	24	23	5	7	2	1				74	7.72	7.77
Females						11	17	6	6	8	3					51	7.84	(125)
April 13:																		
Males					1	6	11	7	10	5	2	2		1		45	8.31	8.28
Females						8	23	12	7	7	5	5				67	8.25	(112)
April 15, 19:																		
Males						10	14	6	2	3	2		1			38	7.61	8.13
Females					4	8	15	8	6	11	4	4	3			63	8.44	(101)
April 23:																		
Males				3	4	19	8	5	3	1				1		44	6.66	7.75
Females				1		3	15	7	4	8	5		4	1		48	8.75	(92)
May 15: Both sexes		42	33	94	8	4	8		1	2						192		3.69
May 17: Both sexes	1	73	49	46	3	2	5	2			1					182		3.12
June 3: Both sexes		32	51	113	27	20	16	5	3	2	2	1	1		1	274		4.32
June 8: Both sexes	1	40	54	90	9	10	8	3	1	1						217		3.72
June 12: Both sexes		21	62	66	6	3	1									159		3.44
June 14, 18: Both sexes		40	59	47	6	2	3		2							159		3.31
Total:																		
April 4–23:																		
Males				5	11	59	88	69	36	21	8	3	1	2		303	7.58	
Females				1	5	31	79	40	28	40	23	11	8	1		267	8.40	
Both sexes				6	16	90	167	109	64	61	31	14	9	3		570		7.96
May 15–June 18:																		
Both sexes	2	248	308	456	59	41	41	10	7	5	3	1	1		1	1,183		3.67

[1] Average number of annuli. [2] Number of fish in parentheses. [3] No females taken on April 6.

difference was twice that of spawning-run samples (0.53 or 0.60). Furthermore, since the average age in late spring (3.67) was less than half that in the spawning run (7.96), the relative variation of age was even greater during the later collection period. The trend in the variation of age was irregular in the early part of the collecting period. The average age dropped from 3.69 on May 15 to 3.12 (the minimum average) on May 17 and rose sharply to the maximum of 4.32 on June 3. Over the period June 3 to June 14 and 18, however, the mean age decreased consistently (from 4.32 to 3.31) as the season advanced. Age-group IV was dominant in 4 of the 6 collections (in the combined collections also) with age-groups II and III the strongest in 1 sample each. Because of the considerable variation of age in late spring, conclusions based on a single sample might vary considerably according to the date of collection. On the basis of only the May 15 collection, for example, one might be inclined to conclude with some confidence that age-group IV (94 fish, or 49 percent of the total sample of 192) was dominant in the late-spring season. Had the one available collection been taken 2 days later (May 17) one might believe that the II group (73 fish, or 40 percent in a total of 182 walleyes) was the strongest. Thus, for the late-spring period a series of samples is desirable. Even so, the variability of the age composition from date to date leaves in some doubt the actual conditions within the population as a whole.

In 1930 (table 6) the mean age of the samples (sexes combined) increased from 4.31 on April 30 to a maximum of 5.05 on May 8, 11, and 13, and thereafter followed a distinct although irregular downward trend. The range of variation was from 5.05 to 3.30 (June 3)—a difference of 1.75. The extent to which ages differed in the earlier and later parts of the collecting period is illustrated by the fact that the highest average age after the May 15 and 17 collection was below the mean in that collection or any earlier one. Furthermore, the average age over the period May 22–June 20 was only 3.74 as compared with 4.50 for April 30–May 17—a difference of 0.76.

The variations in the average age of walleyes from sample to sample in the late spring of 1930 were accompanied by shifts in the dominance of age groups. Three of the first four collections were

TABLE 6.—*Age composition and average age of Saginaw Bay walleyes in 1930*

Date of collection	Number in age group—											Total	Average age [1]	
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII		By sex	Both sexes [2]
April 30:														
Males		19	49	27	3							98	4.14	4.31
Females		4	27	28	6							65	4.55	(163)
May 3, 5:														
Males	1	19	50	25	2	2						99	4.14	4.36
Females		4	19	9	1	1	3		1		1	39	4.92	(138)
May 8, 11, 13:														
Males		7	31	30	3	1	2					74	4.54	5.05
Females		6	16	37	5	9	5	5	1		1	85	5.49	(159)
May 15, 17:														
Males	4	10	31	16								61	3.97	4.12
Females		8	21	7		1		1		1		39	4.36	(100)
May 22, 24:														
Males	2	25	18	1	1	1						48	3.52	3.89
Females	2	32	24	8	2	2		1		1	2	74	4.13	(122)
May 26, 29:														
Males	3	26	21	5		1						56	3.57	4.02
Females	3	36	23	20	2	4	3	1	1			83	4.32	(139)
June 1, 3:														
Males	3	25	19	3								50	3.44	3.30
Females	9	26	16	1								52	3.17	(102)
June 9, 18, 20:														
Males	4	23	27	3		1						58	3.57	3.66
Females	9	37	18	10			2	2	1			79	3.73	(137)
Total:														
Males	17	154	246	110	9	6	2					544	3.94	
Females	23	143	164	120	16	17	13	10	4	2	4	516	4.36	
Both sexes	40	297	410	230	25	23	15	10	4	2	4	1,060		4.14

[1] Average number of annuli. [2] Number of fish in parentheses.

dominated by age-group IV, the fourth (May 8, 11, and 13) by the V group. Every one of the last four collections was dominated by age-group III. Thus 5 of 8 samples each containing 100 or more walleyes [7] disagreed with the combined collections (in which age-group IV dominated) as to which age group was strongest. Again it is seen that a single sample from the late-spring collecting period, even though it be of fair size, can prove misleading and that even with an abundance of samples the variation in age composition inevitably leaves doubt as to the actual situation in the general population.

In earlier discussion of the age composition of the 1929 spawning run it was observed that the mean ages of males and females varied "more or less independently" from sample to sample. In the late-spring collections of 1930 the variations of the ages of males and females were closely correlated. Although this relation is clearly detectable from the data of table 6, the closeness of the correlation can be brought out more forcefully by the figures in table 7 in which the daily mean ages of the sexes are recorded in the descending order of the average ages of the males. So similar were these day-to-day variations that the coefficient of correlation (r) between the two series of averages was 0.913. This figure is far beyond that which ordinarily would be termed highly significant (at $df=15$, $r=0.606$ for $p=0.01$). It is concluded therefore that the factors which determine the day-to-day changes of age composition in late-spring collections operate in the same way on males and females.

[7] A minimum sample of 100 fish was the basis for combining the catches of certain days to form a single sample.

TABLE 7.—*Variation in average age of male and female Saginaw Bay walleyes in daily samples collected in 1930*

[Collections arranged in descending order of mean age of males]

Date of collection	Males		Females	
	Number of fish	Average age [1]	Number of fish	Average age [1]
May 8	9	4.89	18	6.06
May 11	40	4.72	43	5.58
May 3	50	4.24	20	5.45
April 30	98	4.14	65	4.55
May 15	23	4.13	14	5.29
May 13	25	4.12	24	4.92
May 5	49	4.04	19	4.37
May 26	28	3.93	54	4.81
May 17	38	3.87	25	3.84
June 9	29	3.72	33	3.88
June 3	30	3.60	30	3.33
May 24	30	3.57	47	4.55
June 18	4	3.50	3	4.00
May 22	18	3.44	27	3.41
June 20	25	3.40	43	3.60
May 29	28	3.21	29	3.41
June 1	20	3.20	22	2.95
Total or average	544	[2] 3.87	516	[2] 4.35

[1] Average number of annuli.
Unweighted means of averages for the individual collections.

RELATIVE STRENGTH OF YEAR CLASSES

1926–30 collections

The great seasonal variation in age composition of the Saginaw Bay walleye imposes severe limitations on the use of the data of table 4 to estimate the relative strength of the year classes. Obviously, the comparisons of the representation of age groups on which such estimates are based can be made only between samples taken at the same time of year (spawning period, late spring, fall). Difficulties are increased by the circumstance that for only 1 of the 3 periods, late spring, were the two available collections made in consecutive calendar years (1929 and 1930). Despite these limitations, some general ideas concerning the strength of the year classes may be developed.

Year-classes 1914–16 were represented by too few fish to warrant speculation as to their probable strength. For the remaining year classes, estimates of relative strength will be made from (1) comparisons of the percentage age composition of samples from the same collecting season (spawning period, late spring, fall) but from different calendar years, and (2) comparisons of the ratios of numbers of fish in consecutive age groups in different collections.

The evidence from the percentage age composition probably can be presented most effectively in a condensed form (table 8). The manner of reading the table perhaps can be illustrated best by specific examples. The first line, for example, states that the year-class 1917 which made up 3.9 percent of a spawning-run collection as age-group X is estimated to have been weaker than year-class 1919 which accounted for 10.7 percent of a spawning-run sample at the same age. Similarly, the high representation (95.5 percent) of year-class 1925 as the I group of a fall collection suggests that it was stronger than year-class 1927 which accounted for only 73.1 percent at the same age. Finally, the nearly equal representations of 1926 and 1927 year classes as age-group III (26.0 and 28.0 percent, respectively) in late-spring samples indicates that they were of approximately the same strength.

The estimates in table 8 are by no means equally reliable as both the numbers of fish and the differences between pairs of percentages varied widely. Neither can it be assumed that any one of the pairs of percentages offers an unbiased estimate of the true relative strength of the year classes involved. Important but undeterminable factors can intervene to distort the data. It is conceivable, for example, that the relatively weak percentage representation of the older age groups (and hence stronger representation of younger fish) in the 1927 samples as compared with the 1929 spawning run (table 4) may have resulted from a particularly intensive fishery in the years prior to 1927, and hence reflect only a high fishing mortality. Again, the much stronger representation of the I group in 1926 (95.5 percent) than in 1928 (73.1 percent) does not necessarily mean a correspondingly greater relative strength for the 1925 year class as compared with year-class 1927. Year-class 1925 may seem strong only because year-class 1924 was too weak to give the II group its "normal" representation in 1926, or conversely, year-class 1927 may appear weak only because a strong 1926 year class contributed more than the usual number of II-group walleyes in 1928 (actually, there is evidence that year-class 1924 was weak). The same, of course, holds for all collections—age composition can be influenced by earlier fishing intensity and exceptionally strong percentage representation of one age group makes others appear relatively weak, and *vice versa*.

Although the best evidence concerning the relative strength of the year classes probably is that provided by comparisons of the percentage age composition of the samples, some valuable additional information is to be had from data on the ratio of the numbers of fish in successive age groups

TABLE 8.—*Relative strength of certain year classes of the Saginaw Bay walleye as indicated by their percentage representation at corresponding ages in different collections*

Estimated relative strength of year classes	Time of collection [1]	Age group	Percentage representation of age group as—	
			Earlier year class	Later year class
1917<1919	SR	X	3.9	10.7
1918<1920	SR	IX	6.3	11.2
1919=1921	SR	VIII	18.9	19.1
1920=1922	SR	VII	27.6	29.3
1921>1923	SR	VI	26.0	15.8
1922>1924	SR	V	10.2	2.8
1922>1923	LS	VII	3.5	2.2
1923<1925	F	III	.3	6.8
1923>1924	LS	VI	3.5	2.3
1924<1926	F	II	2.3	18.5
1924<1925	LS	V	5.0	21.7
1925>1927	F	I	95.5	73.1
1925=1926	LS	IV	38.5	38.7
1926=1927	LS	III	26.0	28.0
1927>1928	LS	II	21.0	3.8

[1] SR=spawning run; LS=late spring; F=fall.

within collections. The numerical distribution of fish within a sample according to age usually follows a characteristic pattern. Some of the younger age groups may be poorly represented (gear selection or segregation on the basis of maturity or size) but among the older fish increase of age normally is accompanied by a regular decrease in numbers. Any sharp deviation from the typical pattern of decrease is suggestive of abnormal strength or weakness in the year class or classes responsible for the irregularity. To illustrate this point, let us assume that the numbers of fish in age-groups VI and V ordinarily are in about the ratio of 1:2. If a particular collection contains 20 VI-group and 20 V-group fish (ratio of 1:1) we have evidence of weakness in the year class represented by the V group or of strength in the one represented by the VI group. Similarly, a collection with 10 VI-group and 50 V-group individuals (ratio of 1:5) indicates the younger fish belong to the relatively stronger year class. Even among those younger age groups that are subject to selection, deviations from the customary ratio can provide information.

Preliminary to the employment of ratios of numerical representation of age groups, it is necessary to establish as accurately as possible the general pattern of the variation in numbers with age. The basic usable data for the Saginaw Bay walleye (table 9) demonstrate at once that in ratios of numbers as in percentage age composition different kinds of collections (spawning-run, late-spring, and fall) follow different trends. It is true that over the age range XII–XI to VIII–VII the averages at the bottom of the table were based on combinations of spawning-run and late-spring samples. In the data for age-groups VII–VI and VI–V, however, the materials had to be separated since selection as to maturity decreased the representation of the younger age groups of the spawning runs. Similarly, the fall and late-spring collections were treated separately since the trends of numerical abundance with increase in age were dissimilar.

The number of collections contributing to the averages of table 9 was only two or four (the averages given in the footnotes were based on two collections) and certain of the individual ratios were based on extremely small numbers of fish. Despite these obvious inadequacies the averages exhibited remarkably small variation over the range XII–XI to VIII–VII. For the combined collections the range of the ratios was 0.52 to 0.84; the means of the individual ratios varied from 0.56 to 0.82. At the lower ages VII–VI to III–II (data based only on late-spring collections of 1929 and 1930) the ratios ranged from 0.23 to 2.10 (combined collections) and from 0.34 to 4.33 (mean of ratios). Some of them certainly cannot be held to represent typical conditions. The value of 0.96 as the ratio of the numbers of walleyes in age-groups VII and VI, for example, should not be interpreted to indicate that normally the two groups are almost equally plentiful in random samples.

TABLE 9.—*Ratios of the numbers of fish in successive age groups of the Saginaw Bay walleye in the 1926–30 collections*

[Numbers in age groups in parentheses]

Collection	Ratio of numbers and numbers in age groups—										
	XII–XI	XI–X	X–IX	IX–VIII	VIII–VII	VII–VI	VI–V	V–IV	IV–III	III–II	II–I
Fall 1926									[1] 3.00 (3–1)	[1] 0.14 (1–7)	0.02 (7–291)
Fall 1928									[1] 0.12 (1–8)	[1] 0.36 (8–22)	0.25 (22–87)
Spawning run 1927	0.50 (2–4)	0.80 (4–5)	0.62 (5–8)	0.33 (8–24)	0.69 (24–35)	[1] 1.06 (35–33)	[2] 2.54 (33–13)	[2] 13.00 (13–1)			
Spawning run 1929	0.45 (14–31)	0.51 (31–61)	0.95 (61–64)	0.59 (64–109)	0.65 (109–167)	[1] 1.86 (167–90)	[2] 5.62 (90–16)	[2] 2.67 (16–6)			
Late spring 1929	0.33 (1–3)	0.60 (3–5)	0.71 (5–7)	0.70 (7–10)	0.24 (10–41)	1.00 (41–41)	0.69 (41–59)	0.13 (59–456)	1.48 (456–308)	1.24 (308–248)	
Late spring 1930	2.00 (4–2)	0.50 (2–4)	0.40 (4–10)	0.67 (10–15)	0.65 (15–23)	0.92 (23–25)	0.11 (25–230)	0.56 (230–410)	1.38 (410–297)	7.42 (297–40)	
Combined collections:											
Ratio	0.52	0.53	0.84	0.56	0.59	0.97	0.23	0.33	1.43	2.10	0.08
Total number	(21–40)	(40–75)	(75–89)	(89–158)	(158–266)	(64–66)	(66–289)	(289–866)	(866–605)	(605–288)	(29–378)
Average of ratios	0.82	0.60	0.67	0.57	0.56	0.96	0.40	0.34	1.43	4.33	0.14

[1] Data not included at bottom of table. The ratios (combined collections and average ratios, respectively) for the fall collections are 0.44 and 1.56 for age-groups IV–III and 0.31 and 0.25 for age-groups III–II.

[2] Ratio probably affected by selection on basis of maturity; data not included at bottom of table. The ratios (combined collections and average ratios, respectively) in the spawning run are 1.64 and 1.46 for age-groups VII–VI, 4.24 and 4.08 for age-groups VI–V, and 4.14 and 7.83 for age-groups V–IV.

For the next two comparisons (VI–V and V–IV), the ratios are almost certainly too low as the result of a large difference between the original abundance of year-classes 1924 and 1925. High values more than 1.0 at IV–III and III–II in the late-spring collections may be in part the result of a normal scarcity of the younger fish on the grounds at that season. At least one of the ratios, 7.42 at III–II in 1930, must have been high because the younger age group represented a weak year class.

Values of the ratio consistently above 1.0 for comparisons of age-groups VII and VI and for younger fish in the spawning-run samples can be explained, as stated previously, on the basis of selection according to maturity. Despite this selection the ratios indicate conditions at the spawning period and hence have some usefulness in the estimation of the strength of the year classes.

The value of the data for the fall collections is limited greatly by the scarcity of walleyes older than the I group. Here, as with the younger age groups of the late-spring collections, the ratios varied widely, and here also the lowest ratio, 0.02 at II–I in 1926, came from a comparison of year-classes 1924 and 1925.

The sources of error and of distortion of the data just outlined were kept in mind when estimates of the relative strength of successive year classes were made from the data of table 10. Some of the decisions were most difficult, some probably incorrect; yet it is encouraging to observe that the general trends as estimated from the ratios and from the percentage age composition of the samples were similar (table 11).

It is possible from the data of table 11 to form some idea of the rankings of the several year classes. If, for example, 1917 is assigned a "position" of 0 and the later year classes successively assigned higher or lower positions according to their indicated strength (in comparison with the preceding year class or classes), it is possible to arrive at the following sequence of positions which is in conflict with only two estimates of the table (1919=1921; 1925=1926). Both disagreements were unavoidable because of discrepancies among the estimates.

Year class	Position	Year class	Position
1917	0	1923	1
1918	1	1924	0
1919	3	1925	2
1920	2	1926	1
1921	2	1927	1
1922	2	1928	0

Although these rankings are valid to the extent that they conform well with the data of table 11 they are defective in the sense that the positions were determined by the mere occurrence of a stronger or weaker year class in the sequence and took no account of their actual relative strengths. (The increases of two in the positions from 1918

TABLE 10.—*Estimates of the relative strength of certain year classes of the Saginaw Bay walleye as indicated by the ratios of the numbers of fish in successive age groups*

Relative strength of year classes	Time of collection [1]	Earlier year class		Later year class		Ratio of numbers	General ratio of age groups—	
		Age group	Number	Age group	Number		From total numbers	Mean of ratios
1917<1918	1927SR	X	5	IX	8	0.62	0.84	0.67
	1929SR	XII	14	XI	31	.45	.52	.82
	1929LS	XII	1	XI	3	.33		
1918<1919	1927SR	IX	8	VIII	24	.33	.56	.57
	1929SR	XI	31	X	61	.51	.53	.60
	1929LS	XI	3	X	5	.60		
	1930LS	XII	4	XI	2	2.00	.52	.82
1919>1920	1927SR	VIII	24	VII	35	.69	.59	.66
	1929SR	X	61	IX	64	.95	.84	.67
	1929LS	X	5	IX	7	.71		
	1930LS	XI	2	X	4	.50	.53	.60
1920=1921	1927SR	VII	35	VI	33	1.06	1.64	1.46
	1929SR	IX	64	VIII	109	.59	.56	.57
	1929LS	IX	7	VIII	10	.70		
	1930LS	X	4	IX	10	.40	.84	.67
1921=1922	1927SR	VI	33	V	13	2.54	4.24	4.08
	1929SR	VIII	109	VII	167	.65	.59	.56
	1929LS	VIII	10	VII	41	.24		
	1930LS	IX	10	VIII	15	.67	.56	.57
1922>1923	1926F	IV	3	III	1	3.00	.44	1.55
	1927SR	V	13	IV	1	13.00	4.14	7.83
	1929SR	VII	167	VI	90	1.86	1.64	1.46
	1929LS	VII	41	VI	41	1.00	.97	.96
	1930LS	VIII	15	VII	23	.65	59	.56
1923>1924	1926F	III	1	II	7	.14	.31	.25
	1929SR	VI	90	V	16	5.62	4.24	4.08
	1929LS	VI	41	V	59	.69	.23	.40
	1930LS	VII	23	VI	25	.92	.97	.96
1924<1925	1926F	II	7	I	291	.02	.08	.14
	1928F	IV	1	III	8	.12	.44	1.56
	1929SR	V	16	IV	6	2.67	4.14	7.83
	1929LS	V	59	IV	456	.13	.33	.34
	1930LS	VI	25	V	230	.11	.23	.40
1925>1926	1928F	III	8	II	22	.36	.31	.25
	1929LS	IV	456	III	308	1.48	1.43	1.43
	1930LS	V	230	IV	410	.56	.33	.34
1926=1927	1928F	II	22	I	87	.25	.08	.14
	1929LS	III	308	II	248	1.24	2.10	4.33
	1930LS	IV	410	III	297	1.38	1.43	1.43
1927>1928	1930LS	III	297	II	40	7.42	2.10	4.33

[1] SR=spawning run; LS=late spring; F=fall.

TABLE 11.—*Summary of estimates of the relative strength of year-classes 1917 to 1928 of the Saginaw Bay walleye*

[Based on tables 8 and 10]

Basis of estimate	*Estimated relations among year classes*											
Ratios of numbers in successive age groups	1917<	1918<	1919>	1920=	1921=	1922>	1923>	1924<	1925>	1926=	1927>	1928
Percentage age composition of samples	1917	<	1919	=	1921	>	1923	<	1925	>	1927	----
	------	1918	<	1920	=	1922	>	1924	<	1926	------	----
	------	------	------	------	------	1922>	1923>	1924<	1925=	1926=	1927>	1928

to 1919 and from 1924 to 1925 were required by the estimates of table 11 and are not attempts to measure the advantage of the more recent year classes.) The original data are not as a whole sufficiently extensive or dependable to warrant an attempt at greater exactitude than that involved in the assignment of successive positions. In two situations, however, the evidence of extremely large differences between successive year classes is so strong as to make desirable an adjustment of the preceding tabulation. There can be little question that year-class 1925 was far stronger than year-class 1924 and that year-class 1928 was much weaker than year-class 1927. These large differences, if not to be measured exactly, can be accorded some recognition if the change of position from 1924 to 1925 is increased from 2 to 3 and that from 1927 to 1928 from 1 to 3. With these adjustments the new positions for year-classes 1925 to 1929 become: 1925, 3; 1926, 2; 1927, 2; 1928, −1.

If the adjusted positions just given are used and the whole series shifted to a mean position of 0.00, the following final estimate of rank is obtained (see fig. 2):

Year class	Rank	Year class	Rank
1917	−1.42	1923	−0.42
1918	−.42	1924	−1.42
1919	1.58	1925	1.58
1920	.58	1926	.58
1921	.58	1927	.58
1922	.58	1928	−2.42

The preceding "final rankings" are offered merely as the best estimate of the relative strength of the various year classes that could be obtained from difficult data. The treacherous nature of chains of estimates is realized fully. Nor is any claim made that individual decisions were based on fixed objective standards. Because the estimates were based so largely on personal interpretation of diffuse and indefinite evidence, full tabular materials have been provided.

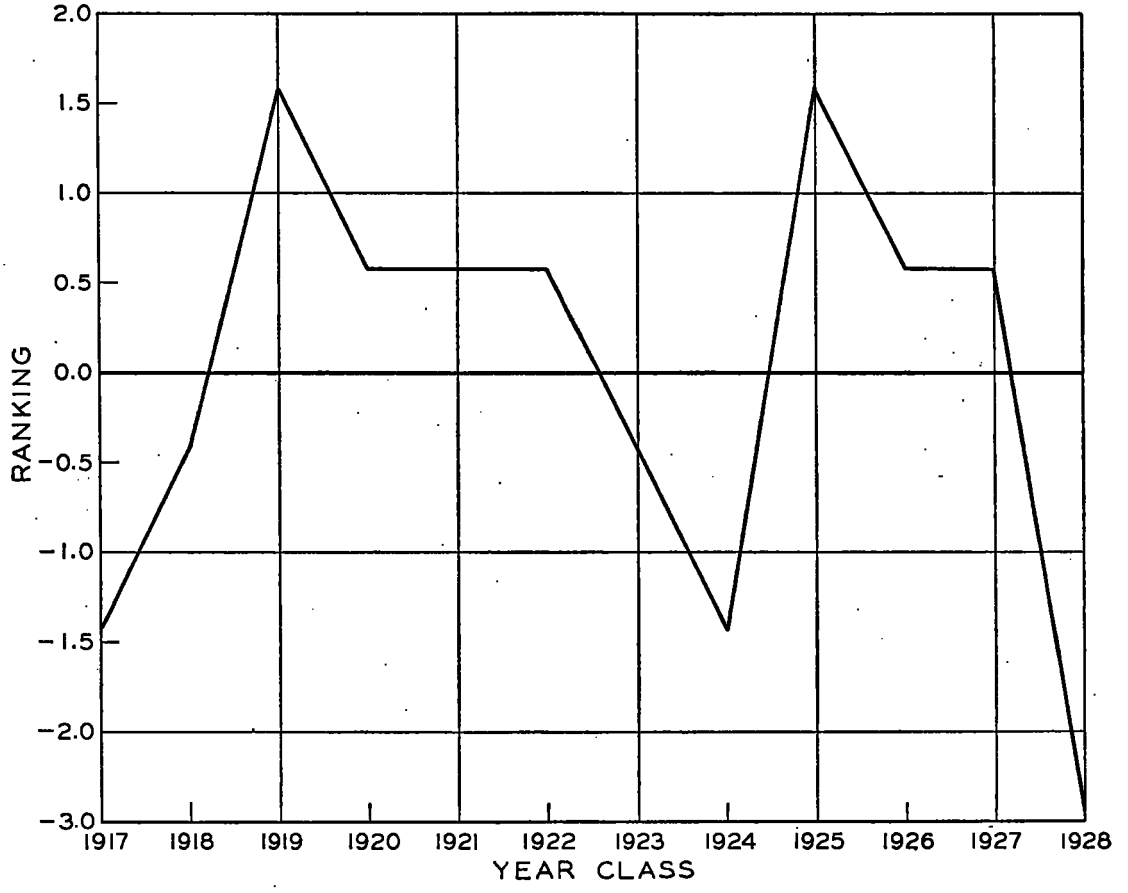

FIGURE 2.—Fluctuations in the relative strength of year-classes 1917 to 1928 of the Saginaw Bay walleye.

Preliminary analyses gave strong evidence for correlation between certain meteorological conditions and the fluctuations in the strength of the 1917 to 1928 year classes. The indicated relation failed completely, however, to hold up for year classes of the 1943 collection, a discussion of which follows. Inquiry into factors influencing the strength of year classes of the Saginaw Bay walleye must wait until work now in progress makes information available over a longer series of years.

1943 collection

Interpretation of the data on age and year-class composition in 1943 (table 12) is made difficult not only by the lack of comparable data for adjacent years but also by some uncertainty as to the proper classification of the sample with respect to "type" of collection. Examination of the gonads revealed that spawning was still in progress; on the other hand, immature fish, ordinarily absent or rare in spawning-run collections, were numerous among the younger females. Presumably the 1943 collection was intermediate between the spawning-run and late-spring samples of earlier years.

TABLE 12.—*Age and year-class composition of Saginaw Bay walleyes collected May 4, 1943*

Year class	Age group	Sex			Percentage of total
		Males	Females	Both	
1930	XIII	----------	2	2	0.7
1931	XII	----------	1	1	.3
1933	X	3	1	4	1.4
1934	IX	3	2	5	1.8
1935	VIII	2	----------	2	.7
1936	VII	5	3	8	2.8
1937	VI	14	16	30	10.4
1938	V	3	1	4	1.4
1939	IV	49	30	79	27.4
1940	III	101	50	151	52.4
1941	II	1	1	2	.7
Total	----------	181	107	288	----------
Average age [1]	----------	3.91	4.30	4.06	----------

[1] Average number of annuli.

Age-group III was strongly dominant (52.4 percent) in 1943 with the IV group second (27.4 percent). The VI group (10.4 percent) held third place. The remaining age groups were represented sparsely (0.3 to 2.8 percent). The extremely low percentage (1.4) for age-group V indicates that the 1938 year class was exceptionally weak. Conceivably, unusual strength of year-class 1937 made year-class 1938 seem weaker than it was in fact. On the other hand, the point should be made that age-groups IX and X were represented as well as or better than the V group. It is highly probable that year-class 1941 also was extremely weak. Segregation on the basis of maturity cannot explain the low representation of the year class since immature fish made up the large majority of the III-group females. Neither does segregation as to size offer a satisfactory explanation as growth of walleyes of the 1943 sample was much more rapid than in earlier years when II-group fish were taken in abundance.

SIZE AT CAPTURE

LENGTH AND WEIGHT OF THE AGE GROUPS

For the presentation of the average lengths and weights of the age groups at capture (table 13) data for fish of the 1926–30 collections that had completed the same number of growing seasons (see footnote to table) have been combined. True, walleyes of corresponding age and sex in different years did not agree perfectly as to average size. The differences that did occur, however, were not large and could be accounted for satisfactorily on the basis of the small numbers of fish in certain collections or as the result of the annual fluctuations in growth rate that are known to have occurred during and preceding the years of collection. Data for the 1943 collection have been tabulated separately since walleyes captured in that year had grown much more rapidly than had the fish of the earlier samples.

A detailed discussion of table 13 is not desirable, as more adequate and detailed information will be available from later tabulations of calculated growth in length and weight. Treatment will be limited, therefore, to brief comments on the general trends of increase of size with age, on sex differences in growth, and on the increased growth of fish of the 1943 collection.

At the end of 2 growing seasons the male and female walleyes of the 1926–30 samples had the same average length (10.0 inches). In 3 years (in this section the terms "years" and "growing seasons" are used interchangeably) the females (12.7 inches) were 0.1 inch longer than the males (12.6 inches). To this advantage the females added consistently to the end of 9 growing seasons when their average length (22.8 inches) was 3.5 inches greater than that of the males (19.3 inches). During the later years of life the length advantage of

TABLE 13.—*Average total lengths and weights of the age groups of male and female Saginaw Bay walleyes collected in 1926–30 and 1943*

[Number of fish in parentheses]

Age groups and number of completed growing seasons [1]	1926–30 collections				1943 collection			
	Males		Females		Males		Females	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight
	Inches	*Lbs.*	*Inches*	*Lbs.*	*Inches*	*Lbs.*	*Inches*	*Lbs.*
I–II	10.0	0.32	10.0	0.31				
(2 seasons)	(170)	(25)	(195)	(50)				
II–III	12.6	0.59	12.7	0.59	16.4	1.41	17.0	1.59
(3 seasons)	(161)	(158)	(153)	(149)	(101)	(101)	(50)	(50)
III–IV	14.4	0.89	14.7	0.96	17.5	1.69	18.6	2.10
(4 seasons)	(251)	(250)	(166)	(166)	(49)	(49)	(30)	(30)
IV–V	15.9	1.28	16.5	1.44	18.5	2.04	21.2	3.38
(5 seasons)	(113)	(110)	(121)	(121)	(3)	(3)	(1)	(1)
V–VI	17.3	1.36	18.6	1.88	19.8	2.59	22.1	3.45
(6 seasons)	(81)	(9)	(68)	(16)	(14)	(14)	(16)	(16)
VI–VII	18.0	1.83	20.1	2.62	20.3	2.61	23.4	4.25
(7 seasons)	(131)	(25)	(131)	(35)	(5)	(5)	(3)	(3)
VII–VIII	18.5	1.85	21.3	3.05	20.2	3.05		
(8 seasons)	(87)	(5)	(70)	(19)	(2)	(2)		
VIII–IX	19.3	2.42	22.8	4.25	21.2	3.33	24.6	4.59
(9 seasons)	(41)	(2)	(48)	(15)	(3)	(3)	(2)	(2)
IX–X	21.1	3.19	23.8	4.91	22.3	3.84	25.0	5.56
(10 seasons)	(24)	(2)	(52)	(7)	(3)	(3)	(1)	(1)
X–XI	21.7	3.71	24.9	5.48				
(11 seasons)	(10)	(1)	(30)	(4)				
XI–XII	22.1		25.9	5.96			26.5	5.75
(12 seasons)	(3)		(19)	(5)			(1)	(1)
XII–XIII	23.5		26.1	6.88			28.9	7.69
(13 seasons)	(2)		(10)	(1)			(2)	(2)
XIII–XIV	21.3		27.3					
(14 seasons)	(2)		(1)					
XIV–XV			28.2	6.75				
(15 seasons)			(1)	(1)				

[1] The age groups at left apply to fall collections taken after completion of season's growth, and those at right to spring collections, made before growth began. Fish enter the next higher age group on January 1.

the females varied irregularly between the minimum of 2.6 inches at the end of 13 seasons (males, 23.5 inches; females 26.1 inches) and the maximum of 6.0 inches at the end of 14 when two males averaged 21.3 inches and the single female was 27.3 inches long. Much of this variation can be ascribed to the small numbers of fish at the higher ages.

The increments of length for the males were 2.6 inches for the third growing season, between 1 and 2 inches in the fourth through the sixth, and less than 1 inch in the seventh through the ninth. For older ages the increments ranged between 1.8 (tenth season) and −2.2 inches (fourteenth). The length increments of the females were 2.7 inches in the third year and from 1.8 to 2.1 inches in the fourth through the sixth years; they did not fall below 1 inch before the thirteenth season.

The weights [8] of the male and female walleyes of the 1926–30 samples were the same or nearly the same at the end of 2 (males, 0.32 pound; females, 0.31 pound) and 3 growing seasons (each sex, 0.59 pound). At the end of 4 years, however, the mean weight of the females (0.96 pound) was 0.07 pound greater than that of males (0.89 pound). The females added to this advantage with a fair degree of consistency during subsequent years. The weight advantage of the females first amounted to more than a half pound at the end of 6 seasons (males, 1.36 pounds; females, 1.88 pounds) and first exceeded a pound at the end of 8 (males, 1.85 pounds; females, 3.05 pounds). In the ninth through the eleventh years the females were the heavier by about 1¾ pounds (no males older than 11 growing seasons were weighed).

The increments of weight of both the male and female walleyes of the 1926–30 collections varied erratically. For the males in the third through the eighth years the values ranged between 0.02 pound (eighth year) and 0.47 pound (seventh). The increments of the ninth through the eleventh years all exceeded a half pound (0.52 to 0.77 pound). The increments of weight for the females were all less than a half pound (0.28 in the third year to 0.48 in the fifth) in the third through the sixth growing season. During the later years the values ranged from 0.43 pound (eighth growing season) to 1.20 pounds (ninth). In only 1 year (tenth) did the weight increment of the males (0.77 pound) exceed that of the females (0.66 pound).

Both the males and females of the 1943 collection averaged longer and heavier than walleyes of corresponding age and sex of the 1926–30 samples (the only exception—weight of females at the end of 12 growing seasons was based on only 5 fish in 1926–30 and 1 in 1943). For the males the length advantage of the 1943 walleyes was greatest at 3.8 inches at the end of 3 years and thereafter followed a downward trend to a minimum of 1.2 inches at the end of the tenth year. For the females the maximum advantage of the 1943 fish (4.7 inches) occurred at the end of the fifth year beyond which point the trend again was downward. The advantages of the 1943 over the 1926–30 walleyes were relatively much greater with respect to weight than length. In 4 of the comparisons the fish of the more recent collection were more than twice as heavy as those of the earlier, and in 7 of them the advantage of the 1943 fish exceeded a pound.

[8] Since in most age groups fewer fish were weighed than were measured, the mean length and the mean weight of an age group do not necessarily correspond.

Sex differences in average size were established at an earlier age in the 1943 than in the 1926–30 collections. At the end of 3 growing seasons, for example, the 1943 females (length, 17.0 inches; weight, 1.59 pounds) averaged 0.6 inch longer and 0.18 pound heavier than the males (length, 16.4 inches; weight, 1.41 pounds). At the same age the advantage of the 1926–30 females over the males was only 0.1 inch with respect to length and was nil with respect to weight. For walleyes of approximately the same average size, however, sex differences in the two collections were similar. As an illustration, the difference between the 1926–30 males and females at the end of 5 seasons (0.6 inch; 0.16 pound) was much the same as that between 1943 males and females (0.6 inch; 0.18 pound) at the end of 3 years. Similarly at the end of 6 seasons the advantage of 1926–30 females over males of the same age (1.3 inches; 0.52 pound) was only a little greater than the advantage of the 1943 females at the end of 4 years (1.1 inches; 0.41 pound). It appears, therefore, that size rather than age determines the time of appearance and the extent of sex differences in the growth of the Saginaw Bay walleye.

LENGTH DISTRIBUTION OF THE AGE GROUPS

Data on the length-frequency distribution of the age groups (tables 14, 15, and 16) are so arranged that the collections of 1926–30 and 1943 are treated separately, and walleyes of the earlier collections that had completed the same number of growing seasons are combined regardless of their age designation.

The range in length of most of the well-represented age groups of males collected in 1926–30 (table 14) fell within the limits of 5 to 8 inches [9] (exception for walleyes that had completed 6 growing seasons). For the females (table 15), which had a somewhat greater scatter, the ranges were mostly between 6 and 9 inches (exception at 9 growing seasons).

These relatively large ranges of length were so much greater than the annual increments of length that extensive overlapping of the distributions characterized the data for both sexes. In a random sample from the general population only one of the ages represented—walleyes that had completed 2 growing seasons—could be expected to form a distinct mode in the frequency distribution for all ages combined (see also p. 25). In later years (and for some 2-year fish) length *per se* is a poor index of age. In the males, for example, every length interval from the one with its center at 13.8 inches to the one at 23.1 inches was represented by from 3 to 7 ages. The maximum range of age was 9 years at 21.8 inches; representatives actually were present for 7 of the 9 ages. The mean range of ages at 13.8 to 23.1 inches was 5.1. Similarly with the females, every length from 12.0 to 28.3 inches was represented by 3 to 7 ages. The maximum range of ages (at 20.5 inches) was 8, of which 7 were represented. The mean range at 12.0 to 28.3 inches was 4.9 years.

The data on the length-frequency distribution of the age groups of the 1943 sample (table 16) are too few to warrant a detailed discussion. The length ranges of the age groups ran smaller in the 1943 than in the 1926–30 samples, but the difference might not have existed had the numbers of fish been greater in 1943.

Changes since 1926 in the minimum legal size of walleyes in Saginaw Bay waters make it desirable to give the percentages of legal fish at different ages as estimated from each of three size limits. A minimum size of 1½ pounds [10] (in the round) was in effect during the 1926–30 collecting period and subsequently through 1932. From 1933 to 1938, inclusive, the minimum legal size was 16½ inches total length, and since that time it has been 15½ inches.

With the exception of a single 3-year-old male that was more than 15½ but less than 16½ inches long, no walleyes of the 1926–30 collections were legal-sized in less than 4 growing seasons under any of the three limits. Some fish were legal (1 to 22 percent according to sex and size limit) at the end of 4 seasons, and the percentage increased rapidly with increase in age. Among the males more than half were legal-sized in 5 years at the 15½-inch limit (57 percent) and in 6 years at limits of 16½ inches (83 percent) and 1½ pounds

[9] In estimating ranges from the tables, 0.8 or 0.9 inch must be added to the differences between the midpoints of the terminal frequency intervals.

[10] Because records of weight were lacking for some of the 1926–30 collections, the percentages of legal-sized fish under the 1½-pound limit as given in tables 14 and 15 were determined on the basis of a legal minimum length of 375 millimeters, standard length (17.1 inches, total length). This length was computed from the general length-weight equation (p. 27) to be equivalent to a weight of 1½ pounds. For table 16 the percentage legal at 1½ pounds was determined from actual weights at capture.

TABLE 14.—*Length frequencies of male Saginaw Bay walleyes of the 1926–30 collections according to number of completed growing seasons*

[Age groups of fall collections combined with next higher age groups of spring collections. Fish enter the next higher age group on January 1]

Total length	Standard length	Number of fish that completed growing season—												
		2	3	4	5	6	7	8	9	10	11	12	13	14
	Mm.													
8.6 in.	185	13												
9.5 in.	204	74												
10.3 in.	224	65	4											
11.1 in.	244	14	16	2										
12.0 in.	263	3	45	4										
12.9 in.	282		64	43										
13.8 in.	302	1	24	63	4	1	1							
14.7 in.	322		7	76	26									
15.5 in.	341			46	32	4								
16.4 in.	360		1	13	32	21	14	2						
17.3 in.	380			3	13	35	42	17	2					
18.2 in.	400			1	6	11	37	21	3					
19.1 in.	419					5	21	25	15					
19.8 in.	438						12	17	15	6				
20.5 in.	458					2	4	2	3	4	1			
21.3 in.	478					2		3	2	8	5	2		2
22.2 in.	497								1	4	2		1	
23.1 in.	516									1	2	1		
24.0 in.	536									1				
24.8 in.	556												1	
Total		170	161	251	113	81	131	87	41	24	10	3	2	2
Average total length (in.)		10.0	12.6	14.4	15.9	17.3	18.0	18.5	19.3	21.1	21.7	22.1	23.5	21.3
Average standard length (mm.)		214	276	314	348	380	397	412	430	472	484	494	525	476
Percentage legal at—														
1½ pounds		0	0	1	13	52	79	93	100	100	100	100	100	100
16½ inches		0	0	4	30	83	94	100	100	100	100	100	100	100
15½ inches		0	1	15	57	98	99	100	100	100	100	100	100	100

TABLE 15.—*Length frequencies of female Saginaw Bay walleyes of the 1926–30 collections according to number of completed growing seasons*

[Age groups of fall collections combined with next higher groups of spring collections. Fish enter next higher age group on January 1]

Total length	Standard length	Number of fish that completed growing season—													
		2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Mm.														
7.7 in.	165	1													
8.6 in.	185	20													
9.5 in.	204	64	2												
10.3 in.	224	87													
11.1 in.	244	20	10												
12.0 in.	263	2	40	5											
12.9 in.	282	1	59	11											
13.8 in.	302		33	43	1										
14.7 in.	322		9	52	9										
15.5 in.	341			34	26	2									
16.4 in.	360			14	41	6	1								
17.3 in.	380			4	26	12	5		1						
18.2 in.	400			1	15	11	9								
19.1 in.	419			2	3	16	13	5	1						
19.8 in.	438					10	33	15	1						
20.5 in.	458					7	36	9	3	2	1		1		
21.3 in.	478					3	26	18	7	2	1				
22.2 in.	497					1	6	10	8	7	1	1			
23.1 in.	516						2	6	10	14	3	2			
24.0 in.	536							3	11	9	5				
24.8 in.	556							3	1	7	5	2	1		
25.7 in.	575							1	3	6	5	5	2		
26.6 in.	595								2	3	7	4	2		
27.4 in.	614									1	1	2	2	1	
28.3 in.	634									1	1	2	2		1
29.2 in.	653											1			
Total		195	153	166	121	68	131	70	48	52	30	19	10	1	1
Average total length (in.)		10.0	12.7	14.7	16.5	18.6	20.1	21.3	22.8	23.8	24.9	25.9	26.1	27.3	28.2
Average standard length (mm.)		216	280	322	364	412	447	475	510	533	557	579	583	610	634
Percentage legal at—															
1½ pounds		0	0	4	32	84	98	100	100	100	100	100	100	100	100
16½ inches		0	0	6	49	94	100	100	100	100	100	100	100	100	100
15½ inches		0	0	22	84	100	100	100	100	100	100	100	100	100	100

TABLE 16.—*Length frequencies of the age groups of Saginaw Bay walleyes of the 1943 collection*

[Ages correspond to numbers of completed growing seasons]

Total length	Standard length	Number of fish by sex (M, male; F, female) in age-group—																
		III		IV		V		VI		VII		VIII	IX		X		XII	XIII
		M	F	M	F	M	F	M	F	M	F	M	M	F	M	F	F	F
	Mm.																	
14.7 in	322	5																
15.5 in	341	20	7	2	1													
16.4 in	360	38	19	12	1													
17.3 in	380	38	18	17	6	1												
18.2 in	400		6	14	8			2				1						
19.1 in	419			4	6	2		5		1								
19.8 in	438				6			3	2	2			1					
20.5 in	458				2			3		1			1					
21.3 in	478						1	1	3	1								
22.2 in	497								9		1	1	1		3			
23.1 in	516								2		1							
24.0 in	536										1			1				
24.8 in	556													1		1		
25.7 in	575																	
26.6 in	595																1	1
27.4 in	614																	
28.3 in	634																	
29.2 in	653																	
30.1 in	673																	
30.9 in	692																	1
Total		101	50	49	30	3	1	14	16	5	3	2	3	2	3	1	1	2
Average total length (in.)		16.4	17.0	17.5	18.6	18.5	21.2	19.8	22.1	20.3	23.4	20.2	21.2	24.6	22.3	25.0	26.5	28.9
Average standard length (mm.)		360	372	383	409	406	475	436	494	448	523	448	470	550	499	559	592	645
Percentage legal at—																		
1½ pounds		41	70	80	93	100	100	100	100	100	100	100	100	100	100	100	100	100
16½ inches		53	80	88	97	100	100	100	100	100	100	100	100	100	100	100	100	100
15½ inches		91	98	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

(52 percent). The maximum ages in completed growing seasons, of undersized males under the three limits were: 15½ and 16½ inches, 7; 1½ pounds, 8. A majority or nearly a majority of female walleyes of the 1926–30 samples reached legal size in 5 seasons under the 15½-inch (84 percent) and 16½-inch limits (49 percent) and in 6 years with the 1½-pound minimum (84 percent). The oldest undersized females were: 15½ inches, 5 seasons; 16½ inches, 6; 1½ pounds, 7. On the whole, males required in the neighborhood of a year longer than females to attain legal size.

As the result of their much more rapid growth, walleyes of the 1943 collection were predominantly legal at a relatively early age (table 16). Only one percentage was less than 50 (41 percent of III-group males legal-sized under the 1½-pound limit) and not one fish that had completed more than 4 growing seasons was undersized under any of the three limits.

LENGTH DISTRIBUTION OF THE CATCH OF IMPOUNDING NETS

The earlier data on age composition and the length-frequency distributions of the age groups were sufficient to make it apparent that the lengths of walleyes in random samples from commercial impounding nets vary considerably not only from year to year but also by seasons within a year. Information on the extent of this variation is summarized in table 17 which is based both on the scale collections[11] and on the measurements of large numbers of walleyes not employed in the study of age or growth. The arrangement of the table is such as to facilitate the ready comparison of the distributions of walleyes captured at the same season but in different years. The major sections illustrate the general trends within a year from the spawning season (in early spring) to autumn.

The spawning-run samples of 1927 and 1929 were distributed so irregularly that it is not possible to discuss them in terms of sharp modes or distinct trends.[12] In 1927, walleyes were most

[11] Fish for which ages could not be determined (reading too uncertain: scales with regenerated centers or otherwise defective) were included in the preparation of the length destributions of table 17.

[12] Transformations of data that were necessary to fit the information on the 1929 spawning run into table 17 have introduced some irregularities that were not present in the original measurements. Most of the walleyes of the collection were measured to the nearest half centimeter of total length. When these measurements were tabulated in terms of centimeter intervals of standard length some intervals included two and others three of the original units of measurement. At some intervals distortion from this source was augmented by an apparent bias in the original measurements favoring full over half centimeters.

TABLE 17.—*Length-frequency distribution of Saginaw Bay walleyes according to year and season of capture*

[Random samples from commercial and experimental impounding nets]

Total length	Standard length	Spawning run			Late spring		Autumn		
		1927	1929	1943[1]	1929	1930	1926	1928	1929
	Mm.								
7.0 in.	151				2				
7.4 in.	160				1				
7.9 in.	170						1	2	
8.4 in.	180					2	3	5	
8.8 in.	190				8	2	26	12	2
9.3 in.	200				16	1	56	33	
9.7 in.	209				71	11	76	72	1
10.1 in.	219				114	9	86	123	1
10.5 in.	229				106	11	35	146	3
10.9 in.	239				142	14	15	109	
11.3 in.	248				98	25	8	41	6
11.8 in.	258				89	59		35	10
12.2 in.	268				134	69		39	13
12.7 in.	278				172	92	1	30	14
13.1 in.	287				190	133		30	3
13.5 in.	297	1			193	110		18	9
14.0 in.	307			1	207	115		13	3
14.5 in.	317			1	221	119	1	9	5
14.9 in.	326			4	218	107	1	12	7
15.3 in.	336	2		6	178	104	1	8	11
15.8 in.	346	2	2	25	129	74		2	11
16.2 in.	356	6	14	29	88	70		1	20
16.6 in.	365	10	26	41	57	60		2	7
17.1 in.	375	11	69	51	59	36		1	15
17.6 in.	385	11	26	29	43	31			5
18.0 in.	395	13	21	10	30	19			10
18.4 in.	404	12	38	21	21	18	1	1	1
18.9 in.	414	10	42	10	20	6			1
19.3 in.	424	11	30	8	7	6			1
19.7 in.	434	3	58	8	13	2			1
20.0 in.	443	4	37	6	19	4			1
20.3 in.	453	7	21	2	12	3			
20.7 in.	463	3	23	5	8	8		1	
21.3 in.	473	7	38	2	15	7			
21.6 in.	482	3	21	4	7	5			
22.0 in.	492	1	17	8	3	6			
22.5 in.	502		19	7	6	4			
22.9 in.	512	3	11	2	4	4			1
23.3 in.	521		18	1	1	1			
23.8 in.	531	3	11		6	3			
24.2 in.	541	2	11	2	2	2	1		
24.7 in.	551	1	10	2	2	1			
25.1 in.	560		4		2	5			
25.5 in.	570		15		3	4			
25.9 in.	580		3			2			
26.4 in.	590	3	9	1	5	1			
26.8 in.	600	1	5	1		1			
27.2 in.	609		3		2	2			
27.7 in.	619				1	2			
28.1 in.	629	1	2			1			
28.6 in.	639				2	1			
29.0 in.	648						1		
29.4 in.	658								
29.9 in.	668								
30.3 in.	678								
30.7 in.	687			1					
Total		131	604	288	2,787	1,372	313	745	162
Average total length (in.)		19.1	20.1	17.9	13.8	14.7	10.0	11.1	14.8
Average standard length (mm.)		422	445	394	304	323	217	242	324
Percentage legal at—									
1½ pounds		80	88	55	10	12	1	[2]0	18
16½ inches		92	97	75	12	17	1	1	26
15½ inches		98	100	96	21	30	1	1	48

[1] From late spawning run.
[2] Less than 0.5 percent.

plentiful over the range,[13] 16.6 to 19.3 inches, which included 78 walleyes, or 60 percent of the entire sample. Most of the remaining fish (42 walleyes, or 32 percent of the total) were longer than 19.3 inches. The larger walleyes were relatively even more plentiful in the 1929 than in the 1927 spawning run. For example, 56 percent (336 fish) of the 1929 collection exceeded 19.3 inches as compared with the 32 percent in 1927. Fish less than 16 inches long were scarce in both years—only 5 in 1927 and 2 in 1929. The greater relative abundance of the larger fish in the 1929 spawning run led to an average length (20.1 inches) 1 inch greater than in 1927 (19.1 inches).

The 1943 collection, as explained previously (p. 8), appears to have been intermediate between the spawning-run and late-spring samples, since it contained considerable numbers of immature fish along with some adults that had not yet spawned and more that were freshly spent. In this sample the walleyes were rather well concentrated toward the lower end of the length range. The interval 15.8 to 17.6 inches included 175 fish, or 61 percent of the total, and a distinct mode was present at 17.1 inches. Only 101 (35 percent) of the fish exceeded 17.6 inches. The mean length of the 1943 walleyes (17.9 inches) was 1.2 and 2.2 inches, respectively, below the averages for the bona fide spawning-run samples of 1927 and 1929.

The late-spring collections of 1929 and 1930 were characterized by large numbers of smaller walleyes with a scattering of larger individuals. In 1929, 2,349 walleyes, or 84.3 percent of the total, were less than 16 inches long and in 1930, 1,057, or 77 percent of the entire collection, were below that length. This situation contrasts sharply with that in the spawning-run samples of 1927 and 1929 in which almost all walleyes were longer than 16 inches. The comparison between spawning-run and late-spring collections of 1929 provides a particularly striking illustration of the extensive changes that can occur in the length distribution of samples in a matter of weeks.

Although the late-spring samples of 1929 and 1930 both contained large numbers of the smaller walleyes, they differed as to the distribution of these shorter fish. In 1929, the numbers of the lesser lengths increased with increase in length to a mode at 10.5 inches, declined to a minimum at 11.8 inches, and then increased again. The second interval with large numbers of fish was relatively long (roughly 12.2 to 15.8 inches) and without sharp peaks. The 1930 collection had the second,

[13] For convenience, statements of range in this section are given in terms of midpoints of the extreme intervals. It is to be understood that the actual range extends about 0.2 or 0.25 inch beyond each of these midpoints.

long, flat concentration but lacked the first one almost entirely. The difference between the 2 years can be attributed to the great scarcity of II-group walleyes (weak 1928 year class—see p. 19). In the 1929 distribution the concentration with a mode at 10.5 inches was made up principally of II-group walleyes and the depression between 11 and 12 inches marks the transition from predominance of age-group II to that of older fish.[14] Age-group II was so sparsely represented in 1930, however, that it did not form a distinct mode in the length-frequency distribution of that year's collection. The scarcity of II-group walleyes was the most important cause of a higher mean length in 1930 (14.7 inches) than in 1929 (13.8 inches).

The three fall collections agreed in that walleyes above a length of about 18 inches were rare in all of them. Below that length, however, the distributions varied widely. The 1926 sample was made up almost exclusively of extremely small fish; 98 percent fell at 11.3 inches and less. This concentration at small lengths can be traced to the overwhelming dominance of age-group I (2 growing seasons) in that year (table 4). The distribution of the 1928 collection which contained a small but appreciable representation of age-group II was less concentrated although by far the bulk of the sample (73 percent) still lay at 11.3 inches or less. The smallest fish were as scarce in 1929 as they were abundant in the earlier fall collections. Intervals at 11.3 inches and less included only 8 percent of the total collection. The bulk of the walleyes (92 percent) were distributed irregularly over the range, 11.8 to 18.0 inches. The scarcity of I-group walleyes in the fall of 1929[15] is in agreement with that of the II group in 1930; both groups were members of year-class 1928 which, according to all evidence, was extremely weak. The overwhelming dominance of age-group I in 1926, the presence of some older fish (especially the II group) in 1928, and the scarcity of the I group in 1929 account for successive increases in the mean length of walleyes captured in the fall from 10.0 to 11.1 to 14.8 inches.

The percentage of legal-sized walleyes, of course, varied enormously according to the mean lengths and length distributions in the different seasons and years. Commercial fishermen could have retained the bulk of the walleyes in the spawning-run samples of 1927 and 1929 (80 and 88 percent, respectively) even at the 1½-pound size limit[16] then in effect. Under the limits that were subsequently in force (see p. 22 for statement of times of change of legal minimum size limits) they could have kept even more (92 and 97 percent at 16½ inches; 98 and 100 percent at 15½ inches). Most of the walleyes (96 percent) of the 1943 late-spawning-run sample were of legal size under the 15½-inch minimum then in force. At 16½ inches 75 percent and at 1½ pounds only 55 percent could have been retained.

The sorting of the catch of walleyes must have been an irritating task for the commercial fishermen of Saginaw Bay in the late spring of 1929 and 1930 and the falls of 1926, 1928, and 1929. Under the 1½-pound limit only 10 and 12 percent, respectively, of the take could be retained in the two late-spring samples. A 16½-inch limit would have been of some small benefit (increases to 12 and 17 percent) whereas a 15½-inch minimum would have permitted better than a doubling of the number of walleyes kept (21 and 30 percent).[17] In the fall of 1926 and of 1928 only a negligible few of the walleyes were legal and no reasonable lowering of the size limit could have benefited the fishermen materially. In 1929, however, 18 percent were legal, at the 1½-pound limit and 26 and 48 percent respectively could have been marketed legally at limits of 16½ and 15½ inches.

LENGTH-WEIGHT RELATION

GENERAL RELATION

Annual and seasonal fluctuations in the length-weight relation and variations related to sex, maturity, and the state of organs have been observed so frequently that their occurrence can be accepted as general. Because of these fluctuations, some of which may be large, a curve based on fish captured

[14] This statement is supported by age records for a large sample of fish—see table 4 for the numbers in the different age groups.

[15] No scale collections were made in the fall of 1929. The general size range of walleyes that had completed 2 growing seasons can be considered well established, however, from data for other 1926–30 collections.

[16] All estimates in table 17 of percentages of legal-sized walleyes under the 1½-pound limit were based on the length distributions. See footnote 10 for statement of procedure.

[17] The high percentages of undersized walleyes in the catches together with a strong market demand for the smaller fish must have been responsible for the large-scale traffic in illegal-sized walleyes that existed prior to the enactment of the 15½-inch limit.

at one time may describe poorly the length-weight relation at another time. From a practical standpoint, it is important to have a single curve that best depicts the general relation even though the curve is not exact for any particular time. To arrive at such a general relation, the most satisfactory procedure appears to lie in the lumping together of the available materials regardless of the year or season of capture, the sex, ... This procedure was followed in the preparation of table 18.

The calculated weights of table 18 were computed by means of the following length-weight equation which was fitted to the empirical mean values of length and weight for length intervals represented by more than 5 fish:

$$W = 1.376 \times 10^{-5} L^{2.989},$$

where W = weight in grams,
and L = standard length in millimeters.

In logarithmic form actually used for calculation the equation is written:

$$\log W = 2.988737 \log L - 4.8613315.$$

The agreement between the empirical and computed weights of the Saginaw Bay walleye (table 18 and fig. 3) can be termed satisfactory. The discrepancy between the two did not exceed 0.03 pound at any point over the range, 7.0 to 16.6 inches (corresponding range of theoretical weight, 0.10 to 1.38 pounds) and was nil or only 0.01 pound at 15 of the 23 intervals. All discrepancies in excess of 0.10 pound were at lengths greater than 19.3 inches (theoretical and empirical weights both 2.16 pounds at that length) and even at these larger sizes the maximum difference in an interval represented by 10 or more fish was only 0.11 pound (at 19.7 inches where the empirical weight was 2.43 pounds and the computed weight was 2.32 pounds). Better agreement than that just described could hardly be expected from heterogeneous materials, particularly when one considers the potential distorting effects of seasonal fluctuations in the length-weight relation (see next sections) in combination with seasonal differences in the length-frequency distributions (table 17).

The total lengths corresponding approximately to certain computed weights of the Saginaw Bay walleye are: ½ pound, 11.9 inches; 1 pound, 14.9 inches; 1½ pounds, 17.1 inches; 2 pounds, 18.9 inches; 3 pounds, 21.2 inches; 5 pounds, 25.2 inches.

TABLE 18.—*Length-weight relation of Saginaw Bay walleye based on combined collections of 1928–30 and 1943*

[Lengths are board measurements equivalent to midpoints of centimeter intervals of standard length as measured with steel tape]

Number of fish	Total length	Weight		Standard length	Weight		K
		Empirical	Calculated [1]		Empirical	Calculated [1]	
	Inches	*Pounds*	*Pounds*	*Millimeters*	*Grams*	*Grams*	
2	7.0	0.10	0.10	151	44	45	1.28
1	7.4	.09	.12	160	40	53	.98
2	7.9	.16	.14	170	71	64	1.45
7	8.4	.18	.17	180	82	76	1.41
17	8.8	.19	.20	190	87	89	1.27
34	9.3	.24	.23	200	107	104	1.34
117	9.7	.26	.26	209	117	118	1.28
207	10.1	.30	.30	219	136	136	1.29
254	10.5	.34	.34	229	153	155	1.27
217	10.9	.37	.39	239	170	177	1.25
148	11.3	.42	.43	248	191	197	1.25
179	11.8	.48	.49	258	219	222	1.28
239	12.2	.54	.55	268	246	249	1.28
298	12.7	.60	.61	278	270	278	1.26
344	13.1	.66	.67	287	299	305	1.26
321	13.5	.73	.75	297	327	338	1.25
332	14.0	.81	.82	307	368	373	1.27
353	14.5	.89	.91	317	405	411	1.27
343	14.9	.97	.99	326	440	447	1.27
304	15.3	1.08	1.08	336	490	489	1.29
240	15.8	1.16	1.18	346	526	534	1.27
208	16.2	1.29	1.28	356	587	581	1.30
170	16.6	1.41	1.38	365	640	626	1.32
166	17.1	1.55	1.50	375	703	679	1.33
119	17.6	1.68	1.62	385	760	734	1.33
72	18.0	1.81	1.75	395	822	793	1.33
64	18.4	1.88	1.87	404	854	848	1.30
41	18.9	2.09	2.01	414	946	912	1.33
26	19.3	2.16	2.16	424	979	980	1.28
28	19.7	2.43	2.32	434	1,103	1,051	1.35
31	20.0	2.53	2.46	443	1,150	1,117	1.32
21	20.3	2.60	2.63	453	1,180	1,194	1.27
23	20.7	2.91	2.81	463	1,319	1,275	1.33
24	21.2	2.95	3.00	473	1,339	1,359	1.27
18	21.6	3.13	3.17	482	1,419	1,437	1.27
18	22.0	3.38	3.37	492	1,532	1,528	1.29
17	22.5	3.63	3.58	502	1,648	1,623	1.30
11	22.9	3.84	3.80	512	1,741	1,722	1.30
3	23.3	4.27	4.00	521	1,937	1,814	1.37
10	23.8	4.22	4.23	531	1,915	1,920	1.28
7	24.2	4.34	4.48	541	1,970	2,030	1.24
6	24.7	4.98	4.73	551	2,257	2,144	1.35
7	25.1	4.59	4.96	560	2,082	2,251	1.19
8	25.5	5.08	5.23	570	2,305	2,373	1.24
2	25.9	4.45	5.51	580	2,020	2,499	1.04
7	26.4	5.68	5.80	590	2,575	2,630	1.25
2	26.8	6.33	6.10	600	2,870	2,766	1.33
4	27.2	6.42	6.38	609	2,913	2,892	1.29
4	27.7	6.74	6.69	619	3,058	3,036	1.29
2	28.1	7.25	7.02	629	3,289	3,185	1.32
3	28.6	6.73	7.36	639	3,052	3,339	1.17
1	30.7	8.91	9.14	687	4,040	4,146	1.25

[1] See text for equation used to determine calculated weights.

The heaviest fish of the combined samples (taken in 1943) had an actual weight of 8.91 pounds and a calculated weight of 9.14 pounds at the length of 30.7 inches. The weight corresponding to the present legal minimum length of 15½ inches is 1.12 pounds. The size limit of 1½ pounds, in effect at the time of collection of the 1926–30 samples was equivalent to total length of 17.1 inches, and the 1933–38 minimum legal length of 16½ inches corresponded to a weight of 1.36 pounds.

Since the value of the exponent in the length-weight equation (2.989) was so close to 3, no distinct trend was to be anticipated in the variation

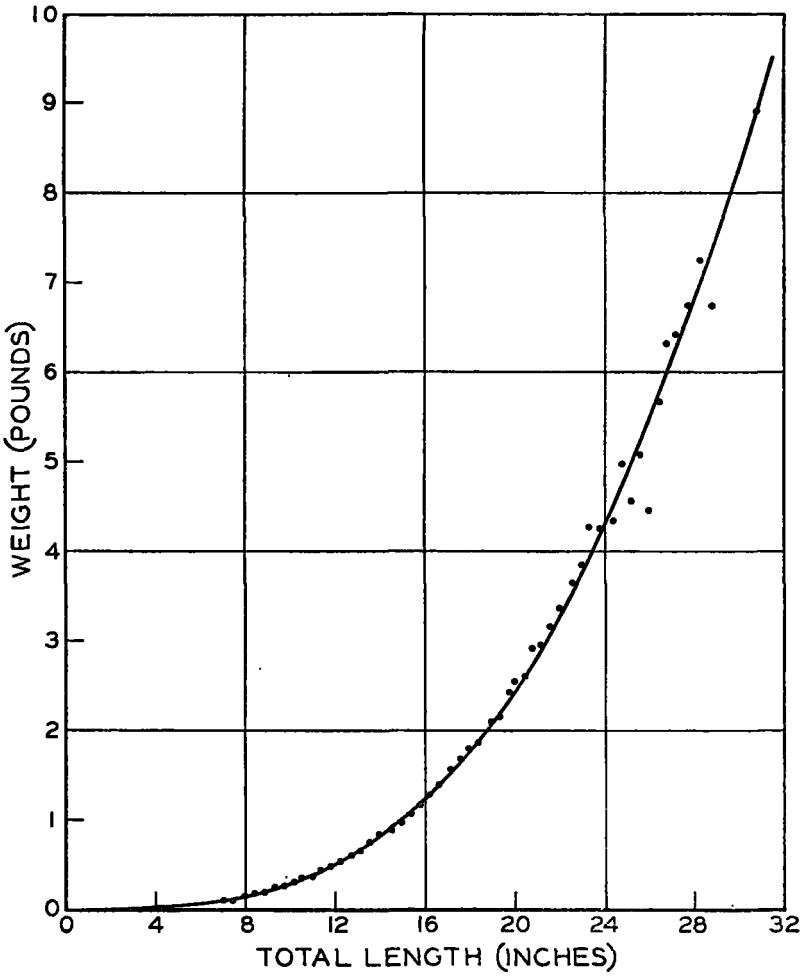

FIGURE 3.—Length-weight relation of the Saginaw Bay walleye. The dots represent the empirical data of table 18. The smooth curve is the graph of the length-weight equation given in the text.

of the coefficient of condition, K,[18] with increase of length. (If the value of the exponent is n, K varies as the $n-3$ power of the length.) The actual values of K (of table 18) conform to this expectation. The mean value of the coefficient for all fish was 1.28. The weight of the walleye seems to be relatively lighter in Saginaw Bay than in Lake of the Woods for which Carlander (1945) reported an average K of 1.47 and in Trout Lake, Wis., where the mean coefficient was 1.45 (Schloemer and Lorch 1942).

FLUCTUATIONS OF WEIGHT IN LATE-SPRING COLLECTIONS

The frequent sampling during late spring of 1929 and of 1930 has made it possible to investigate short-term fluctuations in the weights of walleyes captured in the same nets[19] over periods of approximately 6 weeks and 2 months. Attention will be given first to the data for 1930 since for that year's collections alone were records of sex and maturity available for the individual fish. It is considered desirable to establish the degree to which those factors may affect data on the length-weight relation during the late-spring period.

The preliminary tabulations of the 1930 data brought out the following points: In fish of the same collection no consistent differences occurred between the weights of mature and immature males of corresponding length or between males and immature females; mature females tended

[18] $K=\frac{W\times 10^5}{L^3}$, where W=weight in grams, and L=standard length in millimeters.

[19] The 1929 and 1930 collections were from experimental pound nets fished near Bay Port.

to be somewhat heavier than males and immature females (exceptions to this trend can be ascribed to inadequate numbers of fish); the length-weight relation varied but little within two individual periods, April 25–May 13 and May 19–June 20; walleyes captured during the earlier of these two periods were distinctly the heavier for their length.

The consistency with which weights were higher in the collections of April 25–May 13 than in those of May 19–June 20 may be seen in table 19 (here data are recorded separately for males and immature females despite the small differences between the two groups). Not one exception is to be found even though some of the weights were based on only one or a few fish.[20] Furthermore, the percentage advantage of walleyes of the April 25–May 13 samples over the May 19–June 20 fish tended to group closely about a characteristic value; 27 of 38 values were within the range, 15 to 25 percent, and most of the 11 percentages outside that range came from comparisons based on small numbers of specimens. The unweighted mean values of the percentages were almost identical for the three series of comparisons: males, 20.4 percent; immature females, 19.3 percent; mature females, 19.7 percent. There is no indication that the relative advantage of the walleyes collected April 25–May 13 varied with the length of the fish except possibly in the immature females where the percentages of the last three length intervals were much lower than those of shorter fish. Comments on the possible explanation for a decline of approximately 20 percent in the weight of walleyes within a period of 6 days[21] will be deferred until after the presentation of the data on short-term fluctuations in weight during the spring of 1929.

Changes in the average weights of walleyes captured in the experimental pound nets at Bay Port in 1929 (table 20), although generally smaller than those of 1930, occurred several times rather than once during the collecting season. At the beginning of the collecting period (May 8–15) the walleyes were of intermediate weight but still on

[20] The table covers the range of length over which at least one of the three categories was represented by 5 fish or more in both the April 25–May 13 and May 19–June 20 periods. At an interval meeting this requirement data were included for the remaining categories even though the numbers of fish were less than five.

[21] That a change in the weight composition was occurring between May 13 and 19 was indicated by small numbers of fish taken May 15 and 17. The weights of these fish tended to be intermediate to those of walleyes of the April 25–May 13 and May 19–June 20 periods.

TABLE 19.—*Comparison of weights of Saginaw Bay walleyes captured April 25–May 13 and May 19–June 20, 1930*

[Figures in parentheses listed under average weight are the number of specimens and under difference are the percentage advantage of fish captured April 25–May 13 over those taken May 19–June 20]

Standard length	Total length	Weight of males			Weight of immature females			Weight of mature females		
		Average, April 25–May 13	Average, May 19–June 20	Difference	Average, April 25–May 13	Average, May 19–June 20	Difference	Average, April 25–May 13	Average, May 19–June 20	Difference
	Inches	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
248 mm	11.3	7.3 (6)	5.8 (5)	1.5 (25.9)	8.0 (1)	5.7 (8)	2.3 (40.4)			
258 mm	11.8	8.6 (9)	6.9 (13)	1.7 (24.6)	8.2 (5)	6.7 (14)	1.5 (22.4)			
268 mm	12.2	9.6 (12)	8.1 (23)	1.5 (18.5)	9.4 (2)	8.1 (20)	1.3 (16.0)			
278 mm	12.7	10.1 (14)	8.6 (25)	1.5 (17.4)	11.0 (7)	8.7 (27)	2.3 (26.4)			
287 mm	13.1	11.3 (37)	9.5 (40)	1.8 (18.9)	11.6 (10)	9.8 (27)	1.8 (18.4)	12.2 (1)	11.0 (2)	1.2 (10.9)
297 mm	13.5	12.5 (28)	10.7 (27)	1.8 (16.8)	12.3 (10)	10.6 (36)	1.7 (16.0)			
307 mm	14.0	14.0 (32)	11.7 (28)	2.3 (19.7)	14.6 (20)	11.8 (19)	2.8 (23.7)	13.8 (1)	11.5 (2)	2.3 (20.0)
317 mm	14.5	15.4 (42)	12.8 (19)	2.6 (20.3)	15.0 (19)	12.6 (17)	2.4 (19.0)			
326 mm	14.9	16.9 (31)	13.0 (15)	3.9 (30.0)	17.6 (21)	14.1 (26)	3.5 (24.8)	17.8 (1)	14.5 (5)	3.3 (22.8)
336 mm	15.3	18.3 (36)	15.6 (17)	2.7 (17.3)	18.4 (19)	15.6 (12)	2.8 (17.9)	18.8 (3)	15.6 (3)	3.2 (20.5)
346 mm	15.8	19.6 (26)	16.7 (7)	2.9 (17.4)	20.9 (9)	17.2 (20)	3.7 (21.5)	21.9 (4)	17.5 (3)	4.4 (25.1)
356 mm	16.2	21.7 (15)	17.7 (8)	4.0 (22.6)	20.6 (13)	18.7 (13)	1.9 (10.2)	23.1 (10)	18.5 (4)	4.6 (24.9)
365 mm	16.6	23.6 (17)	20.5 (9)	3.1 (15.1)	20.3 (6)	19.6 (11)	0.7 (3.6)	24.4 (9)	19.3 (2)	5.1 (26.4)
375 mm	17.1	25.3 (11)	21.3 (6)	4.0 (18.8)	25.5 (1)	23.2 (3)	2.3 (9.9)	26.3 (11)	24.1 (4)	2.2 (9.1)
385 mm	17.6	28.8 (8)	23.5 (1)	5.3 (22.6)				29.9 (12)	25.5 (9)	4.4 (17.3)

TABLE 20.—*Comparison of the weights of Saginaw Bay walleyes, sexes combined, captured on various dates, May and June 1929*

[Number of specimens in parentheses]

Standard length	Total length	Average weight of fish caught during period—				
		May 8–15	May 17–27	May 29–31	June 3–8	June 12–18
	Inches	*Ounces*	*Ounces*	*Ounces*	*Ounces*	*Ounces*
209 mm	9.7	4.1 (12)	3.8 (27)	4.3 (12)	4.0 (12)	4.3 (8)
219 mm	10.1	4.5 (21)	4.4 (56)	5.3 (14)	4.4 (13)	4.9 (10)
229 mm	10.5	5.2 (27)	5.1 (80)	5.6 (19)	5.0 (25)	5.4 (15)
239 mm	10.9	6.1 (20)	5.8 (85)	6.4 (7)	5.7 (14)	6.0 (16)
248 mm	11.3	6.6 (11)	6.3 (49)	7.8 (9)	6.6 (13)	6.7 (16)
258 mm	11.8	7.9 (11)	7.2 (35)	8.1 (20)	7.5 (6)	7.9 (17)
268 mm	12.2	8.6 (23)	8.1 (47)	9.4 (23)	8.2 (19)	8.9 (22)
278 mm	12.7	9.6 (28)	9.2 (65)	10.5 (25)	9.0 (20)	9.8 (34)
287 mm	13.1	10.6 (24)	10.1 (69)	11.4 (26)	10.3 (32)	10.7 (39)
297 mm	13.5	12.0 (19)	11.2 (84)	12.1 (30)	11.2 (30)	11.9 (30)
307 mm	14.0	13.1 (32)	12.7 (71)	14.0 (24)	12.3 (49)	13.2 (31)
317 mm	14.5	14.2 (40)	13.7 (85)	14.9 (34)	14.2 (42)	14.9 (20)
326 mm	14.9	16.2 (41)	15.1 (96)	16.3 (14)	14.8 (52)	15.3 (15)
336 mm	15.3	17.1 (33)	16.5 (74)	17.6 (19)	16.8 (32)	17.6 (20)
346 mm	15.8	18.3 (28)	17.6 (61)	18.7 (4)	18.1 (28)	18.3 (8)
356 mm	16.2	20.2 (15)	19.3 (48)	22.2 (6)	20.4 (14)	19.4 (5)

the average 5.0 percent[22] heavier than fish captured May 17–27. The highest level of weight was attained May 29–31. Walleyes captured in this period averaged 12.5 percent heavier than fish of the May 17–27 collections and 10.9 percent heavier than those taken June 3–8. Another increase of weight occurred June 12–18.

In the 1929 data, as in the 1930, the variations of average weight were remarkably consistent. In the entire table only one exception is to be found with respect to the characteristic direction of change of weight in a particular period; at 16.2 inches the walleyes of June 12–18 averaged smaller, not heavier than fish of the preceding period. This average was based, however, on only 5 specimens.[23] Nor does the consistency end here. At the various length intervals the average weights for the five periods tended to fall in the same order of rank (table 21). As an illustration, walleyes collected May 29–31 were heaviest in 13

[22] Unweighted mean of the percentages for the individual length intervals; percentages not included in the table.

[23] The range of length covered by table 20 was determined from the requirement that each average weight be based on five or more fish. One exception was made for the average at 15.8 inches in the May 29–31 samples.

TABLE 21.—*Number of length intervals at which the walleyes of five collecting periods held particular ranks with respect to average weight*

[Based on data of table 20]

Rank	Number of times a rank was held—				
	May 8–15	May 17–27	May 29–31	June 3–8	June 12–18
1			14½		1½
2	4		1½	1	9½
3	11			1	4
4	1	6		8	1
5		10		6	
Average rank	2.8	4.6	1.1	4.2	2.3

of the 16 intervals and were tied for first rank with fish of June 12–18 in the remaining 3. May 29–31, therefore, held first rank 14½ times and second 1½ times. Each of the remaining collecting periods held its "characteristic" ranking in at least half of the length intervals. Thus fish of the June 12–18 samples were second 9½ times; those of May 8–15, third 11 times; those of June 3–8, fourth 8 times; and those of May 17–27, fifth 10 times.

The chance is remote that differences from one period to another in the composition of the samples with respect to sex and maturity had an appreciable effect on the 1929 data. From the 1930 data it was determined that no large or consistent differences existed among the weights of mature males, immature males, and immature females of corresponding length. Only differences in the relative abundance of mature females (which tended to be heavier in 1930 than males and immature females), therefore, could be expected to influence the average weights. In 1929, however, most of the 16 length intervals for which data were available were in a range over which mature females were lacking or scarce (table 47).

It is not believed that the observed short-term fluctuations in the average weights of walleyes in the 1929 and 1930 late-spring samples reflect corresponding losses and gains of weight by individual fish. In 1930, for example, it could hardly be expected that the weight should drop 20 percent from May 13 to May 19, even under conditions of total starvation. The changes were less extreme in 1929 (5 to 12½ percent) but even here it is difficult to believe that the environmental factors contributing to gain or loss of weight were subject to the sudden and sharp changes that would be required to explain the alternating periods of high and low weight.

Fluctuations from period to period in the weight of the stomach contents could produce "apparent" changes in the weight of the whole fish, but this explanation, too, appears to be far from adequate, especially for 1930 when we should have to hypothesize stomachs stuffed to bursting, April 25–May 13, and almost totally unsuccessful foraging, May 19–June 20. A similar explanation for the fluctuations of weight in 1929 may impose a lesser strain on the investigator's credulity. Even so the large and frequent fluctuations of feeding activity that would have to be postulated are too great to make the explanation attractive.

It is believed that the fluctuations of weight of Saginaw Bay walleyes in late spring in 1929 and in 1930 can be explained most logically by the assumption that the population is heterogeneous with respect to the length-weight relation and that different segments of that population dominated the samples during different periods. Speculation as to the source of this heterogeneity, whether it be hereditary or ecological, and as to the basis of the segregation of elements with different length-weight relationships would not be profitable.

The numbers of walleyes measured in the fall (November 7–December 1, 1928, and October 15–November 21, 1929) were too few to permit detailed analysis but such data as were available failed to indicate the existence of short-term fluctuations comparable to those of late spring in 1929 and 1930. No data are available on fluctuation of weight during the spawning period.[24]

DIFFERENCES BETWEEN SPRING AND FALL WEIGHTS

The grand average weights for all walleyes collected in late spring of 1929 and of 1930 (tabulation not presented here) revealed that at most lengths the fish were somewhat the heavier in the former year. These annual differences were small, however, in relation to the within-season fluctuations; the combination of the data for 1929 and 1930 to obtain a general estimate of the length-weight relation in late spring (table 21) accordingly was held to be legitimate. The fall collections likewise exhibited annual differences, for at most lengths fish captured in 1929 were a little heavier than those taken in 1928. Again a combination of materials has been considered justified since in both autumns the walleyes were notably heavier than in late spring of either 1929 or 1930.

It may be seen from table 22 that without exception walleyes collected in the fall were heavier than fish of corresponding length taken in late spring. The examination of the percentage advantages of the autumn-caught fish reveals that

[24] The only collection containing spawning fish for which weights were recorded was that of May 4, 1943. Even this sample perhaps should be designated as intermediate between a true spawning and a postspawning collection.

TABLE 22.—*Comparison of weights of Saginaw Bay walleyes, sexes combined, captured in the fall and spring*

[Figures in parentheses listed under average weight are number of specimens and under difference the percentage advantage of fish captured in fall over those taken in spring]

Standard length	Total length	Weight			Standard length	Total length	Weight		
		Average in fall [1]	Average in spring [2]	Difference			Average in fall [1]	Average in spring [2]	Difference
	Inches	*Ounces*	*Ounces*	*Ounces*		*Inches*	*Ounces*	*Ounces*	*Ounces*
190 mm	8.8	3.6 (7)	2.7 (10)	0.9 (33.3)	297 mm	13.5	13.0 (18)	11.4 (303)	1.6 (14.0)
200 mm	9.3	3.9 (17)	3.6 (17)	0.3 (8.3)	307 mm	14.0	13.5 (9)	13.0 (322)	0.5 (3.8)
209 mm	9.7	4.4 (35)	4.0 (82)	0.4 (10.0)	317 mm	14.5	15.8 (12)	14.2 (340)	1.6 (11.3)
219 mm	10.1	5.2 (34)	4.6 (123)	0.6 (13.0)	326 mm	14.9	17.5 (14)	15.4 (325)	2.1 (13.6)
229 mm	10.5	5.9 (77)	5.2 (177)	0.7 (13.5)	336 mm	15.3	20.5 (16)	17.1 (282)	3.4 (19.9)
239 mm	10.9	6.5 (61)	5.8 (156)	0.7 (12.1)	346 mm	15.8	21.9 (12)	18.3 (203)	3.6 (19.7)
248 mm	11.3	7.5 (25)	6.6 (123)	0.9 (13.6)	356 mm	16.2	24.1 (21)	20.1 (158)	4.0 (19.9)
258 mm	11.8	8.4 (30)	7.6 (148)	0.8 (10.5)	365 mm	16.6	25.9 (8)	21.9 (121)	4.0 (18.3)
268 mm	12.2	9.6 (36)	8.5 (203)	1.1 (12.9)	375 mm	17.1	28.6 (16)	23.8 (99)	4.8 (20.2)
278 mm	12.7	10.3 (32)	9.4 (264)	0.9 (9.6)	385 mm	17.6	28.6 (5)	26.4 (85)	2.2 (8.3)
287 mm	13.1	11.7 (21)	10.5 (323)	1.2 (11.4)	395 mm	18.0	34.2 (10)	27.8 (52)	6.4 (23.0)

[1] Includes fish captured Nov. 7–Dec. 1, 1928, and Oct. 15–Nov. 21, 1929.

[2] Includes fish captured May 8–June 18, 1929, and Apr. 25–June 20, 1930.

their values tended to be higher at 15.3 inches or longer than at the lesser lengths, but that within each of these ranges the percentages clustered rather closely about a characteristic value. Over the range, 8.8 to 14.9 inches, the unweighted mean percentage was 12.7 and 11 of the 15 individual values were from 10.0 to 14.0 percent. The two extreme deviations from the mean—33.3 percent at 8.8 inches and 3.8 percent at 14.0 inches—both came from comparisons in which one of the average weights was based on fewer than 10 fish. At 15.3 to 18.0 inches the mean percentage was 18.5 and 6 of the 7 individual values were within the range of 18.3 to 23.0 percent. Again the outstanding exception—8.3 percent at 17.6 inches—can be attributed to inadequate data since the average weight for fall walleyes was determined from only 5 specimens.

EFFECT OF *LYMPHOCYSTIS* INFECTION ON WEIGHT

The incidence of *Lymphocystis* in the Saginaw Bay walleye was relatively high in the fall of 1942 and the spring of 1943. Although no quantitative data on its occurrence were obtained in 1942, casual observations indicated that the infection was relatively more frequent that fall than in the following spring. Of the 288 walleyes in the sample from which scales were taken on May 4, 1943, 19, or 6.6 percent, were infected.

During visits to Bay Port in mid-November 1942 and early May 1943 the weights of infected walleyes were compared with those of sound fish. The infected fish included, in addition to the 19 specimens mentioned above, legal-sized walleyes that had been discarded by commercial fishermen as unmarketable and undersized fish that had been brought ashore under special authorization from Michigan law-enforcement officials. The sound fish were in part from the collection of May 4, 1943, and in part were weighed during the course of filleting experiments conducted in November 1942 and May 1943 (see Krumholz 1945, for an account of those experiments).

The average weights of sound walleyes exceeded those of fish infected with *Lymphocystis* at 13 of 14 lengths in November 1942 and at 18 of 19 lengths in May 1943 (table 23). The percentage advantage of the sound over the diseased fish varied widely as should be expected in view of the small numbers on which some of the average weights were based. At most lengths with the better numerical representation, however, the percentage was below 10. The weighted-mean percentage (see footnote 2 of the table) was 5.6 for the November 1942 samples and 6.6 for the May 1943. The differences between the weights of sound and diseased walleyes doubtless would have been greater had the "warty" growths been removed from the latter before they were weighed.

TABLE 23.—*Comparison of weights of Saginaw Bay walleyes infected with* Lymphocystis *with weights of uninfected fish collected on the same dates*

[Figures in parentheses under average weight are the numbers of specimens and under difference the percentage difference of weight. Weights given in ounces]

Total length	November 12–16, 1942			May 3–5, 1943		
	Average weight of infected fish	Average weight of uninfected fish	Difference [1]	Average weight of infected fish	Average weight of uninfected fish	Difference [1]
13½ in.	12.5	13.9	1.4	10.5	12.7	2.2
	(1)	(6)	(11.2)	(1)	(8)	(21.0)
14 in.	12.9	13.4	0.5	12.5	13.9	1.4
	(10)	(11)	(3.9)	(1)	(17)	(11.2)
14¼ in.	14.2	15.0	0.8	12.0	14.8	2.8
	(8)	(17)	(5.6)	(1)	(19)	(23.3)
14½ in.	15.9	15.5	−0.4	14.2	15.9	1.7
	(9)	(22)	(−2.5)	(4)	(26)	(12.0)
14¾ in.	16.3	16.9	0.6	15.2	16.3	1.1
	(15)	(21)	(3.7)	(2)	(25)	(7.2)
15 in.	17.5	17.6	0.1	15.4	17.3	1.9
	(28)	(19)	(0.6)	(8)	(29)	(12.3)
15¼ in.	18.5	18.8	0.3	16.6	17.7	1.1
	(27)	(19)	(1.6)	(11)	(22)	(6.6)
15½ in.	19.4	20.3	0.9	18.3	19.1	0.8
	(26)	(16)	(4.6)	(14)	(25)	(4.4)
15¾ in.	19.3	21.7	2.4	18.1	19.8	1.7
	(31)	(20)	(12.4)	(14)	(20)	(9.4)
16 in.	21.0	22.5	1.5	20.0	21.2	1.2
	(30)	(17)	(7.1)	(18)	(25)	(6.0)
16¼ in.	21.9	23.0	1.1	21.2	21.8	0.6
	(18)	(17)	(5.0)	(6)	(30)	(2.8)
16½ in.	22.7	24.8	2.1	22.3	23.0	0.7
	(24)	(18)	(9.3)	(13)	(32)	(3.1)
16¾ in.	23.7	25.9	2.2	23.2	24.7	1.5
	(11)	(11)	(9.3)	(2)	(37)	(6.5)
17 in.	23.8	26.5	2.7	22.4	24.9	2.5
	(9)	(11)	(11.3)	(4)	(36)	(11.2)
17¼ in.				27.2	26.1	−1.1
				(3)	(29)	(−4.0)
17½ in.				21.5	28.6	7.1
				(1)	(12)	(33.0)
18 in.				28.0	30.3	2.3
				(1)	(9)	(8.2)
18½ in.				32.0	32.3	0.3
				(2)	(11)	(0.9)
19¾ in.				31.5	40.6	9.1
				(1)	(6)	(23.9)
Average [2]			5.6			6.6

[1] Advantage of sound over infected fish.
[2] Weighted mean percentages for all fish. The weight for each percentage was the product of the numbers of infected and uninfected fish. For example, the percentage 3.9 at 14 inches in November 1942 received the weight 10×11=110.

CALCULATED GROWTH

GROWTH IN LENGTH

Since, as was explained previously (p. 20), differences (other than those that could be ascribed to inadequate numbers of fish in the samples) in the growth of walleyes of the same age in the

1926–30 collections but taken in different years could be explained on the basis of annual fluctuations in growth rate and members of the same year class captured at different ages in general had closely similar growth, it is not desirable to present the large amount of tabular material required to show the calculated growth history of each age group in each year's collection. Presentation of data on calculated growth in length, accordingly, has been limited to the growth histories of the individual year classes. To obtain the data of tables 24 and 25, the calculated lengths of all age groups belonging to the same year class were combined.[25] In the computation of the growth history of a year class, weighted means of the calculated lengths were employed up to and including the length at capture of the youngest age group. The later calculated lengths were determined by successive addition of the weighted-mean-annual increments of length.

The calculated lengths of the year classes at corresponding years of life varied rather widely. This variation followed a distinct pattern which was similar for the sexes. Among the walleyes of the 1926–30 collections (year-class 1928 and earlier) the older year classes had the higher calculated lengths. From the generally high levels of the earlier year classes, the calculated lengths started on a downward trend, usually with the year class of 1917 or 1918; the onset of the trend varied somewhat according to year of life. The lowest general level of growth was exhibited by year-class 1924. Year-classes 1925 to 1928 grew faster than the 1924 year class but more poorly than the year classes before 1924 (exception in the second-year calculated length of females of year-class 1915).[26]

In the examination of tables 24 and 25 to ascertain the extent of the variations of the average calculated lengths in the 1926–30 collections, attention should be centered on year-classes 1918 to 1928 for the males and 1916 to 1928 for the females as the earlier year classes were represented by only 1 to 4 fish. Among the males the range of the average calculated lengths rose from 1.9 inches at the end of the first year of life (maximum of 7.7 inches and minimum of 5.8) to 3.2 inches at the end of 4 years and thereafter declined to 0.2 inch at the end of 10. The increase of range during the early years indicates an in-

[25] Only one age group was represented in each year class later than 1928.

[26] The relation of this general pattern of growth to annual fluctuations in growth rate will be brought out later.

TABLE 24.—*Calculated growth in length of the males of the year classes of Saginaw Bay walleyes*

Year class	Number of fish	Calculated total length (inches) at end of year of life—													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1914	1	6.3	12.1	14.6	17.2	18.1	18.9	19.8	20.2	20.8	21.1	21.5	21.9	22.2	
1915	2	7.2	10.3	13.2	15.5	16.6	17.6	18.4	19.2	19.8	20.2	20.5	20.7	20.9	21.3
1916	2	7.4	10.9	14.0	16.5	18.0	19.6	20.7	21.5	22.3	22.9	23.4	23.7	24.0	
1917	4	7.6	12.0	14.7	16.9	18.3	19.6	20.6	20.8	21.3	21.9	22.3	22.8		
1918	12	7.4	11.7	14.3	16.1	17.6	18.5	19.2	19.8	20.3	20.7	21.1			
1919	36	7.3	11.5	14.3	16.5	17.5	18.3	19.1	19.7	20.1	20.5				
1920	55	7.2	11.2	13.8	15.7	16.9	17.7	18.4	18.9	19.5					
1921	85	7.7	11.5	14.0	15.5	16.6	17.5	18.1	18.7						
1922	112	7.5	11.2	13.3	15.3	16.5	17.3	18.0	18.9						
1923	66	7.4	11.1	14.0	15.6	16.8	17.6	18.3							
1924	12	5.8	9.5	11.5	13.3	14.9	16.1								
1925	250	6.1	9.9	12.4	14.6	15.9									
1926	256	5.8	9.7	12.6	14.3										
1927	162	6.3	10.5	12.6											
1928	17	6.5	10.3												
1933	3	7.3	12.3	15.4	17.7	19.1	20.1	20.8	21.2	21.7	22.3				
1934	3	6.5	11.4	13.7	15.8	17.6	18.8	19.6	20.4	21.2					
1935	2	5.4	11.2	15.0	16.5	18.0	19.0	19.6	20.2						
1936	5	5.5	10.8	14.4	16.6	18.0	19.3	20.3							
1937	14	6.2	11.0	14.9	17.1	18.7	19.8								
1938	3	6.6	11.2	15.1	17.3	18.5									
1939	49	5.7	10.7	15.1	17.5										
1940	101	6.9	13.0	16.4											
Year-classes 1914–28: [1]															
Standard length (mm.)		144	234	293	336	365	385	401	415	428	440	451	460	468	476
Total length (in.)		6.7	10.7	13.4	15.3	16.6	17.6	18.3	18.9	19.5	20.0	20.4	20.7	21.0	21.3
Increment		6.7	4.0	2.7	1.9	1.3	1.0	.7	.6	.6	.5	.4	.3	.3	.3
Year-classes 1933–40: [1]															
Standard length (mm.)		139	264	346	396	430	456	476	491	507	521				
Total length (in.)		6.4	12.0	15.8	18.1	19.5	20.6	21.4	21.9	22.7	23.3				
Increment		6.4	5.6	3.8	2.3	1.4	1.1	.8	.5	.8	.6				

[1] See text for method of deriving these general growth data.

TABLE 25.—*Calculated growth in length of the females of the year classes of Saginaw Bay walleyes*

Year class	Number of fish	Calculated total length (inches) at end of year of life—														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1914	2	8.6	12.4	14.8	17.0	17.9	19.6	20.2	20.9	21.5	22.1	22.7	23.5	23.9	24.4	24.9
1915	4	8.5	12.0	15.5	17.4	19.7	21.6	22.9	23.6	24.8	25.4	26.1	26.7	27.0	27.4	
1916	12	8.5	12.4	15.5	17.6	19.5	21.1	22.2	23.0	23.9	24.5	25.2	25.7	26.2		
1917	17	8.1	12.3	15.5	17.8	19.9	21.5	22.5	23.2	23.9	24.4	24.9	25.3			
1918	34	7.8	11.9	15.1	17.6	19.6	21.0	21.9	22.6	23.4	24.1	24.7	25.4			
1919	56	7.9	11.9	15.2	17.8	19.4	20.7	21.6	22.3	22.8	23.5	24.0				
1920	54	7.7	12.1	15.2	17.4	19.1	20.2	20.9	21.6	22.3	22.9					
1921	77	7.9	11.9	14.6	16.4	18.1	19.4	20.3	20.9	21.6						
1922	110	7.9	11.7	14.0	16.4	18.1	19.4	20.4	21.2							
1923	48	7.4	11.0	14.5	16.7	18.6	19.7	20.5								
1924	21	5.4	9.5	12.1	14.3	16.1	17.5									
1925	267	6.3	10.1	12.7	15.0	16.3										
1926	170	5.9	9.8	12.8	14.6											
1927	170	6.3	10.5	12.7												
1928	23	6.3	10.2													
1930	2	6.5	12.9	15.5	17.5	20.3	22.0	23.9	25.1	25.9	26.6	27.2	28.1	28.9		
1931	1	6.1	10.6	13.2	16.3	18.9	20.3	21.7	22.6	23.6	24.8	25.6	26.5			
1933	1	7.1	13.0	15.6	18.0	19.9	21.3	22.5	23.2	24.0	25.0					
1934	2	7.0	11.7	15.2	17.3	19.4	21.3	22.5	23.5	24.6						
1936	3	6.6	11.3	14.7	18.1	20.2	21.8	23.4								
1937	16	5.9	10.7	15.4	18.2	20.5	22.1									
1938	1	7.9	13.4	17.0	19.5	21.2										
1939	30	5.9	11.1	16.1	18.6											
1940	50	6.9	13.0	17.0												
Year-classes 1914–28: [1]																
Standard length (mm)		148	238	302	351	391	423	447	466	484	499	513	526	537	547	558
Total length (in.)		6.9	10.9	13.8	16.0	17.8	19.3	20.3	21.0	21.7	22.3	22.9	23.5	24.0	24.5	25.0
Increment		6.9	4.0	2.9	2.2	1.8	1.5	1.0	0.7	0.7	0.6	0.6	0.6	0.5	0.5	0.5
Year-classes 1930–40: [1]																
Standard length (mm)		139	264	357	416	471	509	544	568	589	610	624	644	661		
Total length (in.)		6.4	12.0	16.3	18.9	21.3	22.9	24.3	25.4	26.3	27.3	27.9	28.8	29.5		
Increment		6.4	5.6	4.3	2.6	2.4	1.6	1.4	1.1	0.9	1.0	0.6	0.9	0.7		

[1] See text for method of deriving these general growth data.

creasing variability of the means. The decrease in the range during the later years of life, however, can be considered to a large extent the result of the decreasing number of years for which data were available and hence of lesser opportunity for variation. The extremes and ranges for the ninth and tenth years of life, for example, had to be determined from only three and two mean lengths, respectively. The ranges of the means for the females varied irregularly. From a value of 3.1 inches at the end of the first year (maximum of 8.5 inches and minimum of 5.4) the range dropped to 2.9 at the end of 2 years (12.4 and 9.5 inches) rose to a maximum of 4.0 at the end of 6 (21.5 and 17.5 inches), and then declined (with an irregularity at 8 and 9 years) to 0.4 inch at the end of 12. Here, as with the males, the earlier increases of the range suggest increasing variability of the means, but the subsequent declines cannot be interpreted to represent decreasing variability.

The year classes of the 1943 collection (year-class 1933 and later in table 24; year-class 1930 and later in table 25) had, on the whole, far better growth than those of the 1926–30 samples. An exception must be made for the first-year lengths which were mostly at about the same level of those of year-classes 1924 to 1928 and below that of year classes before 1924. In the second and later years, however, the calculated lengths of the walleyes collected in 1943 were commonly near or above the highest to be found in the 1926–30 samples. The advantage of the 1943 walleyes is more apparent in the later than in the earlier years of life.

To facilitate comparisons of the growth of males and females and of walleyes of the 1926–30 and 1943 collections, the data on "general" growth in length have been summarized in table 26. The lengths in this table were obtained by the successive addition of the average annual increments of length. For the 1926–30 collection, each increment is the weighted mean of the increments for the individual year classes after correction for annual fluctuations in growth rate.[27] Since the data from the 1943 collection provided a much less-

[27] To illustrate the method of correction—a 25-millimeter increment made in a year in which growth was 10.3 percent above average is subject to adjustment as follows: 25/1.103=22.6. See pp. 42–45 for data on the extent of the fluctuations in growth rate.

dependable estimate of annual fluctuations in growth, the increments for the walleyes of that sample are merely the weighted means of the increments for all available fish.

TABLE 26.—*General growth in total length of Saginaw Bay walleyes of the 1926–30 and 1943 collections*

[Data transcribed from tables 24 and 25 to facilitate comparison. Lengths given in inches]

Year of life	1926–30 collections				1943 collection			
	Males		Females		Males		Females	
	Length	Increment	Length	Increment	Length	Increment	Length	Increment
1	6.7	6.7	6.9	6.9	6.4	6.4	6.4	6.4
2	10.7	4.0	10.9	4.0	12.0	5.6	12.0	5.6
3	13.4	2.7	13.8	2.9	15.8	3.8	16.3	4.3
4	15.3	1.9	16.0	2.2	18.1	2.3	18.9	2.6
5	16.6	1.3	17.8	1.8	19.5	1.4	21.3	2.4
6	17.6	1.0	19.3	1.5	20.6	1.1	22.9	1.6
7	18.3	.7	20.3	1.0	21.4	.8	24.3	1.4
8	18.9	.6	21.0	.7	21.9	.5	25.4	1.1
9	19.5	.6	21.7	.7	22.7	.8	26.3	.9
10	20.0	.5	22.3	.6	23.3	.6	27.3	1.0
11	20.4	.4	22.9	.6	-------	-------	27.9	.6
12	20.7	.3	23.5	.6	-------	-------	28.8	.9
13	21.0	.3	24.0	.5	-------	-------	29.5	.7
14	21.3	.3	24.5	.5	-------	-------	-------	-------
15	-------	-------	25.0	.5	-------	-------	-------	-------

The females of the Saginaw Bay walleyes were longer than the males in all but the earliest years of life (fig. 4). In the 1926–30 collection the females averaged the longer even at the end of the first year (females 6.9 inches; males 6.7 inches). The females were unable to add to this 0.2-inch advantage during the second year (second-year length of females, 10.9 inches, and of males, 10.7 inches) but were the longer by 0.4 inch at the end of 3 years (females, 13.8 inches; males, 13.4 inches). The females added to this early advantage in each succeeding year of life with a resulting divergence of the growth curves for the sexes. At the end of 5 years the length of the females (17.8 inches) was more than an inch greater than that of the males (16.6 inches). The advantage of the females had reached 2 inches in 7 years (females, 20.3 inches; males, 18.3 inches), 3 inches in 13 years (females 24.0 inches; males, 21.0 inches), and was 3.2 inches at the end of 14 years, the highest age attained by the males. How great this disparity of growth became with respect

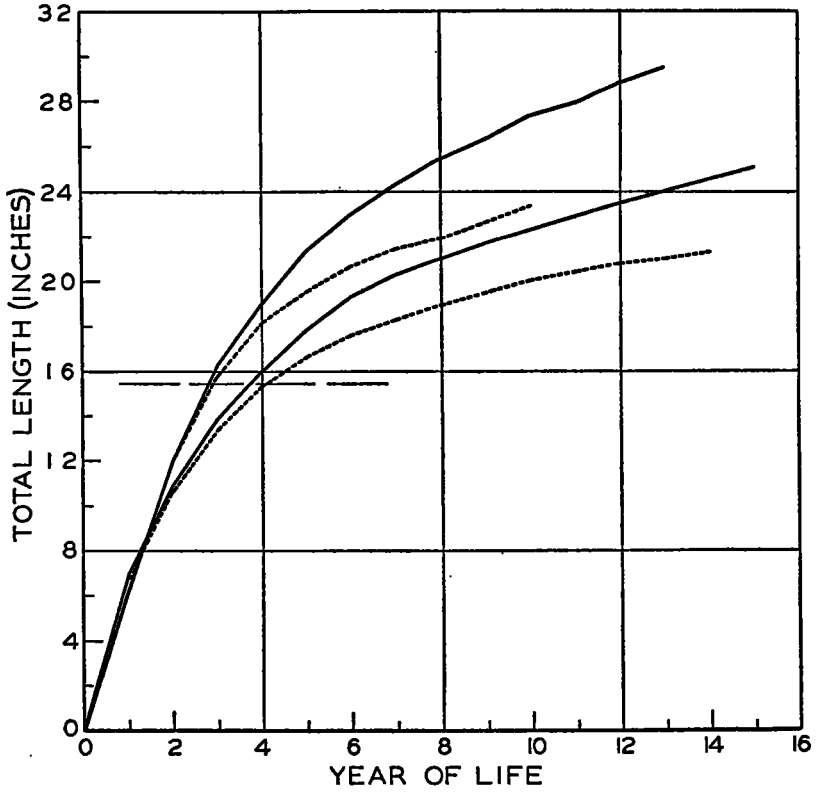

FIGURE 4.—Calculated general growth in length of male (broken lines) and female walleyes (solid lines) of the 1926–30 (lower curves) and 1943 collections (upper curves). The broken horizontal line indicates the minimum legal length of 15½ inches.

to time is well illustrated by the fact that females were longer at the end of 9 years (21.7 inches) than males at the end of 14 years (21.3 inches).

The present legal minimum size of 15½ inches was attained by the 1926–30 males early in the fifth growing season and by the females in the latter part of the fourth. The size limit of 1½ pounds (equivalent to a length of 17.1 inches) which was in effect at the time of collection was reached by the males in the sixth and by females in the fifth year. Finally, males reached the 1933–38 legal minimum length of 16½ inches near the end and the females in the earlier part of the fifth growing season.

Walleyes of both sexes in the 1926–30 collections made by far their greatest growth in length during the first year of life. Beyond that year the increments decreased rather consistently (were equal over periods of 2 or 3 years at certain higher ages). All increments were less than an inch beyond the sixth year of life of the males and the seventh year of the females.

The comparison of the annual increments of the sexes of the walleyes of the 1926–30 collection reveals that the advantage of the females over the males with respect to yearly growth was 0.2 inch in the first year and nil in the second, rose thereafter to a maximum of 0.5 inch in the fifth and sixth years, and ranged from 0.1 to 0.3 inch in the seventh through the fourteenth. Although the absolute advantage of the females over the males tended first to increase and then to decrease, the trend was toward an increase in the relative advantage with advancing age as the following tabulation proves:

Years of life	Growth		Ratio
	Males	Females	
	Inches	*Inches*	
1–2	10.7	10.9	1.02
3–6	6.9	8.4	1.22
7–14	3.7	5.2	1.41

The relation between the growth of the sexes in the 1943 collection was similar to that in the 1926–30 samples (fig. 4). In fish collected in 1943, the calculated lengths of the males and the females were the same at the end of the first (6.4 inches) and second (12.0 inches) years of life. In the succeeding years the females established an advantage that reached 1.8 inches at the end of 5 years (females, 21.3 inches; males, 19.5 inches) and was 4.0 inches at the end of 10 years (females, 27.3 inches; males 23.3 inches). In the seventh growing season females reached a length as great as that of males at the end of 10 full years. In the third through the tenth year of life the advantages of the females over males were consistently greater at corresponding ages in the 1943 than in the 1926–30 collections. The greatest difference occurred at the end of the tenth year when the 1943 females were 4.0 inches longer than the males as compared with a sex difference of only 2.3 inches at the same age in the 1926–30 fish.

The times of attainment of legal length by both males and females of the 1943 sample at the various limits were as follows: 15½ inches—late in the third growing season; 16½ inches and 1½ pounds (17.1 inches)—during the fourth season. The females reached each of these limits earlier than did the males.

In the 1943 sample as in the 1926–30 collections the best growth in length was made in the first year (6.4 inches for each sex) and the trend of the increments was downward during the succeeding years. All length increments of the 1943 males were less than 1.0 inch beyond the sixth year; the same holds for the females beyond the eighth year with the exception of the tenth-year increment of 1.0 inch.

Comparisons of the corresponding annual growth increments of the males and females of the 1943 collection reveal that in the first and second years the sex differences were nil but that in each of the later years the growth of the females was the greater. The largest difference is to be found in the fifth year when the growth of the females (2.4 inches) was a full inch greater than that of the males. In other years the advantage of the females ranged between 0.1 inch (ninth year) and 0.6 inch (seventh and eighth years). Again, we find the relative advantage of the females increasing with increase in age as the following tabulation demonstrates:

Years of life	Growth		Ratio
	Males	Females	
	Inches	*Inches*	
1–2	12.0	12.0	1.00
3–6	8.6	10.9	1.27
7–10	2.7	4.4	1.63

Comparison of this tabulation with the one given previously for the 1926–30 collections shows that the ratios for years 1–2 and 3–6 were closely similar (1.02 and 1.22 for the 1926–30 samples; 1.00 and 1.27 for the 1943 collection). Beyond the sixth year, however, the relative advantage of the females was much greater in the 1943 walleyes (ratio of 1.63) than in the 1926–30 fish (ratio of 1.41). As a result the rate of divergence of the growth curves for the sexes (fig. 4) was greater for the 1943 than for the 1926–30 specimens.

The increase with age in the growth advantage of the females is of interest in connection with the problem of the relation between sex differences in growth rate and in the time of attainment of maturity (with a concomitant depression of growth rate). The earlier attainment of sexual maturity by males frequently has been offered as the explanation of the more rapid growth of females in certain species of fish.[28] In the Saginaw Bay walleye, males do mature at a lesser size and age than do females (p. 56). If attainment of maturity in this stock causes a depression of growth rate, then sex differences in the age at first maturity contributed to the sex differences in growth rate in some of the earlier years. On the other hand, the females maintained their (relative) advantage in growth at ages at which all or practically all walleyes of both sexes were mature (no immature walleyes beyond the VI group in 1930 or the IV group in 1943—see table 48). To a large extent, therefore, the more rapid growth of the females of the Saginaw Bay walleye represents a true sex difference in growth potential and is not the result of later attainment of maturity by fish of that sex.

In earlier comments relative to the data of tables 24 and 25 it was stated without elaboration that the first-year growth of the walleyes of the 1943 collection was no better than that of the 1926–30 samples—indeed was inferior to the first-year growth of the earlier year classes—but that in the later years of life the calculated lengths of fish of the 1943 collection were characteristically near or above the highest corresponding lengths of those of the 1926–30 collections. The true extent of the differences in the growth of the two groups, however, is probably brought out best by the general growth data of table 26.

[28] See Svärdson (1943) for an excellent review of the problem of the relation between sexual maturity and the growth of fish.

Although the walleyes of the 1943 collection were shorter at the end of the first year (calculated length of 6.4 inches for each sex) than the fish of the 1926–30 collections (males, 6.7 inches; females, 6.9 inches) the second-year growth of fish of the more recent sample was so rapid that in 2 years they were the longer by more than an inch. To this advantage they added materially in subsequent years.

By the end of the fourth year of life the 1943 males (18.1 inches) were 2.8 inches longer than 1926–30 fish (15.3 inches). Beyond the fourth year the advantage of the males caught in 1943 varied irregularly and within rather narrow limits from 2.9 inches in the fifth year (lengths of 19.5 and 16.6 inches) to 3.3 inches in the tenth (lengths of 23.3 and 20.0 inches). The 1943 males were as long at the end of 5 years (19.5 inches) as the 1926–30 males at the end of 9 and were longer in 7 years (21.4 inches) than 1926–30 males at the end of 14 (21.3 inches).

Females of the 1943 sample differed from the males in that their advantage over the 1926–30 fish did not tend to level off after 4 years. Rather, they added to their advantage in every later year of life but the eleventh. The length advantage of the 1943 females amounted to 2.5 inches at the end of 3 years (lengths of 16.3 and 13.8 inches), was 4.0 inches in 7 years (lengths of 24.3 and 20.3 inches) and reached a maximum of 5.5 inches in 13 years (lengths of 29.5 and 24.0 inches). Female walleyes of the 1943 sample were longer at the end of 5 years than 1926–30 females at the end of 8 years and were longer in 8 years (25.4 inches) than 1926–30 fish in 15 (25.0 inches).

GROWTH IN WEIGHT

The data of tables 27, 28, and 29 were computed (by means of the length-weight equation given on p. 27) from the standard lengths on which tables 24, 25, and 26 were based. The solutions of the equation, obtained in grams, were subsequently converted to pounds. (Tables 27 and 28 give the general growth in weight in both pounds and grams.)

Data obtained by this procedure have the distinct advantage that the length and weight at a particular age correspond exactly, whereas for a group of fish (as an age group) in which both length and weight vary, the mean weight may be

expected to exceed the normal weight of a fish of average length.[29]

Because tables 27, 28, and 29 were derived from tables 24, 25, and 26, the general patterns of variation must be the same in corresponding pairs of tables. As a result of the increase of weight approximately as the cube of the length, however, the variations are much greater in the tables on weight.

In the 1926–30 collections (year-class 1928 and earlier) the greatest relative variation in calculated weight[30] occurred in the first year of life. In the males the maximum weight of 0.13 pound (year-class 1921) was more than twice the minimum of 0.06 (year-classes 1924 and 1926); in the females the maximum first-year weight of 0.18 pound (year-class 1916) was 3.6 times the minimum of 0.05 pound (year-class 1924). In the later years the relative variability of the calculated weights was less although the actual ranges were greater. The difference between the highest and the lowest calculated weights of male walleyes in corresponding years of life rose from 0.07 pound at the end of the first year to 0.64 pound at the end of the fifth and sixth years, ranged between 0.36 and 0.38 pound in the seventh through the ninth year, and was 0.07 pound at the end of the tenth. For the females this range increased from 0.13 pound at the end of the first year to 1.46 pounds at the end of the sixth, varied between 0.66 and 1.13 pounds in the seventh through the eleventh year, and was 0.24 pound at the end of the twelfth. With the weights, as was true with the lengths, the early increase in the range of the calculated values can be interpreted as an increase in the variability but the subsequent decreases can be ascribed in large part to the lesser number of year classes represented in the data for the later years of life.

As would be expected, since the weights were computed from the lengths, the calculated first-year weights of the year classes of the 1943 collection (year-class 1933 and later of the males; year-class 1930 and later of the females) were at about the same level as those of year-classes 1924 to 1928 of the 1926–30 collections but were generally below

[29] To illustrate this point—given one fish with a length of 1 foot and a weight of 1 pound and another with a length of 2 feet and a weight of 8 pounds, we have a mean length of 1.5 feet and a mean weight of 4.5 pounds. Yet, in a stock with the indicated length-weight relation (weight in pounds equal to the cube of the length in feet) a 1.5-foot fish should weigh only 3.375 pounds.

[30] In statements of variations in calculated weight as with calculated length the data of year-classes 1914–17 of the males and of year-classes 1914–15 of the females have been excluded as inadequately represented.

TABLE 27.—*Calculated growth in weight of the males of the year classes of Saginaw Bay walleyes*

[Weights computed from the standard lengths corresponding to the total lengths of table 24. See p. 27 for length-weight equation]

Year class	Calculated weight (pounds) at end of year of life—													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1914	0.07	0.53	0.94	1.53	1.77	2.03	2.32	2.50	2.76	3.05	3.17	3.33	3.45	------
1915	.11	.32	.69	1.12	1.37	1.63	1.86	2.10	2.33	2.50	2.67	2.79	2.90	3.05
1916	.12	.39	.82	1.35	1.74	2.28	2.74	3.09	3.49	3.82	4.07	4.21	4.40	------
1917	.13	.52	.95	1.44	1.84	2.30	2.53	2.77	3.07	3.35	3.51	3.73	------	------
1918	.12	.48	.87	1.26	1.63	1.90	2.11	2.35	2.58	2.76	2.98	------	------	------
1919	.11	.46	.88	1.34	1.61	1.84	2.07	2.28	2.48	2.69	------	------	------	------
1920	.11	.43	.79	1.16	1.44	1.67	1.86	2.03	2.21	------	------	------	------	------
1921	.13	.46	.82	1.12	1.38	1.61	1.79	1.97	------	------	------	------	------	------
1922	.12	.43	.71	1.08	1.35	1.56	1.75	2.03	------	------	------	------	------	------
1923	.12	.41	.82	1.15	1.42	1.62	1.84	------	------	------	------	------	------	------
1924	.06	.24	.46	.71	.99	1.26	------	------	------	------	------	------	------	------
1925	.07	.28	.58	.94	1.20	------	------	------	------	------	------	------	------	------
1926	.06	.26	.60	.88	------	------	------	------	------	------	------	------	------	------
1927	.07	.35	.61	------	------	------	------	------	------	------	------	------	------	------
1928	.08	.33	------	------	------	------	------	------	------	------	------	------	------	------
1933	.11	.56	1.10	1.66	2.07	2.45	2.77	2.98	3.23	3.51	------	------	------	------
1934	.08	.44	.78	1.19	1.62	1.98	2.30	2.60	2.94	------	------	------	------	------
1935	.04	.43	1.02	1.35	1.74	2.04	2.28	2.55	------	------	------	------	------	------
1936	.05	.37	.90	1.38	1.74	2.19	2.55	------	------	------	------	------	------	------
1937	.07	.40	.99	1.48	1.97	2.35	------	------	------	------	------	------	------	------
1938	.08	.42	1.04	1.56	1.90	------	------	------	------	------	------	------	------	------
1939	.05	.37	1.04	1.59	------	------	------	------	------	------	------	------	------	------
1940	.09	.65	1.32	------	------	------	------	------	------	------	------	------	------	------
Year-classes 1914–28:														
Grams	30	166	325	489	626	734	829	919	1,008	1,095	1,178	1,250	1,316	1,385
Pounds	.09	.37	.72	1.08	1.38	1.62	1.83	2.03	2.22	2.41	2.60	2.76	2.90	3.05
Increment	.09	.28	.35	.36	.30	.24	.21	.20	.19	.19	.19	.16	.14	.15
Year-classes 1933–40:														
Grams	35	238	534	799	1,022	1,218	1,385	1,519	1,672	1,814	------	------	------	------
Pounds	.08	.52	1.18	1.76	2.25	2.69	3.05	3.35	3.69	4.00	------	------	------	------
Increment	.08	.44	.66	.58	.49	.44	.36	.30	.34	.31	------	------	------	------

TABLE 28.—*Calculated growth in weight of the females of the year classes of Saginaw Bay walleyes*

[Weights computed from the standard lengths corresponding to the total lengths of table 25. See p. 27 for length-weight equation]

Year class	Calculated weight (pounds) at end of year of life—														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1914	0.18	0.57	0.97	1.46	1.72	2.27	2.55	2.85	3.17	3.41	3.71	4.09	4.33	4.57	4.86
1915	.18	.52	1.11	1.57	2.32	3.09	3.75	4.16	4.80	5.18	5.65	6.01	6.22	6.53	
1916	.18	.57	1.11	1.64	2.24	2.88	3.41	3.86	4.30	4.68	5.04	5.37	5.68		
1917	.15	.56	1.11	1.68	2.40	3.05	3.54	3.93	4.30	4.57	4.86	5.13			
1918	.14	.51	1.03	1.62	2.28	2.86	3.29	3.66	4.05	4.43	4.75	5.20			
1919	.15	.50	1.05	1.68	2.22	2.74	3.17	3.49	3.77	4.11	4.38				
1920	.13	.54	1.05	1.58	2.07	2.51	2.83	3.17	3.49	3.82					
1921	.14	.51	.93	1.32	1.79	2.19	2.53	2.83	3.17						
1922	.14	.48	.83	1.31	1.79	2.22	2.63	2.96							
1923	.12	.40	.91	1.40	1.91	2.35	2.70								
1924	.05	.24	.54	.88	1.26	1.59									
1925	.07	.29	.62	1.01	1.30										
1926	.06	.27	.63	.93											
1927	.07	.35	.62												
1928	.07	.30													
1930	.08	.64	1.11	1.63	2.58	3.33	4.30	5.02	5.48	5.98	6.34	6.99	7.57		
1931	.07	.36	.69	1.29	2.04	2.58	3.21	3.66	4.16	4.83	5.31	5.86			
1933	.10	.67	1.14	1.75	2.38	2.98	3.54	3.95	4.38	4.94					
1934	.10	.48	1.06	1.56	2.21	2.98	3.54	4.09	4.70						
1936	.08	.43	.96	1.76	2.51	3.25	4.05								
1937	.06	.37	1.10	1.83	2.70	3.41									
1938	.14	.72	1.46	2.27	3.03										
1939	.06	.41	1.24	1.94											
1940	.09	.67	1.46												
Year-classes 1914–28:															
Grams	42	174	355	557	769	973	1,147	1,299	1,455	1,594	1,732	1,866	1,985	2,098	2,227
Pounds	.09	.38	.78	1.23	1.70	2.15	2.53	2.86	3.21	3.51	3.82	4.11	4.38	4.63	4.91
Increment	.09	.29	.40	.45	.47	.45	.38	.33	.35	.30	.31	.29	.27	.25	.28
Year-classes 1930–40:															
Grams	35	238	586	926	1,342	1,692	2,064	2,348	2,617	2,906	3,110	3,417	3,694		
Pounds	.08	.52	1.29	2.04	2.96	3.73	4.55	5.18	5.77	6.41	6.86	7.53	8.14		
Increment	.08	.44	.77	.75	.92	.77	.82	.63	.59	.64	.45	.67	.61		

TABLE 29.—*General growth in weight of Saginaw Bay walleyes of the 1926–30 and 1943 collections*

[Data transcribed from tables 27 and 28 to facilitate comparisons. Weight given in pounds]

Year of life	1926–30 collections				1943 collection			
	Males		Females		Males		Females	
	Weight	Increment	Weight	Increment	Weight	Increment	Weight	Increment
1	0.09	0.09	0.09	0.09	0.08	0.08	0.08	0.08
2	.37	.28	.38	.29	.52	.44	.52	.44
3	.72	.35	.78	.40	1.18	.66	1.29	.77
4	1.08	.36	1.23	.45	1.76	.58	2.04	.75
5	1.38	.30	1.70	.47	2.25	.49	2.96	.92
6	1.62	.24	2.15	.45	2.69	.44	3.73	.77
7	1.83	.21	2.53	.38	3.05	.36	4.55	.82
8	2.03	.20	2.86	.33	3.35	.30	5.18	.63
9	2.22	.19	3.21	.35	3.69	.34	5.77	.59
10	2.41	.19	3.51	.30	4.00	.31	6.41	.64
11	2.60	.19	3.82	.31			6.86	.45
12	2.76	.16	4.11	.29			7.53	.67
13	2.90	.14	4.38	.27			8.14	.61
14	3.05	.15	4.63	.25				
15			4.91	.28				

the first-year weights of year classes earlier than 1924. It was to be expected further that beyond the first year the calculated weights of walleyes of the 1943 collection would characteristically be above the level of the weights of fish of the 1926–30 collections, and that the advantage of the 1943 fish would be relatively greater with respect to weight than it was with respect to length. All of these expectations are met by the data of tables 27 and 28.

Male and female walleyes of the 1926–30 collections had the same calculated weight (table 29; fig. 5) at the end of the first year of life (0.09 pound), and at the end of 2 years the females (0.38 pound) were only 0.01 pound heavier than the males (0.37 pound). In the third year, however, the weight of the females (0.78 pound) was 0.06 pound greater than that of the males (0.72 pound). The females added to this advantage in each succeeding year of life. The sex difference was 0.53 pound at the end of 6 years (females, 2.15 pounds; males, 1.62 pounds), amounted to practically a pound (0.99 pound) in 9 years (females, 3.21 pounds; males, 2.22 pounds) and reached the maximum of 1.58 pounds at the end of 14 years (females, 4.63 pounds; males, 3.05 pounds).

The annual increments of weight of the 1926–30 males increased from 0.09 pound in the first year to a maximum of 0.36 pound in the fourth and thereafter declined (except for the equal ninth- to eleventh-year increments of 0.19 pound) to 0.14 pound in the thirteenth year. The fourteenth-year increment was 0.15 pound. In the females the increase from the first-year increment of 0.09

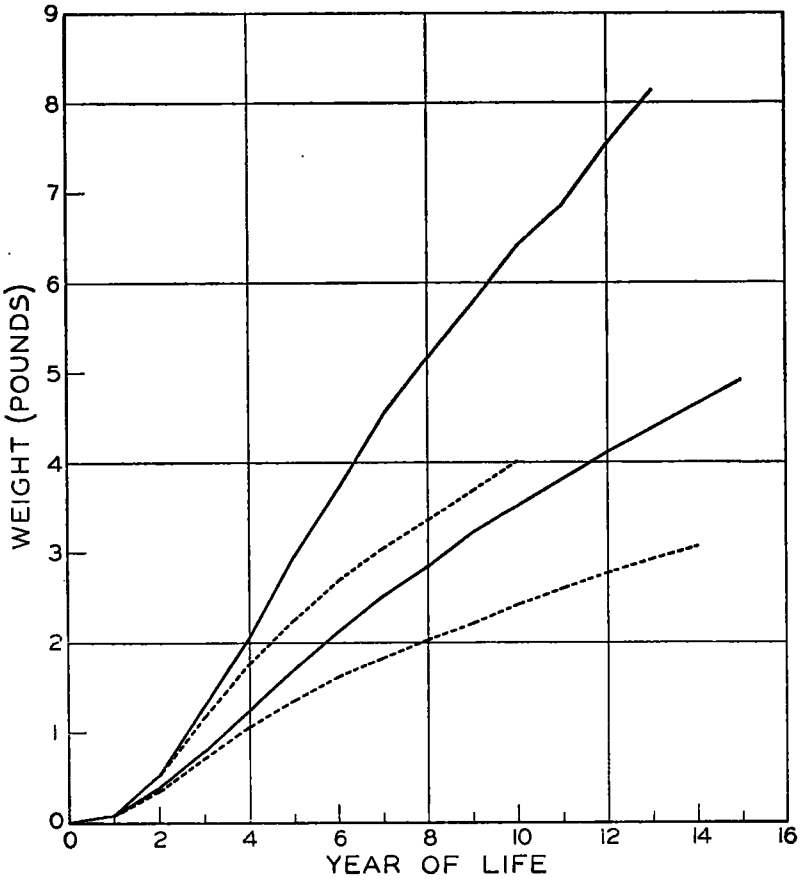

FIGURE 5.—Calculated general growth in weight of male (broken lines) and female walleyes (solid lines) of the 1926–30 (lower curves) and 1943 collections (upper curves).

pound continued through the fifth year when the maximum value of 0.47 pound was reached. During the later years the trend was irregularly downward; the lowest value in these years was 0.25 pound in the fourteenth year of life.

The annual increments of weight of female walleyes of the 1926–30 samples exceeded those of males in every year of life beyond the first. The greatest absolute advantage of the females occurred in the sixth year when their growth of 0.45 pound was 0.21 pound greater than that of males. The relative advantage of the females tended to become greater with advancing age as may be seen from the following tabulation:

Years of life	Growth		Ratio
	Males	Females	
	Pounds	*Pounds*	
1–2	0.37	0.38	1.03
3–6	1.25	1.77	1.42
7–14	1.43	2.48	1.73

A comparison of this tabulation with the corresponding one for growth in length of walleyes of the 1926–30 samples (p. 36) reveals that the progressive increase in the relative advantage of the females was considerably more rapid for weight than for length (higher ratios for growth in weight). The divergence of the curves of growth in weight was correspondingly more pronounced (*cf.* figs. 4 and 5).

The calculated weights of the male and female walleyes of the 1943 sample were the same at the end of the first and second years of life (0.08 and 0.52 pound, respectively). In the later years, however, females had a weight advantage that increased each year from 0.11 pound in the third year (females, 1.29 pounds; males, 1.18 pounds) to 1.04 pounds at the end of the sixth year (females, 3.73 pounds; males, 2.69 pounds), and to 2.41 pounds in 10 years (females, 6.41 pounds; males, 4.00 pounds).

The annual increments of weight of the male walleyes of the 1943 collection rose from 0.08 pound in the first year of life to a maximum of 0.66 pound in the third and then declined to 0.30 pound in the eighth. The ninth- and tenth-year increments were 0.34 and 0.31 pound, respectively. The trends in the annual increments of the females were much more irregular than were those of the males. The upward trend from the first-year increment of 0.08 pound to the maximum of 0.92 pound in the fifth year (2 years later than the maximum for the males) was interrupted in the fourth year, and the subsequent decline from the maximum was decidedly irregular. During the last 6 years of life (eighth through the thirteenth) the increments fluctuated more or less at random between a maximum of 0.67 pound in the twelfth year and a minimum of 0.45 pound in the eleventh.

In every year of life beyond the second the weight increments of the 1943 females exceeded those of the males. The greatest advantage of the females occurred in the seventh year when the increment of 0.82 pound was 0.46 pound greater than the increment of 0.36 pound for the males. The increase in the relative advantage of the females with increase in age was greater for the later years in the 1943 than in the 1926–30 walleyes as may be seen from the comparison of the following tabulation with the one previously given for the earlier collections:

Years of life	Growth		Ratio
	Males	Females	
	Pounds	*Pounds*	
1–2	0.52	0.52	1.00
3–6	2.17	3.21	1.48
7–10	1.31	2.68	2.05

Although the ratios for the periods of years 1 and 2 and 3 to 6 did not differ greatly in the two collections, the growth in weight of the females of the 1943 sample in the years 7 to 10 was 2.05 times that of males whereas the growth of the females of the 1926–30 collection in the years 7 to 14 was but 1.73 times that of the males. The curves of the growth in weight of the sexes accordingly diverge much more prominently in the later years in the 1943 than in the 1926–30 walleyes (fig. 5).

In the years 3 to 6 and 7 to 10 the relative advantages of the females of the 1943 sample were much greater with respect to growth in weight than to growth in length (compare preceding tabulation with the one on p. 36).

The superiority of the growth of the walleyes of the 1943 collection over fish of the 1926–30 collections, much like the advantage of females over males, becomes much greater when the comparison is based on weight rather than length.

Although the calculated weight of the 1943 males (0.08 pound) in the first year of life was slightly less than that of 1926–30 males (0.09 pound), the fish of the more recent collection established an advantage in the second year of life and added to it in every later year. From 0.15 pound at the end of the second year (1943 males, 0.52 pound; 1926–30 males, 0.37 pound), the advantage of the fish of the 1943 sample increased to more than a pound by the end of the sixth year (1943 males, 2.69 pounds; 1926–30 males, 1.62 pounds), and reached 1.59 pounds at the end of 10 years (1943 males, 4.00 pounds; 1926–30 males, 2.41 pounds). With the females, as with the males, the 1943 fish first established an advantage over walleyes collected in 1926–30 at the end of the second year of life when they weighed 0.52 pound or 0.14 pound more than fish of the earlier samples. This advantage had increased to more than 1¼ pounds by the end of the fifth year (1943 females, 2.96 pounds; 1926–30 females, 1.70 pounds), was above 2½ pounds in 9 years (1943 females, 5.77 pounds; 1926–30 females, 3.21 pounds), and at the end of 13 years amounted to more than 3¾ pounds (1943 females, 8.14 pounds; 1926–30 females, 4.38 pounds).

A striking feature of the comparative data lies in the high degree of stability that was attained in the later years of life in the ratios of the calculated weights of 1943 walleyes to the weights of 1926–30 fish of corresponding sex and age (table 30). In the males, this ratio rose sharply from 0.89 at the end of the first year of life to 1.64 at the end of the third, but thereafter exhibited only slight variation (within the range, 1.63–1.67). For practical purposes it can be said that in the third through the tenth year of life the 1943 males were 65 percent heavier than 1926–30 males of the same age. In the females, stability of the ratio was reached at a later age and at a higher level. From 0.89 at the end of the first year the value rose somewhat irregularly to 1.80 at the end of the seventh, and in the seventh through the thirteenth year

was from 1.80 to 1.86. In years of life 7 to 13, therefore, the 1943 females were about 82 percent heavier than 1926–30 females, or, sacrificing some precision in favor of a longer span of years and a round figure, in years of life 5 to 13 the 1943 females were the heavier by 80 percent.

TABLE 30.—*Ratios of the calculated weights of walleyes of the 1943 collection to the weights of fish of corresponding age and sex of the 1926–30 collections*

[Based on data of table 29]

Year of life	Ratio of 1943 to 1926–30 weight		Year of life	Ratio of 1943 to 1926–30 weight	
	Males	Females		Males	Females
1	0.89	0.89	8	1.65	1.81
2	1.41	1.37	9	1.66	1.80
3	1.64	1.65	10	1.66	1.83
4	1.63	1.66	11		1.80
5	1.63	1.74	12		1.83
6	1.66	1.73	13		1.86
7	1.67	1.80			

ANNUAL FLUCTUATIONS IN GROWTH RATE

FLUCTUATIONS FROM 1916 TO 1929

Length

The basic data on the annual fluctuations in growth in length of Saginaw Bay walleyes (tables 31 and 32) are arranged in the following manner: Each column shows the increments for different years of life but in the same calendar year, each horizontal row the increments for the same year of life but in different calendar years, and each diagonal row the growth history of a year class that can be identified by the calendar year in which the first-year growth was made. Omitted from the tables are data for certain of the earlier and poorly represented year classes.

Examination of the length increments of tables 31 and 32 reveals certain rather definite trends that were similar for the males and females. It is obvious, for example, that years prior to 1923 constituted, on the whole, a period of relatively good growth and years subsequent to 1923 one of rather poor growth. Apparent also in certain calendar years is the tendency toward sharp improvement or decline from the growth in the preceding year, whereas in other calendar years no important change from the preceding year can be demonstrated. The downward trend in growth rate was extremely clear cut in 1923 when all 5 increments of the males and all 7 increments of the females were smaller than the corresponding increments for 1922 (table 33). The situation was similar in 1924 when 5 of the 6 increments of the males and all 8 increments of the females were smaller than those of 1923. The general trend was downward also in 1926 (5 of 8 increments of males and 7 of 10 increments of females smaller than in 1925). The most consistent improvements of growth occurred in 1921 (2 of 3 increments of the males and all 5 increments of females larger than in 1920) and in 1925 (5 of 7 increments of the males and 6 of 9 of the females larger than in 1924). In 1928, 8 of 10 increments of the males but only 6 of 12 of the females exceeded those of 1927.

TABLE 31.—*Annual increments of growth in length of male Saginaw Bay walleyes of the 1926–30 collections according to calendar year*

[Each diagonal row gives the growth history of a year class]

Year of life	Increment of standard length (millimeters) in year—											
	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
11											12	
10										10	12	
9									14	12	12	
8								15	14	12	13	20
7							15	16	14	14	15	17
6						20	18	19	19	18	17	27
5					32	23	26	25	26	25	35	27
4				41	47	41	34	44	37	39	48	38
3			57	62	57	54	46	63	49	59	67	47
2		96	96	91	87	85	83	78	82	83	94	86
1	160	156	155	165	161	160	126	132	126	136	140	
Number of fish in—												
1926					3	1	3	145				
1927	3	13	18	13								
1928								4	4	8		
1929	9	23	38	72	107	59						
1930					2	6	9	110	246	154	17	

The data of tables 31 and 32 offer little basis for the belief that the trends of the annual fluctuations in growth rate varied significantly for different years of life. It is true that in the 1927 data for the males the increments for the first 4 years of life all exceeded those for 1926, whereas beyond the fourth year the 1926 growth was the greater in 4 years of life and equalled 1927 growth in the remaining (the seventh). Again, in 1929 growth was superior to that in 1928 in years of life 6 to 8 but poorer in years of life 2 to 5. It might be judged from these two examples that fluctuations in growth tended to follow opposite trends in the earlier and later years of life. This same tendency was almost lacking, however, in the 1926–27 data for the females and was reduced in the 1928–29 data. Furthermore, the disagreements in the remaining data were distributed at

TABLE 32.—*Annual increments of growth in length of female Saginaw Bay walleyes of the 1926–30 collections according to calendar year*

[Each diagonal row gives the growth history of a year class]

Year of life	Increment of standard length (millimeters) in year—													
	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
13													11	
12												12	11	17
11											14	11	13	11
10										15	11	16	13	15
9									19	16	17	15	16	18
8								21	18	18	16	18	17	18
7							27	24	22	23	18	21	25	21
6						38	37	34	31	28	28	30	29	29
5					42	49	47	38	36	38	39	40	40	29
4				48	51	54	57	49	40	51	49	48	50	39
3			67	70	70	73	67	58	52	76	62	62	70	48
2		89	95	93	89	100	92	85	82	87	82	84	96	85
1	183	174	168	171	166	170	171	160	117	135	127	135	135	
Number of fish in—														
1926						1			4	145				
1927	3	5	5	11	17	20								
1928									1	2	6	27		
1929	9	12	25	43	33	46	97	31						
1930			4	2	4	10	13	17	16	120	164	143	23	

TABLE 33.—*Comparison of increments of length of Saginaw Bay walleyes for corresponding years of life in consecutive calendar years*

[Relative sizes of increments are based on comparisons of growth in the more recent with that in the preceding year]

Calendar years compared	Males			Females		
	Larger	Smaller	Same	Larger	Smaller	Same
1916 and 1917				0	1	0
1917 and 1918				1	1	0
1918 and 1919	0	1	0	2	1	0
1919 and 1920	0	1	1	1	2	1
1920 and 1921	2	1	0	5	0	0
1921 and 1922	1	3	0	2	4	0
1922 and 1923	0	5	0	0	7	0
1923 and 1924	1	5	0	0	8	0
1924 and 1925	5	2	0	6	2	1
1925 and 1926	2	5	1	2	7	1
1926 and 1927	4	4	1	7	3	1
1927 and 1928	8	1	1	6	4	2
1928 and 1929	3	4	0	4	6	1

random—that is, not detectably related to age, and in some years, as previously noted, the direction of change was the same at all or nearly all ages. The general conclusion seems warranted that the trends of the annual fluctuations in growth rate did not vary according to the age of the fish.

Although the examination of tables 31 and 32 and of the supplementary records of table 33 provides a useful preliminary measure of the changes which occurred from year to year in the growth of walleyes of the 1926–30 collections, it is only roughly quantitative. Much more exact information is to be had from the analysis of the data to determine the actual percentage changes. The results of this analysis[31] (table 34) are given in terms of percentage deviation from average growth in 1919–28, the longest term of calendar years with data for all three periods—first year, second and later years, and all years of life—for which computations were made. Percentages have been presented separately for the first and for the second and later years as well as for all years combined despite the earlier observation that the trends of the fluctuations were not demonstrably correlated with age. Since young of the year, to our best knowledge, spend the growing season in Saginaw Bay whereas most older fish desert the bay for offshore waters, the most exact comparison possible between growth in the two environments is desired.

It is at once obvious from the percentages of table 34 that the trends of the annual fluctuations all were rather closely similar. First-year growth followed a course resembling that of growth in the second and later years, and in both the first and the later years the fluctuations followed closely those for all years combined. Furthermore, the fluctuations in growth of the males and females were much the same in all three categories. How similar the percentage fluctuations were is well demonstrated by the coefficients of correlation (r) of table 35. Of the coefficients listed, four were far above the level ordinarily termed highly significant ($p=0.01$)—two of the four, indeed, exceeded the value corresponding to $p=0.001$—and the fifth (correlation between the annual fluctuations in the growth of males in the first and in the second and later years) was between the 5- and

[31] See Hile (1941) for a detailed account of the procedure.

1-percent levels of probability. Some differences are to be noted, however, in the ranges of the percentages, which over the common period, 1919 to 1928, were greater for the females than for the males and for the first year than for the later years of life.

The close agreement between the annual fluctuations in the growth of the male and female Saginaw Bay walleyes of the 1926–30 collections constitutes the strongest sort of evidence that the age determinations were accurate for the bulk of the fish up to relatively advanced ages. That these fluctuations should be similar is not surprising—in fact, is to be expected. On the other hand, for this similarity to be so apparent in the analyses made independently for the males and females required that increments showing a certain deviation from the mean be identified with a particular calendar year. This identification in turn called for a correct assessment of age. Furthermore, nearly all of the year classes had to be identified at two or three ages (only exceptionally at one or four—see bottom sections of tables 31 and 32) that were separated by as many as 4 calendar years.

Despite certain discrepancies as to detail and differences in range in the percentage fluctuations in growth in length of walleyes of different sex and/or in different years of life, the general agreement seems to be sufficiently strong to justify the description of the course of growth from 1916 through 1929 on the basis of the percentages as determined for all years of life, sexes combined (bottom row of table 34; see also fig. 6). According to these data the best growth, 12.8 percent above the 1919–28 mean, occurred in 1916, the first year for which we have an estimate. From this maximum the percentage dropped to 7.8 percent in 1917. Variations were small during the 4 years, 1917–20—range from 8.6 percent in 1918 to 6.8 percent in 1920. A rise to the second highest level of the 14-year period (11.7 percent) in 1921 was followed by a rapid decline to the minimum of −14.2 percent in 1924. The fluctuations in the succeeding years were irregular but the general level was low. In only one year (1928) was growth as good as average (0.2 percent). The remaining years were from 4.0 percent (1925) to 11.7 percent (1929) below the 1919–28 mean. This last value was the second lowest of the 1916–29 period. The general trend of growth for the 14-year period can be described as irregularly downward.

TABLE 34.—*Annual fluctuations in the growth in length of the Saginaw Bay walleye expressed as percentage deviations from the 1919–28 mean*

[Percentages for the sexes combined are the unweighted means of the values determined for the sexes individually]

Year of life, and sex	Percentage deviation in calendar year—													
	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
First:														
Males			9.7	7.0	6.3	13.1	10.4	9.7	−13.4	−9.3	−13.4	−6.6	−3.9	
Females	22.1	16.3	12.4	14.4	11.2	13.7	14.4	7.3	−20.5	−8.9	−14.0	−8.9	−8.9	
Both sexes	22.1	16.3	11.0	10.7	8.8	13.4	12.4	8.5	−17.0	−9.1	−13.7	−7.8	−6.4	
Second and later:														
Males				7.2	7.2	7.2	5.1	−4.3	−11.7	−1.8	−9.4	−6.7	7.3	−1.5
Females		−1.5	5.1	5.6	5.2	14.2	9.7	−3.1	−12.5	−1.0	−9.8	−7.3	−1.0	−15.2
Both sexes		−1.5	5.1	6.4	6.2	10.7	7.4	−3.7	−12.1	−1.4	−9.6	−7.0	3.2	−8.4
All years:														
Males			9.3	6.7	6.3	9.5	7.1	1.5	−12.5	−4.5	−11.1	−6.7	3.8	−6.0
Females	12.8	7.8	7.8	9.0	7.4	13.9	11.2	.6	−15.8	−3.4	−11.5	−7.9	−3.3	−17.4
Both sexes	12.8	7.8	8.6	7.8	6.8	11.7	9.2	1.0	−14.2	−4.0	−11.3	−7.3	.2	−11.7

TABLE 35.—*Correlations of annual fluctuations in the growth rate of Saginaw Bay walleyes*

Growth periods correlated	Period of years	Value of r		Degrees of freedom	Value of r at—		
		Length	Weight		p=0.05	p=0.01	p=0.001
First year, males; later,[1] males	1919–1928	0.724	0.806	8	0.632	0.765	0.872
First year, females; later,[1] females	1917–1928	.814	.911	10	.576	.708	.823
First year, males; first year, females	1918–1928	.966	.933	9	.602	.735	.847
Later,[1] males; later,[1] females	1919–1929	.816	.942	9	.602	.735	.847
All years, males; all years, females	1918–1929	.925	.945	10	.576	.708	.823

[1] Exclusive of the first year.

FIGURE 6.—Annual fluctuations in the growth of Saginaw Bay walleyes in length (solid line) and weight (broken line), 1916–29, expressed as percentages of the 1919–28 mean.

Weight

Inasmuch as the calculated weights of tables 36 and 37 were based on the calculated lengths from which tables 31 and 32 were derived, the annual fluctuations of growth in weight of walleyes of the 1926–30 collections can be expected to exhibit trends generally similar to those just described for growth in length. Comparisons of tables 36 and 37 with tables 31 and 32 do show that with weight as with length, in the years prior to 1923 the annual increments tended to be larger and in years later than 1923, smaller than in 1923 itself; the trend toward a sharp improvement or decline was especially noticeable in certain calendar years;

the fluctuations of males and females resembled each other; and, in general, the trends of fluctuations did not differ with age (year of life). The impression is gained also that the range of variations of the annual increments was relatively much greater for weight than for length. The points just listed can be substantiated by comparisons of the actual percentage fluctuations of growth, expressed as deviations from the 1919–28 mean, in length (table 34) and weight (table 38).

The outstanding difference between the annual fluctuations in growth in length and in weight of the 1926–30 collections of walleyes lies in the much greater variation of the latter. This difference has its origin largely in the nature of length-weight relation, namely, the increase of weight approximately as the cube of the length. In consequence of this relation, the increment of weight corresponding to a particular increment of length depends not only on the amount of growth in length but also on the size of the fish at the time the growth is made. To illustrate, under the cube relationship a fish that weighs 1 pound at a length of 10 inches will increase to 1.728 pounds when it grows to a length of 12 inches. A 12-inch fish that experiences the same 2-inch growth (from 12 to 14 inches), will increase its weight by 1.016 pounds (from 1.728 to 2.744 pounds)—an increase 0.288 pound greater than the 0.728-pound increment associated with growth from 10 to 12 inches. Thus it was that during the earlier years of the 1916–29 period the increments of weight were large not only because of above-average increments of length but also because the walleyes were relatively long for their age at the time the growth was made. In the later years, on the contrary, the increments of weight were small by reason both of the small increments of length and the shortness of fish for their age. Here we have the explanation for the fact that 1928, although a year of approximately average growth in length was far below average with respect to growth in weight. The slow growth of preceding years had so reduced the size of the walleyes that with average growth in length they could not make average growth in weight.

Contributing also to discrepancies between estimates of fluctuations of growth in length and in

TABLE 36.—*Annual increments of growth in weight of male Saginaw Bay walleyes*

[Each diagonal row gives the growth history of a year class. See table 31 for numbers of fish

Year of life	Increment of weight (grams) in year—											
	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
11											100	
10										79	93	
9									106	89	82	
8								106	97	77	82	126
7							98	103	85	82	87	102
6						121	107	105	103	95	92	120
5					169	123	127	119	123	122	130	116
4				175	207	166	137	168	150	112	164	127
3			179	192	166	163	128	184	99	136	154	118
2		164	158	145	149	139	128	84	97	92	124	113
1	53	49	48	58	54	58	26	30	26	33	36	

TABLE 37.—*Annual increments of growth in weight of female Saginaw Bay walleyes*

[Each diagonal row gives the growth history of a year class. See table 32 for numbers of fish]

Year of life	Increment of weight (grams) in year—													
	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
13													141	
12												149	122	204
11											166	128	148	119
10										169	123	173	154	147
9									200	169	173	127	148	154
8								205	179	170	148	154	136	148
7							239	219	193	195	143	153	186	161
6						293	298	263	234	201	183	197	198	152
5					269	324	302	245	222	210	215	231	172	132
4				244	261	267	287	241	178	219	221	156	178	136
3			242	250	237	249	233	191	160	232	133	149	165	121
2		180	184	168	162	184	168	152	130	89	100	95	128	106
1	80	68	62	65	59	64	65	53	21	32	27	32	32	

TABLE 38.—*Annual fluctuations in the growth in weight of the Saginaw Bay walleye expressed as percentage deviations from the 1919–28 mean*

[Percentages for the sexes combined are the unweighted means of the percentages determined for the sexes individually]

Year of life, and sex	Percentage deviation in calendar year—													
	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
First:														
Males			26.2	16.9	14.5	37.9	28.6	37.9	−36.9	−27.5	−36.9	−20.5	−13.5	
Females	75.2	49.4	36.5	42.9	30.1	40.8	42.9	17.2	−51.6	−27.9	−38.7	−27.9	−27.9	
Both sexes	75.2	49.4	31.4	29.9	22.3	39.4	35.8	27.6	−44.2	−27.7	−37.8	−24.2	−20.7	
Second and later:														
Males				20.0	16.3	16.3	18.2	2.6	−10.1	−5.0	−19.3	−25.8	−12.7	−14.0
Females		15.5	17.7	15.8	15.5	25.2	23.0	7.8	−7.8	−8.5	−22.4	−25.1	−23.8	−33.2
Both sexes		15.5	17.7	17.9	15.9	20.8	20.6	5.2	−9.0	−6.8	−20.8	−25.4	−18.2	−23.6
All years:														
Males			26.4	18.6	15.3	17.9	18.9	5.1	−11.3	−5.9	−20.2	−25.7	−12.7	−14.0
Females	35.2	19.0	18.2	17.2	16.1	25.7	23.7	8.3	−9.2	−9.2	−23.2	−25.5	−24.2	−33.6
Both sexes	35.2	19.0	22.3	17.9	15.7	21.8	21.3	6.7	−10.2	−7.6	−21.7	−25.6	−18.4	−23.8

weight were differences with respect to the years of life that exerted greatest influence in the computation of year-to-year percentage changes. Under the procedure followed (comparison of 2 consecutive calendar years on the basis of the sums of the increments for all years of life represented in the data for both years), the earlier years of life (particularly the first and second) by reason of their larger increments dominated the estimates of fluctuations of growth in length. In the data on weight, however, the first-year increments were the smallest and those for the second year were far below the increments for intermediate ages (3 to 4 or 5 years of life) and were smaller than many of the increments at still higher ages. Thus the estimates of fluctuations of growth in length were dominated by the data for the earlier years whereas the intermediate years were most important and the later years of life enjoyed increased influence in the estimation of fluctuations of growth in weight. Since, as was brought out earlier, the data for different years of life were not fully consistent with respect to the extent of growth and direction of change of growth from one year to another, this shift in dominance of years of life inevitably affected comparisons of fluctuations of growth in length and weight.

The correlation between the sexes and between the first and the later years of life was even closer for fluctuations in growth in weight than for growth in length. Four of the five coefficients for weight (table 35) were larger than the corresponding coefficients for length and all had values well beyond the 1-percent level of probability (four beyond the 0.1-percent value). With weight as with length the range of the percentages was greater for the first than for the later years of life and for the females than for the males.

For the sexes and all years of life combined (bottom row of table 38; fig. 6) the growth in weight was best in 1916 when it stood at 35.2 percent above the 1919–28 mean. The percentages fluctuated about a lower level during the next 6 years—between a high of 22.3 percent in 1918 and a low of 15.7 percent in 1920. Successive large decreases in 1923 and 1924 carried the value to −10.2 percent in the latter year. A small improvement in 1925 (to −7.6 percent) was followed by a new decline to the minimum of −25.6 in 1927. A rise occurred again in 1928 (to −18.4 percent) but 1929 with a percentage of −23.8 had the second lowest value of the entire 1916–29 period. The year of relatively best growth for both length and weight was 1916. The poorest growth in weight, however, occurred in 1927, 3 years later than the season of poorest growth in length (1924).

With the fluctuations of growth in 1916–29 as with the strength of the year classes in 1917–28 (see p. 20), preliminary analyses indicated a significant correlation with certain meteorological conditions. Furthermore, the limited data on annual fluctuations in growth supplied by the 1943 sample (see section, Improvement in growth after 1929), contrary to the situation with the year classes, tended to confirm conclusions based on 1926–30 collections. Because the 1943 materials were so scanty, it is held desirable to postpone a detailed inquiry into environmental factors influencing changes of growth rate until more extensive information is at hand.

IMPROVEMENT IN GROWTH AFTER 1929

In the earlier comparison of the general growth of the walleyes of the 1926–30 and 1943 collections, it was brought out that first-year growth was much the same in the two groups but that fish of the 1943 collection had grown by far the better in the second and later years of life. Although the data for the 1943 sample (tables 39, 40, 41, and 42) do contain fragmentary information on first-year growth as far back as 1930 and on growth beyond the first year as early as 1931, the representation of some of the year classes was so weak (females of year-classes 1932 and 1935 were lacking; males included no year classes earlier than 1933) as to limit sharply the dependability of estimates of annual fluctuations by means of procedures followed with the 1926–30 collections. These tables do provide, however, some information on the question of the time of occurrence of the improvement in growth rate from the low level of the late 1920's to that which characterized walleyes of the 1943 collection as a group.

The trends of growth of the 1943 walleyes in the second and later years of life are not clear cut. A possible exception to this statement is offered by the increments for the third year of life which were at a distinctly higher level in the more recent years (after 1935 or 1936) than in earlier years. For other years of life this trend toward improved growth in the more recent years is relatively weak or lacking. It is largely the pronounced upward trend in the third-year increments together with the obviously good growth of 1941 that gives the impression that the general trend during the years covered by the data from the 1943 collection was irregularly upward.

TABLE 39.—*Annual increments of growth in length of male Saginaw Bay walleyes of the 1943 collection*

[Each diagonal row gives the growth history of a year class]

Year of life	Increment of standard length (millimeters) in year—									
	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942
10										14
9									13	19
8								11	18	16
7							19	21	16	22
6						24	27	22	32	25
5					30	38	32	29	37	26
4				50	46	32	49	48	48	51
3			69	52	84	80	85	87	97	76
2		112	108	130	118	107	103	113	136	
1	157	141	116	118	134	142	122	148		
Number of fish	3	3	2	5	14	3	49	101		

Regardless of what the trends of growth may have been during the years covered by the data of the 1943 collection, such information as we have suggests strongly that much of the advantage of the 1943 walleyes over those collected in 1926–30 had become established in the early and middle 1930's. For example, the second-year growth of females in 1929 was 85 millimeters (table 32), a figure far below any of the second-year increments of 1943 females in 1931–35 (101 to 143 millimeters). Similarly, the third-year increment in 1929 (48 millimeters) was less than the 1932–35 figures of 56 or 57 millimeters and was much below the 1936 value of 78 millimeters. The continuation of these comparisons to other years of life and to the data on growth in length of males and on growth in weight of walleyes of both sexes leads to the general conclusion that a sharp upturn in growth rate must have occurred soon after 1929. Any uncertainty arising from the small numbers of fish on which data on growth in the early and

TABLE 40.—*Annual increments of growth in length of female Saginaw Bay walleyes of the 1943 collection*

[Each diagonal row gives the growth history of a year class]

Year of life	Increment of standard length (millimeters) in year—												
	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942
13													17
12												20	19
11											12	18	
10										17	27		22
9									17	22		18	25
8								28	22		19	25	
7							44	34		28	28		37
6						40	34		34	45		40	37
5					64	59		43	47		50	56	44
4				47	68		53	46		73	63	59	57
3			57	56		56	78		75	103	79	108	86
2		143	101		134	106		105	108	123	117	138	
1	139	132		152	150		143	127	170	127	148		
Number of fish	2	1		1	2		3	16	1	30	50		

TABLE 41.—*Annual increments of growth in weight of male Saginaw Bay walleyes of the 1943 collection*

[Each diagonal row gives the growth history of a year class. See table 39 for numbers of fish]

Year of life	Increment of weight (grams) in year—									
	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942
10										130
9									114	155
8								92	135	119
7							148	144	110	161
6						171	165	139	207	172
5					187	196	176	161	220	155
4				254	186	148	219	226	234	251
3			246	152	270	237	266	282	304	305
2		202	164	173	149	150	153	144	254	
1	50	36	20	21	31	37	24	42		

middle 1930's are based is more than compensated for by the consistency and the degree to which growth was better than in 1929.

GROWTH IN SAGINAW BAY COMPARED WITH THAT IN OTHER AREAS

Studies of the growth of the walleye in Lake Erie by Deason (1933) and in Lake of the Woods by Carlander (1945)[32] make possible the comparison of growth in three major centers of commercial production in the United States (table 43 and fig. 7). In the interest of uniformity, the data of those two investigators were submitted to certain adaptations. For Carlander's data only a conversion from standard length in millimeters to total length in inches was required. With the Lake Erie data the calculated lengths, which were computed by direct proportion for Deason's preliminary report, were recalculated on the basis of an intercept of 50 millimeters (see p. 10). These corrected calculated lengths were then converted from tape to board measurement (see p. 9) and from standard to total lengths. The data of table 43 were carried only through those years of life for which reasonably adequate data were available (records for Saginaw Bay walleyes were dependable beyond the ninth year but comparable data were not available from other localities).[33] The lengths for walleyes from Lake of the Woods and Lake Erie were based on the sexes combined; for Saginaw Bay they are the unweighted means of the lengths determined for males and females separately.

[32] See Carlander's paper and Eschmeyer (1950) for additional references on the growth of the walleye.

TABLE 42.—*Annual increments of growth in weight of female Saginaw Bay walleyes of the 1943 collection*

[Each diagonal row gives the growth history of a year class. See table 40 for numbers of fish]

Year of life	Increment of weight (grams) in year—												
	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942
13													263
12												292	247
11											167	219	
10										225	303		254
9									211	226		192	277
8								323	207		189	252	
7							442	284		254	254		362
6						339	245		270	349		333	321
5					431	340		287	295		341	397	347
4				238	274		278	226		364	331	366	318
3			212	148		213	263		238	330	338	374	361
2		255	134		256	173		159	141	261	161	260	
1	35	30		46	44		38	27	64	27	42		

TABLE 43.—*Comparison of the growth of walleyes in Lake of the Woods and Lake Erie with that in Saginaw Bay*

[Total length in inches]

Year of life	Lake of the Woods [1]		Lake Erie [2]		Saginaw Bay			
					1926-30		1943	
	Length	Increment	Length	Increment	Length	Increment	Length	Increment
1	6.4	6.4	6.0	6.0	6.8	6.8	6.4	6.4
2	9.3	2.9	9.7	3.7	10.8	4.0	12.0	5.6
3	11.5	2.2	12.1	2.4	13.6	2.8	16.0	4.0
4	13.5	2.0	15.1	3.0	15.7	2.1	18.5	2.5
5	14.9	1.4	18.0	2.9	17.2	1.5	20.4	1.9
6	16.7	1.8			18.5	1.3	21.7	1.3
7	18.2	1.5			19.3	.8	22.8	1.1
8	19.9	1.7			20.0	.7		
9	21.6	1.7			20.6	.6		

[1] Data adapted from Carlander (1945).
[2] Data adapted from Deason (1933).

The most noteworthy features of the data of table 43 are the high calculated lengths of Saginaw Bay walleyes of the 1943 collection and the differences between Saginaw Bay fish and those from Lake of the Woods and Lake Erie in the trend of

[33] The record of lengths for walleyes from Lake of the Woods was terminated at the end of 9 years because of the sharp disagreement at higher ages between growth curves as based on grand-average lengths and as determined from the summation of grand-average annual increments.

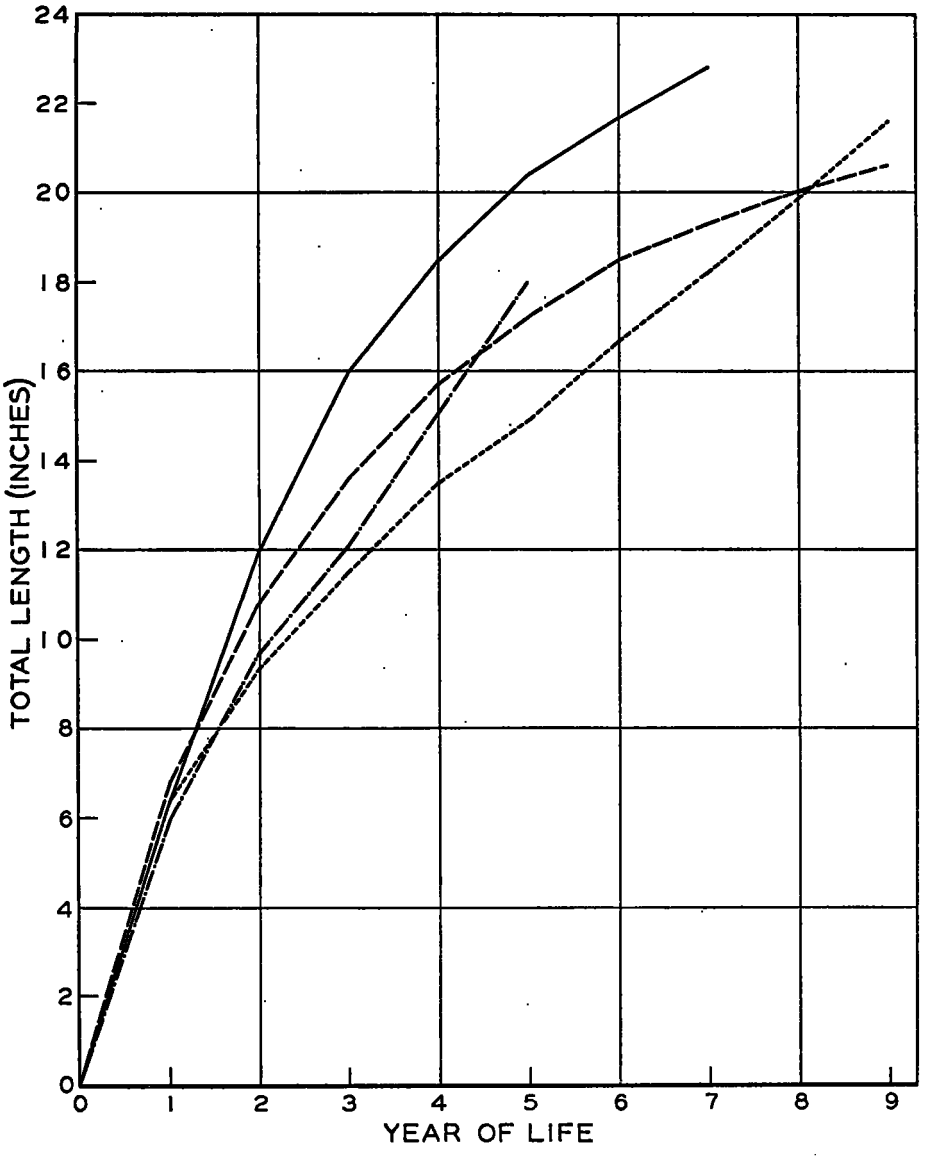

FIGURE 7.—Comparison of growth in length of walleyes in Saginaw Bay (1926–30 collection, long dashes; 1943 collection, solid line), Lake Erie (dots and dashes), and Lake of the Woods (short dashes).

the annual increments during the later years of life. Examination of the increments reveals that the advantage of Saginaw Bay walleyes of the 1943 collection over those of other localities or collections was established entirely or principally in the earlier years of life—in the first through the third with respect to Lake Erie fish and in the second through the fifth with respect to walleyes of Lake of the Woods and of the Saginaw Bay 1926–30 collections. The increments of Saginaw Bay walleyes collected in 1943 declined so rapidly with increase in length that Lake Erie fish had better growth in the fourth and fifth years and Lake of the Woods walleyes in the sixth and seventh; the growth of Saginaw Bay walleyes of the 1926–30 samples equaled that of the 1943 fish in the sixth year but again was the smaller in the seventh.

Differences between Saginaw Bay fish and walleyes from Lake of the Woods and Lake Erie in the trends of growth during the later years of life led to two distinct types of growth curves. In both of the Saginaw Bay collections the consistent decrease of the annual increments with increase of

age resulted in a progressive decrease in the slope of the curves. In Lake Erie, on the other hand, no downward trend can be demonstrated beyond the third year—in fact, the fourth- and fifth-year increments were greater than the third—and in fish from Lake of the Woods the variation of the increments in the fifth through the ninth years of life may be termed irregular. The sustained growth in the later years permitted Lake Erie walleyes to overtake and pass the Saginaw Bay fish of the 1926–30 collection during the fifth year. The Lake of the Woods walleyes, however, did not overtake the 1926–30 fish from Saginaw Bay until the ninth year of life. This relationship among growth curves of walleyes in which the populations (or collections) with the greater lengths in the earlier years lost much or all of their advantage during later years is closely similar to that observed in five populations of rock bass of northern Wisconsin (Hile 1942).

SEX RATIO

CHANGES WITH INCREASING AGE

Despite pronounced irregularities in the trends of changes in the sex ratio with each successive increase of age, male walleyes of the Saginaw Bay collections tended strongly to be relatively less abundant at the higher than at the lower ages in both the combined spawning-run samples of 1927 and 1929 and the late-spring collections of 1929 [34] and 1930 (table 44). In the spawning-run collections, the representation of males dropped from 71.4 percent in age-group IV to 52.5 percent in age-group VII, increased to 61.7 percent in age-group VIII, and thereafter declined consistently to a minimum of 18.2 percent in age-group XIII.

[34] Sex data available only for the VII group and older in 1929—see footnote to table 44.

Two of the three fish in age-group XIV were males. The general trend in the changes of the percentage of males with increasing age is brought out by the following tabulation:

Age groups	Number of males	Number of females	Percentage males
IV-IX	322	244	56.9
X-XIV	37	94	28.2

Thus it is seen that the relative abundance of the males was twice as great in age-groups IV to IX as in age-groups X to XIV.

In late spring, the representation of males rose from 42.5 percent in age-group II to 60.0 percent in age-group IV, declined to 36.0 percent in age-group VI, increased again to 41.7 percent in age-group VII, and ranged between 22.0 and 11.8 percent in age-groups VIII to XI; all 7 fish more than 11 years old were females. The general trend may be seen in the following summary:

Age groups	Number of males	Number of females	Percentage males
II-V	527	450	53.9
VI-VII	34	51	40.0
VIII-XV	10	52	16.1

Here the extreme scarcity of males at the highest ages is striking. Relatively, males were 2½ times as plentiful in age-groups VI to VII and more than 3 times as abundant in age-groups II to V as in age-groups VIII to XV. The downward trend that culminated in this low percentage of males at the higher ages perhaps cannot be held to have started until after the fifth year since the percentage of males in the V group (47.8), although substantially less than that in the IV group (60.0) was still above the value for age-group II (42.5)

TABLE 44.—*Variation of the sex ratio with age in spawning-run and late-spring collections of Saginaw Bay walleyes*

Collection	Representation of sexes in age group—														All ages
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	
Spawning run (1927, 1929):															
Number of males	----	----	5	18	72	106	82	39	21	9	3	2	2	----	359
Number of females	----	----	2	11	51	96	51	33	45	26	13	9	1	----	338
Percentage males	----	----	71.4	62.1	58.5	52.5	61.7	54.2	31.8	25.7	18.8	18.2	66.7	----	51.5
Late spring (1929, 1930): [1]															
Number of males	17	154	246	110	9	25	5	2	2	1	----	----	----	----	544
Number of females	23	143	164	120	16	35	19	15	7	4	5	1	----	1	516
Percentage males	42.5	51.9	60.0	47.8	36.0	41.7	20.8	11.8	22.2	20.0	.0	.0	----	.0	51.3

[1] Adequate records of sex were available only for the VII group and older fish in 1929; although the 1929 records were included in the data for individual age groups, the totals at the right are based on the 1930 collections alone.

and not much less than that for age-group III (51.9).

At corresponding ages the percentages of males were consistently higher (usually by a wide margin) in the spawning-run samples than in those of late spring. The nearly equal percentages in the two collections for all age groups combined (51.5 percent males in the spawning run; 51.3 percent males in late spring—1930 only) was the result of the greater age of the spawning-run fish. Given the same age distribution, males should be much more plentiful in spawning-run than in late-spring collections.

The only collections in addition to those covered in table 44 for which sex data were recorded for all or nearly all individuals were poorly suited for the study of the relation of the sex ratio to age. In the samples taken in the fall of 1926, 291 of the 305 walleyes were of the same age (I group). In this group 145 were females, 145 were males, and sex of 1 fish was undetermined. Dominance of a single age group was not so sharp in the collection of May 4, 1943 (52.4 percent of the total in age-group III—see table 12), but even here only 3 of the 11 age groups contributed more than 90 percent of the total number. Although the data from the 1943 sample exhibited no distinct trend as to sex ratio, it is to be noted that all 3 fish more than 10 years old were females.

Greater destruction of males than of females in the fishery may have contributed to the lower percentages of males at the higher ages. During the spawning period, at which time the heaviest fishing is carried on and practically all fish captured are adults, the males may be much the more vulnerable sex, since as will be shown in the next section, they tend to mature at an earlier age than do females. Hence during the years of life when at least some of the males are mature, but below the age at which all fish of both sexes have attained maturity, males are on the spawning grounds in numbers out of proportion to their true representation in the age groups as a whole. To some extent the effects of earlier attainment of maturity of the males should have been offset at the time of collection of the 1926–30 samples by the fact they attained the then legal minimum size of 1½ pounds in the sixth year as compared with the fifth year for the females. To what degree the males actually benefited from this theoretically greater protection is problematic for it is known that in the years of the 1½-pound limit large if undetermined quantities of undersized males ("jacks" in the parlance of commercial fishermen) were marketed illegally.

The explanation of the decreasing relative abundance of males with increasing age on the basis of their earlier attainment of maturity cannot account for the continuing decline in the percentage of males at those higher ages at which no fish of either sex are immature (beyond age-group VI if the 1930 data hold for all fish of the 1926–30 collections). Here, a higher rate of destruction of the males can take place only if they are the easier to catch, that is, remain longer on the spawning grounds than do females or are the more active. That males may be more catchable than females during the spawning season is evidenced by the fact that for all ages, including those at which all fish are mature, the percentage of males ran higher in the spawning-run than in the late-spring samples.

There is no reason to believe that the rates of commercial exploitation of the sexes at corresponding ages differed at periods other than the spawning season except possibly for the questionable additional protection that males may have received as the result of their later attainment of legal size.

Belief that the reduced percentage of males in the higher age groups of the walleyes was the result of their greater mortality in the commercial fishery is supported by the earlier observation that no real downward trend in the percentage could be demonstrated among the younger fish (that is, fish largely immature and of less than legal size).

Even though a relatively high exploitation rate for spawning-run males resulting from their earlier maturity and greater activity may seem adequate to explain their decreasing percentage with increase of age, the possibility should not be overlooked that the natural mortality rate as well as the rate of exploitation may be higher for males than for females. Strong evidence that the natural death rate of males is higher than that of females has been presented by a number of investigators. (See Hile 1936 and 1941, and Deason and Hile 1947 for discussion and references to literature on the changes of the sex ratio with increase of age.)

CHANGES WITHIN COLLECTING PERIODS

Spawning period

It is commonly believed that males tend to predominate in the earlier and females in the later part of the spawning period. This belief is supported by the data on collections made over the period, April 4–23, 1929 (table 45). Males were in the majority on both April 4 (56.3 percent) and April 7 (59.2 percent) and made up 58.0 percent of the combined samples. (The April 6 sample, which is obviously abnormal, is discussed later in this section.) They were in the minority, however, in each of the three samples of April 13–23 and comprised but 41.6 percent of the combined samples.

In view of the relation between sex ratio and age demonstrated in the preceding section, changes in the age composition and hence in average age must be considered as a possible factor in fluctuations of that ratio. An explanation of the lower percentage of males in the April 13–23 samples on the basis of age is not acceptable, however. It is true that these fish averaged older than walleyes collected April 4 and 7, but the difference between the averages—only 0.19 year—was extremely small. Furthermore, the examination of the data on mean age and sex ratio for the individual samples fails to reveal a correlation between the two. Finally, the trend toward fewer males on the later collecting dates was exhibited by four of the five best-represented age groups as well as by all age groups combined.[35] The shift toward a lesser relative abundance of males in the last three samples, therefore, was a real, not an apparent phenomenon, traceable to changes in age composition. Whether the change represents a shifting about within a single stock or the successive domination of the catch by different stocks with different sex ratios cannot be stated.

The April 6 sample in which all 53 fish were males is precisely the type that causes grave concern as to the possible inaccuracy of records. Unfortunately it was impossible to consult the collector concerning the sampling.[36] The following circumstances, however, lead to the conclusion that the collection of April 6 almost certainly was a true sample of the catch: First, the serial numbers ran consecutively from the largest fish of the April 4 sample to the smallest one of the April 7 sample; second, in none of the remaining five collections had the scale envelopes for males and females been separated—hence the possibility seems remote that the envelopes were sorted according to sex and those for females subsequently lost.

To determine whether any unusual weather conditions existed near the time of the April 6 collection the meteorological records were examined for the Saginaw Bay area. This examination revealed that a severe storm accompanied by heavy rainfall (amounting to 2.10 inches at Bay City) occurred on April 5. Whether this storm actually caused males only to be taken on April 6, and if so, how that result was produced are strictly matters for speculation at this time.

Late spring

In the late spring of 1930, as in the spawning season of 1929, the sex ratio fluctuated considerably from sample to sample (table 46). Again it is possible to divide the collecting season into two periods. In the samples of April 30–May 17,

[35] See table 5 for the numerical representation of males and females in the various age groups on the several dates.

[36] Dr. Jan Metzelaar who made the collections from the 1929 spawning run met his untimely death later in that same year.

TABLE 45.—*Fluctuations in sex ratio and relation of the ratio to average age during the spawning season of 1929*

Date of collection	Percentage males in age group—					All ages combined			Average age (sexes combined)
	VI	VII	VIII	IX	X	Number of males	Number of females	Percentage males	
April 4	88	68	56	64	25	49	38	56.3	8.05
6	100	100	100	100	100	53	0	100.0	7.68
7	48	59	79	45	47	74	51	59.2	7.77
April 4–7	59	62	71	56	39	123	89	58.0	7.88
April 13	43	32	37	59	42	45	67	40.2	8.28
15, 19	56	48	43	25	21	38	63	37.6	8.13
23	86	35	42	43	11	44	48	47.8	7.75
April 13–23	65	38	40	47	26	127	178	41.6	8.07

males comprised 59.3 percent of the total whereas they made up only 42.4 percent of the collections of May 22–June 20. Within each of these two periods no trend is discernible. The largest deviation from the general level in the earlier period was the value of 46.5 percent for May 8, 11, and 13. This figure was still higher, however, than the mean for May 22–June 20. In the later period the percentage of 49.0 for June 1 and 3 was well above the average but still below the mean for the earlier period.

Differences of age do not account for the lower percentage of males in the second period. On the contrary, had age been an important factor the younger walleyes of May 22–June 20 (average age, 3.74 years) should have included a higher, not a lower, percentage of males than the fish of April 30–May 17 (average age, 4.50 years). Furthermore, in these samples, as in the spawning-run samples of 1929, the tendency toward a lower percentage of males in the latter part of the collecting period is to be found in the data for the best represented individual age groups III to V.[37]

TABLE 46.—*Fluctuations in sex ratio and relation of the ratio to average age in the spring of 1930*

Date of collection	Percentage males in age group—			All ages combined			Average age (sexes combined)
	III	IV	V	Number of males	Number of females	Percentage males	
April 30	83	64	49	98	65	60.1	4.31
May 3, 5	83	72	74	99	39	71.7	4.36
8, 11, 13	54	66	45	74	85	46.5	5.05
15, 17	56	60	70	61	39	61.0	4.12
April 30–May 17	71	66	55	332	228	59.3	4.50
May 22, 24	44	43	11	48	74	39.3	3.89
26, 29	50	48	20	56	83	40.3	4.02
June 1, 3	49	54	[1] 75	50	52	49.0	3.30
9, 18, 20	38	60	23	58	79	42.3	3.66
May 22–June 20	45	51	24	212	288	42.4	3.74

[1] Based on only four fish.

The question arises again as to whether the differences in the sex ratio in two parts of the same general collecting period represent a change in the distribution (or activity) of males and females within a single stock or whether the catches were dominated in successive periods by different stocks with different natural sex ratios. The data presented earlier (p. 29) on fluctuations of weight during the late spring of 1930 would seem to favor the latter assumption. At that time it was pointed out that walleyes captured April 25–May 13 were approximately 20 percent heavier than fish of corresponding length taken May 19–June 20. The opinion was expressed that this decline was greater than could reasonably be accounted for as the result of weight losses by individual fish and hence that the stock probably was heterogeneous as regards the length-weight relation. Since the late-spring samples of 1930 can be grouped in approximately the same periods with respect to weight and sex ratio (fish were weighed on some days scale samples were not taken; collections of May 15 and 17, held to be intermediate between the April 25–May 13 and May 19–June 20 fish in weight, agreed well with the walleyes of the earlier period in sex ratio), the assumption of heterogeneity in sex ratio as well as in weight is attractive.

SIZE AND AGE AT MATURITY

Data on both sex and state of organs on all or nearly all walleyes were recorded only for the collections of April 25–June 20, 1930, and May 4, 1943. The reliability of the latter collection for the study of maturity is held questionable, because of the presence of spawning fish and the consequent possibility of a certain, if unmeasured, segregation on the basis of maturity. This collection did contain numbers of immature fish (all of them females) but they might have been more plentiful in samples taken after the completion of spawning activities. The data on the relation between length and maturity (table 47) accordingly are based entirely on the 1930 materials. The necessary breakdown of the data so reduced the numbers of specimens in the individual entries that the variation of the percentages of maturity with length was at times decidedly irregular. To overcome the difficulty occasioned by these irregularities the percentages were plotted and curves fitted to them by inspection (fig. 8). Values read from the curves, although certainly approximations, have some superiority over individual percentages.

[37] See table 6 for the numerical representation of males and females in the different age groups on the several dates.

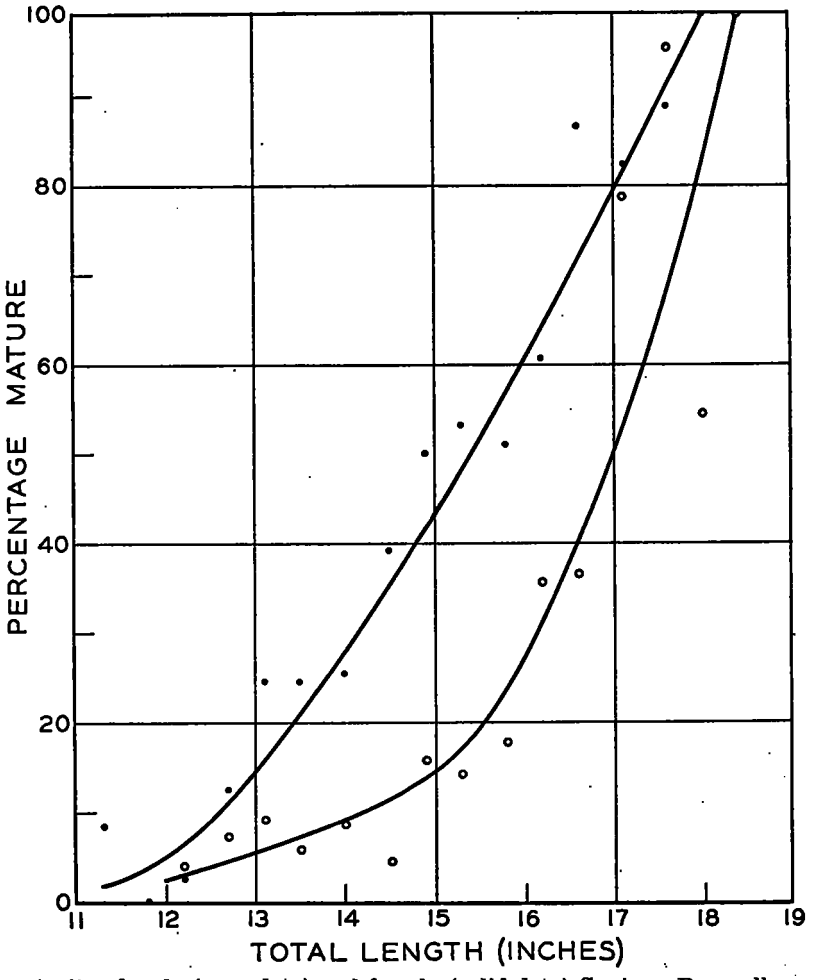

FIGURE 8.—Percentage maturity of male (open dots) and female (solid dots) Saginaw Bay walleyes according to length. The curves were fitted by inspection.

The difference between the sexes with respect to the size of the smallest sexually mature fish and that at which all were mature was small. The shortest mature female was 12.2 inches, and only one shorter mature male (11.3 inches) was observed. At the other extreme, the males attained 100-percent maturity at 18.0 inches and the females at 18.4 inches. Between these points the trends of the percentages of maturity with increase of length differed sharply in males and females. In the males, the percentage rose rather steadily as length increased. But for a slight upward curvature of the line the increases could be termed proportional. The line for the females, on the other hand, was flat at the smaller lengths, curved sharply upward at about 15–16 inches, and was steep at the greater lengths. The difference in the shape of the curves caused the disparity between the percentages of mature males and females to be greatest at intermediate lengths (with the largest disagreement at about 16 inches). At the 1½-pound (17.1-inch) minimum legal size in effect in 1930 the percentages of sexually mature fish as estimated from the curves were slightly above 80 percent for the males and a little better than 50 percent for the females. At the present minimum legal length of 15½ inches the percentages are just above 50 percent for the males and roughly 20 percent for the females.

The large percentage of immature females at 15½ inches indicates that they derive relatively small protection from the present minimum legal size. They do, however, enjoy a most effective "biological" protection. Since the heaviest catches are made during the spawning season and since walleyes captured at that time are almost exclu-

TABLE 47.—*Relation between length and sexual maturity of walleyes captured from April 25 to June 20, 1930*

Standard length [1]	Total length	Males			Females		
		Immature	Mature	Percentage mature	Immature	Mature	Percentage mature
	Inches						
180 mm.	8.4	1		0.0	1		0.0
190 mm.	8.8				2		.0
200 mm.	9.3				1		.0
209 mm.	9.7	4		.0	7		.0
219 mm.	10.1	4		.0	5		.0
229 mm.	10.5	7		.0	4		.0
239 mm.	10.9	9		.0	5		.0
248 mm.	11.3	11	1	8.3	12		.0
258 mm.	11.8	31		.0	23		.0
268 mm.	12.2	39	1	2.5	24	1	4.0
278 mm.	12.7	42	6	12.5	37	3	7.5
287 mm.	13.1	64	21	24.7	40	4	9.1
297 mm.	13.5	43	14	24.6	48	3	5.9
307 mm.	14.0	50	17	25.4	42	4	8.7
317 mm.	14.5	45	29	39.2	42	2	4.5
326 mm.	14.9	25	25	50.0	48	9	15.8
336 mm.	15.3	29	33	53.2	36	6	14.3
346 mm.	15.8	17	18	51.4	32	7	17.9
356 mm.	16.2	11	17	60.7	27	15	35.7
365 mm.	16.6	4	26	86.7	19	11	36.7
375 mm.	17.1	3	14	82.4	4	15	78.9
385 mm.	17.6	1	8	88.9	1	21	95.5
395 mm.	18.0		8	100.0	5	6	54.5
404 mm.	18.4		5	100.0		13	100.0

[1] All fish of lengths greater than those shown in the table (5 males and 76 females) were mature.

sively mature individuals, the mere state of immaturity provides almost complete exemption from capture during the period of greatest exploitation. That an excessive destruction of immature fish has not taken place under the 15½-inch limit is demonstrated by the continuing success of the spawning-run fishery. Because of this success there is no reason to believe that the recent scarcity of walleyes in Saginaw Bay is to be attributed to the destruction of immature fish. At the present time there is no reason to hold that an increase in the size limit is needed.

Walleyes seem to mature sexually at a greater size in Saginaw Bay than in Lake Erie where Deason (1933) found that males 13½ inches long and larger and females 15 inches long and larger were practically all mature.

The data on the percentage of sexually mature fish at different ages in 1930 (table 48) reveal that no II-group walleyes of either sex were mature and that the percentages were small in the III group (males, 13.6 percent; females, 4.2 percent). The percentages increased consistently in the succeeding age groups. In 5 years, 49.2 percent, or nearly half, of the females and 71.8 percent of the males were mature. Immature fish were distinctly in the minority in age-group VI (77.8 percent of the males and 68.8 percent of the females mature) and no immature fish were found beyond the VI group.

All males, including one II-group fish, and all females older than the IV group were mature in the rapidly growing fish of the May 4, 1943, collection. As was pointed out previously, however, the value of this sample for the study of maturity is open to question.

TABLE 48.—*Percentage maturity by age and sex of Saginaw Bay walleyes in 1930 and 1943*

Date of collection, and sex	Item	Age group—				
		II	III	IV	V	VI
Apr. 30–June 20, 1930: Males	Total length (inches)	10.6	12.7	14.4	16.0	16.4
	Number in age group	17	154	246	110	9
	Number mature	0	21	85	79	7
	Percentage mature	.0	13.6	34.6	71.8	77.8
Females	Total length (inches)	10.1	12.8	14.7	16.5	17.6
	Number in age group	23	143	164	120	16
	Number mature	0	6	26	59	11
	Percentage mature	.0	4.2	15.9	49.2	68.8
May 4, 1943: Males	Total length (inches)	15.2	16.4	17.5	18.5	19.8
	Number in age group	1	101	49	3	14
	Number mature	1	101	49	3	14
	Percentage mature	100.0	100.0	100.0	100.0	100.0
Females	Total length (inches)	14.0	17.0	18.6	21.2	22.1
	Number in age group	1	50	30	1	16
	Number mature	0	6	22	1	16
	Percentage mature	.0	12.0	73.3	100.0	100.0

SUMMARY

1. The average annual catch of the Saginaw Bay walleye was 1,149,000 pounds in 1891–1919, 652,000 pounds in 1920–31, 1,466,000 pounds in 1932–43, and only 396,000 pounds in 1944–51. The commercial take was under 100,000 pounds in each of the 3 years, 1949–51.

2. The age and growth studies were based on the determination of age for 3,652 fish and the computation of individual growth histories (from scale measurements) for 2,427 specimens collected in 1926–30 and 1943. Growth computations were made on the assumption that the body-scale relation of the Saginaw Bay walleye is described by a straight line with an intercept of 50 millimeters on the (standard) length axis.

3. Age composition and mean age varied widely according to season of capture in the 1926–30 collections. The two fall samples were dominated by age-group I and had a mean age (average number of annuli) of 1.28. Spawning-run collections were dominated by age-group VII and had a mean age of 7.60. Age-group IV dominated the two late-spring collections; the mean age was 3.90. The 1943 sample taken near the end of the spawning

season was dominated by age-group III and had an average age of 4.06.

4. Records of age composition of the subsamples (that is, collections of fish made on a single day or over a few days) of the 1929 spawning run revealed only limited variation within the spawning season. Age composition was much more variable in the late-spring collections of 1929 and 1930, and in both years the mean age exhibited a distinct downward trend toward the end of the collecting period.

5. Shortcomings of the original data (variation of age composition between and within seasons; lack of fall and spawning-run samples in any 2 consecutive years) prohibited a precise evaluation of the relative strength of the year classes. A ranking of the 1917–28 year classes into five categories was made, nevertheless. From the strongest year classes (1) to the weakest (5), the rankings were as follows: (1) 1919, 1925; (2) 1920, 1921, 1922, 1926, 1927; (3) 1918, 1923; (4) 1917, 1924; (5) 1928. In the 1943 collection, year-classes 1937 and 1940 appeared to be stronger and year-classes 1938 and 1941 weaker than average.

6. Seasonal differences in the age composition of walleyes of the 1926–30 collections were reflected in differences in length distribution, mean length, and percentage of legal-sized fish in random samples from impounding nets. In the fall collections, the average total lengths and the percentages of walleyes legal at the present minimum length of 15½ inches were for 1926—10.0 inches, 1 percent; 1928—11.1 inches, 1 percent; 1929—14.8 inches, 48 percent. In the late-spring collections, the lengths and percentages of legal-sized fish were for 1929—13.8 inches, 21 percent; 1930—14.7 inches, 30 percent. In the spawning-run collections the figures were for 1927—19.1 inches, 98 percent; 1929—20.1 inches, 100 percent. The late-spawning-run sample of 1943 averaged 17.9 inches long and included 96 percent of legal-sized fish.

7. The length distributions of successive age groups overlapped extensively in both the 1926–30 and 1943 collections. At the higher lengths as many as 7 age groups were represented in a single length interval of approximately 0.9 inch.

8. The relation between the standard length in millimeters (L) and the weight in grams (W) of 5,080 Saginaw Bay walleyes captured in different seasons and calendar years was described satisfactorily by the equation, $W=1.376\times10^{-5}L^{2.989}$.

9. The weights of walleyes of corresponding lengths and captured in the same nets exhibited pronounced short-term fluctuations during the late spring in both 1929 and 1930. The period May 8–June 18, 1929, could be divided into 5 subperiods in which the mean weights of walleyes differed by 5 to 12½ percent from those of adjacent subperiods. In 1930 walleyes captured April 25–May 13 averaged about 19 to 20 percent heavier than fish captured May 19–June 20. It was concluded that the population is probably heterogeneous with respect to the length-weight relation and that different segments of the population dominated the samples at different times.

10. Walleyes collected in the fall in 1928 and 1929 averaged heavier than fish caught in the late spring in 1929 and 1930 by 12.7 percent at 8.8 to 14.9 inches and 18.5 percent at 15.3 to 18.0 inches. The mean weights of sound walleyes averaged 5½ to 6½ percent heavier than those of fish of corresponding length infected with *Lymphocystis*.

11. Differences of growth between the sexes and between the 1926–30 and 1943 samples made necessary the use of four separate curves for the description of the growth of the Saginaw Bay walleye. Sex differences of growth were small or nil during the first 2 years of life but in the third and later years both the average size and the annual growth increments of females exceeded those of males of corresponding age. The first-year growth of the 1943 walleyes was slightly less than that of fish of the 1926–30 collections. For all later years the actual sizes and for practically all years of life the annual increments of the fish collected in 1943 exceeded those of 1926–30 walleyes of corresponding sex and age.

12. The limited data on annual growth available from walleyes of the 1943 collection indicated that much of the advantage of the 1943 over the 1926–30 walleyes with respect to rate of growth had become established in the early and middle 1930's.

13. Maximum annual growth in length occurred during the first year of life of both males and females in both collecting periods. During later years the increments exhibited a rather consistent

downward trend. Times of attainment of the present minimum legal total length of 15½ inches were for 1926–30 males—early in fifth year (more properly fifth growing season); 1926–30 females—latter part of fourth year; 1943 males—near end of third year; 1943 females—past the middle of the third year. Latest years of life for which data were available and corresponding calculated lengths were for 1926–30 males—14 years, 21.3 inches; 1926–30 females—15 years, 25.0 inches; 1943 males—10 years, 23.3 inches; 1943 females—13 years, 29.5 inches.

14. Annual fluctuations of growth in length were similar for males and females and for first-year and later growth. The quality of growth for both sexes and all years of life expressed as percentage deviation from the 1919–28 mean, stood at the maximum of 12.8 percent above average in 1916. Growth was 6.8 to 11.7 percent above average during the next 6 years, 1917–22, but dropped rapidly from 9.2 percent in 1922 to 1.0 in 1923 and −14.2 percent in 1924. An improvement to −4.0 percent in 1925 was followed by another drop to −11.3 in 1926. Improvements in both 1927 and 1928 brought growth slightly above average (0.2 percent) in the latter year but another sharp decline occurred in 1929 (to −11.7 percent).

15. The first-year calculated increments of growth in weight were small (less than 0.1 pound) for both sexes in both collecting periods. These increments increased to (with one irregularity) a maximum in the third to fifth year of life and thereafter exhibited a fairly consistent downward trend (not pronounced in the 1943 females). Times of attainment of the weight of 1 pound were for 1926–30 males—near end of fourth year; 1926–30 females—middle of fourth year; 1943 males—latter part of third year; 1943 females—past the middle of third year. Latest years for which data were available and corresponding calculated weights were for 1926–30 males—14 years, 3.05 pounds; 1926–30 females—15 years, 4.91 pounds; 1943 males—10 years, 4.00 pounds; 1943 females—13 years, 8.14 pounds.

16. Growth in weight (as estimated from data for both sexes and for all years of life) was at the maximum of 35.2 percent above the 1919–28 mean in 1916. During the next 6 years, 1917–22, the percentage ranged between 15.7 and 22.3. Sharp decreases carried the value from 21.3 percent above average in 1922 to 6.7 in 1923 and −10.2 in 1924. A slight recovery (to −7.6 percent) in 1925 was followed by further declines that carried to the minimum figure of −25.6 in 1927. An improvement to −18.4 in 1928 was followed by another drop to −23.8 in 1929.

17. Comparison of the growth in length of Saginaw Bay walleyes of the 1926–30 and 1943 collections with published records of growth of walleyes in Lake Erie and Lake of the Woods revealed only small differences in first-year growth among the four groups. In the later years of life the Saginaw Bay fish collected in 1943 enjoyed a substantial advantage over the other groups at all ages for which comparative data were available. The 1926–30 walleyes from Saginaw Bay were longer than Lake Erie walleyes in the second through the fourth year but were shorter than Lake Erie fish at the end of the fifth year. The length of the 1926–30 walleyes exceeded that of fish from Lake of the Woods in the second through the eighth year but was smaller at the end of the ninth.

18. The percentage of males exhibited a distinct tendency to decrease with increase in age both in the spawning-run samples of 1927 and 1929 and in the late-spring collections of 1929 and 1930. In the spawning-run collections the percentage of males was 56.9 in the combined age-groups IV to IX and 28.2 in age-groups X to XIV. The percentages for various combinations of age groups in the late-spring collections were for II–V, 53.9 percent; VI–VII, 40.0 percent; VIII–XV, 16.1 percent. A higher rate of exploitation of males than of females was suggested as an important cause of the decrease in the percentage of males with increase in age.

19. Males were more plentiful (58.0 percent) in the early part of the 1929 spawning season (April 4–7) than in the latter part (41.6 percent—April 13–23). The percentage of males decreased also during the late spring of 1930 (59.3 percent males for collections of April 30–May 17 and 42.4 percent for May 22–June 20). With a single exception, shifts in the sex ratio occurred in individual age groups as well as in all age groups combined.

20. Lengths at which 50 percent of the walleyes had reached sexual maturity were about 15½ inches for the males and 17 inches for the females.

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MORTALITY OF SALMON FINGERLINGS EXPOSED TO PULSATING DIRECT CURRENT

BY GERALD B. COLLINS, CHARLES D. VOLZ
AND PARKER S. TREFETHEN

FISHERY BULLETIN 92

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Influences of voltage gradient, current density, pulse frequency, and duration of exposure on the mortality of salmon fingerlings exposed to pulsating direct current were examined experimentally in relation to the length of fish, water temperature, and pulse duration, using a current of square-wave form.

The experiments indicated that mortality increased with an increase in voltage gradient, in current density, or in both. The effect of voltage gradient increased with the duration of exposure. The total voltage to which the fish were subjected (fish length × voltage gradient) was the effective factor in mortality, rather than the voltage gradient, and the effect of total voltage on mortality was actually greater on shorter fish when the exposure was only 30 seconds. Pulse duration was not a lethal factor, and there was no direct relation between mortality and the total energy applied per unit of time. Under the conditions of these experiments, mortality increased with the pulse frequency, and the effect of pulse frequency on mortality increased with the length of the fish and the duration of exposure.

The mortality of the fingerlings exposed to pulsating d. c. increased with the duration of exposure, and the effect of duration of exposure increased with the length of the fingerlings. Mortality increased with the water temperature, and the effect of water temperature on mortality increased with the duration of exposure. The effect of water temperature on mortality was greater on fish of greater length.

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By GERALD B. COLLINS, CHARLES D. VOLZ, and PARKER S. TREFETHEN, *Fishery Research Biologists*

HISTORICAL BACKGROUND

Protection of salmon fingerlings on their downstream migrations is one of the major problems to be solved if the salmon fishery of the Pacific Northwest is to be maintained at its present level. Water resources are being developed for power, irrigation, navigation, and flood control at a rapidly accelerating pace, and the cumulative effect of many dams and water diversions seriously threatens this important natural food resource.

Mechanical screening is used at some of the smaller installations to prevent fingerlings from being swept into turbine intakes or into water diversions, but it is expensive to install and difficult to maintain. At larger dams, where huge volumes of water are involved, mechanical screens are generally considered impractical.

Electric screens have been in use for more than 30 years, with most applications endeavoring to establish an electrical field as a barrier or "fence" to prevent entrance of fish into a given area. These have generally been unsatisfactory with migrating fish, and particularly so with downstream-migrating salmon. The fingerlings seem unable to avoid the electrical field and are stunned or even killed rather than diverted.

Attention has been turned to the use of the directional properties of electric fields as a means of diverting the downstream migrants from hazardous areas. For many years it has been known that under certain conditions when fish are subjected to direct current (d. c.), the fish tend to move toward the positive electrode. Advances in the field of electronics now make it seem likely that this behavior can be put to practical use in controlling the movements of salmon fingerlings. Toward this end the United States Fish and Wildlife Service has initiated a program of research on electrical fish guiding which includes basic laboratory studies as well as large-scale field experiments. The material presented here is a report on one aspect of the research in progress.

A prerequisite to field experiments on electrical fish guiding is a knowledge of the electrical conditions that are injurious or lethal to fish. The range of electrical conditions to which fish can be subjected safely should be defined in advance to avoid the possibility of destroying large numbers of migrating fish during field tests.

Although the effect of electric current upon fish has been a subject of interest and research for at least 50 years, relatively little attention has been paid to its effect upon the mortality of fishes. Scheminzky (1924) outlined the reactions of fish subjected to electric current that occur at successively higher energy levels as follows: (1) The threshold of sensory recognition, (2) electrotaxis, (3) electronarcosis, and (4) at the highest energy level, death. Most of the research has been concerned with the responses at the three lower levels, and observations on mortality have been largely incidental.

Experimenting with electric fish screens, McMillan (1928) described tests using alternating current (a. c.), in which the mortality of salmon fingerlings increased with increases in voltage gradient and current density. He also pointed out the direct relation of mortality to the duration of exposure. Groody, Loukashkin, and Grant (1950), investigating electrotaxis of sardines, reported a relation between current density and mortality that depended upon the size of the fish and the duration of exposure, which relation they found to be "especially true when nonpulsating current was used." Similar observations by research workers studying the effects of electric fish screens and electric fish shockers were usually based on reactions to continuous d. c. or to a. c. In general, the observations on mortality which were made during investigations of recognition thresholds, electrotaxis, or electronarcosis, were inadequate for the purposes of the present study on electrical guiding of salmon

fingerlings. A more detailed understanding of the factors affecting the mortality of salmon fingerlings exposed to pulsating or interrupted d. c. was needed. In the laboratory experiments described in the following pages, the mortality of salmon fingerlings subjected to pulsating d. c. was measured in relation to factors such as the voltage gradient, current density, pulse frequency (pulse repetition rate), pulse duration (pulse width), water temperature, size of fish, and duration of exposure.

Charles Ellis, supervisor of hatcheries, State of Washington, and Lewis Garlick, regional supervisor, Branch of Game Fish and Hatcheries, Fish and Wildlife Service, made available the supply of salmon fingerlings used in this study. The cooperation of personnel at the Green River, Issaquah, and Samish hatcheries of the State of Washington and the Leavenworth hatchery of the Fish and Wildlife Service is gratefully acknowledged. Fishery aids Robert H. Lander and Gene D. Chard of the Fish and Wildlife Service carried out many of the tests and assisted in compiling the data and in preparing the material for publication. Professor Lorne Kersey, University of British Columbia, Professor George Hoard and Leon Verhoeven, University of Washington, and Harlan Holmes and Elizabeth Vaughan, Fish and Wildlife Service, critically reviewed the manuscript and offered many helpful suggestions.

MATERIALS AND METHODS

The experiments were conducted from May to August 1952, at the laboratory of the United States Fish and Wildlife Service in Seattle, Wash. Chinook fingerlings (*O. tshawytscha*) which were used in all tests (the one exception is noted) were transported in milk cans from the Washington State hatcheries at Green River, Issaquah, and Samish, and from the Federal hatchery at Leavenworth, Wash., and were placed in circular, wooden holding tanks 4 feet in diameter and 3 feet in depth. The maximum holding period at the laboratory before the fingerlings were used in the experiments was 4 days.

METHOD

A direct experimental approach was used in which two or three of the factors whose influence was to be examined were each varied while other factors were maintained relatively constant. The influence of voltage gradient, current density, pulse frequency, and duration of exposure upon the mortality of salmon fingerlings exposed to pulsating d. c. was examined directly in relation to the length of the fish, water temperature, and pulse duration. Fingerlings were held in uniform alinement with reference to the direction of the electrical field and were subjected for a specified time to a pulsating d. c. field with defined characteristics. The fingerlings were then held 1 hour after exposure, and the number of mortalities was recorded.

Mortality was interpreted to include any fish that had not completely recovered equilibrium within 1 hour after exposure to the electrical field. This arbitrary definition was based on exploratory tests in which 96 percent of the fish that had not recovered equilibrium within 1 hour after exposure died within the next 6 hours.

APPARATUS

The experiments were performed in a rectangular plastic tank (fig. 1) in which two flat, stainless-steel, screen electrodes were suspended perpendicular to the long axis. The electrodes exactly fit the inside dimensions of the tank to ensure a uniform electrical field. Vertical stalls, 2 cm. deep, 1.5 cm. wide, and 12 cm. long, made of thin plastic were placed between the electrodes, parallel to the long axis of the tank, to keep the fish in alinement parallel to the field. In the tests in which fish were alined across the field, stalls made of plastic screening were used. Plastic screening at the end of the stalls and a plastic cover on the top prevented the fingerlings from jumping out when electric current was applied. The sides of the tank were marked in centimeter units for convenience in establishing the distance between the electrodes.

Throughout the experiments, a current of square-wave form was used (fig. 2). The pulsating, or interrupted, d. c. was supplied by a specially constructed square-wave generator (fig. 3) which was made up of seven units. Unit 1, the pulse-rate frequency generator, used a gas triode (6D4) as a relaxation oscillator, producing a saw-tooth wave of variable frequency (2 to 15 pulses a second.) The flyback of the saw-tooth was differentiated by an RC network, and the negative pulses produced were amplified and inverted by a pentode (6AC7) pulse amplifier, unit 2. The

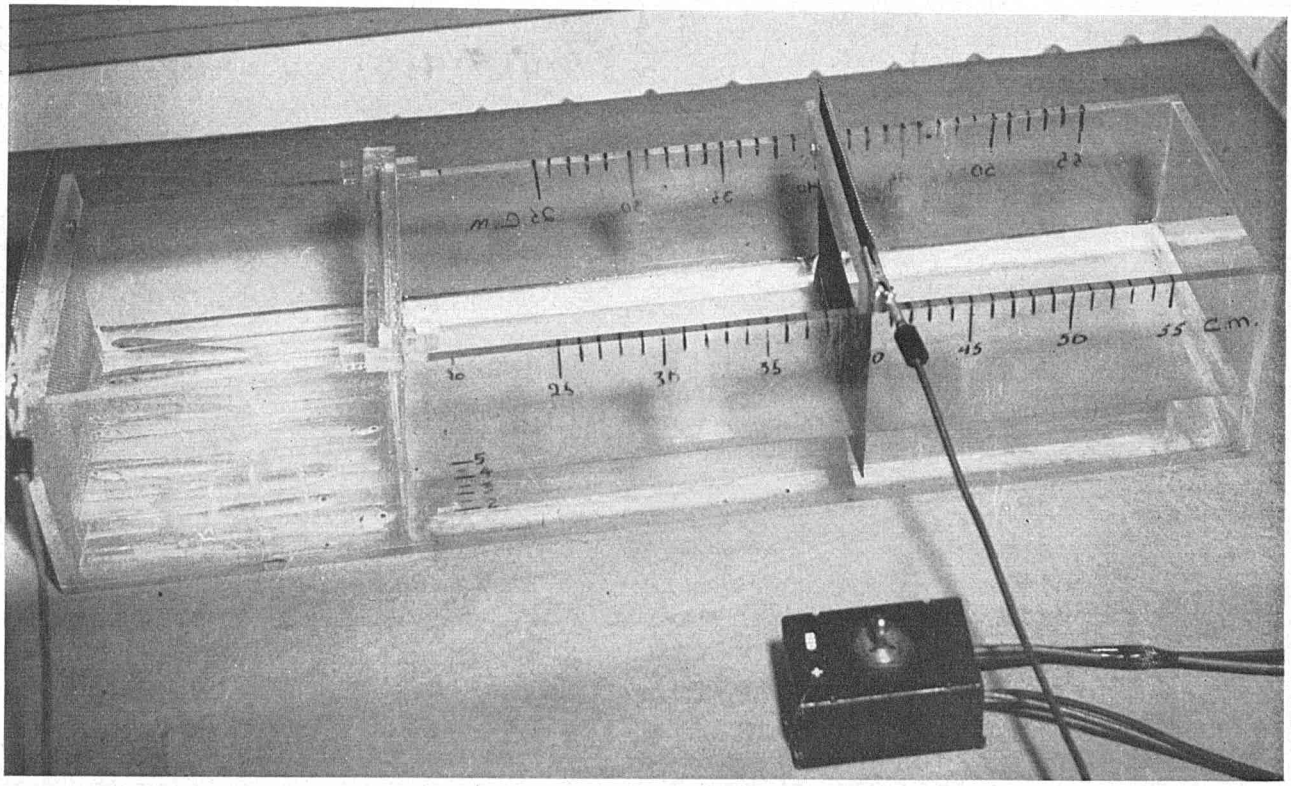

FIGURE 1.—Experimental tank, 60 cm. x 15 cm. x 11 cm.

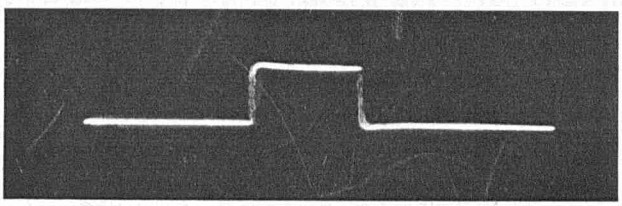

FIGURE 2.—Photograph of wave form on oscilloscope.

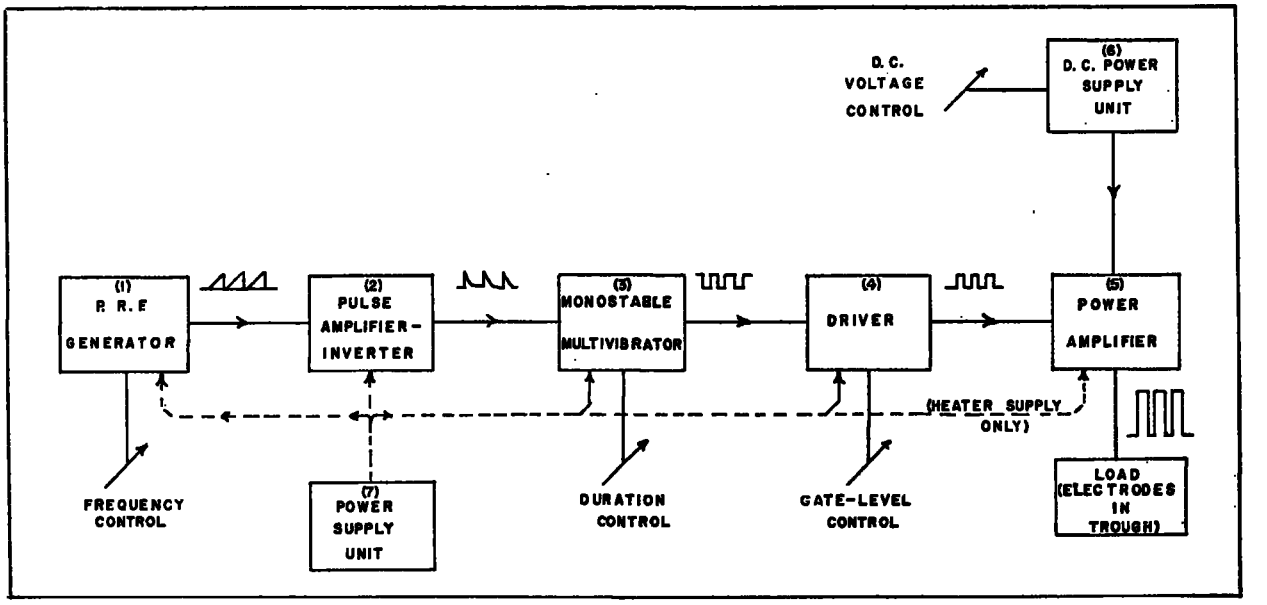

FIGURE 3.—Block diagram of square-wave generator.

positive pulses from unit 2 triggered unit 3, two dual triodes (6SN7) as a monostable multivibrator with a variable period of 5 to 300 milliseconds, which controlled the duration of the pulse. The negative square wave from unit 3 controlled the power pentode (6L6) driver stage, which inverted the pulse to produce a positive square wave to drive the power amplifier (unit 5), two dual triodes (6AS7G). The gate-level control on stage 4 controlled the cutoff bias of the power-amplifier stage and was used as a zero-set and fine-voltage control for the output. The plate supply for the power amplifier contained two mercury-vapor rectifiers (872–A). The primary voltage of the plate transformer was controlled to provide output-voltage control, variable from 0 to 600 volts, at a maximum drain of 1.25 amperes. The square-wave output of unit 5 was taken across a resistor in the cathode returns of the 6AS7G tubes. Plate, bias, and heater voltages were supplied by a separate power unit (7), which had power-rectifier (5V4G), bias-rectifier (6X4), and voltage-regulator tubes (2–OD3, 1–OB3, and 1–OA2), plus the necessary transformers, chokes, capacitors, and resistors.

MEASUREMENTS

All measurements of electrical characteristics were accurate to within 10 percent and most to within 5 percent.

Voltage was measured with a calibrated cathode-ray oscilloscope. Voltage gradient was calculated from the distance between electrodes and the total voltage across the electrodes, since measurements made with the plastic stalls and screens in place showed the field to be uniform within the limits of the measuring equipment.

The specific resistance of the water was measured by a conductivity bridge. Current density was computed from the resistance of the water and the voltage gradient. Current-density computations were checked against measurements made by reading voltage across a precision resistor (1 percent).

Pulse frequency was calibrated by a low-frequency oscillator and checked frequently by means of a stop watch at low rates, and by visual oscilloscope comparison with 60-cycle sine waves at rates of from 5 to 16 pulses a second. Frequency stability was within 1 percent.

Pulse duration was calibrated against a low-frequency oscillator by use of a direct-coupled electronic switch. The accuracy and stability was 1.0 millisecond.

Fish lengths are total lengths from tips of snouts to extreme ends of tails.

PROCEDURE

Fingerlings, in groups of 10, were placed in the stalls in the area between the electrodes in the

plastic tank. No attempt was made to head the fish toward either electrode after exploratory experiments failed to reveal any significant difference in mortality between fingerlings headed toward the positive electrode and fingerlings facing away from it. A cover was placed over the top to prevent the fish from jumping out, then the electric current was turned on, and the duration of exposure was timed by a stop watch. Immediately after exposure the fingerlings were placed in aerated glass bowls where they were held for 1 hour. At the end of that time the dead fish and those that had not completely recovered equilibrium were removed, and their number and lengths recorded. The number and lengths of the remaining fish were also recorded.

During most of the tests, to minimize the need for adjustment to new water conditions, the water used in the experimental tank and in the aerated bowls for holding the fish after exposure was taken from the large holding tank when the fish were brought into the laboratory. The temperature and resistance of the water were usually measured every fourth exposure; however, during tests examining the effect of current density, the resistance of the water was measured before each exposure and the water was adjusted to the desired resistance by the addition of distilled water or an NaCl solution.

During tests examining the influence of water temperature, fingerlings were placed in large aerated containers, and temperatures were gradually raised or lowered at a rate of change less than 2° C. per hour until the desired temperature was reached. The fish were exposed to the electrical field at the desired temperature and were held for 1 hour after exposure at the same temperature.

Throughout these experiments fingerlings were exposed to an electrical field only once (a fish surviving one test was never used in another) to avoid any possible effect due to conditioning.

CONTROLS

To ensure that mortality was not the result of handling, confinement, temperature change, et cetera, with each new supply of fishes, a control group was subjected to the same treatment as the experimental fish with the exception that power was not turned on. Among 2,800 fingerlings used as controls the mortality was only 0.5 percent.

EXPERIMENTAL LIMITATIONS

Lack of control over water temperatures in holding tanks and water sources for experiments (except in the circumstances described in Procedure) resulted in experiments being carried out under a rather wide range of temperatures. The experiments began in May and continued until August with water temperatures increasing from 10° to 19° C.

The procedure followed in the experiments tended to minimize the effect of variation of temperature upon the slope of the curves shown. Fingerlings in groups of 10 were subjected to a complete range of the variables being examined each time the tests were run. The entire experiment was then repeated several times at a later date until the numbers of fish were sufficiently large. Thus one part of the curve was not determined at one temperature and another part at a different temperature. The curves represent the effect at the median temperature of the range shown.

The experiments began with fingerlings in the smaller size ranges, and as the season progressed the sizes increased. Usually only a limited range of length was available at one time. The fish were taken from four different hatcheries throughout a period of 4 months. They were transported and held under a variety of conditions, and undoubtedly some groups were in better physical condition than others. An attempt was made to expose the fish from each group to the entire range of all the variables being examined. For the experiments in which large numbers of fish were used, the data include the reactions of several groups of fish, and the curve represents the effect on fish of the average physical condition.

Fluctuations in water temperature and the physical condition of the fish are probably responsible for some of the scatter shown in the data. However, the validity of relations shown by the compiled data was verified by examining the same relations in single tests with one group of fish under a single set of conditions. Examples of this method of verification are shown by the circled data in figure 12 and the insert in figure 14.

Another factor that must be considered is the distortion of the lines of current flow due to the difference between the resistance of the fish and resistance of the water. The voltage gradients and current densities shown in the graphs are

those existing in the water before the fish were placed in it and are not the voltage gradients and current densities created within the fish. Measurements made during those experiments in which there would be a maximum distortion of the field (minimum electrode spacing, large fish, and water of high resistance) indicated that the maximum error due to distortion of the field

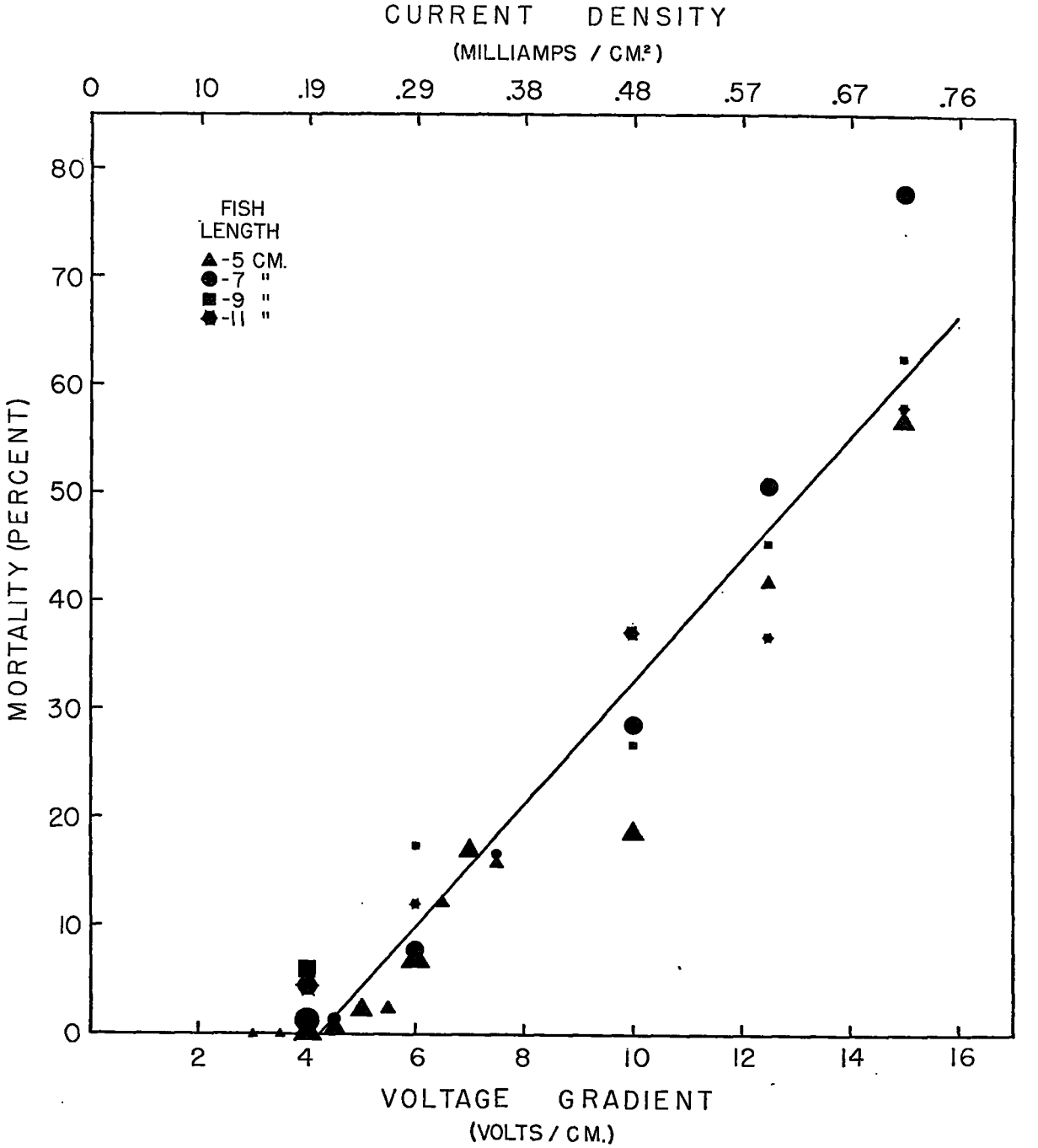

FIGURE 4.—Combined effects of voltage gradient and current density in relation to fish length upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 2 pulses/sec., pulse duration 20 millisecs., temperature range 10.0° to 19.9° C., duration of exposure 30 seconds. Sizes of symbols correspond to fish number categories: 10–49, 50–99, 100–199, and 200–227.

was less than 10 percent. For example, measurements of the total current across the electrodes made with no fish in the apparatus, with one fish in each stall, and with two fish in each stall, with electrode spacings varying from 20 cm. to 50 cm. at a gradient of 1 volt/cm., and a water resistance of 16,000 ohms/cm.[3], were all in agreement within 10 percent. It is probable that some of the scatter in the data may be due to the distortion of the electrical field, or perhaps to electrolysis; however, it is unlikely that the errors are great enough to seriously affect the relations shown.

GRAPHS AND COMPUTATIONS

The curves shown in figures 4 to 14 were calculated by the method of least squares weighted to the number of fish at each point and include all data with mortality values greater than zero and less than 80 percent. Some of the relations shown would probably be best described by sigmoid curves if the data were more complete, but for simplification straight lines of regression have been used to describe them.

The fish lengths indicated in the graphs are the midvalues of 2 cm. groupings (e. g., 5 cm. includes lengths from 4 cm. to 5.9 cm.).

EXPERIMENTS

VOLTAGE GRADIENT AND CURRENT DENSITY

To examine the combined effects of voltage gradient and current density in relation to fish length upon the mortality of salmon fingerlings exposed to pulsating d. c., a series of experiments was run in which chinook fingerlings of different sizes were subjected to a pulsating field at various levels of voltage gradient and current density. During each of these experiments, water temperature, water resistance, pulse frequency, pulse duration, and duration of exposure were maintained constant. The results of the tests are summarized in figure 4, and the numerical data are given in table 1.

The data indicate that above a certain threshold, mortality increases in proportion to each increase in voltage gradient and current density. There is no indication of a relation between the length of the fingerlings and the combined effect of voltage gradient and current density upon mortality.

The situation in the experiments described above was comparable to what would exist in field applications of d. c. for guiding fish, in that the resistance of the water remained constant while the current density changed as the voltage gradient was varied. To complete the study, it was decided to examine independently the effect of current density upon mortality of fingerlings exposed to pulsating d. c. A series of experiments was run in which fingerlings of different lengths were exposed at various levels of current density while the voltage gradient was held constant. This was achieved by modifying the resistance of the water with NaCl solution. Water temperatures, pulse frequency, pulse duration, and duration of exposure were also held constant during each of these experiments. The tests are summarized in figure 5 and the numerical data are shown in table 2.

TABLE 1.—*Combined effects of voltage gradient and current density in relation to fish length on mortality of salmon fingerlings*

	Fish length of—											
	4 to 5.9 cm.			6 to 7.9 cm.			8 to 9.9 cm.			10 to 11.9 cm.		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
3 volts/cm	24	0	0									
3.5 volts/cm	12	0	0									
4 volts/cm	227	1	.4	241	3	1.2	102	6	5.9	125	6	4.8
4.5 volts/cm	137	1	.7	69	1	1.4						
5 volts/cm	123	3	2.4									
5.5 volts/cm	79	2	2.5									
6 volts/cm	200	14	7.0	130	10	7.7	23	4	17.4	25	3	12.0
6.5 volts/cm	89	11	12.4									
7 volts/cm	100	17	17.0									
7.5 volts/cm	88	14	15.9	12	2	16.7						
10 volts/cm	167	31	18.6	154	44	28.6	30	8	26.7	86	32	37.2
12.5 volts/cm	91	38	41.8	148	75	50.7	22	10	45.4	19	7	36.8
15 volts/cm	104	59	56.8	135	105	77.8	24	15	62.5	14	8	57.0

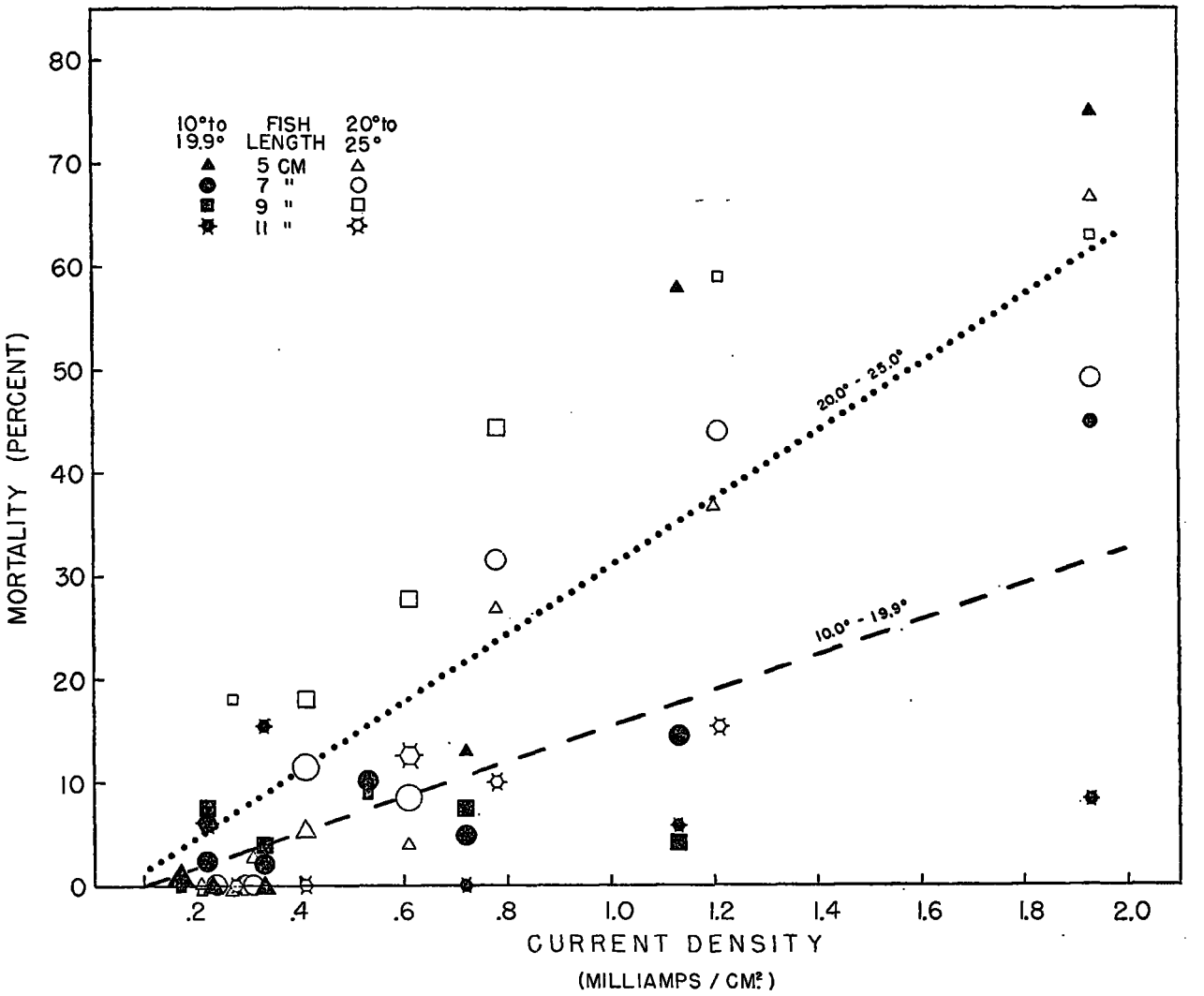

FIGURE 5.—Effect of current density in relation to fish length and water temperature upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 4 volts/cm., 2 pulses/sec., pulse duration 20 milliseconds., duration of exposure 30 seconds. Sizes of symbols correspond to fish number categories: 28–74, 75–149, and 150–443.

TABLE 2.—*Effect of current density in relation to fish length and water temperature on mortality of salmon fingerlings*

Current density	Temperature (° C.)	Fish length of— 4 to 5.9 cm.			6 to 7.9 cm.			8 to 9.9 cm.			10 to 11.9 cm.		
		Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
0.17 milliamps/cm²	10.0–19.9	157	1	0.6				11	0	0			
0.21 milliamps/cm²	20.0–25.0	17	0	0	66	0	0	10	0	0			
0.22 milliamps/cm²	10.0–19.9	53	0	0	89	2	2.2	81	6	7.3	100	6	6.0
0.27 milliamps/cm²	20.0–25.0	15	0	0	58	0	0	28	5	17.9	14	0	0
0.31 milliamps/cm²	20.0–25.0	39	1	2.6	44	0	0						
0.33 milliamps/cm²	10.0–19.9	68	0	0	111	2	1.8	77	3	3.9	13	2	15.4
0.41 milliamps/cm²	20.0–25.0	96	5	5.2	297	34	11.5	50	9	18.0	11	0	0
0.53 milliamps/cm²	10.0–19.9				89	9	10.1	34	3	8.8			
0.61 milliamps/cm²	20.0–25.0	25	1	4.0	156	13	8.3	54	15	27.8	48	6	12.5
0.72 milliamps/cm²	10.0–19.9	23	3	13.0	83	4	4.8	81	6	7.4	28	0	0
0.78 milliamps/cm²	20.0–25.0	41	11	26.8	108	33	31.5	45	20	44.4	10	1	10.0
1.13 milliamps/cm²	10.0–19.9	19	11	57.8	69	10	14.5	120	5	4.2	34	2	5.9
1.21 milliamps/cm²	20.0–25.0	30	11	36.7	84	37	44.0	34	20	58.8	26	4	15.4
1.93 milliamps/cm²	10.0–19.9	20	15	75.0	20	9	45.0				12	1	8.3
1.93 milliamps/cm²	20.0–25.0	27	18	66.7	59	29	49.2	19	12	63.2			

The data, although there is considerable scatter, particularly where only small numbers of fish are used, show a pattern similar to that in the experiments in which both current density and voltage gradient were varied. Above a certain threshold mortality increased in proportion to the increase in current density, and there was no discernible relation between fish length and the effect of current density under the conditions of the experiments. The range of water temperatures in which the experiments were run was so great that the data were divided into two groups to reveal the influence of water temperature upon the mortality of fingerlings exposed to pulsating d. c.

The effect of voltage gradient in relation to current density was calculated (fig. 6) from the combined effects of voltage gradient and current density (fig. 4) and from the effect of current density alone (fig. 5). Mortality is shown to be proportional to the voltage gradient. The relative influence of voltage gradient and current density under the experimental conditions is illustrated by the insert in figure 6.

During the tests, the fingerlings were held in uniform alinement with the direction of the electrical field (see Procedure). This subjected the longer fish to a greater difference in potential. When the data shown in figure 4 are replotted in terms of the total voltage to which the fish were subjected (fish length × voltage gradient), they

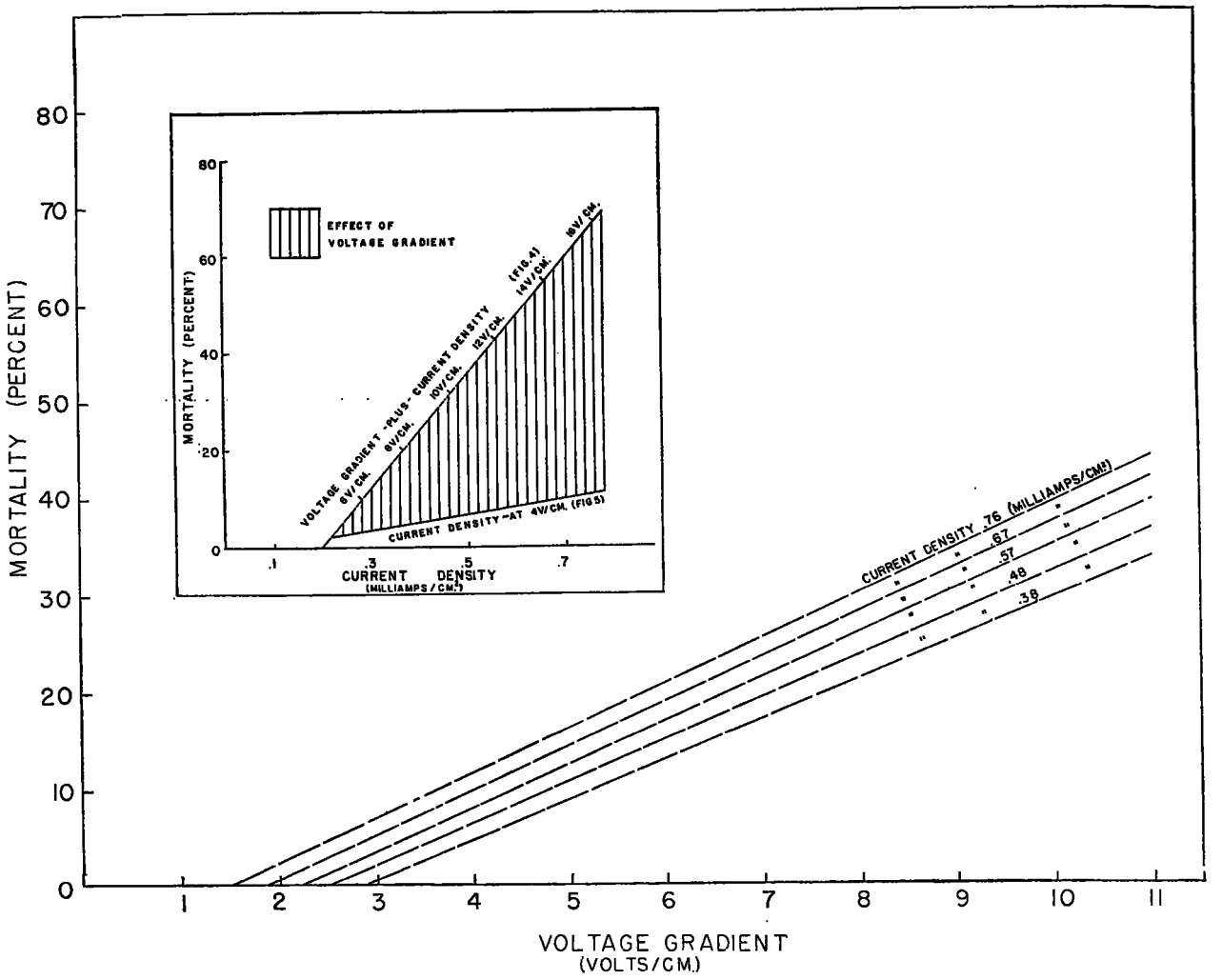

FIGURE 6.—Effect of voltage gradient in relation to current density upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. calculated (see insert) from the combined effects of voltage gradient and current density (fig. 4) and the effect of current density (fig. 5).

indicate that the shorter fish are actually affected to a greater degree (fig. 7).

To determine whether the voltage gradient or the total voltage to which the fish were subjected was the effective factor, a group of tests was made with silver salmon (*O. kisutch*) in which the mortality of fingerlings alined parallel to the electrical field was compared with the mortality of fingerlings alined perpendicular to the field. Evidence (table 3) that the total voltage to which the fish were subjected is the effective factor in mortality was very conclusive. Electrical conditions that proved fatal to 77.6 percent of the fingerlings alined parallel to the field had no discernible injurious effect on fingerlings alined perpendicular to the field.

Experiments made to examine the effect of duration of exposure upon fingerlings subjected to pulsating d. c. in relation to the combined influence of voltage gradient and current density are summarized in figure 8, and the numerical data are shown in table 4. During these tests, pulse frequency, pulse duration, water temperature, water resistance, and fish length were maintained constant. Similar experiments examining the effect of duration of exposure in relation to current density alone are shown in figure 9, and the numerical data are listed in table 5. In these tests, pulse frequency, pulse duration, voltage gradient, water temperature, and fish size were held constant while the resistance of the water was modified.

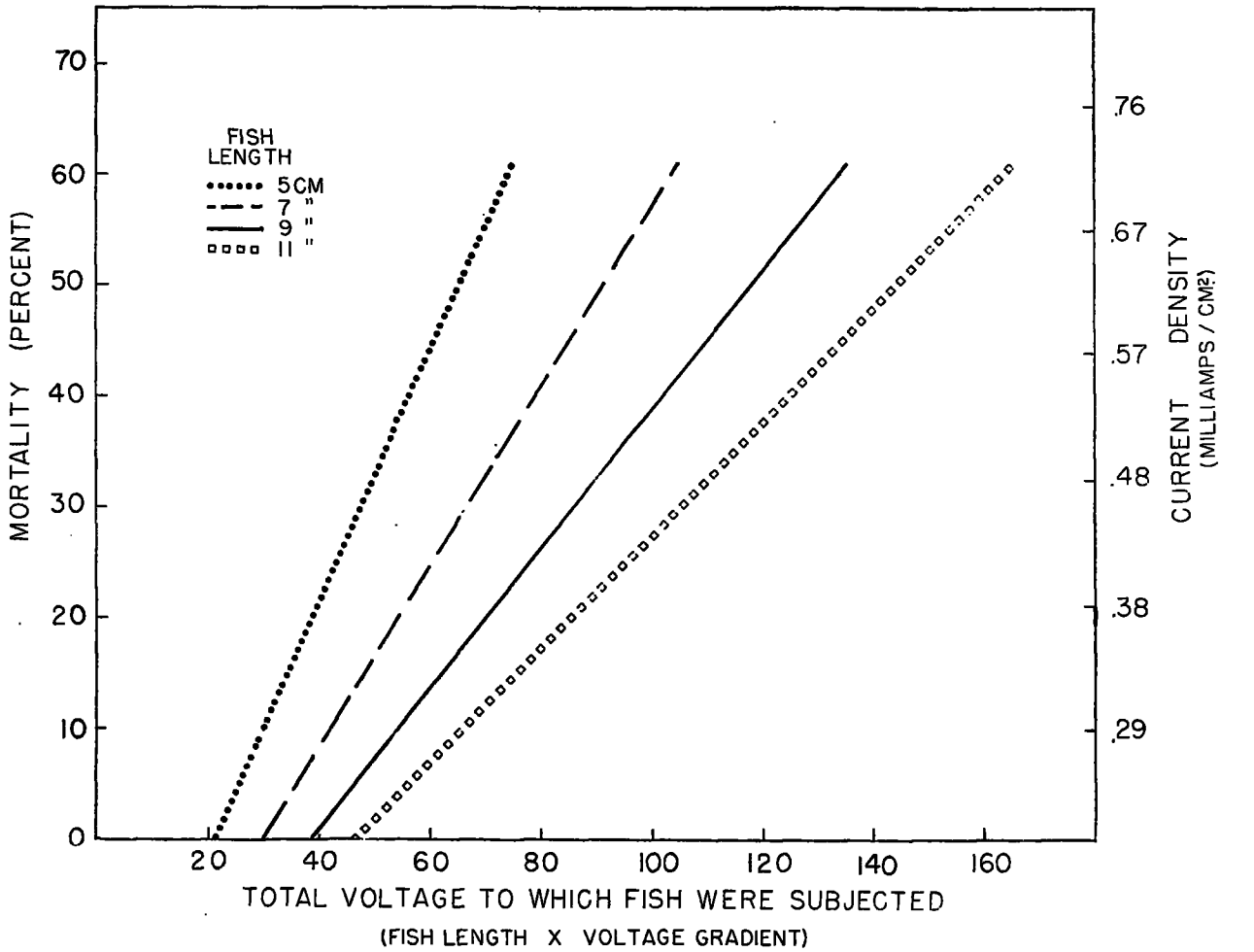

FIGURE 7.—Effect of the total voltage to which the fish were subjected in relation to fish length and current density upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. (fig. 4 replotted in terms of the total voltage to which fish were subjected).

TABLE 3.—*Relative effects of voltage gradient and total voltage to which fish were subjected on mortality of salmon fingerlings* (Oncorhynchus kisutch) *exposed to pulsating d. c.*

[Tests run at 8 pulses/sec., pulse duration 40 milliseconds, water temperature 16.5° C., duration of exposure 1 minute; fish length, 7 cm.]

Fish alinement relative to electrical field	Voltage gradient (volts/cm.)	Total voltage to which fish were subjected	Number exposed	Number dead	Mortality (percent)
Parallel	6	[1] 42	107	83	77.6
Perpendicular	6	[2] 6	105	0	0

[1] Fish length × voltage gradient.
[2] Fish width × voltage gradient.

The results of both groups of experiments indicate, as would be expected, that the mortality of fingerlings exposed to pulsating d. c. is proportional to the duration of exposure. The results further suggest that the effect of voltage gradient increases with the duration of exposure while the effect of current density may actually decrease with an increase in duration of exposure. However, because of the scatter in the data, additional evidence should be obtained to substantiate this latter conclusion.

TABLE 4.—*Effect of duration of exposure in relation to the combined effects of voltage gradient and current density on mortality of salmon fingerlings*

Duration of exposure	Fish exposed to—								
	1 v./cm. and 0.05 ma/cm.[2]			2 v./cm. and 0.10 ma/cm.[2]			4 v./cm. and 0.19 ma./cm.[2]		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
0.5 min							241	3	1.2
1 min							198	9	4.5
2 min							179	8	4.5
3 min				31	0	0	84	7	8.3
4 min				16	0	0			
5 min				63	4	6.4	98	12	12.3
6 min							99	17	17.2
7 min							99	19	19.2
7.5 min				52	6	11.5			
8 min							142	38	26.8
9 min							129	41	31.8
10 min				37	12	32.4	125	65	52.0
11 min							23	9	39.1
12 min							25	12	48.0
13 min							17	13	76.5
15 min	48	1	2.1	20	6	30.0			
20 min	117	20	17.1						

TABLE 5.—*Effect of duration of exposure in relation to current density on mortality of salmon fingerlings*

Duration of exposure	Fish exposed to—					
	0.10 ma./cm.[2]			0.17 ma./cm.[2]		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
2 min				46	2	4.4
3 min	58	2	3.5	49	3	6.1
3.5 min	45	1	2.2			
4 min	27	3	11.1	16	7	43.6
5 min	67	9	13.2	55	15	36.8
7.5 min	65	21	32.2	19	11	58.0
10 min	27	16	59.3	25	12	48.0

PULSE FREQUENCY

The effect of pulse frequency in relation to fish length upon mortality of fingerlings exposed to pulsating d. c. was examined experimentally by subjecting fingerlings of different lengths to a range of pulse frequencies while the voltage gradient, current density, pulse duration, water temperature, and the duration of exposure remained constant.

The data summarized in figure 10 (numerical data shown in table 6) reveal that the mortality

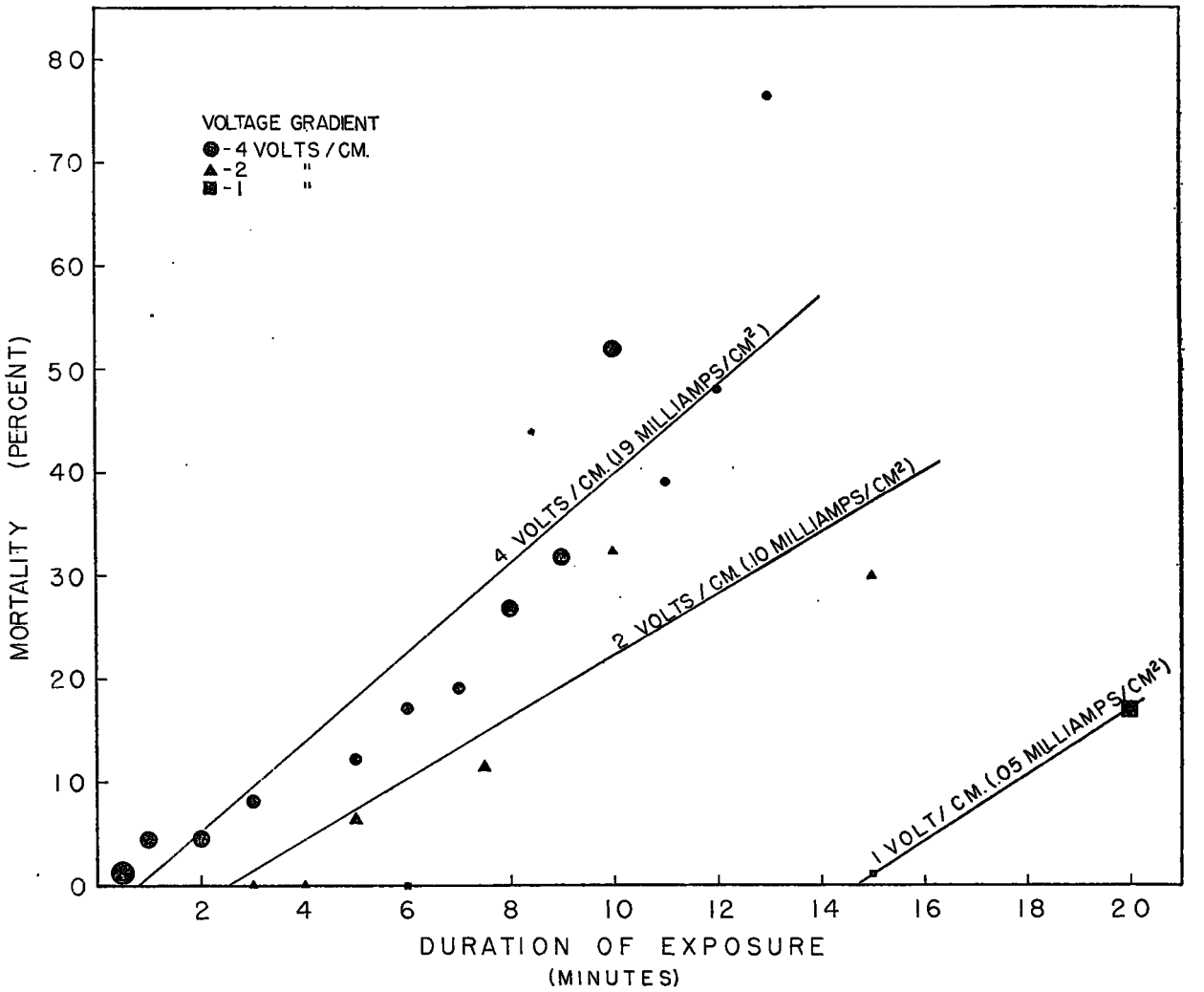

FIGURE 8.—Effect of duration of exposure in relation to the combined effects of voltage gradient and current density upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 2 pulses/sec., pulse duration 20 millisecs., temperature 10.0° to 19.9° C., fish length 7 cm. Sizes of symbols correspond to fish number categories: 17–49, 50–99, 100–199 and 200–241.

of salmon fingerlings exposed to pulsating d. c. increases with the pulse frequency and that the effect of pulse frequency upon mortality increases with the length of the fingerlings.

The relation of pulse frequency to the effect of duration of exposure was explored in the group of tests summarized in figure 11 (numerical data are shown in table 7). Fingerlings were exposed to a pulsating d. c. field for various lengths of time at two different pulse frequencies while the voltage gradient, current density, pulse duration, and water temperature were held constant. The effect of pulse frequency upon mortality was found to increase with the duration of exposure.

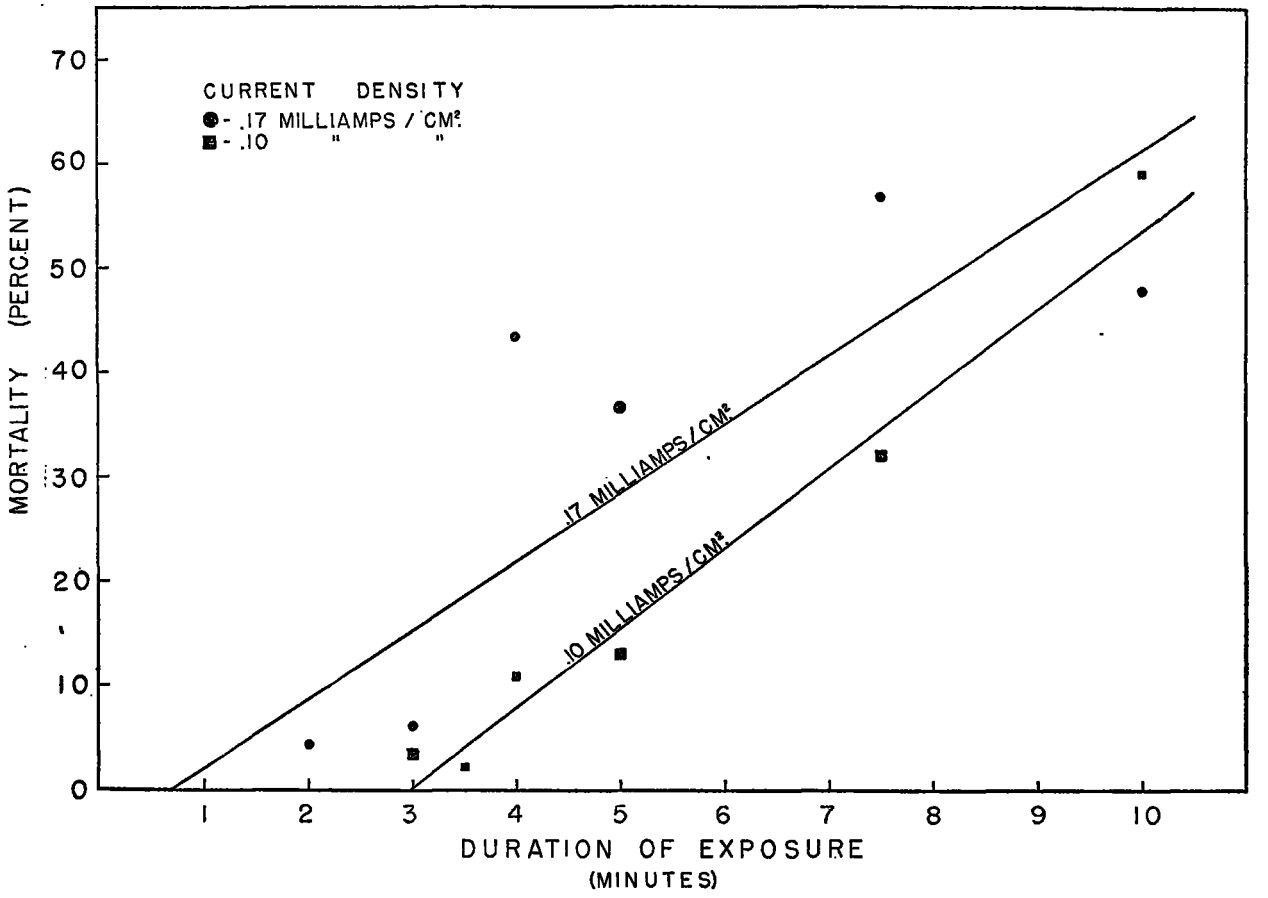

FIGURE 9.—Effect of duration of exposure in relation to current density upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 2 volts/cm., 2 pulses/sec., pulse duration 20 millisecs., temperature range 10.0° to 19.9° C., fish length cm. Sizes of symbols correspond to fish number categories: 16–49 and 50–65.

PULSE DURATION

To study the relation of pulse duration to the effect of duration of exposure upon the mortality of fingerlings exposed to pulsating d. c., tests were run in which fingerlings were subjected to different pulse durations while the voltage gradient and current density, pulse frequency, water temperature, and fish length were held constant. On their face, the data, graphically shown in figure 12 and numerically presented in table 8, suggest that pulses of long duration may be less injurious than pulses of short duration.

Since the tests with the 20-millisecond pulse duration and the tests with the 80-millisecond pulse duration were made several days apart and with fish from two sources, an experimental check was made (see circle, fig. 12) testing fish from only one source on the same day. Fingerlings used in this experimental check were from the group of fish used in the 80-millisecond pulse-duration tests. The results of the check fall along the trend of the 80-millisecond pulse-duration tests, indicating that the difference shown between the reaction to the 20-millisecond and to the 80-millisecond pulse duration is probably due to

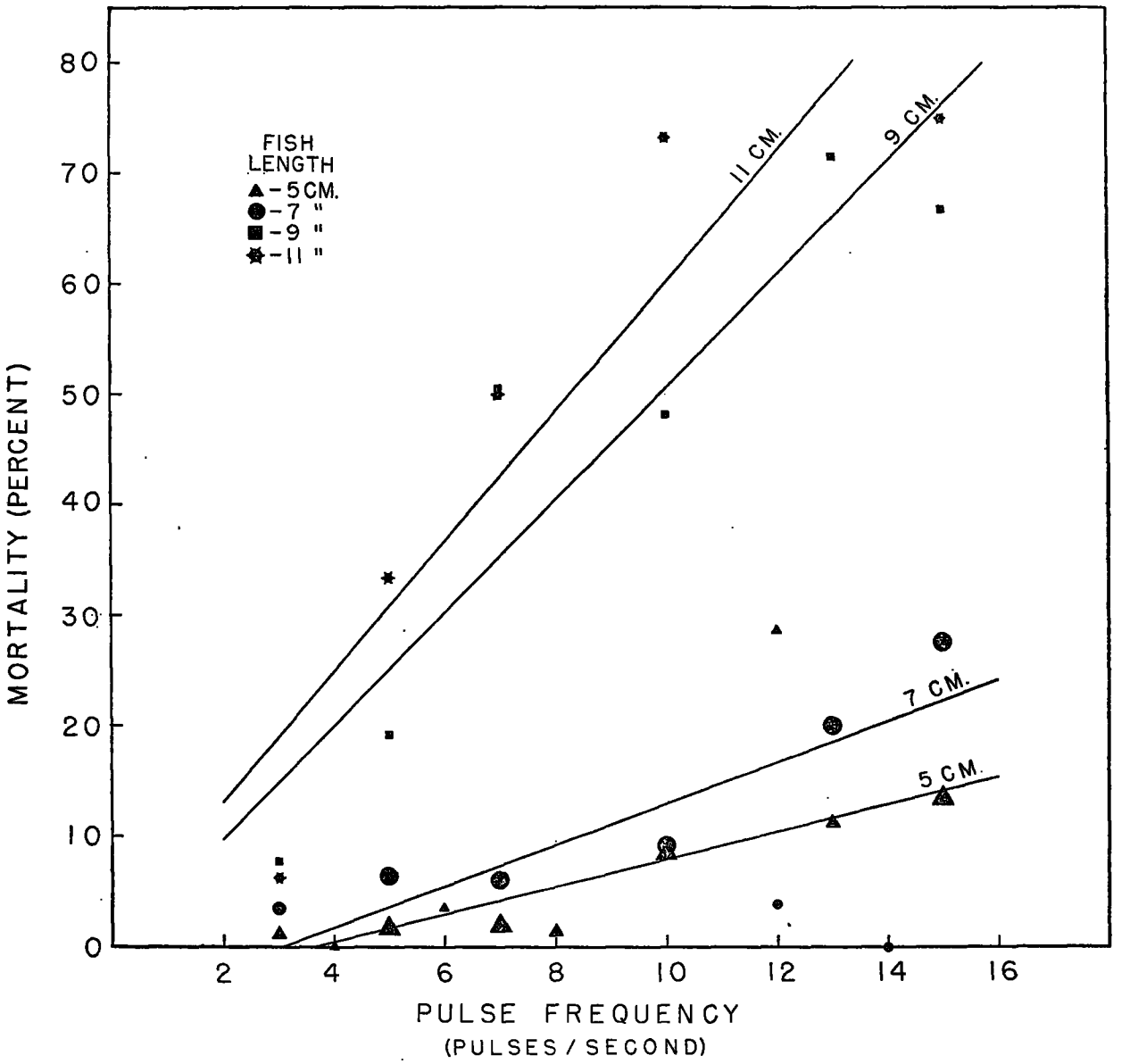

FIGURE 10.—Effect of pulse frequency in relation to fish length upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 4 volts/cm., current density range 0.15 to 0.27 milliamps./cm.^{2}, pulse duration 20 millisecs., temperature range 10.0° to 19.9° C., duration of exposure 30 seconds. Sizes of symbols correspond to fish number categories: 10–49, 50–99, and 100–199.

TABLE 6.—*Effect of pulse frequency in relation to fish length on mortality of salmon fingerlings*

Pulse frequency	Fish length of—											
	4 to 5.9 cm.			6 to 7.9 cm.			8 to 9.9 cm.			10 to 11.9 cm		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
3 pulses/sec	92	1	1.1	59	2	3.4	26	2	7.7	16	1	6.3
4 pulses/sec	10	0	0									
5 pulses/sec	187	3	1.6	125	8	6.4	26	5	19.2	12	4	33.3
6 pulses/sec	29	1	3.5									
7 pulses/sec	107	2	1.8	133	8	6.0	30	15	50.0	18	9	50.0
8 pulses/sec	77	1	1.3									
10 pulses/sec	199	17	8.5	158	14	8.9	27	13	48.2	15	11	73.3
12 pulses/sec	14	4	28.6	26	1	3.8						
13 pulses/sec	98	11	11.2	170	34	20.0	35	25	71.4			
14 pulses/sec				24	0	0						
15 pulses/sec	178	24	13.5	170	47	27.6	27	18	66.7	12	9	75.0

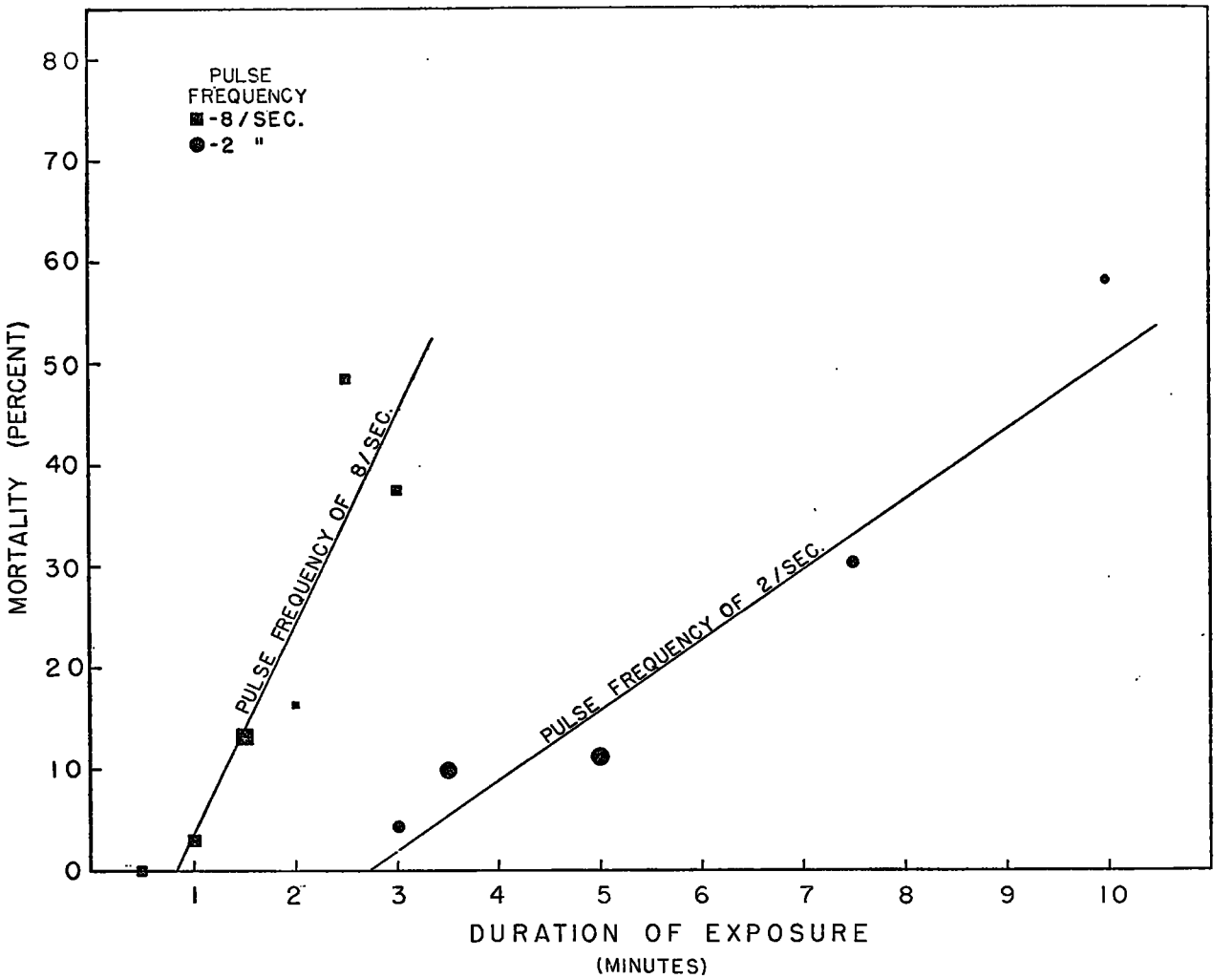

FIGURE 11.—Effect of duration of exposure in relation to pulse frequency upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 2 volts/cm., current density range 0.08 to 0.13 milliamps./cm.^{2}, pulse duration 20 millisecs., temperature range 12.0° to 19.9° C., fish length 9 cm. Sizes of symbols correspond to fish number categories: 27–49, 50–99, and 100–111.

TABLE 7.—*Effect of duration of exposure in relation to pulse frequency on mortality of salmon fingerlings*

Duration of exposure	Fish exposed to pulse frequency of—					
	2 pulses/sec.			8 pulses/sec.		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
0.5 min				71	0	0
1.0 min				65	2	3.1
1.5 min				105	14	13.3
2.0 min				49	8	16.3
2.5 min				58	28	48.3
3.0 min	69	3	4.4	64	24	37.5
3.5 min	101	10	9.9			
5.0 min	171	19	11.1			
7.5 min	69	21	30.4			
10.0 min	36	21	58.3			

TABLE 8.—*Effect of duration of exposure in relation to pulse duration on mortality of salmon fingerlings*

Duration of exposure	Fish exposed to pulse duration of—					
	20 milliseconds			80 milliseconds		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
0.5 min	71	0	0			
1.0 min	14	0	0	50	2	4.0
1.5 min	56	11	19.6	49	5	10.1
2.0 min	46	8	17.4	48	7	14.6
2.5 min	58	28	48.2			
3.0 min	15	8	53.3	45	17	37.8

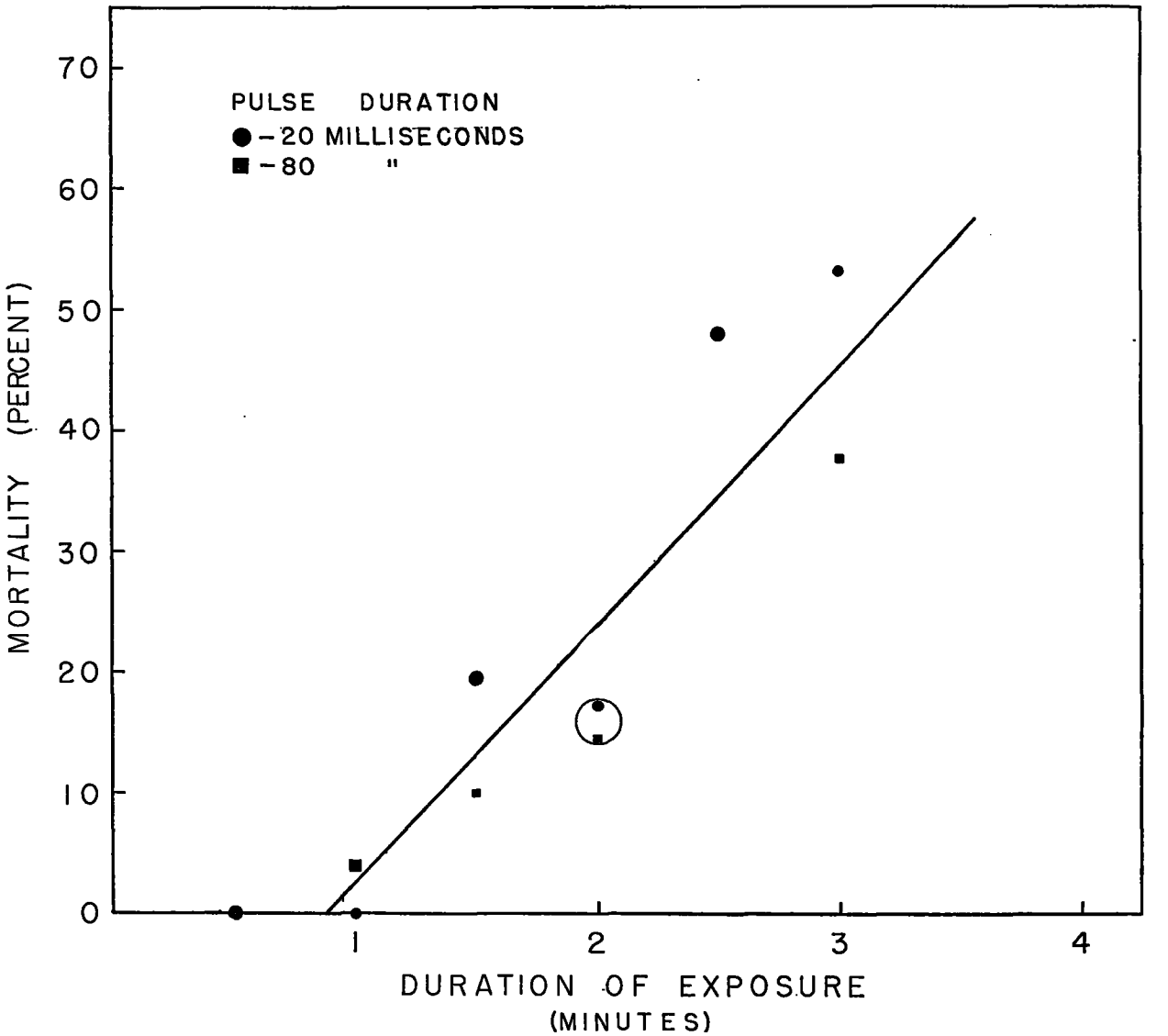

FIGURE 12.—Effect of duration of exposure in relation to pulse duration upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d.c. Tests run at 2 volts/cm., current density 0.10 milliamps./cm.², 8 pulses/sec., temperature range 10.0° to 16.0° C., fish length 9 cm. For explanation of circled data see text. Sizes of symbols correspond to fish number categories: 14–49 and 50–58.

variation in condition of the two groups of fish. Therefore, the data are interpreted (as shown in fig. 12) to mean that under the conditions of these experiments the pulse duration has no relation to the effect of the duration of exposure upon mortality of fingerlings exposed to pulsating d. c.

An examination of the data thus interpreted shows that the mortality of fingerlings exposed to a pulse duration of 20 milliseconds at a frequency of 8 pulses per second (power on 16 percent of the time) is equal to the mortality of fingerlings exposed under similar conditions to a pulse duration of 80 milliseconds at a frequency of 8 pulses per second (power on 64 percent of the time). It is

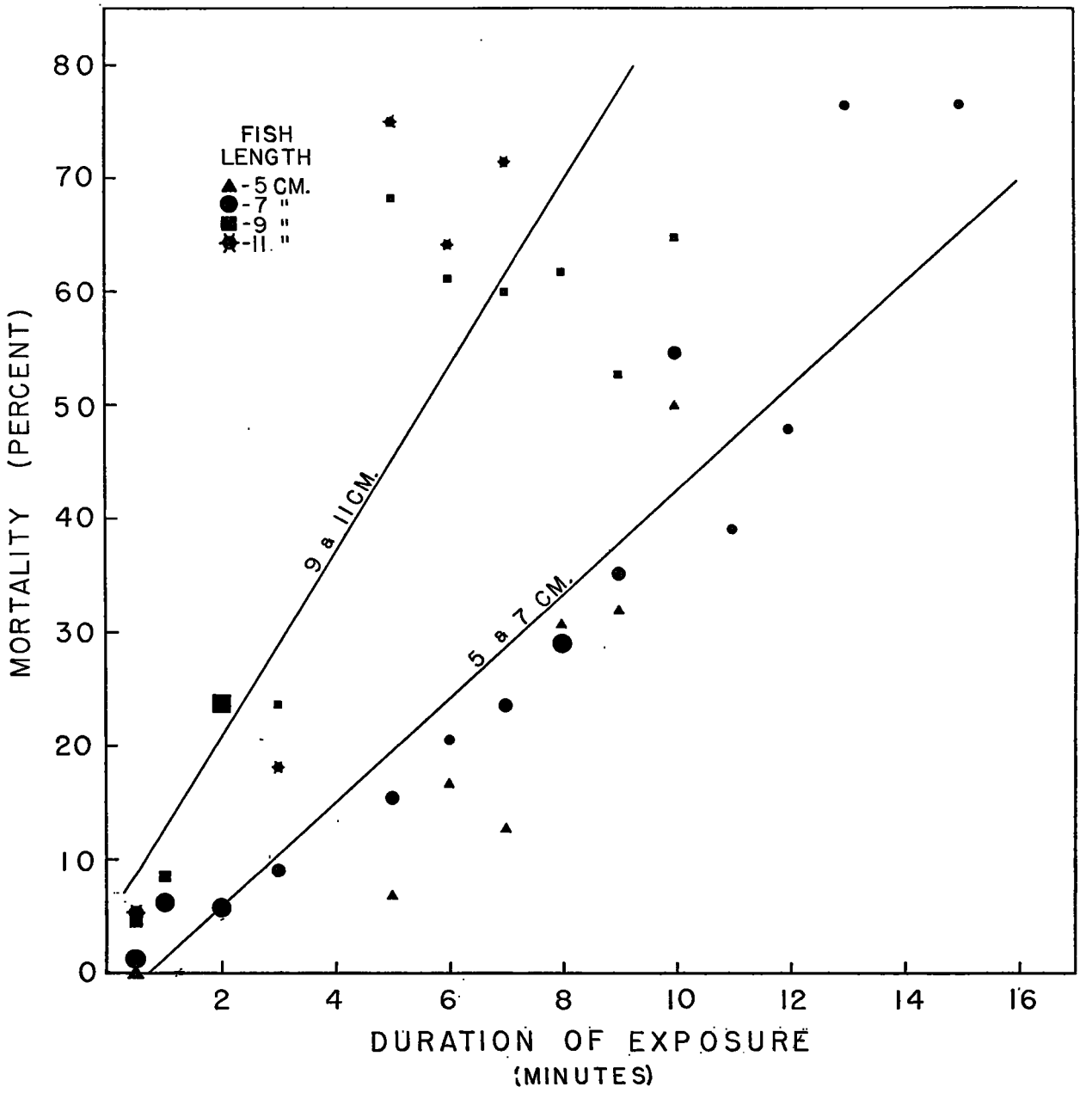

FIGURE 13.—Effect of duration of exposure in relation to fish length upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 4 volts/cm., current density range 0.14 to 0.27 milliamps./cm.^{2}, 2 pulses/sec., pulse duration 20 millisecs., temperature range 15.0° to 19.9° C. Sizes of symbols correspond to fish number categories: 11–49, 50–99, and 100–154.

TABLE 9.—*Effect of duration of exposure in relation to fish length on mortality of salmon fingerlings*

Duration of exposure	Fish length of—											
	4 to 5.9 cm.			6 to 7.9 cm.			8 to 9.9 cm.			10 to 11.9 cm.		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
0.5 min	92	0	0	154	2	1.3	65	3	4.6	56	3	5.4
1.0 min				126	8	6.3	93	8	8.5			
2.0 min				122	7	5.7	105	25	23.8			
3.0 min				77	7	9.1	21	5	23.8	11	2	18.2
4.0 min												
5.0 min	29	2	6.9	71	11	15.5	19	13	68.3	16	12	75.0
6.0 min	18	3	16.7	68	14	20.6	18	11	61.2	14	9	64.2
7.0 min	31	4	12.9	76	18	23.7	20	12	60.0	14	10	71.5
8.0 min	26	8	30.8	113	33	29.2	21	13	61.9			
9.0 min	25	8	32.0	99	35	35.3	17	9	52.9			
10.0 min	12	6	50.0	99	54	54.6	20	13	64.9			
11.0 min				23	9	39.1						
12.0 min				25	12	48.0						
13.0 min				17	13	76.5						
14.0 min												
15.0 min				17	13	76.5						

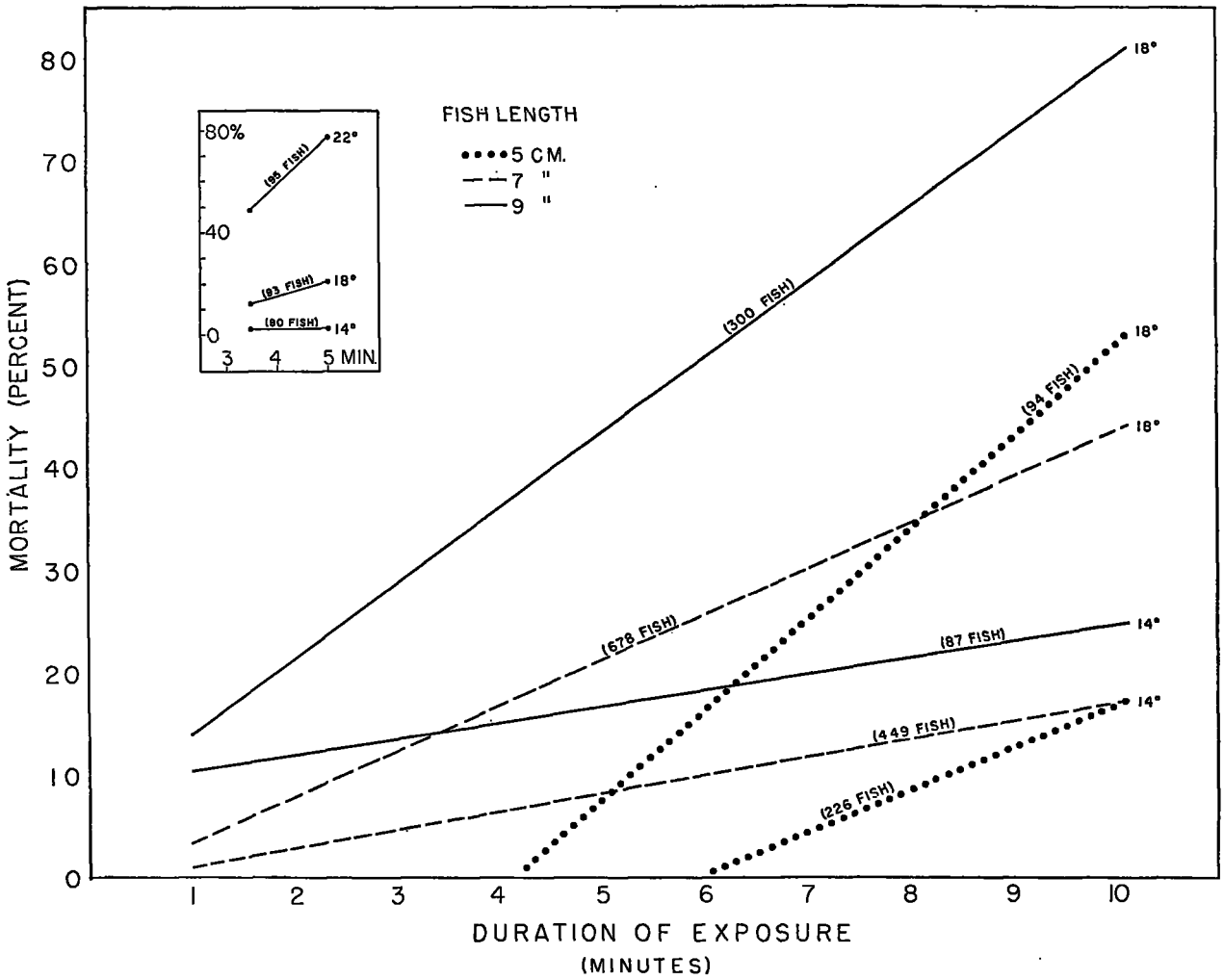

FIGURE 14.—Effect of duration of exposure in relation to temperature and fish length upon mortality of salmon fingerlings (*Oncorhynchus tshawytscha*) exposed to pulsating d. c. Tests run at 4 volts/cm., current density range 0.14 to 0.27 milliamps./cm.², 2 pulses/sec., pulse duration 20 millisecs. (Insert: tests run at 2 volts/cm., current density range 0.09 to 0.11 milliamps./cm.², 2 pulses/sec., pulse duration 20 millisecs., fish length 9 cm.)

TABLE 10.—*Effect of duration of exposure in relation to temperature and fish length on mortality of salmon fingerlings*

Duration of exposure	Fish length of—								
	4 to 5.9 cm.			6 to 7.9 cm.			8 to 9.9 cm.		
	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)	Number exposed	Number dead	Mortality (percent)
1 minute:									
14° C.	[1] 5	0	0	83	1	1.2	[1] 60	0	0
18° C.	[1] 6	0	0	115	8	7.0	84	8	9.5
2 minutes:									
14° C.	[1] 2	0	0	77	2	2.6	67	8	11.9
18° C.	[1] 4	0	0	102	6	5.9	98	22	22.5
3 minutes:									
14° C.	[1] 10	0	0	27	0	0	3	0	0
18° C.	[1] 8	0	0	57	7	12.3	19	5	26.3
4 minutes:									
14° C.									
18° C.							6	2	33.3
5 minutes:									
14° C.	[1] 52	0	0	21	1	4.8	4	1	25.0
18° C.	21	2	9.5	51	11	21.6	17	12	70.6
6 minutes:									
14° C.	55	2	3.6	53	8	15.1	3	1	33.3
18° C.	12	2	16.7	46	9	19.6	5	3	60.0
7 minutes:									
14° C.	60	1	1.7	48	4	8.3	2	0	0
18° C.	17	3	17.7	51	15	29.4	19	12	63.2
8 minutes:									
14° C.	47	3	6.4	52	9	17.3	2	1	50.0
18° C.	20	8	40.0	90	26	28.9	20	13	65.0
9 minutes:									
14° C.	51	6	11.8	48	11	22.9	[1] 1	1	100.0
18° C.	13	5	38.5	81	30	37.0	17	9	52.9
10 minutes:									
14° C.	13	2	26.3	40	21	52.5	6	1	16.7
18° C.	11	6	54.6	85	44	51.8	15	12	80.0

[1] Data not included in calculation of curves.

concluded that pulse duration is not a lethal factor, at least within the range of conditions examined, and that there is no direct relation between mortality and the total energy applied per unit of time.

FISH LENGTH AND DURATION OF EXPOSURE

The relation of fish length to the effect of duration of exposure upon the mortality of chinook fingerlings exposed to pulsating d. c. was examined in a series of experiments in which fingerlings of different lengths were subjected for various periods of time to a pulsating electrical field with voltage gradient, current density, pulse frequency, pulse duration, and water temperature held constant.

The data graphically presented in figure 13 and numerically shown in table 9 indicate that the effect of duration of exposure upon mortality increases with the length of the fish.

TEMPERATURE

The relation of water temperature to the effect of duration of exposure on the mortality of chinook fingerlings subjected to pulsating d. c., was demonstrated by a group of experiments in which fingerlings of different lengths were subjected to pulsating d. c. at different water temperatures for various lengths of time. During these tests, voltage gradient, current density, pulse duration, and pulse frequency were held constant.

The data graphically shown in figure 14 and numerically presented in table 10 reveal that above a certain threshold exposure the influence of water temperature on the mortality of chinook fingerlings exposed to pulsating d. c. increases with the duration of exposure and that the influence of water temperature upon mortality is greater upon longer fish. The pattern of response was verified (see insert, fig. 14) by testing fingerlings from a single source on the same day. The curves shown in the insert illustrate the greater effect of water temperature at higher temperature levels. The marked difference in mortality related to temperature in the current density experiments (fig. 5), where exposure to the electrical field was only 30 seconds, may have been due to the higher temperature levels involved.

DISCUSSION

The results of these experiments are in general agreement with the findings of other research workers investigating the effect of electric current on fish. McMillan's (1928) experiments with a. c.

showed an increase in mortality with an increase in voltage gradient and current density and with an increase in the duration of exposure. Similar results were obtained in the present study with pulsating d. c. That the total voltage received by the fish is the effective factor rather than the voltage gradient has been pointed out several times in the literature (Okada 1929, Bramsnaes et al. 1942, Kuroki 1951). The evidence indicating that shorter fish are affected to a greater degree by total voltage than longer fish (fig. 7) agrees with the findings of Kuroki, whose conclusions were based on a study of the reactions of *Carassius auratus* in approximately the same length range as those used in this study.

There is some evidence suggesting that the relation of fish length to the influence of total voltage upon mortality may be a function of the duration of exposure. Figure 7 indicates that shorter fish are more affected by the total voltage than longer fish when the exposure is only 30 seconds. A comparison, in terms of the total voltage to which the fish were subjected, of mortality of fingerlings of different lengths subjected to pulsating d. c. under almost similar conditions at exposures of 4 minutes and 8 minutes (figs. 8, 11, and 13), suggests that the relation may reverse with increased exposure. At a 4-minute exposure the effect of total voltage is approximately equal for fish of 7-cm. and 9-cm. lengths while with an 8-minute exposure the longer fish are affected to a greater degree. The data, however, do not make clear whether the increased mortality of the longer fish is due solely to the greater effect of total voltage upon longer fish with increased duration of exposure or to the increased effect of some other factor such as pulse frequency.

In several of the experiments that showed a significant relation between mortality and fish length (see figs. 10, 13, and 14), the difference in mortality related to fish length was greater between the 7-cm. and 9-cm. lengths than it was between the 7-cm. and the 5-cm. lengths or between the 9-cm. and the 11-cm. lengths. This suggests the possibility that the difference in mortality may also be a function of some other aspect of the size of fish such as the cross-sectional area of the body.

One of the relations brought out by the experiments is the influence of water temperature upon the mortality of fingerlings exposed to pulsating d. c. The importance of water temperature, apart from its effect upon the resistance of water, is clearly shown by the marked increase in mortality occurring under similar electrical conditions with an increase of a few degrees in water temperature (see figs. 5 and 14). The experience of Larimore, Durham, and Bennett (1950) in stunning fish with an electric fish shocker indicates that the effect of temperature upon mortality shown in the laboratory experiments will also be found in the field. Larimore et al. found that during cold weather the speed of their collecting operation was slowed down because a longer exposure was required to stun the fish.

Since pulse duration does not appear to be a lethal factor and since there does not appear to be a direct relation between mortality and the total energy applied per unit of time, as contrasted with the marked effect of pulse frequency upon mortality, the evidence points to the probable importance of wave form. If the increased mortality caused by an increase in pulse frequency is not due to the increase in total energy applied per unit of time, it must be due to the increase in the number of changes in potential. If change in potential is the effective factor, then the rate of change in potential should be of great importance.

The relation between mortality of the fish subjected to pulsating d. c. under the experimental conditions just described and mortality of wild fish subjected to pulsating d. c. under natural stream conditions must remain a matter of speculation until it is examined experimentally. Differences in the condition of wild fish and of hatchery fish might result in a marked difference in their ability to withstand subjection to electric current. The definition of mortality used in the laboratory experiments allowed 1 hour after exposure for recovery, during which time the fingerlings were held in aerated glass bowls. Whether the proportion of recoveries would be as great or greater under stream conditions where factors such as turbulence and predation would be in operation during that hour is open to conjecture.

In general, one might expect the greater mortality under the laboratory treatment. The fingerlings had to be netted several times, transported, held in tanks, and subjected to several complete water changes. During their exposure to the electrical field the fish were restricted by plastic stalls, and this may have resulted in some mechanical injury due to violent movements when

the current was first applied. The fingerlings were always held in alinement parallel to the direction of the electrical field (the one exception is noted on p. 69) and would therefore be continually subjected to a maximum voltage. In a stream the free-swimming fish may be alined directly parallel to the field for only a part of the total exposure.

Interpretation of the data from these laboratory experiments for use in electrical fish-guiding experiments in the field must take into consideration other factors as well. The maximum width of a directional electrified zone that could be used would be determined by the rate at which the fish swim out of the electrified zone and by the maximum duration of exposure that is "safe" for the fish. Assuming that the fingerlings are distributed at random throughout the stream, only those fish entering at the extreme negative end of the electrified zone would be subjected to the entire width of the zone in moving to the positive end. Thus, a 15-percent expected mortality for those fish exposed to the maximum field width may represent only a negligible mortality in terms of the total number of fish being directed by the electrified zone. It may be possible to safely direct fingerlings in ranges of electrical conditions which produced a mortality of 30 or 40 percent in the laboratory experiments. One of the tasks of field experiments in electrical fish guiding will be to determine the relation between mortality under standardized laboratory conditions and that under conditions in the stream.

The experiments reported here emphasize one point—a significant part of the ranges of electrical characteristics desirable in fish guiding are lethal to some degree for salmon fingerlings. The possibility of injurious effects of a nonvisible nature (e. g., an effect upon reproductive ability) is being explored. Although this study is not yet complete enough to draw many conclusions, it is clear that the application of the principle of electrotaxis to the protection of salmon fingerlings will require an intimate knowledge of the relation between the electrical-energy levels producing electrotaxis and those detrimental to the fish.

SUMMARY

The influence of voltage gradient, current density, pulse frequency, and duration of exposure upon the mortality of salmon fingerlings exposed to pulsating direct current was examined experimentally in relation to the length of fish, water temperature, and pulse duration. A current of square-wave form was used and the following ranges were explored: Voltage gradient, 0.5 to 15 volts/cm.; pulse frequency, 2 to 15/sec.; pulse duration, 20 to 80 milliseconds; current density, 0.05 to 1.9 milliamps./cm.^{2}; duration of exposure, 0.5 to 20 minutes; fingerling lengths, 4 to 12 cm.; and temperature, 10° to 25° C.

For simplification, the assumption was made that a straight line of regression was the most satisfactory description of the relations examined, and the results of the experiments, above threshold values, were interpreted as follows:

1. Mortality increased in a constant ratio with an increase in voltage gradient, an increase in current density, or an increase in both. The effect of voltage gradient increased with the duration of exposure.

2. The total voltage to which the fish were subjected (i. e., fish length×voltage gradient) was the effective factor in mortality rather than the voltage gradient, and the effect of total voltage upon mortality was actually greater on the shorter fish when the exposure was only 30 seconds.

3. Fingerlings exposed to a pulse of 20 milliseconds at a frequency of 8/sec. (power on 16 percent of the time) had the same mortality as fingerlings exposed under similar conditions to a pulse of 80 milliseconds duration at a frequency of 8/sec. (power on 64 percent of the time), indicating that under the conditions of the experiment pulse duration was not a lethal factor and that there was no direct relation between mortality and the total energy applied per unit of time.

4. Mortality increased with the pulse frequency, and the effect of pulse frequency upon mortality increased with the length of fish and the duration of exposure.

5. Mortality of fingerlings exposed to pulsating d. c. increased with the duration of exposure, and the effect of duration of exposure increased with the length of the fingerlings.

6. Mortality increased with the water temperature, and the effect of water temperature upon mortality increased with the duration of exposure. The effect of water temperature upon mortality was greater on fish of greater length.

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DISTRIBUTION AND ABUNDANCE OF EGG AND LARVAL POPULATIONS OF THE PACIFIC SARDINE

BY ELBERT H. AHLSTROM

FISHERY BULLETIN 93

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

A marked decrease in abundance of the Pacific sardine (*Sardinops caerulea*) in recent years led to the initiation in 1949 by the California Cooperative Oceanic Fisheries Investigations of continuing studies to determine the factors responsible for the fluctuations in abundance, distribution, and availability of this important species. The egg and larval populations are being sampled by means of quantitative plankton hauls made over an established pattern of stations occupied at regular intervals during the year.

Sardine spawning in 1950 and 1951 was mainly confined to two major spawning centers, one located off southern California and adjacent Baja California, the other off central Baja California. The latter was by far the more important center, supplying approximately 82 percent of the sardine eggs collected in 1950, and 94 percent of the eggs collected in 1951. Sardine eggs have been obtained during every month of the year off central Baja California, although in both 1950 and 1951 most spawning occurred during a 4-month period, February through May. In the more northern center, the season of spawning has been more sharply delimited, being mostly confined to the months of April, May, and June.

The estimated number of sardine eggs spawned in 1950 was 286,000 billion; in 1951 the total amounted to 611,000 billion. The survival from newly spawned eggs to the end of the planktonic phase of life was about 1 in 1,000 in both 1950 and 1951.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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DISTRIBUTION AND ABUNDANCE OF EGG AND LARVAL POPULATIONS OF THE PACIFIC SARDINE

By ELBERT H. AHLSTROM, *Fishery Research Biologist*

The population of the Pacific sardine, or pilchard (*Sardinops caerulea*), is subject to rather considerable fluctuations in abundance. In recent years there has been a marked decrease in abundance of the sardine over much of its range. To better understand the complex interrelationships responsible for fluctuations in population size, distribution, and availability, there has been an intensification of research on the sardine.

Investigation of the distribution and abundance of egg and larval populations of the Pacific sardine is one facet of the California Cooperative Oceanic Fisheries Investigations, a program sponsored by the Marine Research Committee and carried out cooperatively by the Scripps Institution of Oceanography of the University of California, the Bureau of Marine Fisheries of the California Department of Fish and Game, the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences. The oceanographic-biological survey program, commenced in March 1949 and continued since without interruption, is mainly the responsibility of the first three organizations.

A major line of research is directed toward determining the amount of spawn and the rate of larval survival in relation to environmental conditions. Inasmuch as the amount of spawn probably would be directly proportional to population numbers, this offers a means of estimating the size of the spawning population. The size of the larval population that survives to the postplanktonic stage may bear a direct relation to the subsequent number of individuals of the year class that reach commercial size. The larval studies are predicated on the assumption that such a relation exists. A correlation of the rate of larval survival with hydrographical, meteorological, and biological conditions may clarify the relation between survival rate and environmental conditions. Such information would have predictive value with regard to year-class size.

Personnel of the Scripps Institution of Oceanography and the California Department of Fish and Game cooperated in the collection of data at sea. Staff members of the South Pacific Fishery Investigations of the Fish and Wildlife Service contributed to this investigation, with the majority devoting full time to it. Suggestions of John C. Marr and Theodore Widrig were most helpful during preparation of the paper, and James R. Thrailkill and George Mattson prepared the figures and graphs.

RÉSUMÉ OF PREVIOUS RESEARCH

Eggs and larvae of the Pacific sardine, or pilchard *Sardinops caerulea* (Girard) 1854, were described by Scofield and Lindner (1930) from material collected off southern California in June 1929, during the first year of an investigation of the distribution of sardine spawning.

Results of 4 years (1929–32) of investigation of sardine spawning by the California Department of Fish and Game were reported by Scofield (1934). The surveys of 1929 and 1930 were preliminary. In 1929, both sardine eggs and larvae were taken in a number of hauls made off southern California in June, but neither eggs nor larvae were found in hauls made off central California during April and May. Sardine eggs were obtained in 7 out of 9 hauls made off central California during May and June 1930, a season in which "warmer water than average prevailed along the entire California coast" (ibid.: 19). As in 1929, the largest concentrations of eggs and larvae were obtained off southern California.

Unusually warm temperatures prevailed during the period of the 1931 survey. Scofield (ibid.: 11) noted that in March "warm water of 16° C. was found to be present north of Point Conception, and, as might have been expected, the eggs and larvae of sardine were found there in considerable

numbers." The 1931 survey was more intensive and more extensive than earlier surveys. Furthermore, quantitative plankton sampling was initiated during this season and continued in 1932. As in previous years, most of the collections were made off southern and central California. Two survey cruises were made also along the coast of Baja California: The first, in April 1931, extended into the Gulf of California; the other, in February 1932, sampled as far south as Magdalena Bay. Although not many sardine eggs were taken on the southern survey cruises, large collections of sardine larvae were obtained off central Baja California during February 1932. Both the 1931 and 1932 year classes were outstandingly large, as measured by their representation in the commercial catches of the 1934–35 and 1935–36 seasons (Eckles 1954).

On the basis of 4 years of survey, Scofield (1934) concluded that the region of maximum spawning was a comparatively small area 200 miles long and 100 miles wide, situated off the coast of southern California between Point Conception and San Diego. General spawning was found to occur at least as far south as Magdalena Bay, Baja California, as far north as San Francisco, and offshore to a distance of more than 250 miles.

From a study of maturing ova in commercially landed fish, Clark (1934) determined that the spawning season for fish landed off southern California extended from February to August, with the height of the season in April and May. From fish landed at Monterey, she concluded that sardines from that area would probably spawn between February and July. Her data also led her to infer that the sardine spawned from 30,000 to 65,000 eggs in a batch, depending on size of the fish, and perhaps as many as 3 batches a season.

Tibby (1937) gathered together data on the relation between surface-water temperatures and the occurrence of sardine spawning. He based his analysis on data collected by Scofield in 1929–32 and on data obtained in 1936 on two trips along the coast of Baja California. Altogether, data were used from 81 collections, 62 from off California and 19 from Baja California waters. Tibby concluded that the minimum temperature at which sardine spawning would take place was approximately 13° C., that the optimum temperature for spawning was between 15° and 18° C., and that some spawning would occur at temperatures as high as 24° C. Subsequent investigations by us have confirmed the importance of 13° C. as a threshold temperature for spawning, but they have not substantiated the optimum temperature reported by Tibby. It must be taken into consideration that Tibby's data were heavily weighted by collections made during 1930 and 1931, years when water temperatures off California were unusually high. The five records of spawning at temperatures above 20° C. came from southern California in 1931.

Concerning the spawning off Baja California during 1936, Tibby (ibid.: 134) states, "Although no attempt was made at quantitative estimates, it was apparent that there was a sizable spawning in the Sebastian Viscaino Bay region and some localized spawnings were found as far south as Cape San Lucas. The importance of this southern spawning cannot as yet be told."

Clark (1938) records that 20 small sardines, 34 to 53 millimeters standard length, were taken off Oregon during September 1937. The sardines were obtained from the stomachs of albacore caught about 30 miles at sea off the mouth of the Columbia River. These juvenile sardines must have come from spawning in these northern waters; hence, this record constitutes a northerly extension of the known spawning grounds of the sardine.

Research on sardine recruitment through collections of eggs and larvae was undertaken in the spring of 1939, when the United States Fish and Wildlife Service entered into a collaborative program with the Scripps Institution of Oceanography to investigate sardine recruitment in conjunction with hydrographic conditions off the Pacific coast of the United States. The sea work was done on the research vessel *E. W. Scripps*, operated by the Scripps Institution of Oceanography. The investigation was continued through 1940 and 1941, after which it was discontinued because of war.

A primary purpose of the 1939 survey was to determine whether the entire spawning range of the sardine could be delimited. On a cruise of 2 months (*E. W. Scripps*, cruise 8), an area approximately 1,200 miles long by 300 miles wide was surveyed. Moderate numbers of sardine eggs were collected at several stations on the most northerly of the lines occupied. This line, off

Cascade Head, Oreg., was worked on May 22 to 25. The largest concentration of sardine eggs was encountered on a line off Monterey, worked on June 11 to 14. Sardine eggs were taken at eight contiguous stations on this line, the largest number occurring at a station located about 160 miles from shore. Most of the larvae were obtained on a line off Point Fermin in southern California, worked on June 16 to 23. Unfortunately, this cruise took place too late in the season to sample the southern spawning adequately. Sardine eggs were taken in only 1 of the 34 hauls made to the south of Point Conception between June 15 and July 10. Sardine eggs had been rather abundant in the area off southern California in April 1939, however, when a series of hauls was taken to develop sampling techniques.

Experience gained during the 1939 season indicated that the spawning range was too extensive to be surveyed adequately by one vessel. Consequently, during the following 2 years the investigation was confined to the more limited area off the coast of southern California previously shown by Scofield to be an area of abundant spawning. This concentration of effort served several purposes. It permitted continuation by the Scripps Institution of Oceanography of studies on the oceanography of the southern California area commenced in former years. Another consideration was that by surveying a limited area of abundant spawning, it should be possible to determine from the quantitative sampling of eggs and larvae the amount of spawning within the area and the rate of mortality during the planktonic existence of the sardine. Abundant spawning was found in the area in 1940 and 1941, and two papers dealing with the results of the spawning surveys have been published (Sette and Ahlstrom 1948; Ahlstrom 1948).

Godsil (1941) reported that in January and February 1940, sardine eggs and larvae were collected in the Gulf of California, and maturing fish also were taken there by the research vessel *N. B. Scofield.* This constitutes the first record of sardines spawning in the Gulf of California.

Moderate numbers of sardine eggs and larvae were taken in plankton hauls off San Francisco in June 1946 (Smith and Ahlstrom 1948), from the motorship *Pearl Harbor*, a purse-seine vessel chartered by the San Francisco Sardine Association to explore for sardines with echo-ranging and echo-sounding gear.

In February 1948, prior to the commissioning of the vessels to be used on the expanded oceanographic-biological surveys, a preliminary survey was made off central Baja California aboard the *E. W. Scripps* to obtain additional data on the amount of sardine spawning in that area. Effort was concentrated in the area between Point San Eugenio and Point Abreojos, and abundant spawning was found in a coastal strip about 50 miles wide.[1] This is the area that has proved, since 1949, to be the principal spawning ground of the sardine.

In brief, before the commencement of the California Cooperative Oceanic Fisheries Investigations, sardines were known to spawn over a very considerable area, from the Gulf of California in the south (Godsil 1941) to at least as far north as Cascade Head, Oreg. (Ahlstrom 1948). There was considerable evidence that during the very successful spawning season of 1939 some spawning had taken place as far north as British Columbia (Walford and Mosher 1941; Hart 1943). Within this range it was known that the area off southern California was a center of abundant spawning (Scofield 1934; Sette and Ahlstrom 1948), but it was not definitely known whether there were other important spawning areas.

Sardine eggs and larvae had been taken north of Point Conception during a number of seasons. Did spawning occur in these waters every year, or only during certain years when conditions were more favorable than usual? Scofield (1934) reported taking sardine eggs and larvae off central California in 1930 and 1931, but these were unusually warm years. He had not taken them in this area on cruises made during April and May in 1929 and again in 1932. Would he have taken them in these seasons if his sampling had extended over a longer portion of the year? In 1939, large numbers of sardine eggs had been taken on a line off Monterey, especially at a station located 160 miles from shore (Ahlstrom 1948), but 1939 may have been a season of unusually widespread spawning. Moderate numbers of sardine eggs and larvae had been taken off San Francisco in early June 1946 (Smith and Ahlstrom 1948). Evidence was accu-

[1] Elbert H. Ahlstrom and J. L. McHugh, A record of Pacific sardine (*Sardinops caerulea*) and other fish eggs and larvae collected off central Baja California during February 1948. MS.

mulating that spawning did occur off central California during most years; however, we still did not know how important a segment of sardine spawning this constituted. There were only 2 seasons that sardine spawning to the north of California was definitely documented: off Oregon in 1937 (Clark 1938) and off Oregon (and probably Washington and British Columbia) in 1939 (Ahlstrom 1948; Walford and Mosher 1941; Hart 1943).

Information on the distribution and abundance of sardine spawning off Baja California was fragmentary. Scofield had visited this area only twice during the early period of survey, and on these cruises had taken few sardine eggs. He had made several large collections of sardine larvae off central Baja California, but had underestimated their importance. Tibby (1937: 134) reported making two additional cruises off Baja California in 1936, at which time he had found "sizable spawning in the Sebastian Viscaino Bay region." During 1939, sardine eggs or larvae were taken in only 2 out of 24 hauls off Baja California in late June and early July (Ahlstrom 1948); however, this cruise was made too late in the season to adequately sample the eggs or larvae off Baja California. Godsil (1941) reported taking eggs and larvae in the Gulf of California in January and February 1940. Our best evidence of the importance of central Baja California as a spawning center was obtained during the cruise of the *E. W. Scripps* in February 1948. Even this was fragmentary, being confined to a limited area off central Baja California during one cruise. Hence, nothing very definite was known concerning either the season of spawning, or the distribution and abundance of spawning off Baja California previous to the initiation of the investigations reported in this paper.

SARDINE SPAWNING SURVEYS, 1949–51

1949 SURVEY

Large-scale oceanographic-fishery survey cruises began in March 1949. The area surveyed at monthly intervals during 1949 was a strip of water approximately 400 miles wide and 1,320 miles long. It had its northern limit off the mouth of the Columbia River and its southern off Point San Eugenio, central Baja California. Within this area 12 lines of stations were spaced at intervals of 120 miles, the lines extending seaward normal to the general trend of the coastline. Along each line were 10 or 11 stations spaced at 40-mile intervals. Three vessels participated in the monthly coverage of the area.

The purpose of the initial year of survey, 1949, was exploratory, since information on place and time of sardine spawning as well as on the broad features of oceanic circulation and environment was needed.

Sardine eggs and larvae were collected by hauling a plankton net obliquely from about 70 meters below the surface to the surface. On taking a haul, the net was lowered on 100 meters of wire (¼-inch cable) at the rate of 50 meters a minute, and retrieved at the rate of 5 or 10 meters a minute. The actual depth reached by the net varied from haul to haul, depending on speed of the vessel and state of the sea. The nets used in 1949, and subsequently, measure 1.0 meter in diameter at the mouth, by about 5 meters in overall length. They are constructed of No. 30xxx grit gauze, a rugged grade of Swiss silk bolting cloth with mesh openings of about 0.7 millimeter when new but shrinking to about 0.55 millimeter on use.

To obtain a measure of the volume of water strained during a haul, an Atlas-type current meter was fastened in the center of the mouth of each net. The method used to standardize hauls was described by Ahlstrom (1948). This standard adjusts the number of eggs or larvae in a haul to the number in 10 cubic meters of water strained per meter of depth fished by the net. If the vertical range of the eggs or larvae has been completely traversed (as it has in the case of the sardine), this value is equivalent to the number of eggs or larvae under 10 square meters of sea surface. This area is referred to as a "standard area." For a more detailed discussion of the method of sampling sardine eggs and larvae see Ahlstrom (1948).

The 1949 collections were inadequate both for quantitative estimation of the amount of spawning and for determination of the rate of survival of larvae. Sardine eggs were taken in only 34 of the 924 hauls made during 1949; samples containing 100 or more eggs numbered only 7, and most of the eggs were collected at one station, the inner station on the southernmost line off Point San Eugenio. Sardine larvae were taken in 41 hauls, with 30 of the samples containing 5 or fewer larvae per haul, and only 3 having 100 or more larvae. The seasonal distributions of sardine

eggs and larvae taken in 1949 are shown in figure 1.

Despite the quantitative inadequacy of the 1949 collections, the results of the survey were of considerable value in planning a more intensive coverage of the sardine spawning centers. They established the importance of the spawning center off central Baja California and the need for more thorough coverage of it. The area off southern California was again observed to be an important spawning center, and it was found that spawning in this area sometimes occurred at a considerable distance from shore. Some spawning was found along the length of the California coast and, judging from the number of larvae taken off Point Sur, considerable spawning must have occurred off central California.

The results obtained in 1949 also indicated a northward progression of spawning as the season advanced. During March and April the only large collection of eggs and all hauls containing larvae were obtained off central Baja California (tables 1 and 2). The height of spawning occurred in the southern California area during May. By the following month, spawning had spread to central California (off Point Sur), while still occurring in a continuous belt south to Point San Eugenio. On the July cruise, all sardine eggs

TABLE 1.—*Stations at which sardine eggs were collected, 1949*

[Number per standard haul]

Station	March (cruise 1)	April (cruise 2)	May (cruise 3)	June (cruise 4)	July (cruise 5)	August (cruise 6)	September (cruise 7)	Total
401		0	0	0	0	26	0	26
601	0	0		0	210	0	0	210
701	0	0	0	14	1	0	0	15
801	0	0	0	5	0	0	0	5
901	1	3	0	47	0	0	0	51
902	0	0	0	38	0	0	0	38
903	0	1	1,810	17	172	0	0	2,000
904	0	0	15	0	0	0	0	15
905	0	7	121	0	0	0	0	128
908	0	0	1	0	0	0	0	1
1001	0	88	1,119	9	0	0	0	1,216
1002	0	0	79	0	0	0	0	79
1004	0	1	0	0	0	0	0	1
1101	1	2	4	0	0	0	0	7
1102	0	0	14	0	0	0	0	14
1104	0	5	0	0	0	0	0	5
1105	6	0	0	0	0	0	0	6
1106	0	3	0	0	0	0	0	3
1201		20,421	67	1,264	0	0	0	21,752
1202	0	0	7	0	0	0	0	7
1203	0	32	0	0	0	0	0	32
Total	8	20,563	3,237	1,394	383	26	0	25,611

TABLE 2.—*Stations at which sardine larvae were collected, 1949*

[Number per standard haul]

Station	March (cruise 1)	April (cruise 2)	May (cruise 3)	June (cruise 4)	July (cruise 5)	August (cruise 6)	September (cruise 7)	Total
203			0		0	0	0.8	0.8
601	0	0		0	0	3.7	0	3.7
701	0	0	0	0	261.7	0	0	261.7
702	0	0	0		15.5		0	15.5
803	0	0	0	0	4.8	0	0	4.8
901	0	0	0	1.0	2.6	0	0	3.6
903	0	0	0	14.6	16.3	0	0	30.9
904	0	0	1.1	11.0	1.8	0	0	13.9
905	0	0	1.5	2.7	0	0	0	4.2
906	0	0	5.4	1.4	0	0	0	6.8
907	0	0	0.4	0	0	0	0	0.4
1001	0	0	3.6	4.4	0	0	0	8.0
1002	0	0	0	9.0	0	0	0	9.0
1003	0	0	0.8	0	0	0	0	0.8
1007	0	0	1.4	0	0	0	0	1.4
1101	2.7	379.8	0.9	2.1	0	0	0	385.5
1102	1.6	0	0	30.1	0	0	0	31.7
1103	0.5	0	0	0	0	0	0	0.5
1107	0	0.4	0	0	0	0	0	0.4
1201		105.0	1.5	7.7	0	0	0	114.2
1202	3.0	0	0.7	0	0	0	0	3.7
1203	1.0	0	0.6	0	0	0	0	1.6
1204	1.3	0	0	0	0	1.8	0	3.1
1205	0	3.9	0	0	0	0	0	3.9
1206	0	3.8	0	0	0	0	0	3.8
Total	10.1	492.9	17.9	84.0	302.7	5.5	.8	913.9

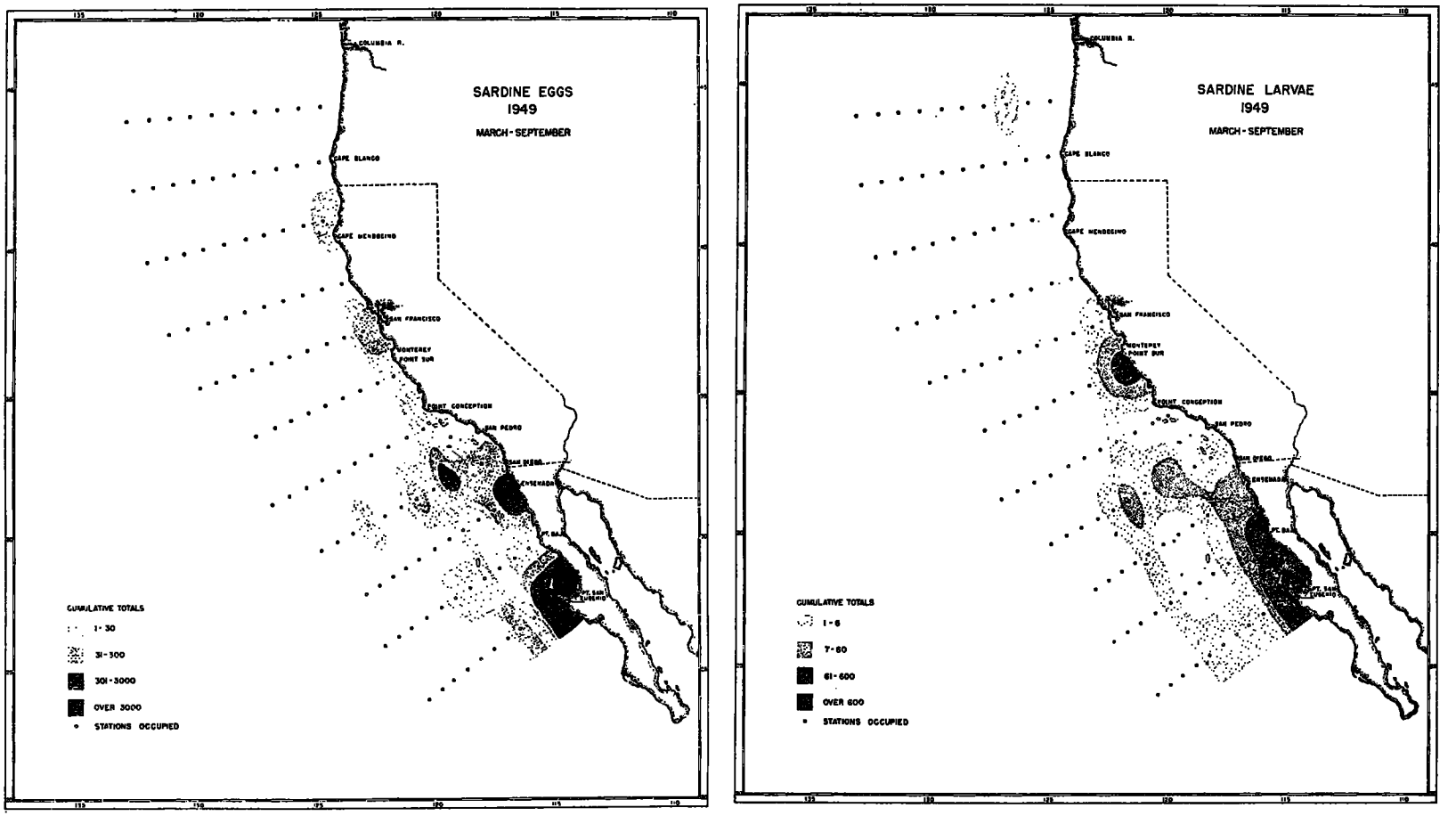

FIGURE 1.—Distribution and abundance of sardine eggs and sardine larvae, March through September, 1949.

and larvae obtained were taken off central and southern California; moderately heavy spawning was sampled off San Francisco, and a large collection of larvae was obtained off Point Sur. Few eggs or larvae were taken in August, but a collection of eggs was obtained off Cape Mendocino, indicating that some spawning occurred off northern California. A single larva was collected off Oregon in September.

A relation between water temperature and the occurrence of sardine spawning was indicated, as almost all of the sardine eggs were found in water with temperatures between 13° and 16° C. (figs. 2–3). Although we subsequently found that the temperature relation is neither as simple nor as clear cut as it appears from the 1949 data, the limiting effect of low temperatures on spawning seems to be an important factor. Only a negligible amount of spawning has been found at any time in waters below 13° C.

1950 SURVEY

The survey was intensified during the 1950 season in the two areas known to be important sardine spawning centers. Four lines of stations were added in the area between Point Conception and Ensenada, Baja California; consequently, the distance between lines in this area was reduced to 40 miles, a distance equivalent to the spacing of stations on the lines. To more adequately sample the spawning off central Baja California, 3 short lines of stations were added to the south of the area covered in 1949. These lines, spaced 40 miles apart, extended the survey area south from Point San Eugenio to Point Abreojos. Inshore stations were added between the remaining station lines. A fairly extensive coverage was maintained to the north of Point Conception during 1950 to sample any important sardine spawning that might occur in this area. The cruises routinely extended as far north as the Oregon-California border, and in August and September they were extended northward to Oregon waters. The stations regularly occupied on the 1950 survey cruises are shown in figure 4. The same sampling procedures were followed as in 1949. The average depth reached by the net was 68 meters.

Two of the 1950 cruises were extended to areas not routinely sampled. During cruise 18 (September), lines 70 and 90 were extended for an additional 600 miles seaward. No sardine eggs or larvae were taken on these lines. During cruise 20 (November) two vessels occupied stations off central and southern Baja California, between Point San Eugenio and Cape San Lucas. Thirty of the stations occupied on this cruise had been regularly occupied on routine survey cruises, and 60 stations were added. This cruise was made for a twofold purpose: (1) to extend the coverage in order to obtain a better understanding of the oceanic circulation off Baja California, and (2) to determine the amount and extent of sardine spawning off central and southern Baja California during this season. Regarding the latter, results were almost entirely negative: sardine larvae were obtained in only one haul, off Magdalena Bay, and no sardine eggs were taken during the entire cruise. It has been learned since that off-season spawning (i. e., fall spawning) is often close inshore, and more positive results might have been obtained had additional stations been occupied inshore.

In place of the regular survey cruise in October, three stations on line 70 were occupied repeatedly to obtain data on short-period variations in physical, chemical, and biological properties, especially those of a periodic nature. Six other stations on line 70 were occupied once. Sardine eggs and larvae were not found in any of the 185 plankton hauls made during this cruise.

The month-by-month coverage during 1950 in different parts of the survey area is summarized in table 3. Omitted from this tabulation are stations occupied only on the September or November cruises. The stations worked repeatedly during October are recorded in the table as if each had been occupied but once. With these deletions, the number of station occupancies in 1950 was 964. The largest number of hauls, 376, was obtained to the north of Point Conception; 358 samples were obtained between Point Conception and Ensenada, Baja California; and 230 hauls were made off central Baja California.

Location and importance of the spawning center off central Baja California were definitely established by the 1950 survey cruises. The center of abundant spawning was found to lie within about 50 miles of the coast between Point San Eugenio (off line 120) and Point Abreojos (off line 130). Approximately 82 percent of the sardine eggs and 70 percent of the larvae collected during 1950 were taken in this area. Most of the remainder were taken in the spawning center off

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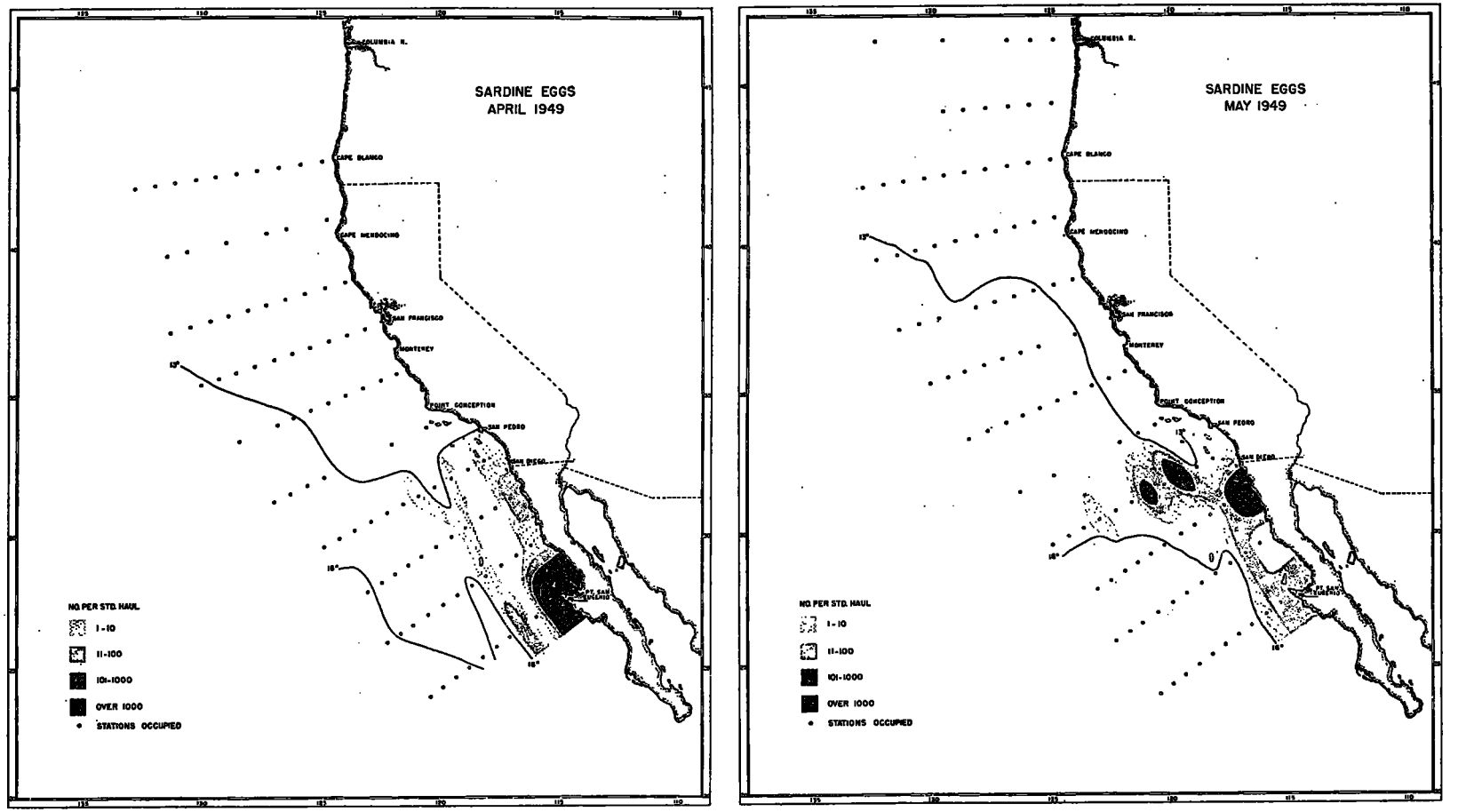

FIGURE 2.—Monthly distribution of sardine eggs in relation to temperature (at the 15-meter level), April and May 1949. The 13° and 16° C. isotherms are shown.

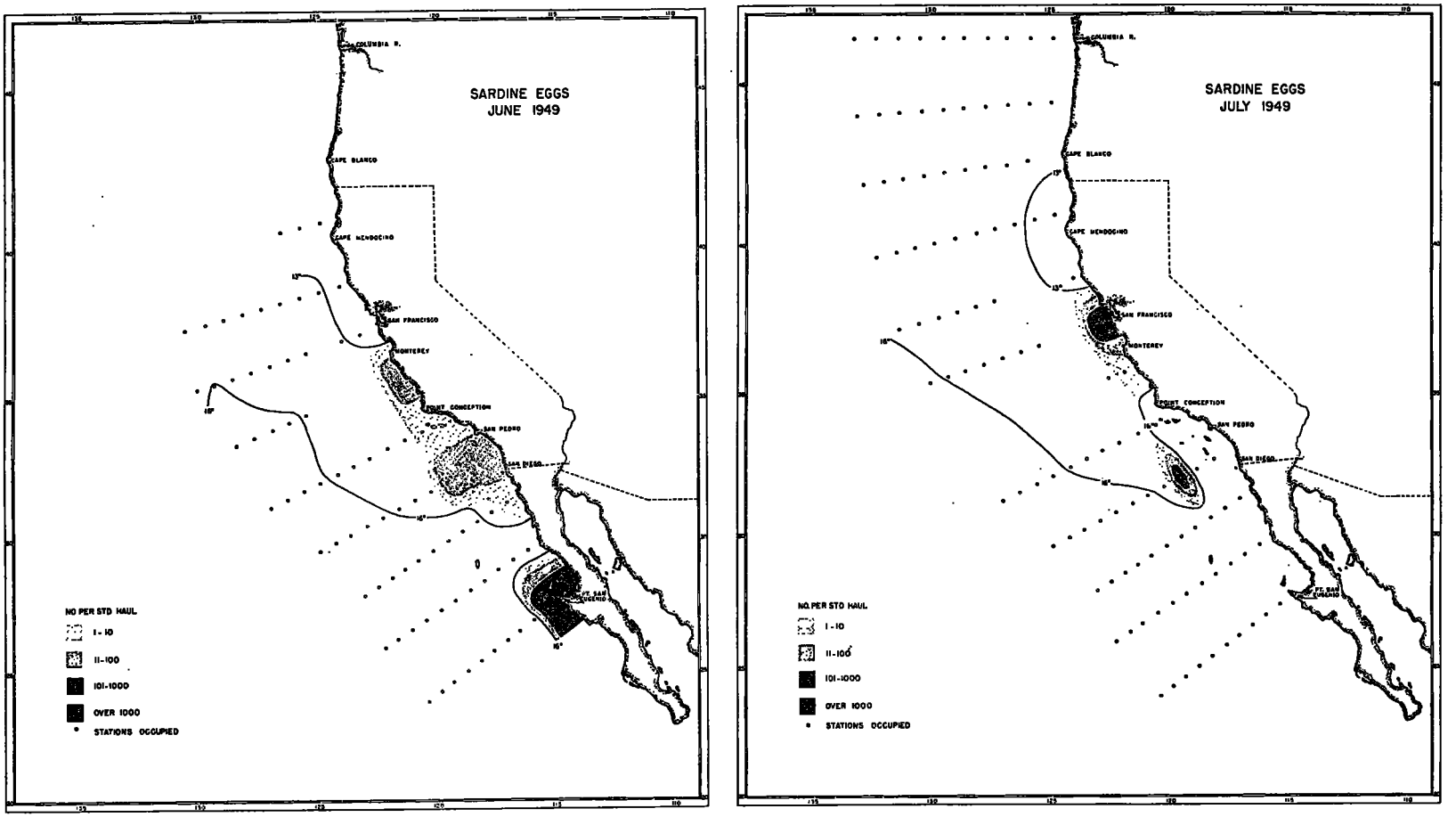

FIGURE 3.—Monthly distribution of sardine eggs in relation to temperature (at the 15-meter level), June and July 1949. The 13° and 16° C. isotherms are shown.

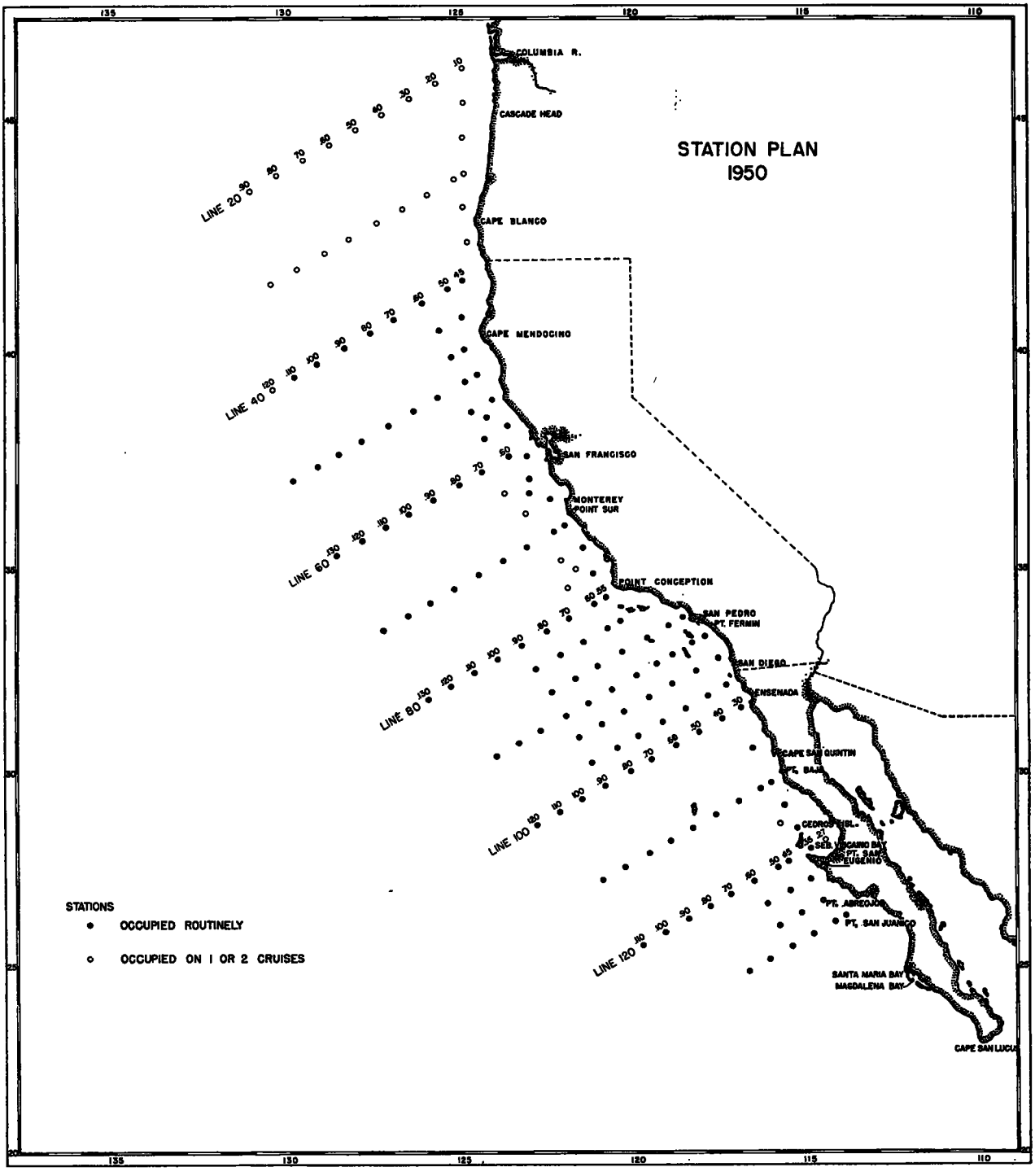

FIGURE 4.—Location of stations occupied during the regular survey cruises of 1950.

TABLE 3.—*Number of stations occupied monthly during survey cruises, 1950*

	February (cruise 11)	March (cruise 12)	April (cruise 13)	May (cruise 14)	June (cruise 15)	July (cruise 16)	August (cruise 17)	September (cruise 18)	October (cruise 19)	November (cruise 20)	Total
Lines 20–37	0	0	0	0	0	0	22	11	0	0	33
Lines 40–57	10	22	22	21	18	25	24	26	0	0	168
Lines 60–77	17	19	19	19	26	26	22	[1] 18	9	0	175
Lines 80–87	21	15	20	21	20	21	14	0	0	4	136
Lines 90–97	24	12	21	25	24	25	11	[1] 11	0	1	154
Lines 100–105	11	11	11	11	2	11	0	10	0	1	68
Lines 110–117	10	11	11	11	3	11	0	11	0	3	71
Lines 120–127	15	15	15	15	10	15	0	14	0	15	114
Line 130	6	6	6	6	3	6	0	6	0	6	45
Total	114	111	125	129	106	140	93	107	9	30	964

[1] Totals for cruise 18 do not include stations occupied on the seaward extension of lines 70 and 90.

southern California and adjacent Baja California. Less than 1 percent of the eggs and larvae were taken to the north of Point Conception (see table 4). The number (standard haul totals) of sardine eggs and larvae taken at each station occupied in 1950 is given in Ahlstrom (1952).

Although sardine eggs and/or larvae were taken off central Baja California on every cruise made in this area in 1950, most of them were collected during a 3-month period, March through May. In the spawning center off southern California and adjacent Baja California, over 99 percent of the sardine eggs and larvae were collected during April, May, and June. To the north of Point Conception eggs and larvae were obtained in June, July, and August. The season of occurrence in different parts of the spawning range was quite similar to that found in 1949.

The relation between temperature and distribution of sardine eggs was similar to that found in 1949. Approximately 98.5 percent of the sardine eggs were taken within a 3.5 degree temperature range, 12.5° to 16.0° C.

1951 SURVEY

During 1951, additional lines of stations were added within the spawning areas off Baja California, both in the area between Ensenada and Point San Eugenio and to the south of Point Abreojos. In all, 6 lines of stations were added, bringing to 18 the number of lines routinely occupied between Point Conception and central Baja California, all of which were spaced 40 miles apart.

Because of more intensive work south of Point Conception, the survey off northern California was less extensive than in 1949 and 1950. Stations were occupied to the north of San Francisco only on the July and August cruises, the time of year spawning had occurred in this area in previous surveys; however, the work between San Francisco and Point Conception was about as

TABLE 4.—*Occurrence and abundance of eggs and larvae, by month and area, in hauls made during 1950*

[Based on standard haul totals]

	Central California (lines 40–77)				Southern California (lines 80–93)				Northern Baja California (lines 97–105)				Central Baja California (lines 110–130)				All areas combined			
	Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae	
	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number
January																				
February	0	0	0	0	0	0	0	0	0	0	0	0	4	1,193	6	349	4	1,193	6	349
March	0	0	0	0	0	0	1	1	0	0	0	0	9	5,887	14	327	9	5,887	15	328
April	0	0	0	0	4	173	0	0	6	1,998	5	139	12	25,487	13	1,947	22	27,658	18	2,086
May	0	0	0	0	7	855	6	353	5	136	14	734	8	5,149	11	3,321	20	6,140	31	4,408
June	6	378	4	15	9	5,733	15	1,007	0	0	6	298	5	249	5	10	20	6,360	30	1,320
July	1	2	5	20	1	22	5	19	0	0	1	3	3	379	3	27	5	403	14	69
August	1	3	2	15	0	0	0	0									1	3	2	15
September	0	0	0	0	0	0	0	0	0	0	0	0	1	59	3	16	1	59	3	16
October	0	0	0	0													0	0	0	0
November									0	0	0	0	0	0	0	0	0	0	0	0
December																				
Total	8	383	11	50	21	6,783	27	1,380	11	2,134	26	1,164	42	38,403	55	5,997	82	47,703	119	8,591

intensive as previously. No stations were occupied off Oregon.

Beginning with the August cruise a number of inshore stations were added, and as a result, offshore work was somewhat reduced. At the same time, routine investigation of shore temperatures between San Francisco and central Baja California was begun. The additional inshore stations have proved exceedingly valuable for sampling off-season sardine spawning, especially off central Baja California. During three cruises of 1951, spaced at 3-month intervals, coverage was extended to Cape San Lucas. The stations occupied during 1951 are illustrated in figure 5.

The month-by-month coverage in different parts of the survey area is summarized in table 5. Including the tows made at 29 nonroutine stations occupied off central California during both September and October, 1,440 plankton hauls were made at stations in 1951. Of these, 288 were taken north of Point Conception, 597 between Point Conception and Cape San Quintin, 466 off central Baja California, and 89 off southern Baja California.

TABLE 5.—*Stations occupied monthly during survey cruises, 1951*

	January (cruise 21)	February (cruise 22)	March (cruise 23)	April (cruise 24)	May (cruise 25)	June (cruise 26)	July (cruise 27)	August [1] (cruise 28)	September [1] (cruise 29)	October [1] (cruise 30)	November [1] (cruise 31)	December [1] (cruise 32)	Total
Lines 20–30	0	0	0	0	0	0	0	0	0	0	0	0	0
Lines 40–57	0	0	0	0	0	0	23	22	0	0	0	0	45
Lines 60–77	15	0	0	22	21	26	24	20	[2] 41	[2] 40	20	14	243
Lines 80–87	16	13	14	21	11	19	8	12	11	13	12	9	159
Lines 90–97	25	25	25	25	25	24	22	24	15	15	14	12	251
Lines 100–107	21	14	20	22	22	18	7	11	14	14	12	12	187
Lines 110–117	19	18	19	19	19	19	2	10	9	9	9	9	161
Lines 120–127	15	14	15	15	15	15	13	17	12	15	13	9	168
Lines 130–137	14	14	14	14	14	15	10	13	10	10	9	0	137
Lines 140–157	0	0	30	0	0	34	0	0	25	0	0	0	89
Total	125	98	137	138	127	170	109	129	137	116	89	65	1,440

[1] Totals for cruises 28 through 32 include 17 to 24 additional inshore stations added to the regular grid pattern beginning with cruise 28.
[2] Included in the total of lines 60–77 on cruises 29 and 30 are 29 closely spaced inshore stations, not a part of the regular grid pattern.

A greater depth stratum was sampled in oblique net hauls made during 1951 than in preceding years. Where depth of water permitted, the net was lowered with 200 meters of wire out, instead of 100 meters as had been routinely used on earlier cruises. The actual depth reached by the net averaged approximately 130 meters. One of the chief reasons for increasing the depth of the hauls was to be certain of sampling completely the mixed layer above the thermocline on offshore stations. The deeper hauls also provided better sampling of the general plankton, and of the larvae of a number of species of fish, including hake and anchovy.

It was definitely established in 1951 that sardine spawning took place in every month of the year off central Baja California (see table 6). Off-season

TABLE 6.—*Occurrence and abundance of eggs and larvae, by month and area, in hauls made during 1951*

[Based on standard haul totals]

	Central California (lines 40–77)				Southern California (lines 80–93)				Northern Baja California (lines 97–107)				Central Baja California (lines 110–137)				All areas combined			
	Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae	
	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number
January	0	0	0	0	0	0	0	0	0	0	0	0	5	3,005	2	82	5	3,005	2	82
February	------	------	------	------	1	32	1	7	0	0	1	2	5	10,465	6	297	6	10,497	8	306
March	------	------	------	------	2	22	3	6	3	23	3	4	13	61,226	10	871	18	61,271	15	881
April	0	0	0	0	6	72	7	148	6	491	7	98	14	16,729	16	1,543	26	17,292	30	1,789
May	0	0	0	0	4	2,265	3	55	8	598	8	531	12	18,163	20	2,930	24	21,026	31	3,516
June	1	4	1	2	6	827	6	73	7	2,182	8	125	3	34	13	1,483	17	3,047	28	1,683
July	0	0	0	0	3	56	3	24	0	0	0	0	3	1,855	5	67	6	1,911	8	91
August	0	0	0	0	0	0	0	0	1	26	0	0	5	2,044	12	1,279	6	2,070	12	1,279
September	0	0	0	0	0	0	0	0	0	0	0	0	2	89	8	84	2	89	8	84
October	0	0	0	0	0	0	0	0	0	0	0	0	3	4,652	4	139	3	4,652	4	139
November	0	0	0	0	0	0	0	0	0	0	0	0	2	1,248	5	729	2	1,248	5	729
December	0	0	0	0	0	0	0	0	0	0	0	0	4	330	9	416	4	330	9	416
Total	1	4	1	2	22	3,274	23	313	25	3,320	26	760	71	119,840	110	9,920	119	126,438	160	10,995

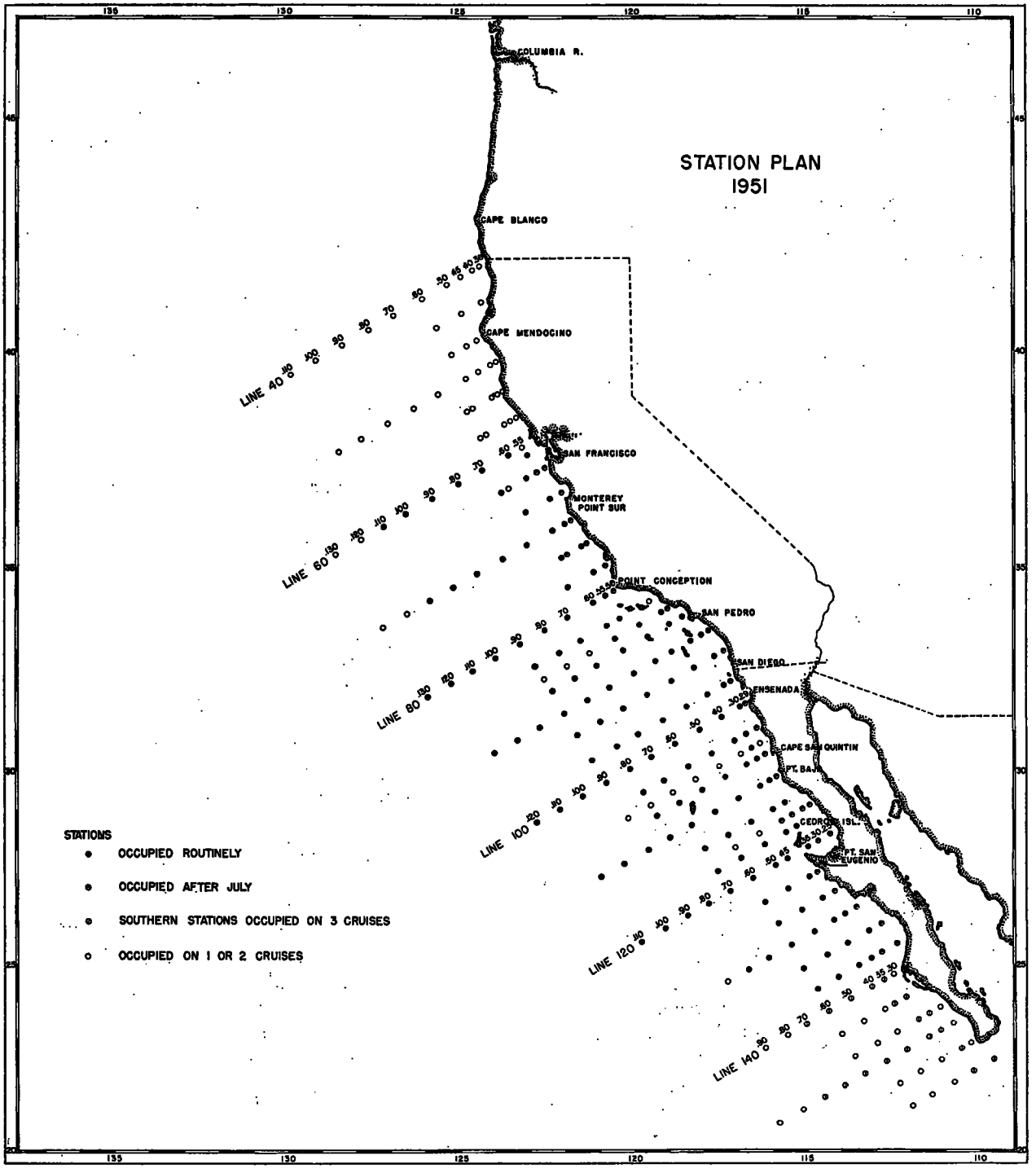

FIGURE 5.—Location of stations occupied during survey cruises made in 1951.

spawning was found to be confined mainly to Sebastian Viscaino Bay.

As in previous years, spawning was mostly confined to two centers: the more important, off central Baja California, the other, off southern California and adjacent Baja California. The latter had declined in importance since 1950. Practically no spawning was found to the north of Point Conception, and very little off southern Baja California. The number (standard haul total) of sardine eggs and larvae taken at each station occupied in 1951 is given in Ahlstrom (1953).

The relation between temperature and spawning was found to be more complex than previously supposed. During the first 6 months of 1951, approximately 98.7 percent of the sardine eggs were taken within a 3-degree temperature range, 13.5° to 16.5° C., but in the off-season, spawning occurred at much higher temperatures, mostly over 19° C.

ESTIMATING ABUNDANCE OF SARDINE EGGS, 1950 AND 1951

Enumeration of the total number of eggs spawned each season is prerequisite to the objectives of our research on the sardine, and the information is of value in several phases of the research. An estimate of the number of eggs spawned is one of the values needed in determining survival rate of larvae during the period of their planktonic existence. It can be used in conjunction with data on fecundity to obtain an estimate of the size of the spawning stock. The distribution of sardine eggs affords, at present, the only reliable information on the distribution of the sardine spawning stock during the spawning period.

It is possible that the extent of the area over which sardine spawning takes place may have an important bearing on the success or failure of year classes of sardines. The 1939 year class, an exceptionally large one, is known to have resulted from very widespread spawning. It is likely that spawning was equally widespread during the warm year of 1931 (*cf.* Hart 1943: 59), a season that produced another successful year class. The sardine spawning area has been contracting each year during the recent survey period, and the year classes have been below average.

The egg, or embryonic stage, is only the first of several stages concerning which information is needed in studying the rate of replenishment of the sardine stock through its productive processes. Others include larval and juvenile stages. Our research is presently limited to those stages that can be sampled by quantitative plankton techniques, i. e., eggs and larvae. Surveys of the distribution and abundance of juveniles are being conducted by the Bureau of Marine Fisheries of the California Department of Fish and Game (Phillips and Radovich 1952).

The methods used to obtain an estimate of the number of sardine eggs spawned in a year have been discussed in detail by Sette and Ahlstrom (1948). The basic data have been obtained from systematic sampling at regular time intervals at a number of stations distributed rather evenly through space. The data from each cruise have been treated as a problem of integration over space, and the combining of the data from the monthly cruises as a problem of integration on time. Two important assumptions underlie this method of treatment: (1) The distribution of egg concentrations through space and through time are continuous, and (2) the egg concentration gradients between points in space and time are linear. A number of special studies have been made in the past 2 years to test the validity of these assumptions. As the material is still under study, the findings are not available for inclusion in this paper. It appears unlikely that the results will materially alter our methods of estimation; rather, they should aid us in assigning values to the reliability of our estimates.

DEFINITION OF SYMBOLS

For consistency, I have used wherever possible the symbols used by Sette and Ahlstrom (1948); it was necessary to make several changes in the definitions of symbols, and to add several symbols.

c_i—Any of several estimates of the number of sardine eggs spawned per day in a standard area representing 10 square meters of sea surface at the ith station.

c_i'—The total number of sardine eggs in a standard haul or standard area at the ith station.

c_i''—The total number of sardine eggs in a standard haul at the ith station belonging to "complete" age categories, i. e., c_i' less incomplete age categories.

$\bar{c}_i'$—Any of several estimates of c_i, derived by dividing c_i' by the number of days' eggs represented in the haul at the ith station.

$\bar{c}_i'$—An estimate of c_i, derived by dividing c_i' by the number of complete age categories.

$\bar{c}_{i_d}'$—An estimate of c_i, derived by dividing c_i' by d.

$\bar{c}_{i_g}'$—An estimate of c_i, derived by dividing c_i' by g.

d_i—An estimate for each station of the time in days from spawning to hatching, determined from the relation between rate of development and temperature at the 10-meter level.

g_i—The total number of age categories, complete or incomplete, represented in a standard haul at the ith station.

t_i—The time weighting given to the ith station, equal to one-half the time elapsing since the preceding occupancy plus one-half the time elapsing prior to the succeeding occupancy.

w_i—The weighting factor for space, in standard areas, that is proportional to the area of the polygon assumed to be presented by the ith station on a given cruise.

C—The estimated number of eggs spawned over the complete survey area during the period of a cruise, according to

$$C=\Sigma(c_i w_i t_i)$$

C_s—The estimated number of eggs in the survey area during the period of survey; i. e., the sum of C for all cruises.

C_S—The estimated number of eggs spawned over the complete survey area during the spawning season.

The steps followed in obtaining the monthly and yearly estimates of egg numbers will be briefly described.

DETERMINING NUMBER OF EGGS SPAWNED PER DAY

The number of eggs taken in any given haul has been made comparable with the numbers from other samples by referring all collections to a common basis—the number of eggs under a standard area of 10 square meters. The number of eggs taken under a standard area may represent an accumulation of eggs from as many as 4 days' spawning or as few as 2 (occasionally 1 day's), depending on the water temperature at which they have been developing. Incubation is slower at lower temperatures, more rapid at higher temperatures (Ahlstrom 1943), hence it is necessary to determine for each collection the number of eggs spawned per day.

Two methods have been employed in estimating the number of eggs spawned per day, and estimates based on both methods will be given. The simpler of the two methods is to divide the total number of eggs in a standardized sample by the estimated number of days from spawning to hatching, as determined from the relation between rate of development and temperature. In previous studies (Ahlstrom 1943), the temperature at the 15-meter level was used in determining the relation between temperature and rate of development of sardine eggs. Temperature determination at this level, being an interpolated value, is not always readily available, but temperatures at the 10-meter level, measured directly from reversing thermometers, are available soon after the completion of each cruise. The 10-meter temperatures are now being used, and for most stations they are quite similar to the temperatures at 15 meters. The original choice of the 15-meter level had been based on the results of several series of horizontal hauls made with closing nets (*cf.* Silliman 1943). Most sardine eggs had been found to occur above a depth of 20 meters, usually between 10 and 20 meters, although in several series the largest concentration occurred within the upper 10 meters. Hence, there is as much justification for using the temperature at 10 meters as at 15 meters.

Estimates of the duration of the incubation period (time from spawning to hatching) are approximations. It is difficult to determine the exact duration of this period since embryos seldom are obtained in the act of hatching; however, our collections contain abundant material of eggs in the stage of development immediately preceding hatching. A determination has been made of the relation between water temperature at the 10-meter level and the rate of development of eggs to this stage. I have utilized data from 7 years of survey that met the following requirements: (1) At least 5 late-stage eggs in the sample, and (2) a nearly uniform temperature throughout the upper 20-meter stratum (difference between surface, 10- and 20-meter depths should not exceed 0.5° C.). Consequently, the determination is relevant not only for the 10-meter level, but for the upper 20-meter depth range. The regression line shown in figure 6 is very similar to that given for this stage by Ahlstrom (1943: fig. 1).

The incubation period was estimated from the regression line by adding 1½ to 4 hours, depending on the temperature. Several independent means of checking the accuracy of these estimates have been used. Miller (1952) reported that the majority of artificially fertilized sardine eggs,

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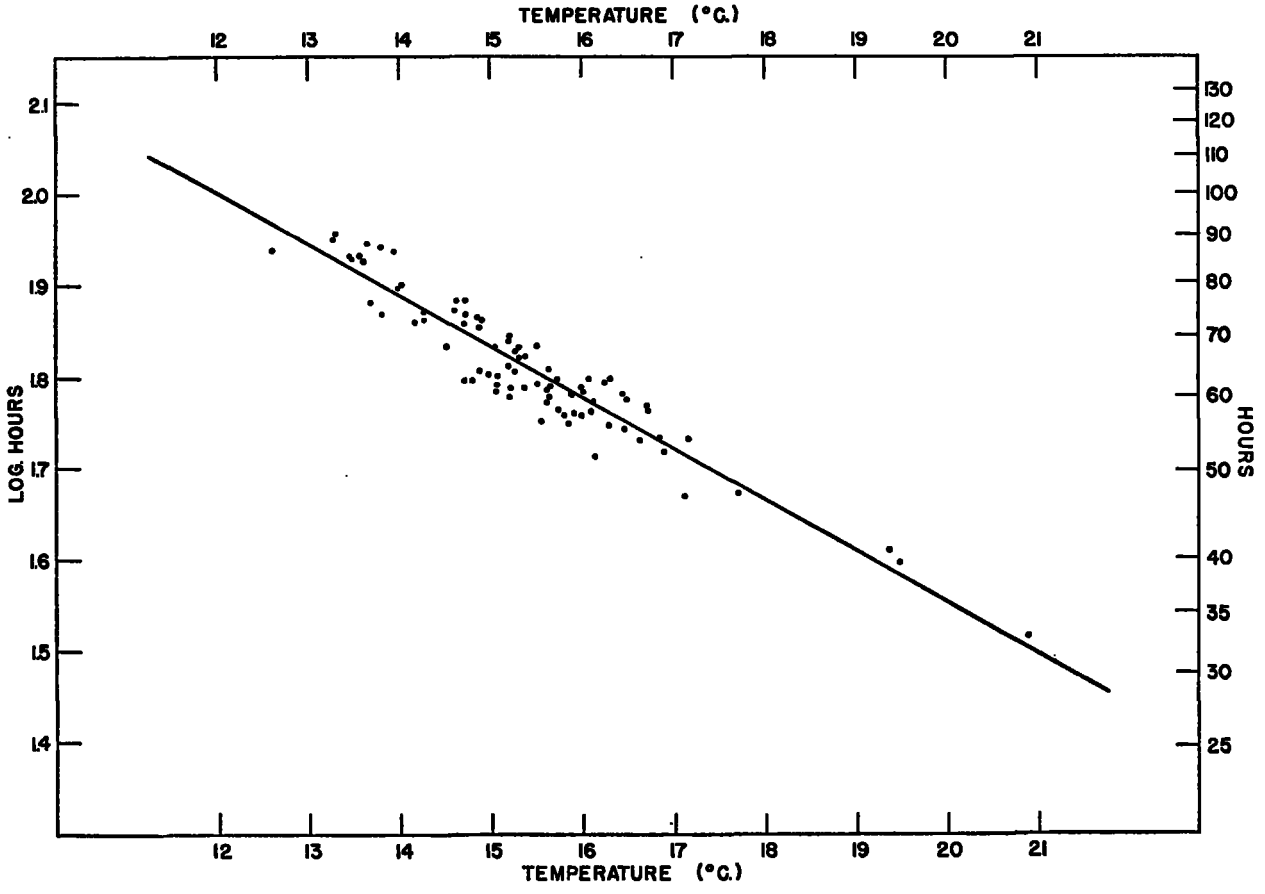

FIGURE 6.—Regression diagram showing influence of temperature (°C.) on time of development (log hours) of sardine eggs to the stage of development immediately preceding hatching. The linear-regression line was fitted to the scatter of points by the method of least squares. Data for the linear-regression line, based on the formula $y=a+bx$: $\bar{x}=15.40$, $\bar{y}=1.809$, $a=2.67$, $b=-0.0558$, s (standard error of estimate)$=0.0258$.

reared at a constant temperature of 16.8° C., hatched between 54 and 56 hours after fertilization. My estimate for incubation at this temperature is 54 hours. A comparison was made of the average incubation period for sardine eggs as estimated from temperature data and the average number of age categories represented in the same hauls for the 1950 and 1951 seasons. The agreement is very close.

Average accumulation of eggs (in days):	*1950*	*1951*
Determined from regression of time of development on temperature	3.20	2.685
Determined from age categories	3.16	2.760
Ratio	1.013	0.972

The alternative method of determining the number of eggs spawned per day requires separation of the eggs in each sample into the several age categories represented. Although time consuming, the separation seldom presents any difficulty, even when one or more of the categories are represented by "zero" abundance. To obtain the average number of eggs spawned per day, the standard haul total is divided by the number of age categories involved. In practice, complicating features arise, owing to some collections having been made while spawning or hatching was actively taking place. There are two alternatives for dealing with this problem, either use all age categories whether complete or incomplete, or set up criteria for identifying incomplete age categories, and eliminate these from consideration when determining the per-day spawning at a station.

An age category may be incomplete because a haul was made while spawning was taking place.

Based on the time of collection of newly spawned eggs, spawning was found to be confined mostly to the 4-hour period from 8 p. m. to midnight (Ahlstrom 1943). Nevertheless, the most recent day's eggs are underrepresented in the collections, not only during these hours, but between midnight and 6 a. m. as well (*cf.* Sette and Ahlstrom 1948: 520). Although the reason for this underrepresenation cannot be given, it is too marked to be ignored. Consequently, the youngest age category collected between 8 p. m. and 6 a. m. has been designated "incomplete."

It is more difficult to determine when an age category is incomplete because a portion of the oldest age group has hatched. A criterion, admittedly somewhat arbitrary, has been established: If over 80 percent of the eggs of the oldest age category are in the stage immediately preceding hatching, some of the eggs of the category would have hatched already, and the category should be judged incomplete.

The question may be asked, Why use two different methods for determining the number of eggs spawned per day? Why not standardize on a single method of determining c_i? The reason is that no one method is entirely satisfactory. Determination based on age categories would be satisfactory were it not for the problem of incomplete age categories. A strict adherence to the criteria established for eliminating incomplete age categories results, at times, in a "zero" estimate for a station at which a considerable number of eggs were collected. Furthermore, it is less than satisfactory in dealing with collections of sardine eggs that have developed at temperatures above 17° C. In such samples, because of the rapidity of development at higher temperatures, only 1 or 2 age categories are present and, too often, 1 or occasionally both have to be classed as incomplete.

Because of the complication arising from incomplete age categories, it seemed desirable to make estimates using all age categories to determine how serious an underrepresentation would result. For purposes of this study, the spawning day was assumed to begin at midnight. Newly spawned eggs obtained between 8 p. m. and midnight were not considered; otherwise, all categories were used.

Determination of per-day spawning using $\overline{c}_{id}$ is a much less direct method than that based on age categories. Based on the relation between rate of development and temperature, it introduces another variable, temperature, into every determination. Incorrect temperature values for a given station would result in an inaccurate estimate of c_i for that station. Occasionally we lack any temperature data for a haul, and for such samples this method is inapplicable. Furthermore, if egg concentrations at any given station occur at a different level than 10 meters, and if the temperature at that level is higher or lower than at the 10-meter level, the estimate will be inaccurate by the amount of this difference. Also, the temperature at the time of collection may not represent the temperature during the entire period of development. Another defect in this method of estimating per-day spawning is that the value for any individual determination is not as reliable as the estimate based on age categories.

DETERMINING THE AREA OF STATIONS

There are various methods of accomplishing a linear integration over space. Isometric lines commonly are employed to define areas of equal abundance. I have used this technique for illustrating distribution, but only occasionally for estimating total quantities. The objection to this method as a tool for estimating abundance is twofold: (1) There is some subjectivity in drawing the lines, with the result that the linear interpolation is approximate rather than precise, and (2) the method is time consuming.

A more precise method of integration over space, presented by Sette and Ahlstrom (1948), involves a concept which we have termed "area of station." A basic assumption of this procedure is that the catch at a particular station is not only an estimate of abundance at that point, but representative of the abundance over a larger area. To define this area for any particular station, a polygon is constructed, the sides of which are the perpendicular bisectors of lines drawn from that station to all surrounding stations. The result is a unique polygon surrounding each station (except peripheral ones). If the concentration at each station is then weighted to the area of the polygons and the values are summed, the resulting total value will be identical to that obtained by linear interpolation between stations. Because of the regularity in our spacing of stations and station lines, the polygon for most stations is a square, 40 miles on a side.

This has greatly simplified the determination of the area represented by each station. There has been no problem in assigning an area to peripheral stations. The boundary of an outer station on a line is defined as if there were another outlying station at the regular spacing of 40 miles. For delimiting the area of the stations on the most northerly line occupied during a cruise, the stations are treated as if the next adjacent line to the north had been occupied; similarly for the most southerly line. An advantage of this method of integration over space is that the sum of the weights given to the stations equals the area surveyed. It has the added advantage of being completely objective.

DETERMINING TIME WEIGHTING TO BE APPLIED TO A STATION

The concentration found at a station is assumed to represent the concentration for an adjacent period of time. The survey cruises are spaced at monthly intervals, hence the time interval represented by each cruise approximates 30 days; however, the time interval between successive occupancies of any given station is somewhat irregular. An individual time-weighting factor has been applied to each haul made at a station, which is equal to one-half the total time elapsing between the previous and succeeding occupancies of the station. By this method of weighting for time, a value is obtained that is exactly equivalent to a linear interpolation in time.

ESTIMATING EGG ABUNDANCE

An estimate of the number of sardine eggs spawned during each cruise (= month), was obtained from

$$C = \Sigma(c_i\, w_i\, t_i)$$

The seasonal total is a summation of the monthly estimates of egg numbers. Three estimates of abundance of sardine eggs are given for each season. All estimates make use of the same weighting factors for area and time, but differ in the method of determining c_i. These estimates, summarized by month and season, are given in table 7.

TABLE 7.—*Comparison of estimates of the number of sardine eggs, 1950 and 1951*

[In billions of eggs. Estimate based on formula $C = \Sigma(c_i\, w_i\, t_i)$]

Month	1950				1951			
	Estimate using—			Average	Estimate using—			Average
	$\bar{c}_i''$	$\bar{c}'_{i_g}$	$\bar{c}'_{i_d}$		$\bar{c}_i''$	$\bar{c}'_{i_g}$	$\bar{c}'_{i_d}$	
January					11,436	15,388	18,352	15,058
February	10,488	10,596	10,929	10,671	69,598	67,151	53,163	63,304
March	36,916	41,625	44,886	41,142	265,277	253,378	285,752	268,136
April	150,118	132,759	152,768	145,215	65,368	73,995	82,592	73,985
May	53,020	51,551	52,407	52,326	100,935	92,319	95,573	96,275
June	28,745	29,909	32,339	30,331	18,054	14,452	16,040	16,182
July	5,951	5,037	5,505	5,498	30,525	29,105	40,615	33,415
August	16	16	16	16	9,663	12,545	15,458	12,555
September	423	605	786	605	353	345	408	369
October					30,736	30,736	38,361	33,278
November	0	0	0	0	6,932	6,041	8,492	7,155
December					1,971	2,116	2,530	2,206
Total	285,677	272,098	299,636	285,804	610,848	597,571	657,336	621,918

For both years, the estimate using $\bar{c}'_{i_g}$ for determining per-day spawning is the lowest; the estimate using $\bar{c}_i''$ (per-day abundance based on complete age categories only) is intermediate; while the estimate based on $\bar{c}'_{i_d}$ is highest. For the 1950 season, the lowest estimate is 90.8 percent of the highest; for the 1951 season, the lowest is 90.9 percent of the highest.

How do estimates based on $\bar{c}'_{i_g}$, where use is made of all age categories, compare with estimates based on $\bar{c}_i''$, where per-day spawning is determined from complete age categories only? For 1950, the estimate using $\bar{c}'_{i_g}$ is 95.2 percent as high as that based on $\bar{c}_i''$; for 1951, it is 97.8 percent as high as the estimate based on complete age categories. Hence the underestimation resulting from the inclusion of incomplete age categories is not particularly important in either the 1950 or the 1951 determinations.

It undoubtedly is due to chance that the estimates of egg abundance using $\bar{c}'_{i_d}$ are larger than estimates otherwise obtained for 1950 and 1951. This is evident if a comparison is made of estimates of egg abundance based on this method with

those based on complete age categories for two different periods, as shown in the following tabulation:

Year and area	Estimate using $\bar{c}'_{id}$	Estimate using $\bar{c}''_i$	Ratio $\bar{c}'_{id}/\bar{c}''_i$	Difference $\bar{c}'_{id}$ from $\bar{c}''_i$
				Percent
1940 (southern California)	179,943	190,026	0.947	−5.3
1941 (southern California)	150,728	163,689	0.921	−7.9
1950 (all areas)	299,636	285,677	1.049	+4.9
1951 (all areas)	657,336	610,848	1.076	+7.6

Estimates obtained by this method are about as much lower than estimates based on complete age categories for 1940 and 1941 as they are higher than those for 1950 and 1951.

RELIABILITY OF ESTIMATES

An extended discussion of the reliability of estimates of egg abundance, determined in the manner previously outlined, is given by Sette and Ahlstrom (1948). Three sources of variability are of particular concern: Sampling variability of hauls, mortality during the incubation period, and errors introduced by interpolations.

Sampling variability of hauls.—To obtain information on sampling variability, duplicate hauls were taken at most stations occupied during 1940. The two hauls were taken successively, not simultaneously, but in an identical manner. In his analysis of variability in the numbers of sardine eggs in a set of 24 paired hauls, Silliman (1946) was able to separate the variability due to real differences in egg concentrations at different stations (time-place of hauls) from the sampling variability between the two hauls at a station. He found that differences in concentration between stations roughly accounted for 90 percent of the total variability. In regard to sampling variability between paired hauls at a station, he concluded that the number of eggs in one haul could not be considered significantly different (at the level $P=0.05$) from the number in the other unless it was about one-half or double.

Using Silliman's data as a basis for further analyses, Sette and Ahlstrom (1948) found that sampling variability became moderate for the sum of all hauls made during a season, amounting to about 5 percent at the one standard-deviation limit. The conclusion was reached that this source of error was not important enough to warrant attempting further refinements aimed at decreasing haul variability.

Inasmuch as routine sampling procedures have been improved during recent years, there is no reason to suppose that the variability from this source can introduce a significant error in determinations.

Mortality during the incubation period.—It takes one to several days for sardine eggs to develop from spawning to hatching. During this period some mortality is inevitable. Because of this mortality, one would expect to find a decrease in abundance of older stages as compared with younger. Contrary to expectation, the youngest age group of eggs is not much more abundant than the next older age category, as the following table illustrates:

Year	Number of eggs aged—	
	8–32 hours	32.1–56 hours
	c_a	c_b
1940	55,923	54,263
1941	30,586	33,980
1950	12,596	12,645
1951	28,986	26,588
Total	128,091	127,476

To ensure that only complete age categories were used in this tabulation, newly spawned eggs collected between 8 p. m. and 6 a. m. were omitted. Hence the youngest age group includes eggs collected between 6 a. m. and 6 a. m. estimated to be between 8 to 32 hours old, while the group a day older is estimated to be between 32.1 and 56 hours old. In determining the age of sardine eggs, the hour of 10 p. m. was selected as the "zero" point, as it represents the midpoint of spawning, which has been shown to be confined mostly to the 4-hour period, 8 p. m. to midnight (Ahlstrom 1943: 4). Age categories with eggs 56.1 to 80 hours old were not included in the tabulation, inasmuch as they would be "completely" represented in only a fraction of the hauls. The largest haul made during 1951 was omitted from the totals for that year. If included, the value for c_a for 1951 would be 34,805, for c_b, 47,880. This unusually rich haul, containing twice as many eggs as any other ever obtained on a regular survey cruise, would unduly influence the total. Otherwise the two age groups are about equally abundant, hence it may be as-

sumed that mortality during the embryonic period is negligible.

Errors introduced by interpolation.—Of greater consequence than the preceding sources of variability are the errors introduced by interpolations over space and time. As stated earlier, a basic assumption of the method followed is that each of the egg concentrations sampled has a linear continuity in space and time. As Sette and Ahlstrom (1948) pointed out, this assumption would tend toward validity as the spacing of stations in space and time became infinitesimally small. Hence the question arises whether the rather wide spacing of stations in space and time introduces too great a variability in our estimates.

Unfortunately, no definite answer to this problem is possible from routine survey data. The problem must be approached through a study of the distribution of sardine eggs in a limited area where stations can be closely spaced, and frequently occupied. Several such studies have been made during the past 2 years, but the data are only partly processed. Even these studies will afford only partial answers, but when supplemented by additional studies, they will permit a fairly precise evaluation of the variability introduced by interpolations.

GEOGRAPHICAL DISTRIBUTION OF SARDINE EGGS, 1950 AND 1951

Quantitative estimates of the number of sardine eggs taken monthly in different parts of the spawning range are given in table 8 for 1950 and in table 9 for 1951. The estimates are summarized by station lines. These are grouped into the following five areas:

1. Area north of Point Conception: Includes all stations occupied to the north of line 80. Lines 40–77 were routinely occupied during 1950, lines 60–77 during 1951.

2. Southern California area: From Point Conception to San Diego (lines 80–93). This area includes the region surveyed during 1940–41.

3. Northern Baja California area: From the International Border south to Point San Quintin (lines 97–107). The southern California and northern Baja California areas together make up one of the two major sardine spawning centers.

4. Central Baja California area: From Point Baja to Point San Juanico (lines 110–137). This constitutes the other major sardine spawning center.

5. Southern Baja California area: From Point San Juanico to Cape San Lucas (lines 140–157). This area is not routinely covered; however, it

TABLE 8.—*Estimated number of sardine eggs in survey areas, 1950*

[In billions. Estimate based on formula $C=\Sigma\ (\bar{c}_i'' w_i t_i)$]

	February (cruise 11)	March (cruise 12)	April (cruise 13)	May (cruise 14)	June (cruise 15)	July (cruise 16)	August (cruise 17)	September (cruise 18)	Total	Percent of total
Area north of Point Conception:										
Lines 40–57	0	0	0	0	0	0	16	0	16	
Lines 60–77	0	0	0	0	2,278	12	0	0	2,290	
Total	0	0	0	0	2,278	12	16	0	2,306	0.8
Southern California area:										
Line 80	0	0	0	0	570	0	0		570	
Line 83	0	0	0	331	0	0	0		331	
Line 87	0	0	36	0	23,345	0	0		23,381	
Line 90	0	0	0	15	402	137	0	0	554	
Line 93	0	0	768	6,612	507	0			7,887	
Total	0	0	804	6,958	24,824	137	0	0	32,723	11.4
Northern Baja California area:										
Line 97	0		1,707	145	0	0			1,852	
Line 100	0	0	14,475	0		0		0	14,475	
Sta. 105.35	0	0	61	54	0	0		0	115	
Total	0	0	16,243	199	0	0		0	16,442	5.8
Central Baja California area:										
Lines 110–117	0	50	7,319	710	418	0		0	8,497	
Line 120	10,468	4,122	5,466	40,184	0	5,802		0	66,042	
Line 123	0	1,338	73,921	3,568	72	0		0	78,899	
Line 127	0	0	937	0	0	0		0	937	
Line 130	20	31,406	45,428	1,401	1,153	0		423	79,831	
Total	10,488	36,916	133,071	45,863	1,643	5,802		423	234,206	82.0
Grand total	10,488	36,916	150,118	53,020	28,745	5,951	16	423	285,677	100.0
Percent	3.7	12.9	52.5	18.6	10.1	2.1	0	0.1	100.0	

TABLE 9.—*Estimated number of sardine eggs in survey areas, 1951*

[In billions. Estimate based on formula $C=\Sigma\,(\bar{c}_i''\,w_i t_i)$]

	January (cruise 21)	February (cruise 22)	March (cruise 23)	April (cruise 24)	May (cruise 25)	June (cruise 26)	July (cruise 27)	August (cruise 28)	September (cruise 29)	October (cruise 30)	November (cruise 31)	December (cruise 32)	Total	Percent of total
Area north of Point Conception:														
Lines 40–57							0	0					0	
Lines 60–77	0			0	0	0	0	0	0	0	0	0	0	
Total	0			0	0	0	0	0	0	0	0	0	0	0.0
Southern California area:														
Line 80	0	0	28	0	0	219	0	0	0	0	0	0	247	
Line 83	0	0	0	0	0	0	0	0	0	0	0	0	0	
Line 87	0	0	0	99	0	2,240	0	0	0	0	0	0	2,339	
Line 90	0	0	183	45	8,023	1,606	315	0	0	0	0	0	10,172	
Line 93	0	0	0	58	2,904	0	0	0	0	0	0	0	2,962	
Total	0	0	211	202	10,927	4,065	315	0	0	0	0	0	15,720	2.6
Northern Baja California area:														
Line 97	0	0	0	2,338	711	8,736	0	42	0	0	0	0	11,827	
Line 100	0	0	11	52	1,015	18	0	0	0	0	0	0	1,096	
Line 103	0	0	50	285	615	4,792	0	0	0	0	0	0	5,742	
Line 107	0	0	0	0	14	0	0	0	0	0	0	0	14	
Total	0	0	61	2,675	2,355	13,546	0	42	0	0	0	0	18,679	3.1
Central Baja California area:														
Line 110	0	0	0	15	558	0	0	0	0	0	0	0	573	
Line 113	0	0	2,953	4,569	51	0							7,573	
Line 115								0	0	28,922	0	0	28,922	
Line 117	0	0	9,129	31	138	34							9,332	
Line 120	1,026	52,336	75,122	18,189	18,744	359	26,396	6,916	306	1,814	6,932	1,933	210,073	
Line 123	9,897	17,262	177,177	24,718	40,784	0	0	162	47	0	0	38	270,085	
Line 127	130	0	257	11,330	27,344	0	0	0	0	0	0		39,061	
Line 130	383	0	367	3,639	34	0	0	2,543	0	0	0		6,966	
Line 133	0	0	0	0	0	0	3,814	0	0	0	0		3,814	
Line 137	0	0	0	0	0	0	0	0	0	0	0		0	
Total	11,436	69,598	265,005	62,491	87,653	393	30,210	9,621	353	30,736	6,932	1,971	576,399	94.4
Southern Baja California area:														
Line 140			0			0			0				0	
Line 143			0			50			0				50	
Line 147			0			0			0				0	
Line 150			0			0			0				0	
Line 153			0			0			0				0	
Line 157			0			0			0				0	
Total			0			50			0				50	0.0
Grand total	11,436	69,598	265,277	65,368	100,935	18,054	30,525	9,663	353	30,736	6,932	1,971	610,848	100.1
Percent	1.9	11.4	43.4	10.7	16.5	3.0	5.0	1.6	0.1	5.0	1.1	0.3	100.0	

was occupied during the November cruise of 1950, and during the March, June, and September cruises of 1951.

The distribution of sardine eggs as determined from the 1950 survey cruises is illustrated in figure 7. The concentrations shown at each station are cumulative totals for 8 monthly cruises made February through September. To facilitate comparison, the distribution of sardine larvae during 1950 is shown in an adjacent chart.

Similar charts for the 1951 survey period are shown in figure 8. To emphasize the restricted distribution of sardine spawning during the off-season, the location of sardine eggs during the latter part of the year, August through December, is shown as an inset, while the distribution during the main spawning period, January through July, is shown in the full-sized chart. For ready comparison, the distribution of sardine larvae during 1951 is given in a companion chart.

Estimates of the abundance of sardine eggs in different parts of the spawning range in 1950 and 1951 were as follows:

Areas	1950		1951	
	Number of eggs	Percent of total	Number of eggs	Percent of total
	Billions		*Billions*	
Area north of Point Conception	2,306	0.8	0	0
Southern California area	32,723	11.4	15,720	2.6
Northern Baja California area	16,442	5.8	18,679	3.1
Central Baja California area	234,206	82.0	576,399	94.4
Southern Baja California area	0	0	50	0
Total	285,677	100.0	610,848	100.1

Area north of Point Conception.—Sardine spawning off central and northern California has decreased each year during the period of survey. In 1949, there was evidence of fairly extensive spawning to the north of Point Conception. Sardine

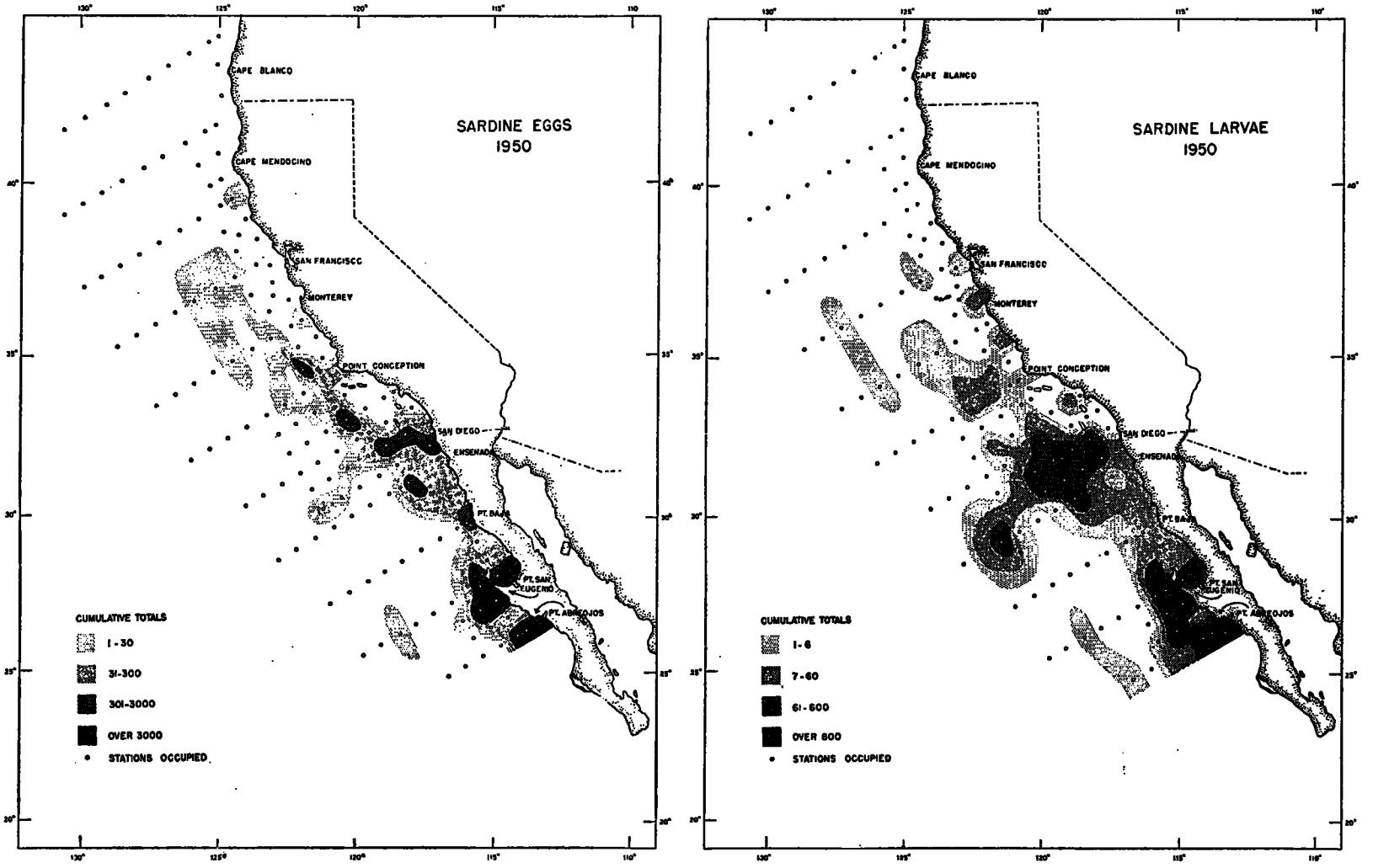

FIGURE 7.—Distribution and abundance of sardine eggs and sardine larvae during 8-month period, February through September, 1950.

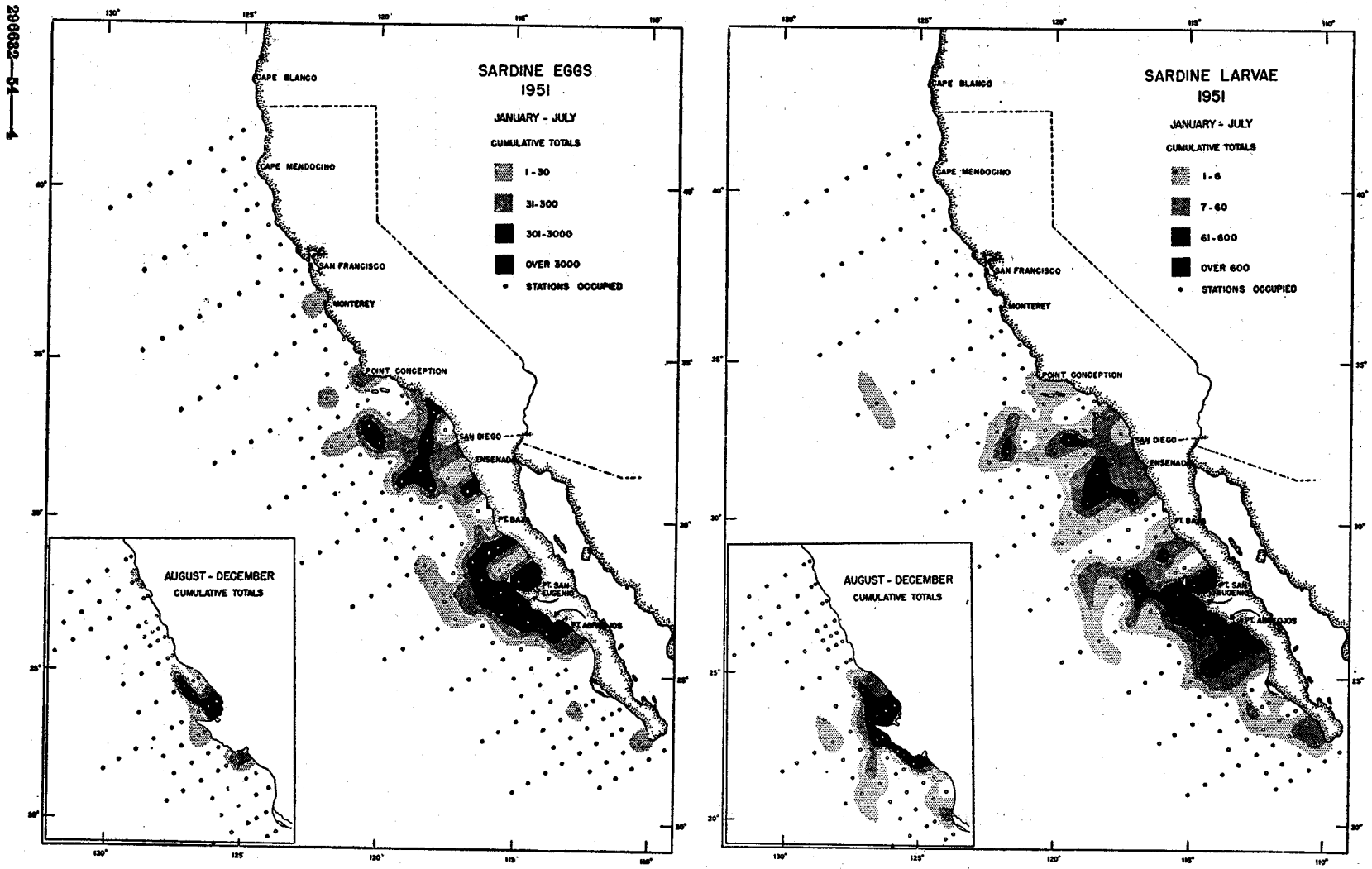

FIGURE 8.—Distribution and abundance of sardine eggs and sardine larvae during 1951. Distributions during the main spawning period, January through July, are shown in the main charts, while distributions during remainder of the year, August through December, are shown in the insets.

eggs were taken as far north as Cape Mendocino and one larva was taken off Oregon. A large number of sardine larvae were taken in a haul made off Point Sur. During 1950, there was evidence of widespread but light spawning off central California. Sardine spawning was almost absent from this area in 1951; only one egg and one larva were taken in hauls made to the north of Point Conception.

Southern California and northern Baja California areas.—Although the contributions of southern California and adjacent Baja California have been segregated in tables 8 and 9, the distribution of sardine spawning is continuous between these areas, and together they constitute one of the major centers of sardine spawning.

The importance of southern California as a sardine spawning area has been known for many years. Scofield (1934) first called attention to it, and the United States Fish and Wildlife Service conducted systematic surveys over a portion of the area during 1940 and 1941. In a subsequent report, the results obtained then will be compared with findings in this area during current surveys.

Spawning off southern California and adjacent Baja California may occur at considerable distances from shore. Sardine eggs have been collected about 250 miles offshore, and larvae at even greater distances; but large concentrations of eggs are seldom taken farther from shore than 150 miles.

Spawning in this center was less abundant in 1951 than in 1950, and a larger part of it occurred off northern Baja California. Decline for the center as a whole was about 33 percent in actual numbers of eggs taken. When expressed as a percentage of the total eggs taken throughout the spawning range, the decline appears more precipitous, the drop being from 17.21 percent to 5.63 percent.

Central Baja California area.—In recent years, this area has been the major sardine spawning center. The heaviest concentrations of sardine eggs have been taken between Cedros Island and Point Abreojos. During the 1950 season there were two areas of heavy spawning; one was located within a radius of 50 miles of Point San Eugenio, the other offshore from Point Abreojos. During 1951, heavy spawning was concentrated in the vicinity of Point San Eugenio. Egg estimates are not decreasing in amount in this area, as is the case in more northerly waters. As a consequence, the percentage contribution of this area has been increasing; in 1950 it amounted to 82 percent, while in 1951 it was over 94 percent.

Southern Baja California area.—Although this area has not been routinely covered, it was surveyed 4 times between November 1950 and September 1951. Sardine eggs were taken in only two hauls. If these collections were representative of the spawning off southern Baja California, this area is unimportant as a spawning center. Sardine eggs and larvae have been taken in most hauls made in Magdalena and Santa Maria Bays, however, and it is likely that sardines spawn there during much of the year. These bay areas are not included in the regular survey pattern.

DISTRIBUTION OF SPAWNING IN TIME, 1950 AND 1951

The seasonal abundance of sardine eggs in different parts of the spawning range is summarized in table 10, and is illustrated by a series of charts showing the monthly distribution of sardine eggs and larvae during 1950 and 1951 (figs. 9–28).

Area north of Point Conception.—Since 1949, sardine eggs have been collected off central and northern California during the 3-month period, June through August. In 1949, eggs were taken off Point Sur in June, off San Francisco in July, and off Cape Mendocino in August, suggesting a northward progression of spawning even within this area. In 1950, sardine eggs were taken as far north as San Francisco in June; however, the few eggs collected off northern California were obtained in August, as in 1949. The only haul containing sardine eggs from this area in 1951 was obtained in June.

Spawning had been found in this area as early as March, in the unusually warm year of 1931 (Scofield 1934). Hence, it is likely that spawning in this area will be early or late, depending on whether water temperatures are warmer or colder than usual. In recent years they have been colder.

Southern California and northern Baja California areas.—In recent years most of the sardine spawning in this center has been confined to a 3-month period, April through June. In 1950, 99.7 percent of sardine eggs were taken during these months; in 1951 over 98 percent. The 1950 and 1951 seasons appear to have been a month

TABLE 10.—*Abundance of sardine eggs, by month and area, 1950 and 1951*
[In billions. Estimate based on formula $C=\Sigma\,(c_i''' w_i t_i)$]

Month	Area north of Point Conception				Southern California and northern Baja California areas				Central Baja California area			
	1950		1951		1950		1951		1950		1951	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
January			0	0			0	0			11,436	2.0
February	0	0			0	0	(1)	0	10,488	4.5	69,598	12.1
March	0	0			0	0	272	0.8	36,916	15.8	265,005	46.0
April	0	0	0	0	17,047	34.7	2,877	8.4	133,071	56.8	62,491	10.8
May	0	0	0	0	7,157	14.6	13,282	38.6	45,863	19.6	87,653	15.2
June	2,278	98.8	(1)	0	24,824	50.5	17,611	51.2	1,643	0.7	393	0.1
July	12	0.5	0	0	137	0.3	315	0.9	5,802	2.5	30,210	5.2
August	16	0.7	0	0	0	0	42	0.1			9,621	1.7
September	0	0	0	0	0	0	0	0	423	0.2	353	0.1
October			0	0			0	0			30,736	5.3
November			0	0			0	0	0	0	6,932	1.2
December			0	0			0	0			1,971	0.3
Total	2,306	100.0	0	0	49,165	100.1	34,399	100.0	234,206	100.1	576,399	100.0

[1] Sardine eggs were collected, but when estimates were based on the formula $C=\Sigma\,(c_i''' w_i t_i)$, no values were obtained.

later than the spawning seasons of 1940 and 1941. This will be discussed in more detail in a subsequent report. Some spawning occurred off southern California from February to August in 1951.

Central Baja California area.—Sardine eggs have been collected off central Baja California in every month of the year; however, in 1950, the majority of sardine eggs were taken during a 3-month period, March through May. In 1951, the main spawning in this area was from February through May. The peak of spawning in 1951 was somewhat earlier than in 1950. The off-season spawning, especially that occurring from August through December, was largely confined to Sebastian Viscaino Bay. The off-season spawning was not adequately sampled in 1950.

Southern Baja California area.—This area has been surveyed too infrequently to permit an adequate determination of the season of spawning. In bays, such as Magdalena Bay, spawning probably occurs throughout the year.

DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF SARDINE LARVAE, 1950 AND 1951

A basic reason for conducting sardine larval studies is to test the widely held assumption that the early postembryonic period is one of the most critical periods, if indeed it is not the most critical period, in the life of a pelagic fish in regard to mortality. Infant mortality is high and it is variable. It is assumed that the success or failure of year classes of sardines and other fishes probably is determined during this period.

Theoretical considerations appear to justify this assumption. It is known, from a study of a number of fisheries, that there is considerable variation in the success of year classes. Good year classes have been recorded that were 50 times as large as poor ones (e. g., herring and cod). The sardine is more at the mercy of its environment during its planktonic existence than at any other period of its life. On hatching, the larva is small and defenseless. It lacks a functional mouth, pigmented eyes for vision, or fins for locomotion. It must develop in an environment where there is sufficient food of the right kind that it can obtain as soon as its yolk supply is depleted, or it will perish.

Studies on food requirements of the young sardine larva have shown that its initial food is composed almost entirely of copepod eggs and nauplii. The larva is severely restricted in the size of food it can utilize, and at first it is limited to food smaller than 80 microns in length.[2]

In addition to rigid food requirements, the small larva is at the mercy of a much larger group of predators than at any other period of life. Not only is it preyed on by many of the larger filter-feeding animals—fish, crustacea, and molluscs—but even by many organisms in the

[2] The food requirements of sardine larvae are being investigated by David Arthur, of Scripps Institution of Oceanography. Results were reported upon briefly in California Cooperative Sardine Research Program Progress Report, 1 January 1951 to 30 June 1952.

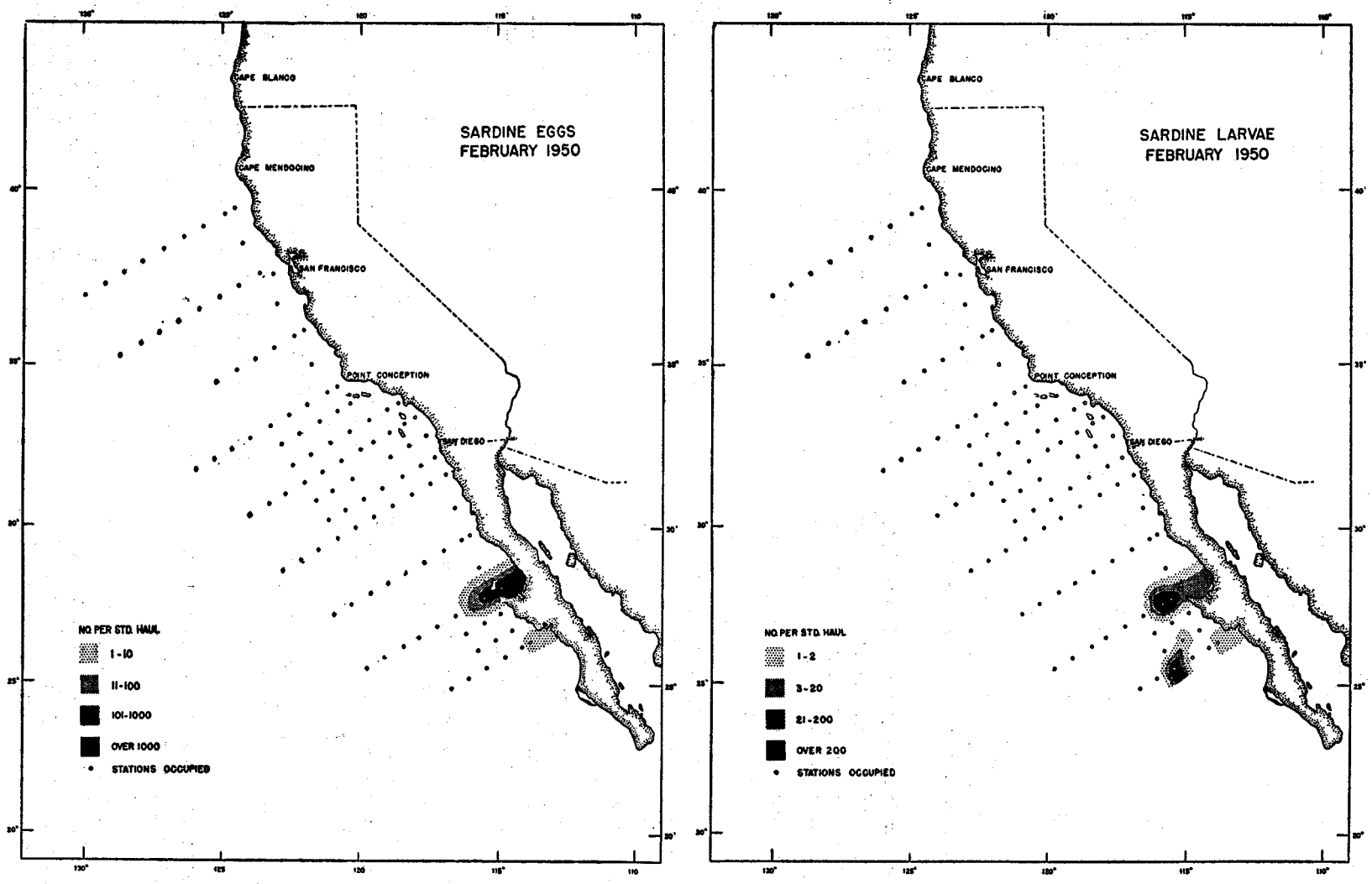

FIGURE 9.—Distribution and abundance of sardine eggs and larvae, February 1950.

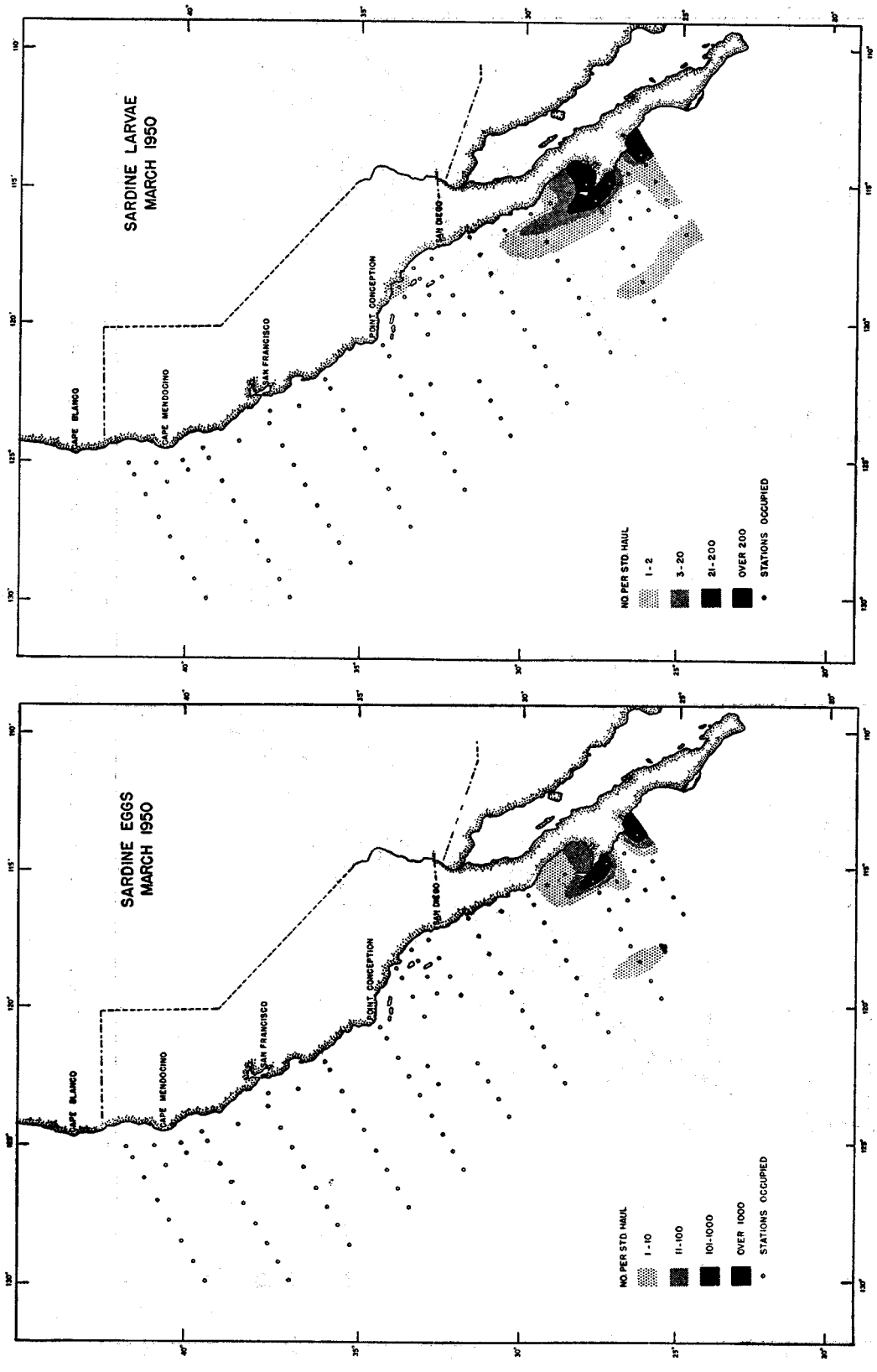

FIGURE 10.—Distribution and abundance of sardine eggs and larvae, March 1950.

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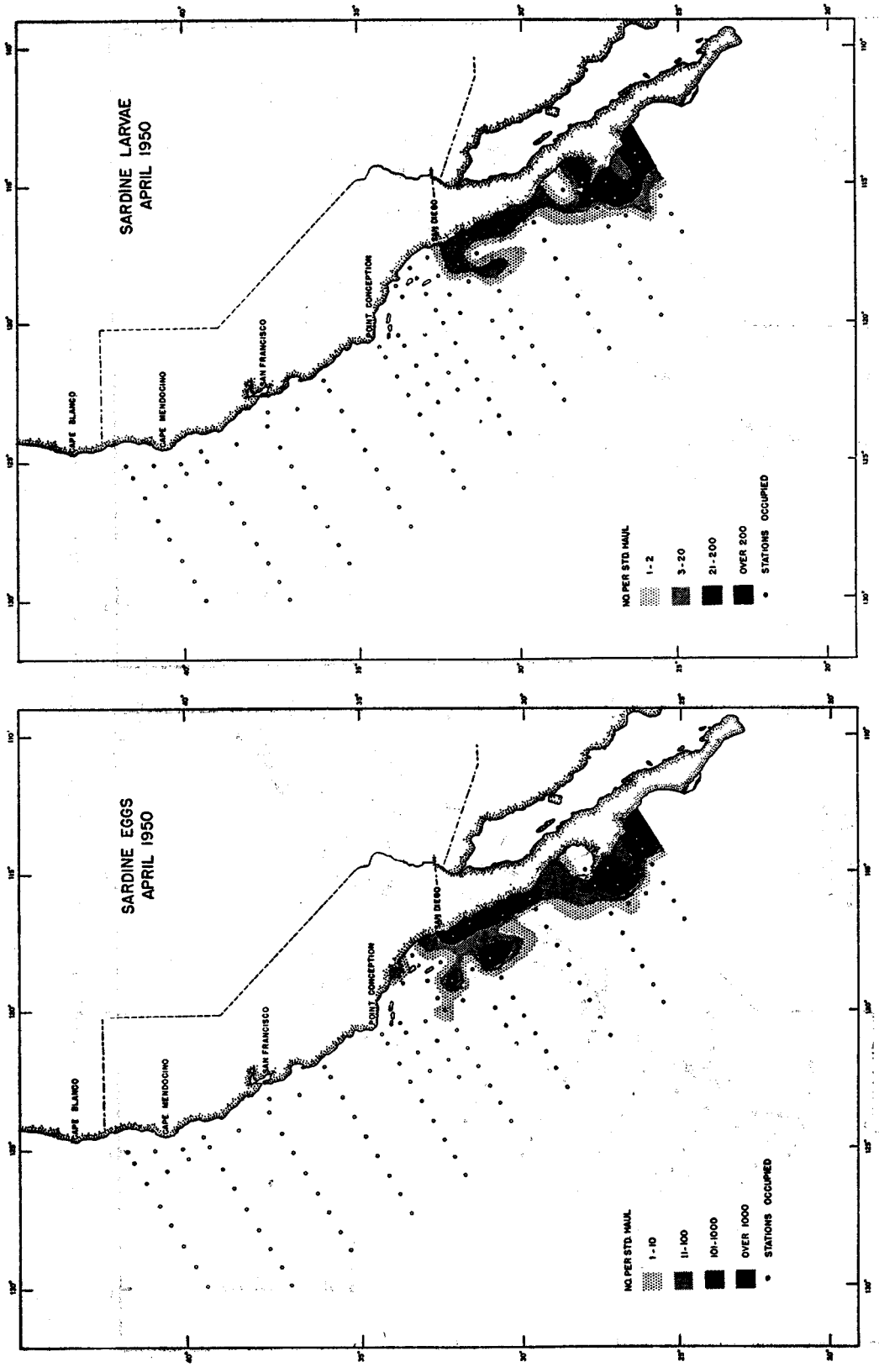

FIGURE 11.—Distribution and abundance of sardine eggs and larvae, April 1950.

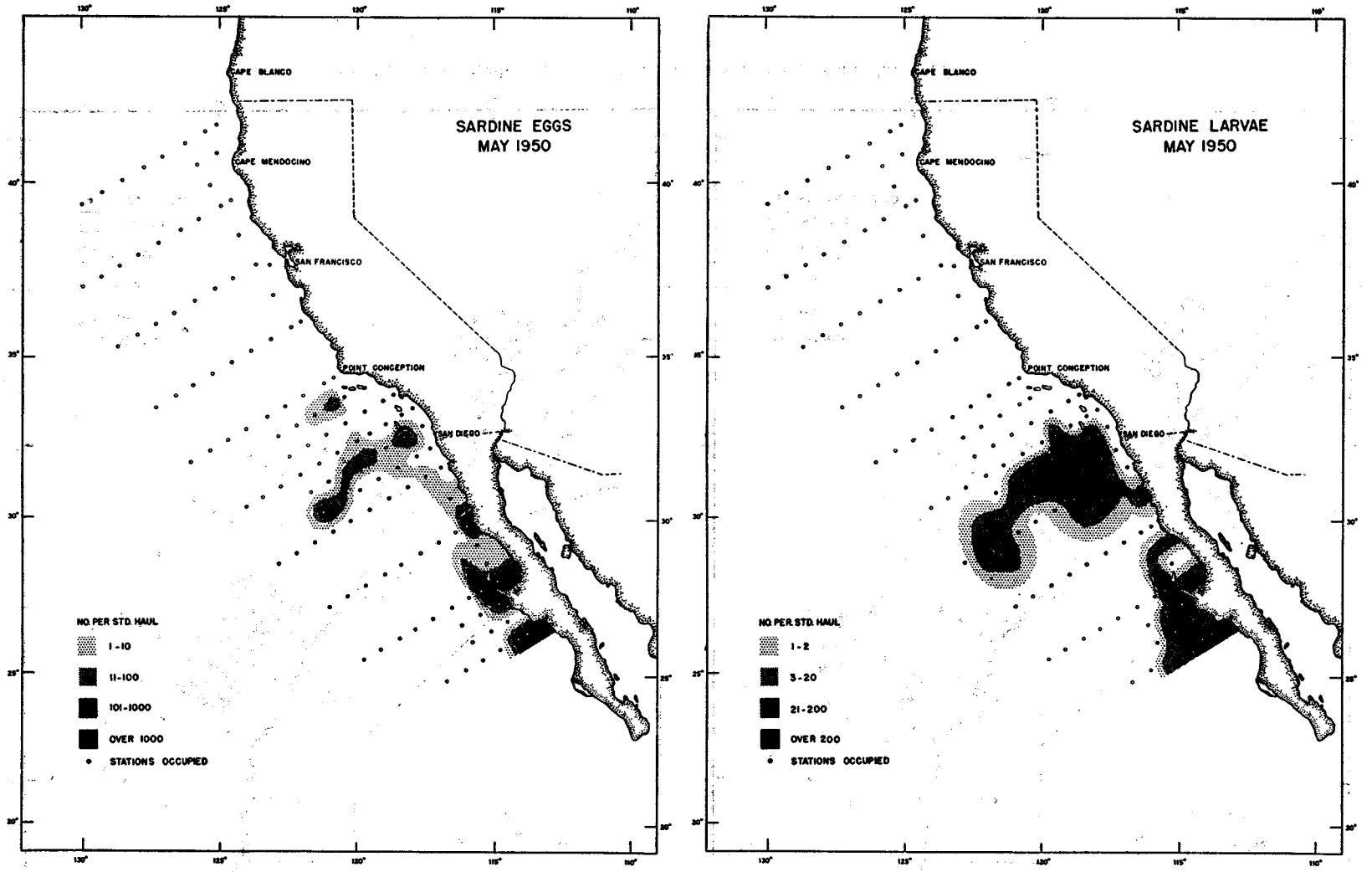

FIGURE 12.—Distribution and abundance of sardine eggs and larvae, May 1950.

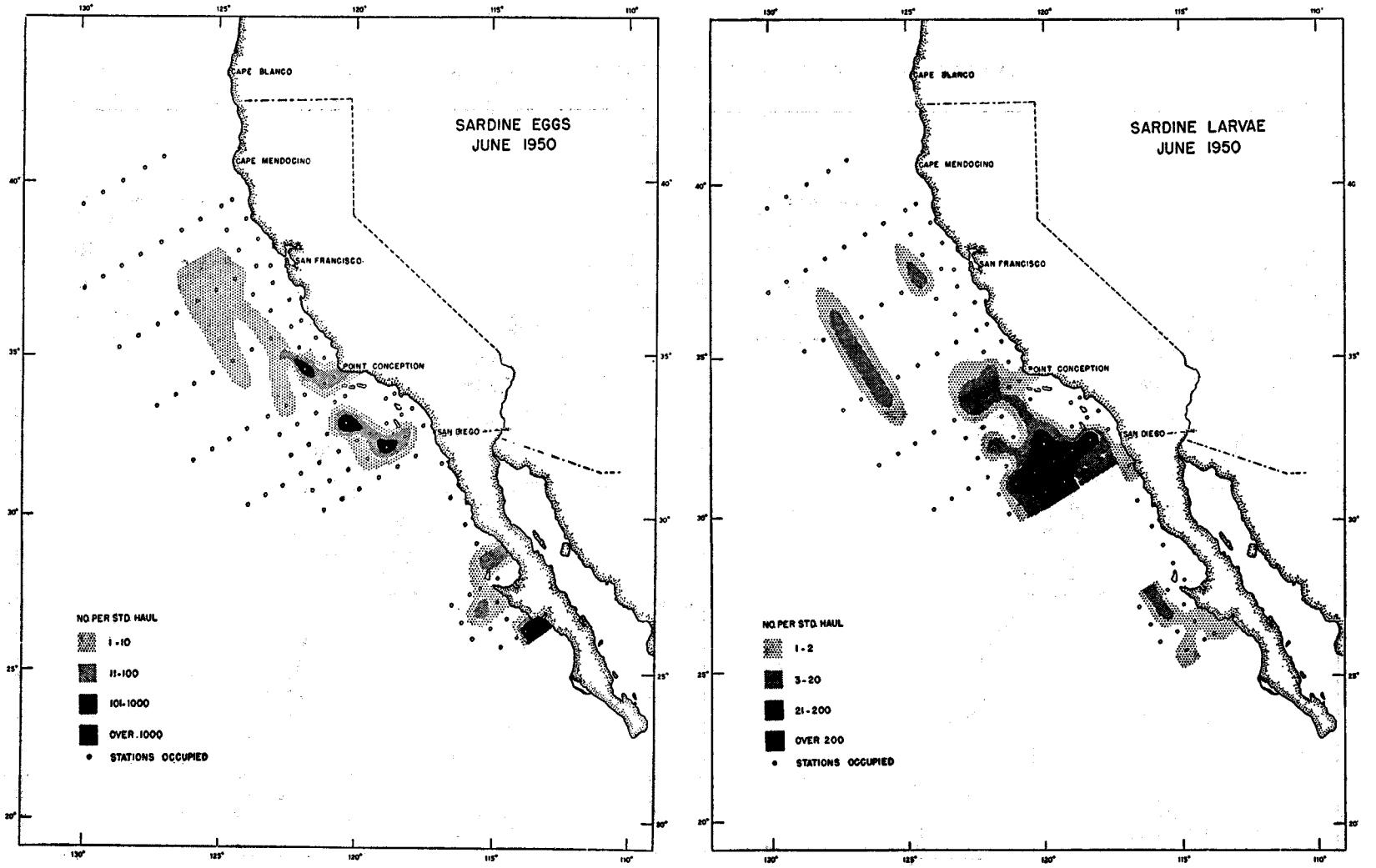

FIGURE 13.—Distribution and abundance of sardine eggs and larvae, June 1950.

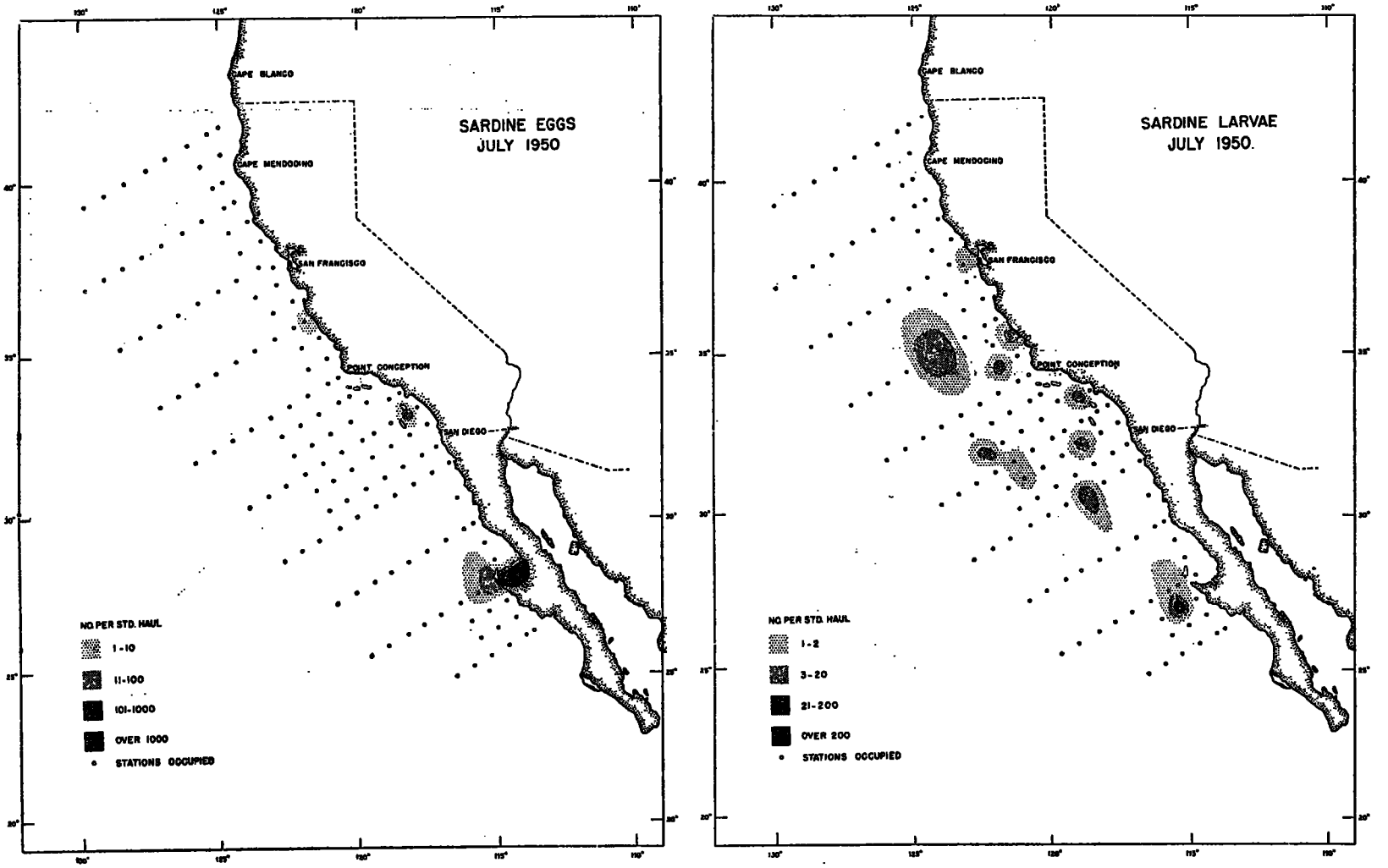

FIGURE 14.—Distribution and abundance of sardine eggs and larvae, July 1950.

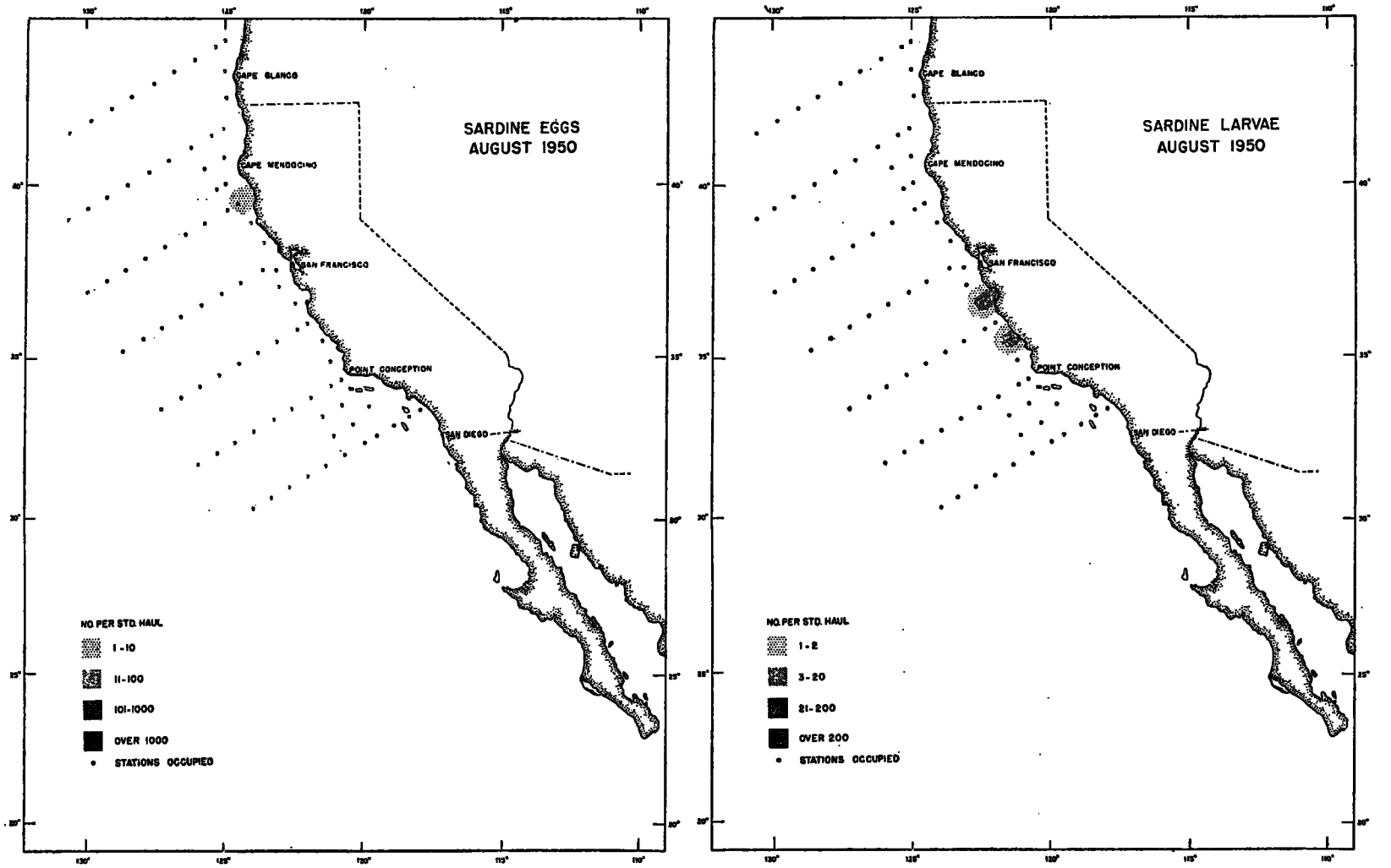

FIGURE 15.—Distribution and abundance of sardine eggs and larvae, August 1950.

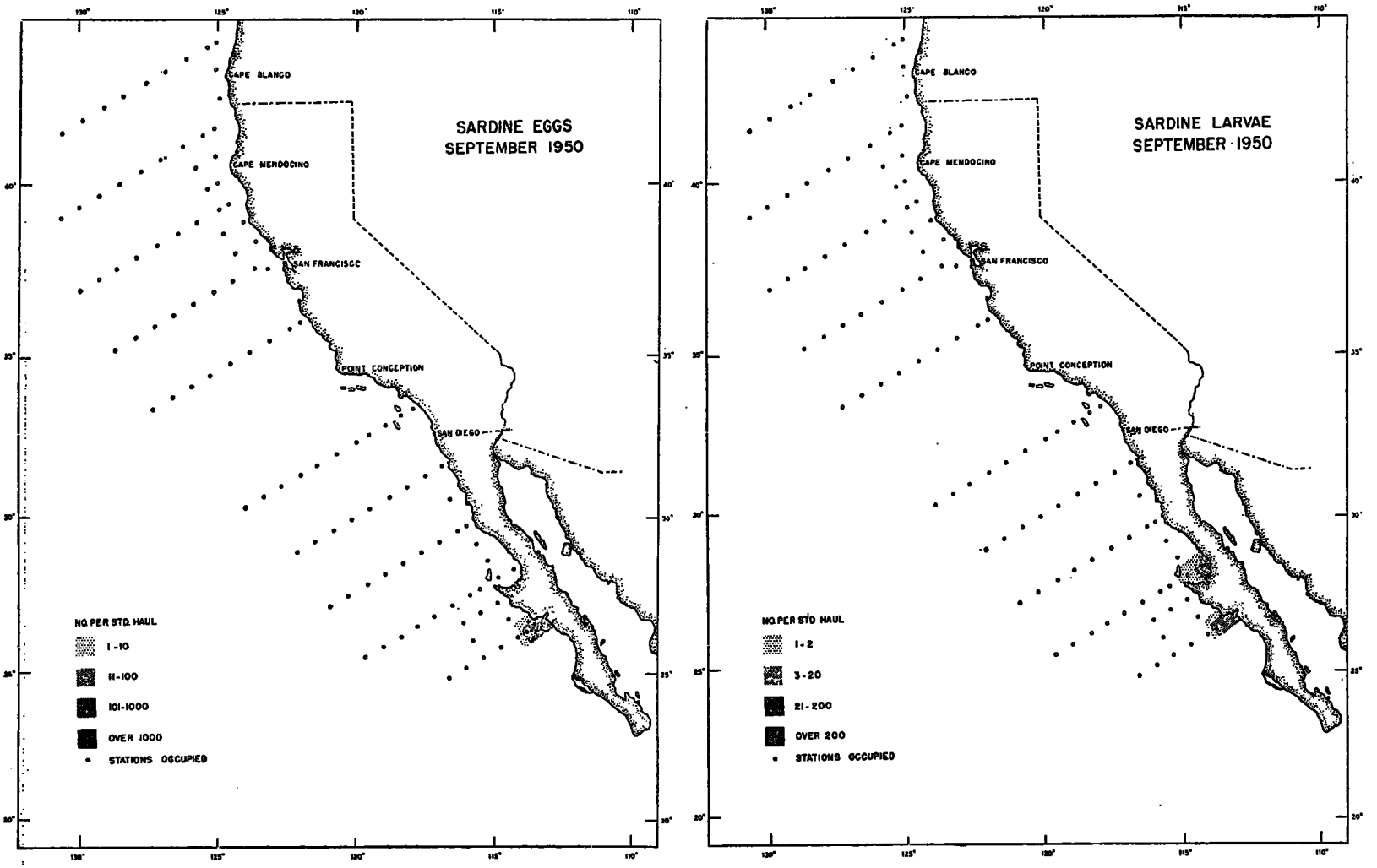

FIGURE 16.—Distribution and abundance of sardine eggs and larvae, September 1950.

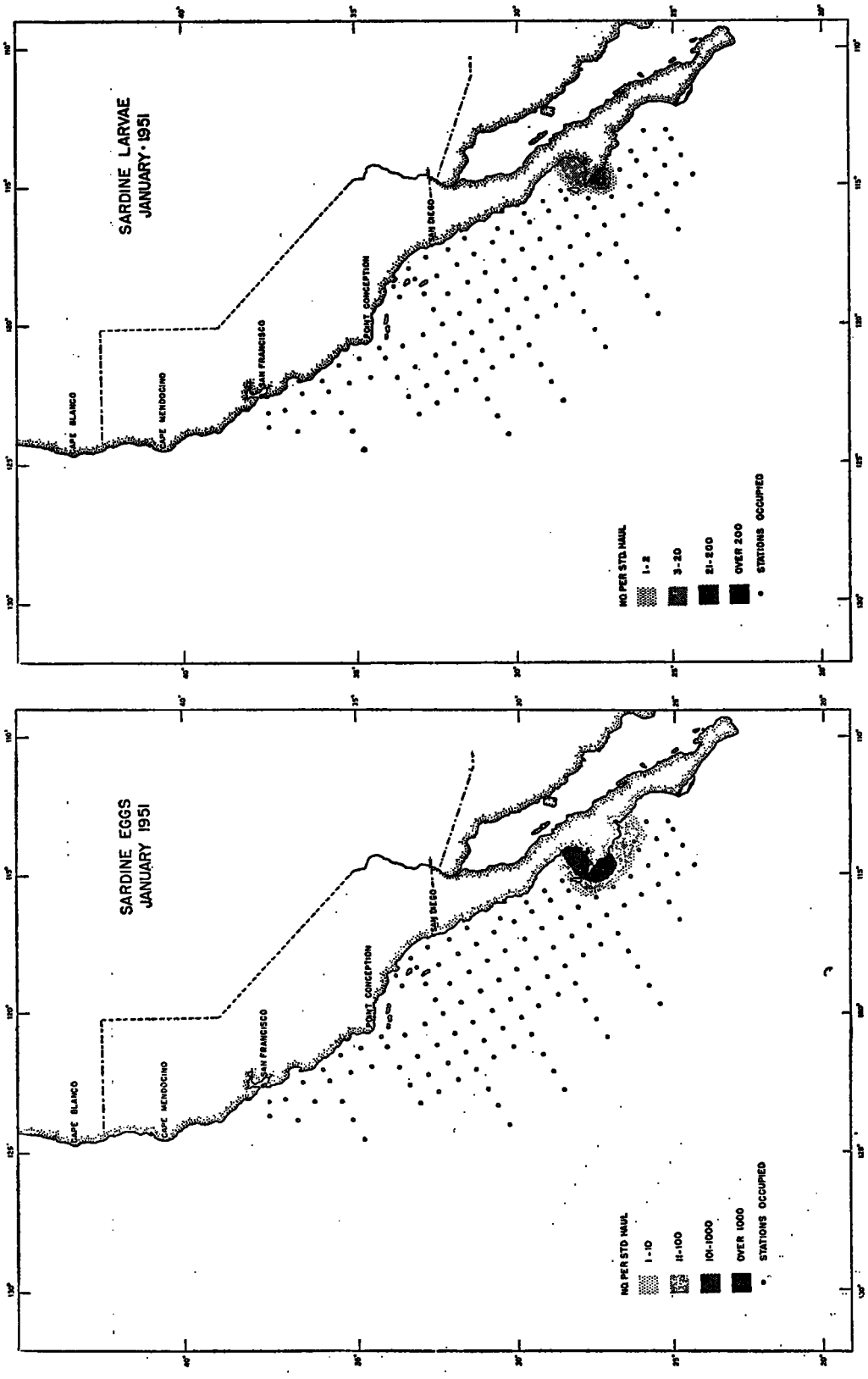

FIGURE 17.—Distribution and abundance of sardine eggs and larvae, January 1951.

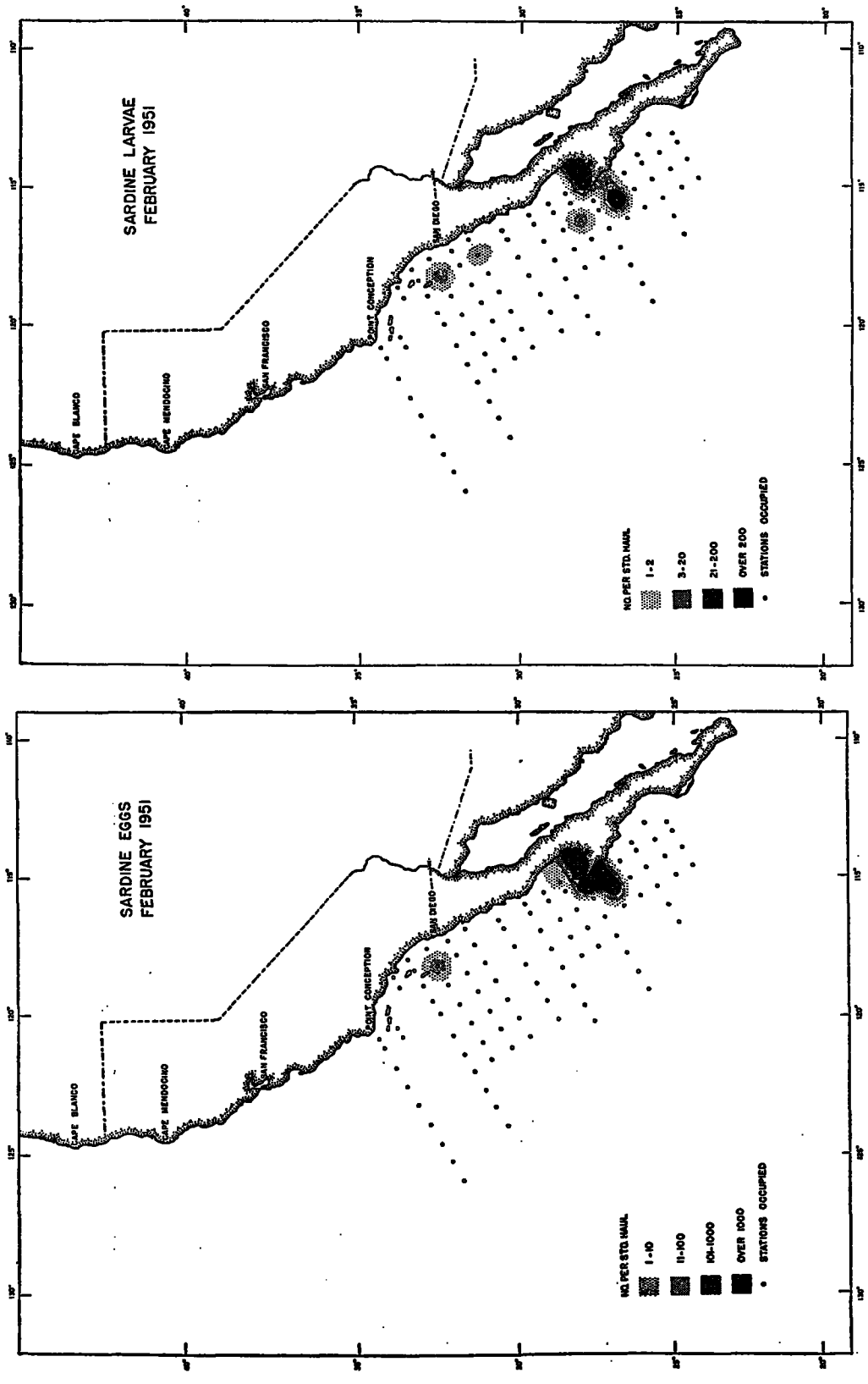

FIGURE 18.—Distribution and abundance of sardine eggs and larvae, February 1951.

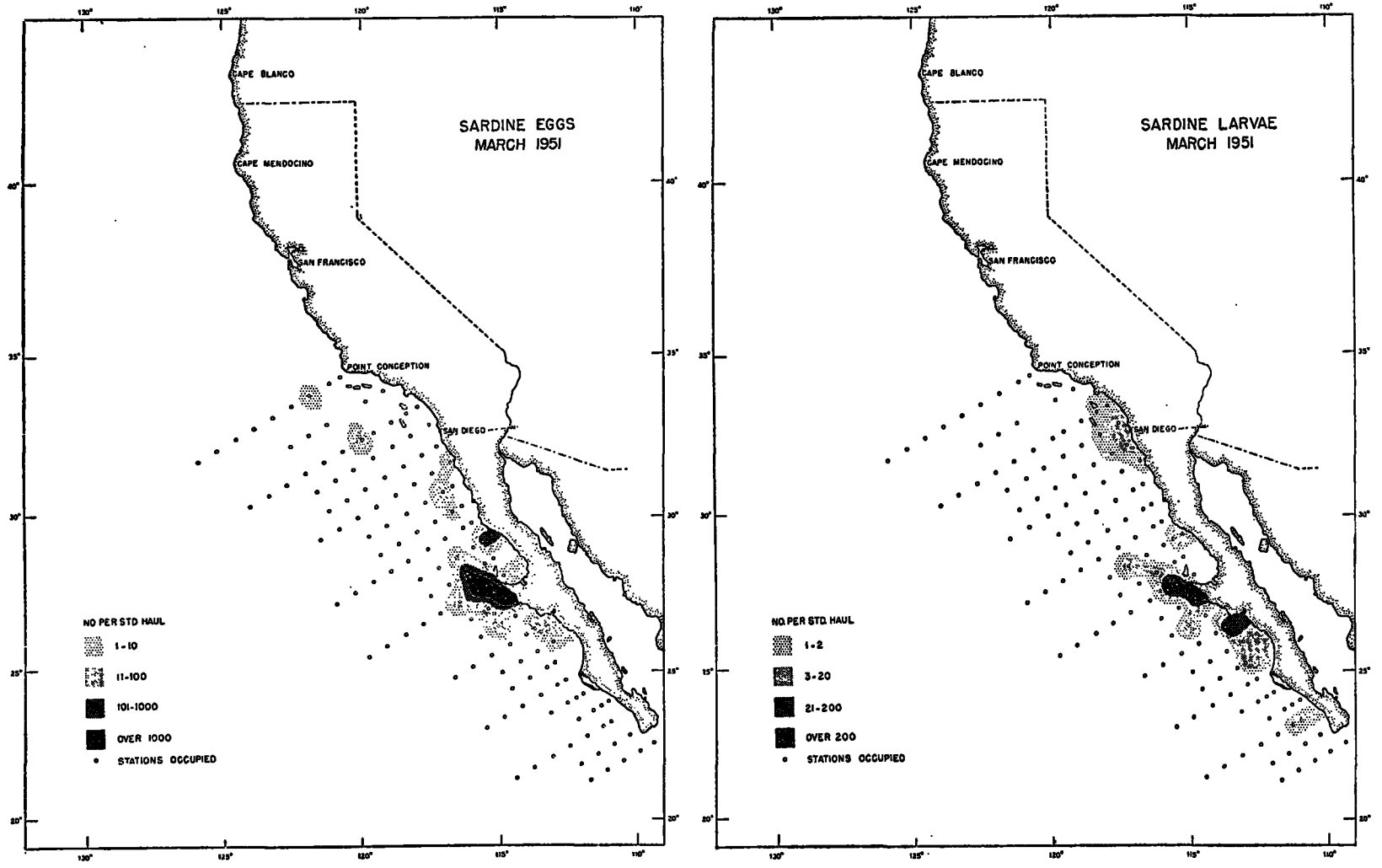

FIGURE 19.—Distribution and abundance of sardine eggs and larvae, March 1951.

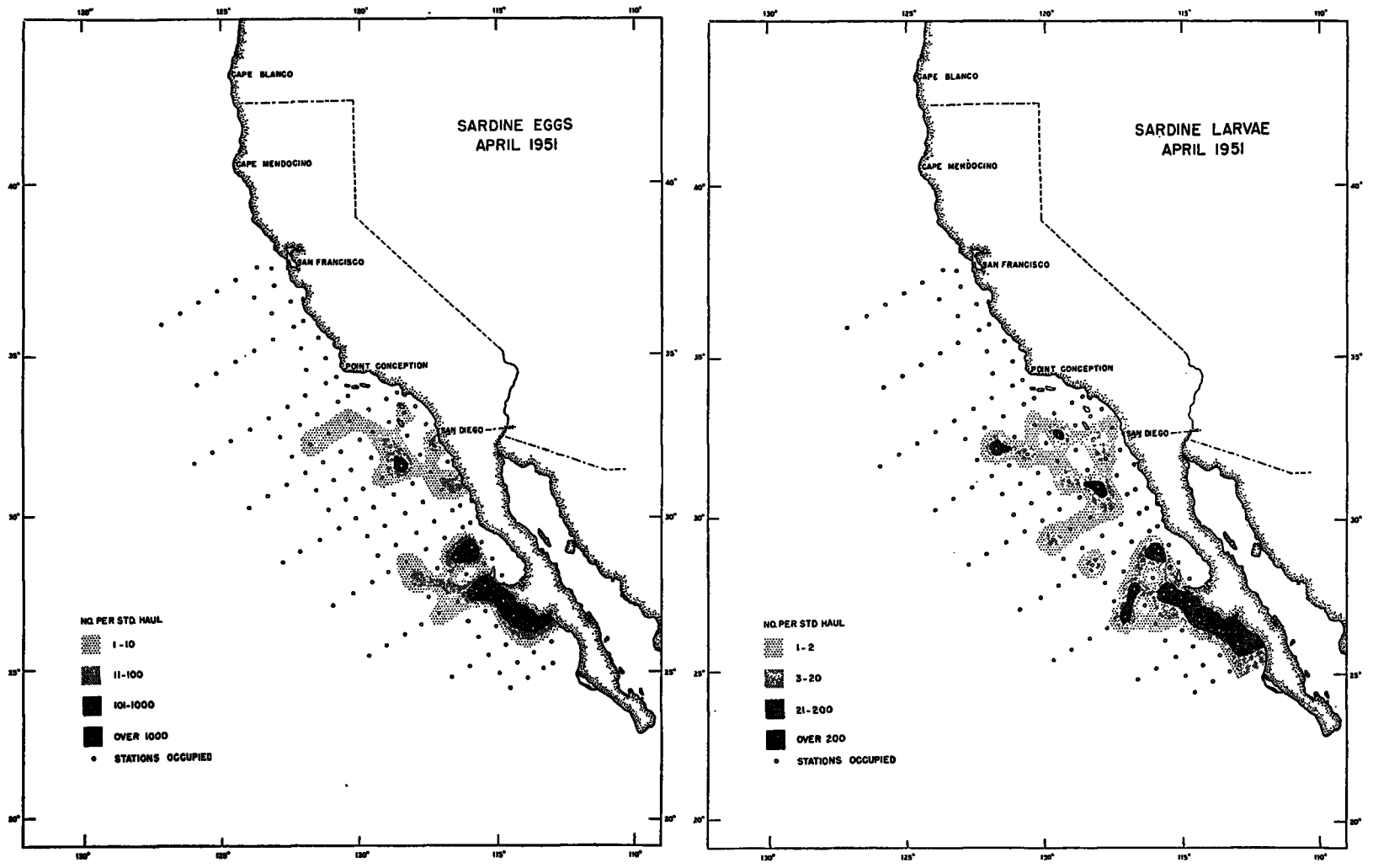

FIGURE 20.—Distribution and abundance of sardine eggs and larvae, April 1951.

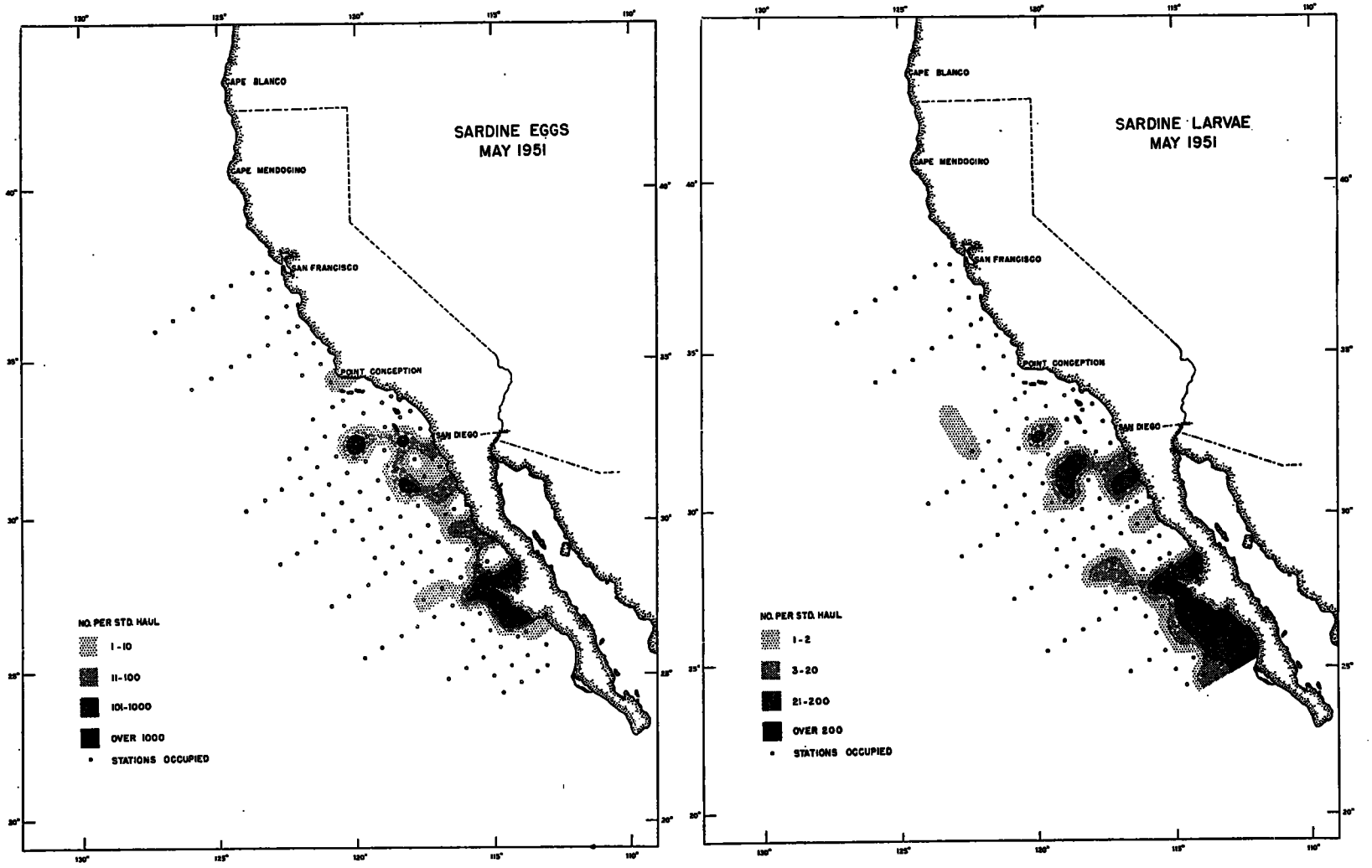

FIGURE 21.—Distribution and abundance of sardine eggs and larvae, May 1951.

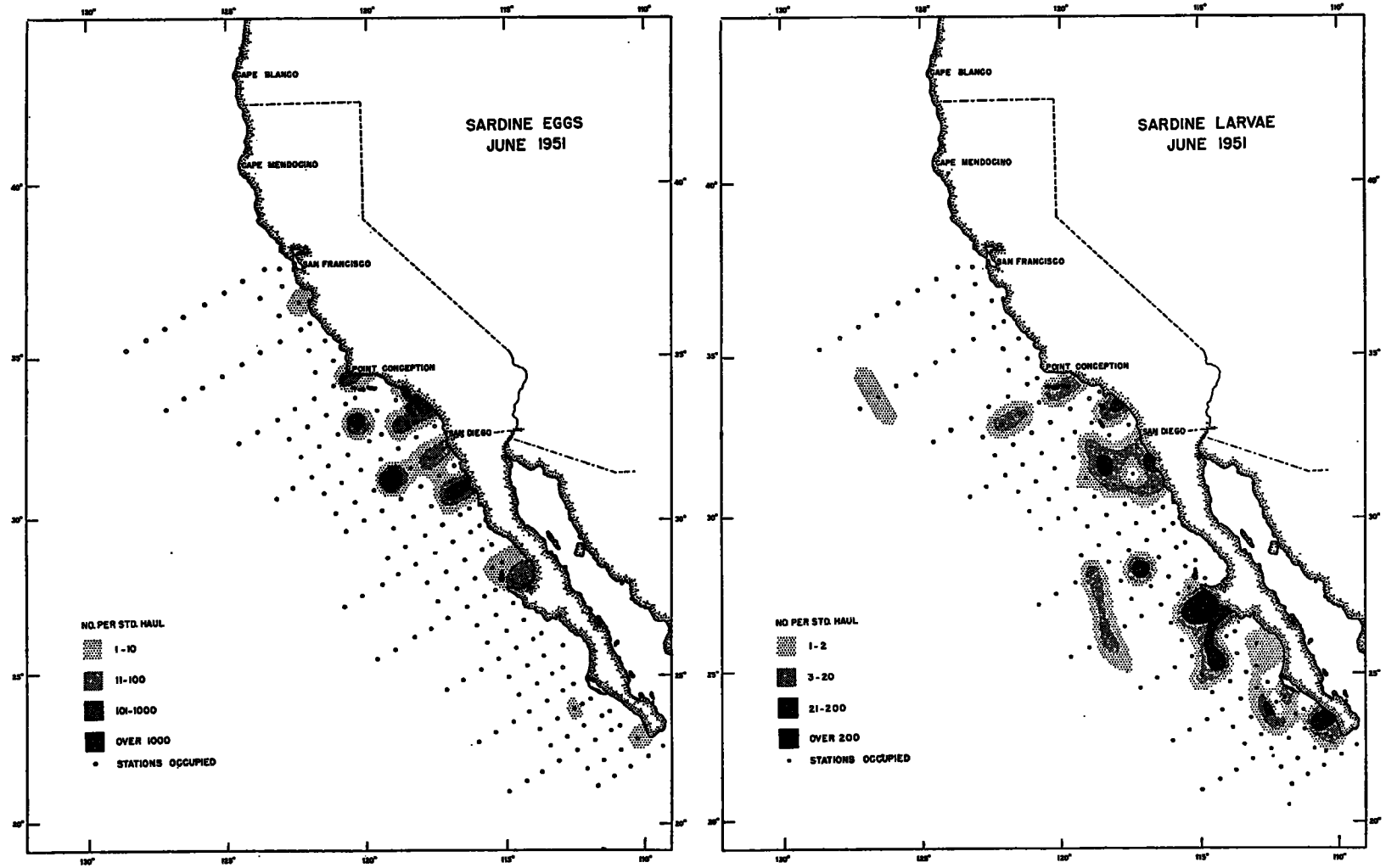

FIGURE 22.—Distribution and abundance of sardine eggs and larvae, June 1951.

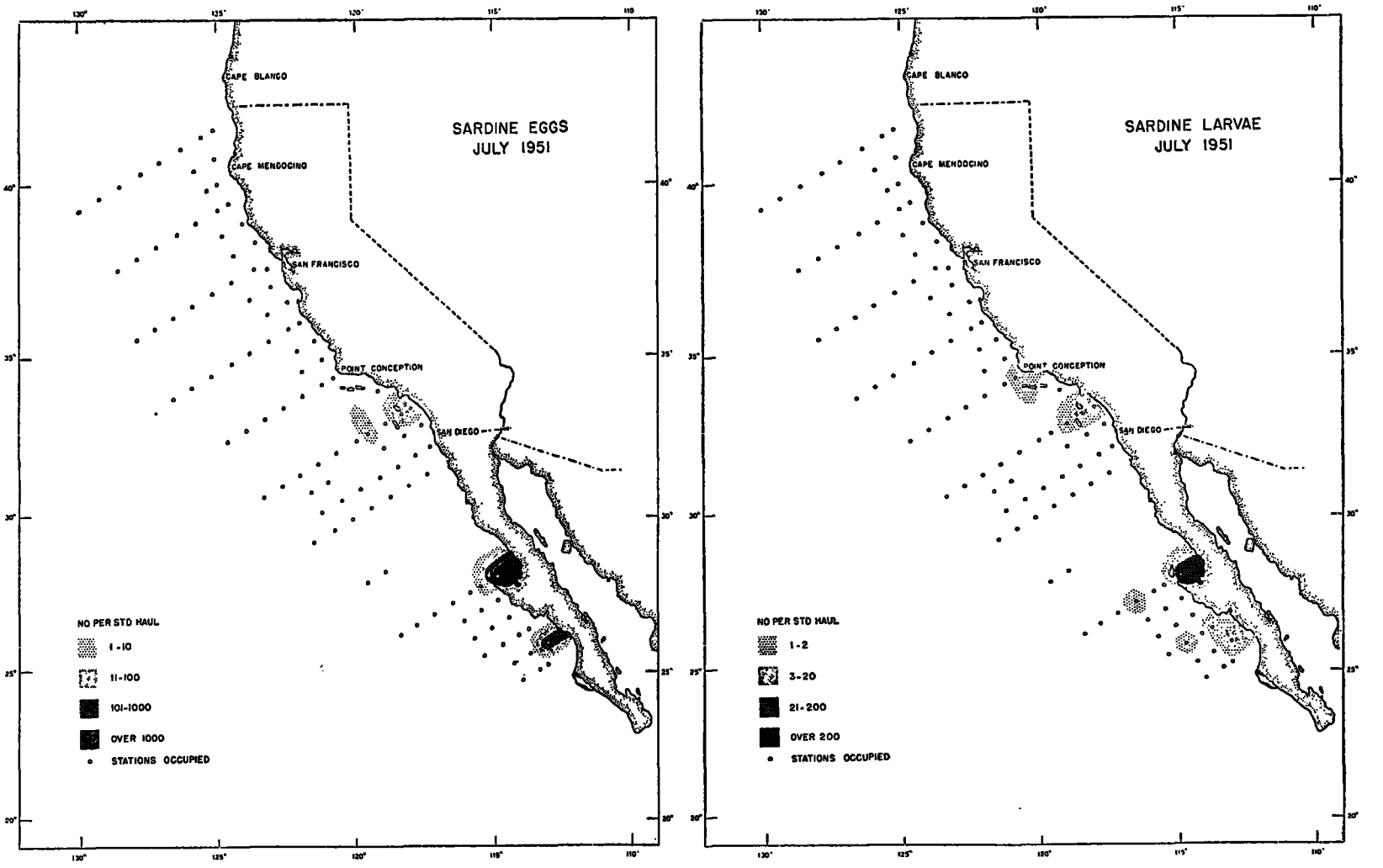

FIGURE 23.—Distribution and abundance of sardine eggs and larvae, July 1951.

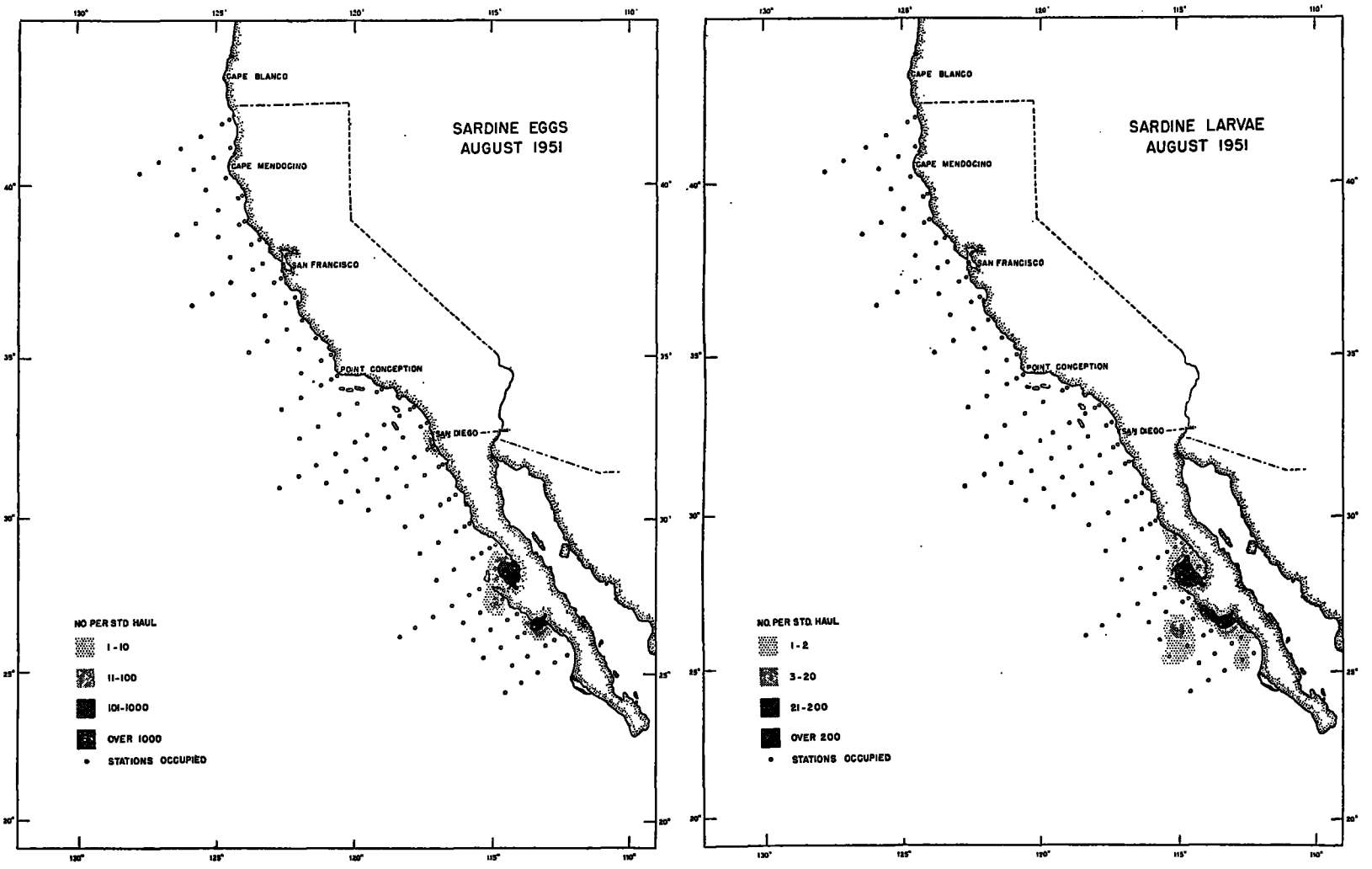

FIGURE 24.—Distribution and abundance of sardine eggs and larvae, August 1951.

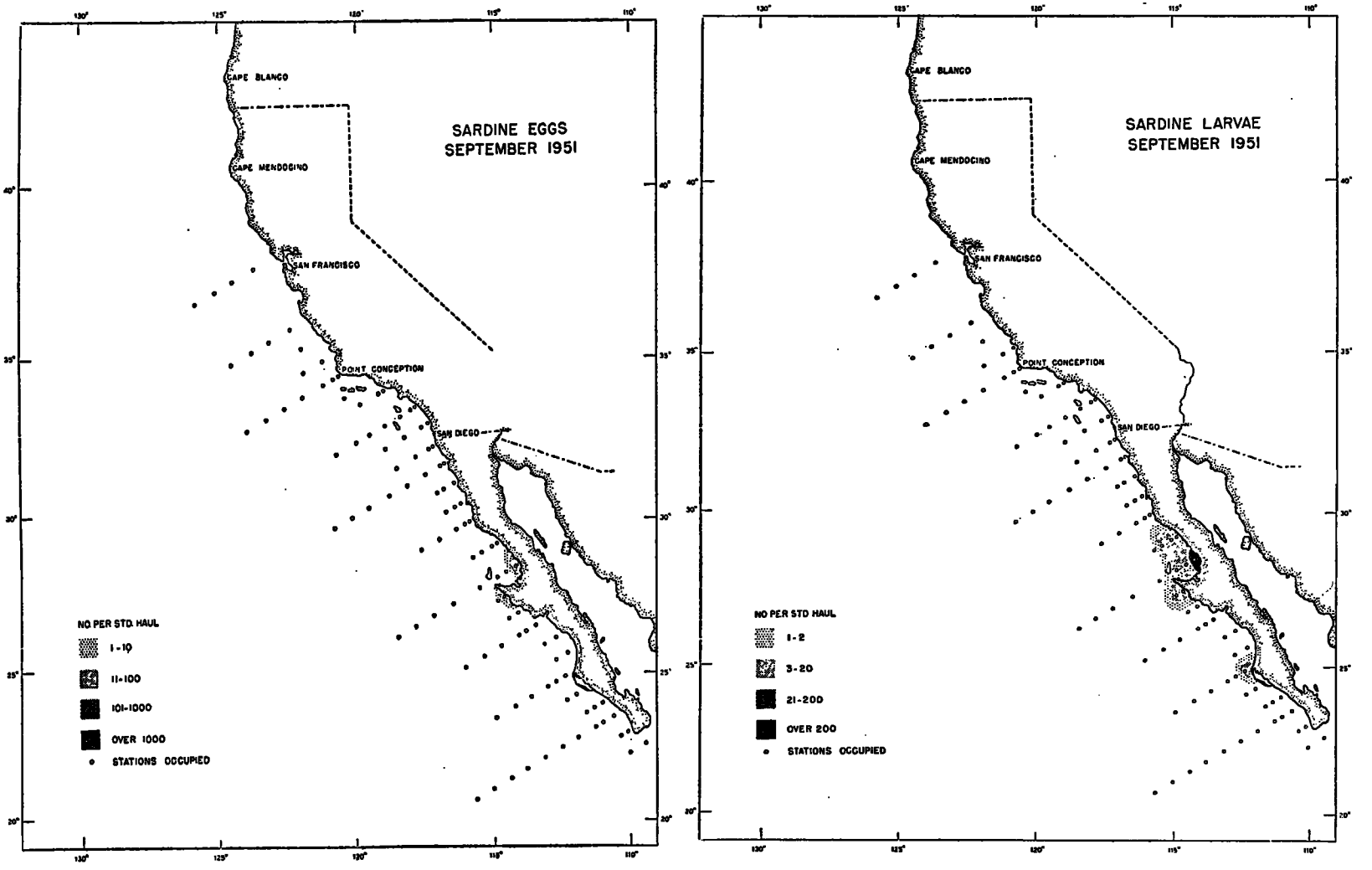

FIGURE 25.—Distribution and abundance of sardine eggs and larvae, September 1951.

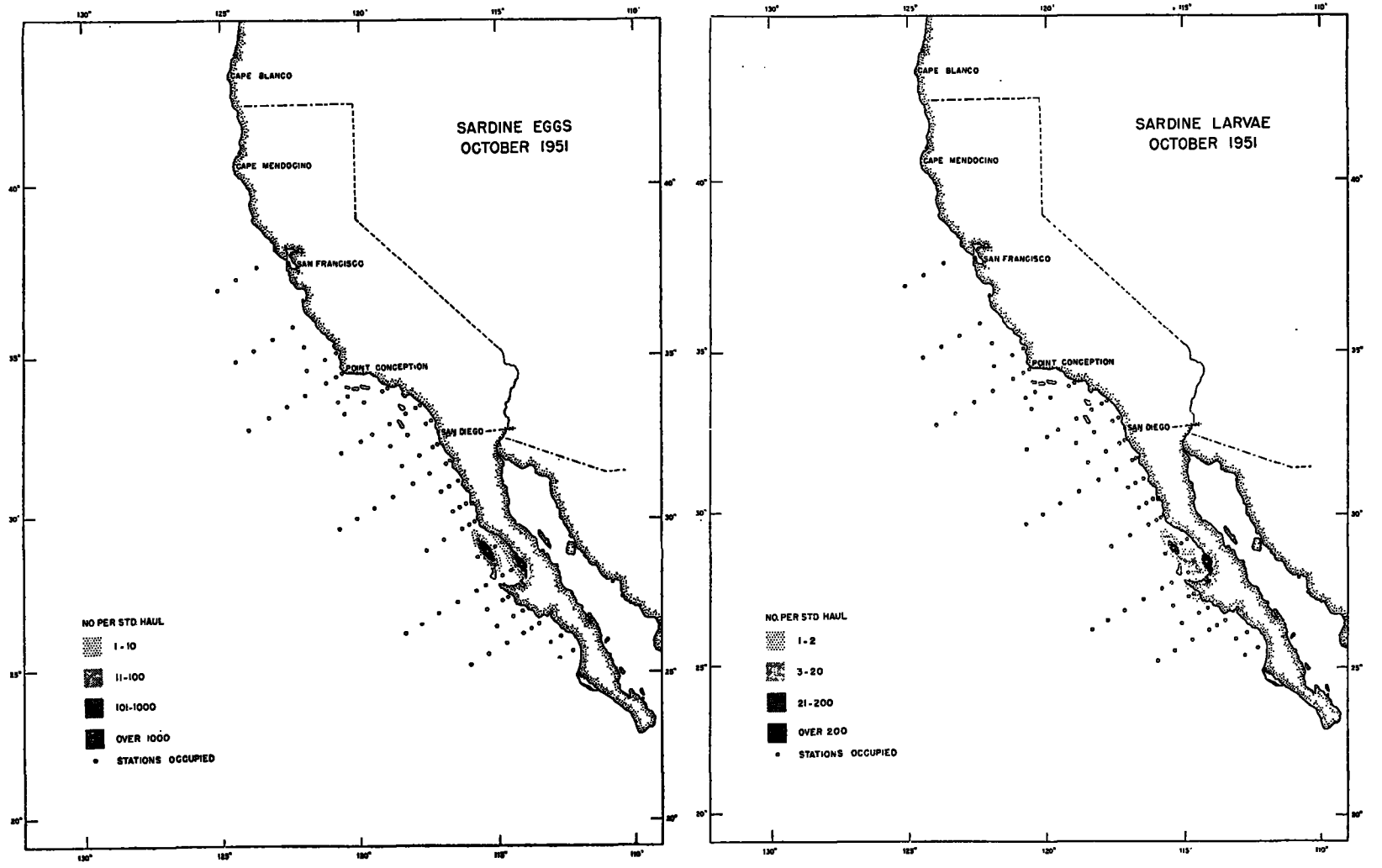

FIGURE 26.—Distribution and abundance of sardine eggs and larvae, October 1951.

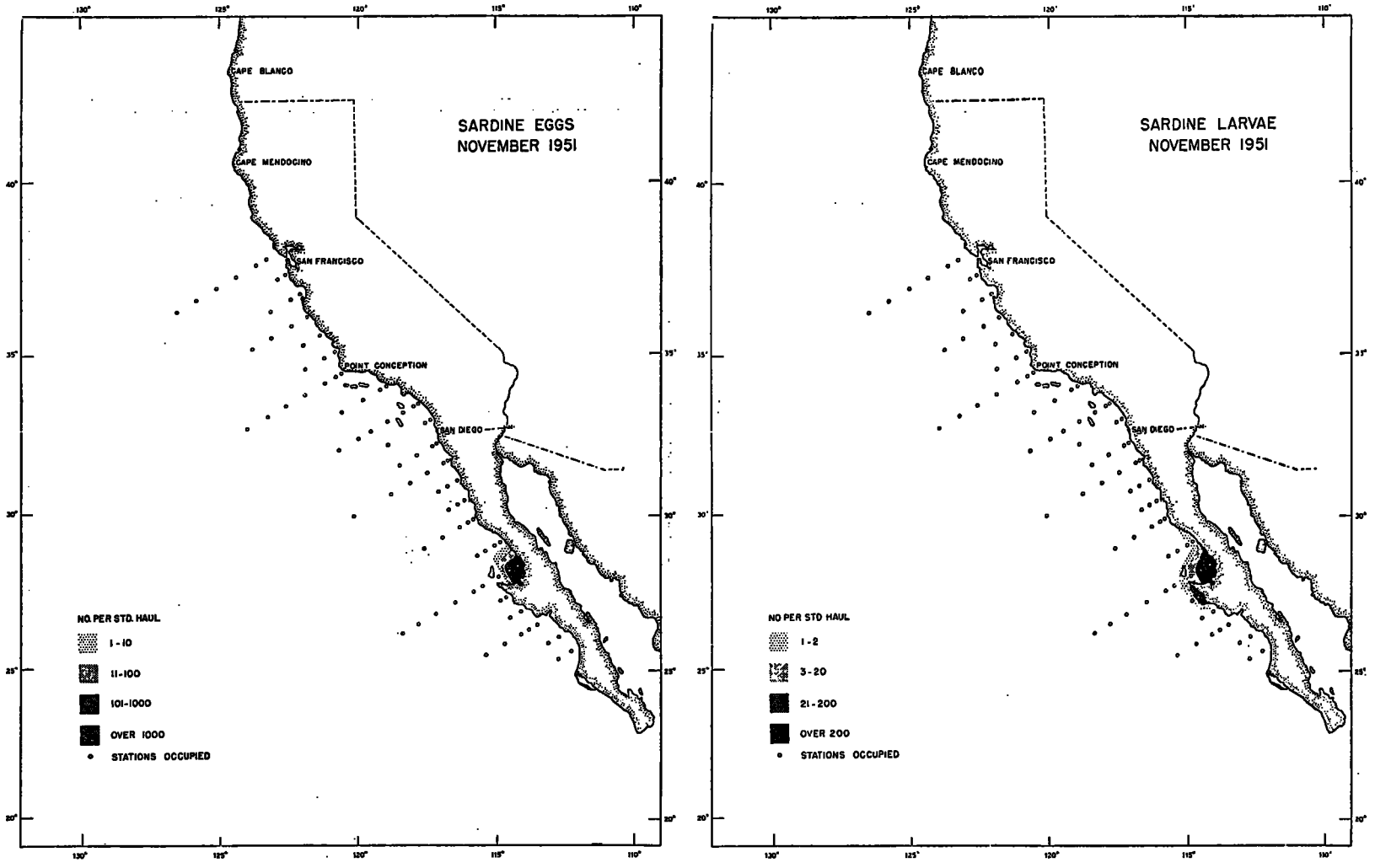

FIGURE 27.—Distribution and abundance of sardine eggs and larvae, November 1951.

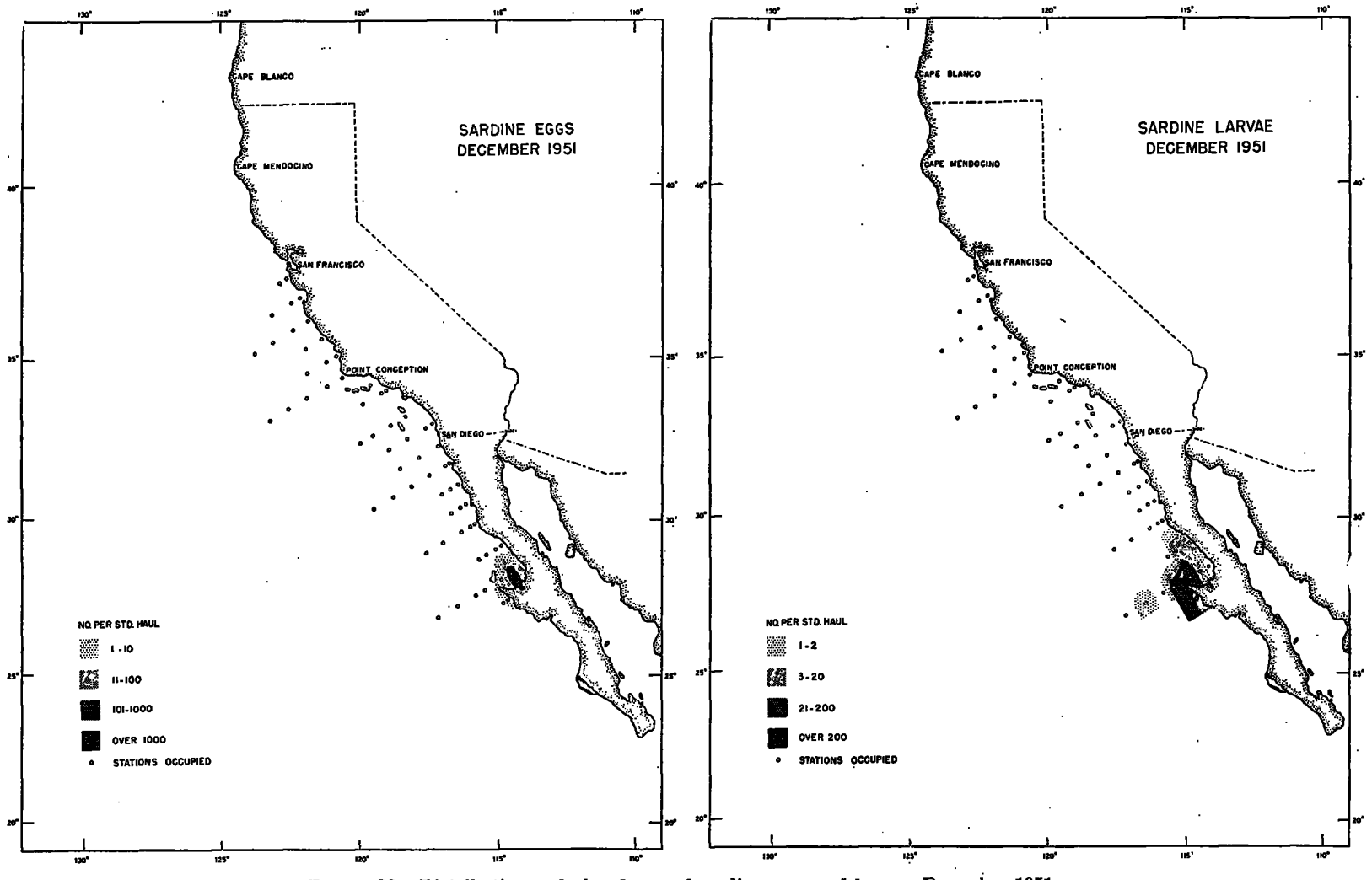

FIGURE 28.—Distribution and abundance of sardine eggs and larvae, December 1951.

plankton, as arrow worms, medusae, carnivorous copepods and ctenophores, to mention a few. Furthermore, it is at the mercy of its physical environment, since it is passively carried by currents.

As the larva develops, it becomes better able to cope with its environment. It can utilize a larger segment of the plankton as food and can move about in search of food. It develops the ability to escape predators. Furthermore, as it increases in size, the number of potential predators in the plankton community becomes fewer.

The validity of the theory that the survival of larvae during the planktonic period is critical in determining the success or failure of year classes can be tested, but it may require a number of years of investigation. If this theory is valid, there will be a correlation between good survival of larvae and successful year classes; between poor survival and poor year classes. But to test the theory, it is necessary that we measure the survival of larvae with sufficient accuracy, that we have a measure of the strength of each year class as adults, and that we obtain a range of survival rates of larvae from good to poor, or a range of year-class sizes from good to poor. If the theory is substantiated, it should be possible to predict year-class strength from survival data on larvae. Furthermore, if the relation between survival rate and environmental conditions can be established, a prediction may be possible from "skeletal" observations of critical factors in the environment. If, on the other hand, no correlation is found between larval survival and year-class strength, it must be concluded either that the aforementioned conditions cannot be satisfactorily fulfilled, or that the survival during the larval period is not critical as regards subsequent success or failure of year classes.[3]

SIZE OF LARVAE TAKEN IN PLANKTON HAULS

The sardine larva at time of hatching is about 3 mm. in length. It has a slender, threadlike form. The yolk is absorbed in 3 to 5 days, during which time the larva increases in length to about 4.5 mm. Most of the larvae taken in plankton hauls are between 3 and 24 mm. standard length, but occasionally larvae up to 30 mm. are taken.

PROBLEMS IN SAMPLING LARVAE

Quantitative sampling of sardine larvae presents a number of difficulties not involved in sampling sardine eggs. The eggs are large enough to be fully retained by the plankton nets, and are passive, so they cannot elude capture. A portion of the smaller-sized larvae, however, have been lost through the mesh openings of the several kinds of plankton nets employed, introducing a problem in net selectivity. The larger larvae have been markedly undersampled during daylight hours, posing a problem in daytime escapement.

Net selectivity.—The problem of net selectivity was first brought to our attention following the 1940 survey season, when it was discovered in analyzing the data that the smaller larvae were not being fully sampled by the plankton nets. The nets then routinely employed were constructed either of No. 24xxx silk grit gauze, or of a cotton scrim netting of similar mesh size. These materials had mesh openings about 0.9 to 1.0 mm. wide in new netting, shrinking to about 0.7 to 0.8 mm. wide after use. To obtain data on net selectivity, two nets having different mesh sizes were hauled side by side at most stations occupied during 1941. The finer-meshed net was constructed on No. 40xxx grit gauze, with openings 0.45 mm. wide in new netting, shrinking to about 0.3 mm. wide after use. It was found that the coarser-meshed nets retained most larvae about 9 mm. in length, but that their retention of smaller sizes might be as low as 7 percent. There is evidence that even the fine-meshed control nets did not retain all of the very small sardine larvae.

All nets employed since 1949 have been constructed of No. 30xxx silk grit gauze. The openings between threads in this grade of grit gauze measure about 0.70 mm. wide in new material, shrinking to about 0.55 mm. after use. The mesh openings are intermediate in size between those of the nets tested during 1941. The extent of the loss of larvae through the openings of this netting material has not been determined. Until the present analysis was made, the nets were considered sufficiently fine-meshed to retain most sizes of sardine larvae. However, from the slope of

[3] The extent of the area over which sardine spawning takes place may have an important bearing on the success or failure of year classes of sardines. Good year classes may result from unusually widespread spawning, poor year classes from contracted spawning. If so, important data would be derived from the surveys, even though we might not be able to measure survival satisfactorily.

the survival curves for sardine larvae, obtained for both 1950 and 1951, it has been concluded that net selectivity must still be an important consideration. We plan to obtain more definite information on the extent of loss of smaller larvae through the mesh openings of No. 30xxx grit gauze. It should not be difficult to check on net selectivity. We plan to enclose a standard plankton net constructed of No. 30xxx grit gauze in a larger net constructed of mesh fine enough to retain all sizes of larvae. By this means it will be possible to determine the proportion of the larvae of each size category usually retained by standard gear.

Undersampling of sardine larvae in daylight hours.—Larger sardine larvae are markedly undersampled during daylight hours. This is obvious from a comparison of the numbers taken in day and in night hauls. To determine extent of the undersampling, a comparison was made, by size, of larvae taken in day and night hauls during 4 years of surveys, 1940, 1941, 1950, and 1951, excluding from the comparison only those taken at sunrise or sunset. (The time of sunrise or sunset for any given date and locality was determined from Tide Table, West Coast for the appropriate years.) A total of 626 hauls was used: 316 collected during the night, 310 during daylight hours. The results are shown in figure 29.

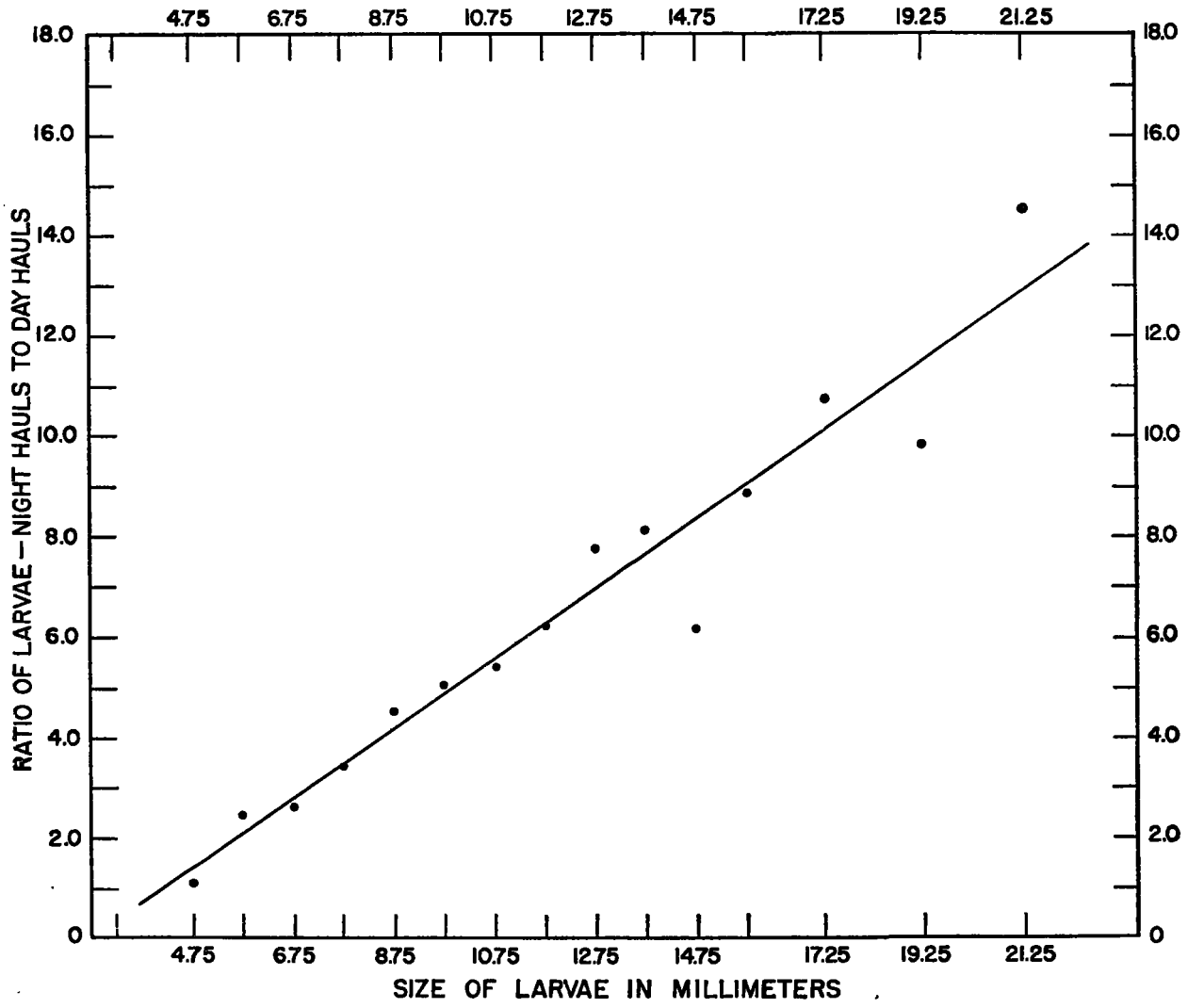

FIGURE 29.—Undersampling of sardine larvae in daylight hauls as compared with those in night hauls as a function of size. The linear-regression line was fitted by the method of least squares. Values for the line in the formula $y=a+bx$: $\bar{x}=12.05$, $\bar{y}=6.48$, $a=-1.9154$, $b=0.6971$, $s=0.957$.

The extent of undersampling of sardine larvae in the day hauls can be conveniently expressed as a ratio of the relative abundance of each size group in night hauls as compared to day hauls. This ratio for the two smallest size groups, 3.25 mm. (larvae 2.26 to 4.25 mm.) and 4.75 (larvae 4.26 to 5.25 mm.), was about equal: 1.35 for the smallest category, 1.15 for the 4.75 mm. group. The fact that the ratios are slightly greater than 1 probably is due to chance, as the smaller larvae have too feeble powers of locomotion to avoid the net. Larvae 5.75 mm. (5.26 to 6.25 mm.) were 2.5 times as abundant in night hauls as in day hauls. Thereafter the disparity became progressively greater with increase in larval size. Larvae 9.75 mm. in length (9.26 to 10.25 mm.) were five times as numerous in night hauls as in day hauls; larvae 15.75 mm. in length (15.26 to 16.25 mm.) were nearly nine times as numerous. Were no correction made for day escapement, the larger larvae would be underestimated by nearly one-half.

A part of the larger larvae may escape capture in hauls made during the night. If this happens, the estimates of abundance of larger larvae will always be minimal, and mortality would be overestimated; however, the percentage error should be reasonably constant from year to year.

Undersampling sardine larvae during daylight hours is probably due either to migration below the level routinely sampled by the net or to avoidance of the net. The weight of evidence favors the latter explanation. Very few sardine larvae have been taken deeper than 60 meters. For example, on the 1940 survey cruises, a 1-meter closing net was used below the upper net at a majority of the stations occupied. The approximate depth zone sampled by the closing net was between 125 and 55 meters. The average depth sampled by the upper net was between 73 meters and the surface. The upper net took sardine larvae at 109 of the stations where both nets were used, the closing net at only 5. In numbers taken (standardized for comparability), 5,900 larvae were taken in the upper-net hauls as compared with 38 in the closing-net hauls. The lower net took only two-thirds of 1 percent as many larvae as the upper net. This finding was reinforced by similar evidence obtained from other studies and was discussed in some detail by Silliman (1943) and Ahlstrom (1948).

The problem of day escapement is not unique for sardine larvae. To a greater or lesser degree it seems to apply to all clupeid larvae and many other pelagic-fish larvae. Russell (1926, 1928) called attention to a similar discrepancy in the number of pilchard, sprat, and herring larvae taken in day hauls as compared with those in night hauls. Marshall, Nicholls, and Orr (1937) found daylight sampling of herring larvae to be so inadequate that sampling was restricted to night collections. Furthermore, if the data given by Sette (1943) for Atlantic mackerel are analyzed for day versus night abundance, the difference in numbers taken in night hauls as compared with those in day hauls is even more marked for the larger sizes of mackerel than it is for the sardine.

LARVAL GROWTH RATE

Sette (1943) has summarized the available information on growth of fishes during the larval and postlarval periods. He concluded, after analyzing the data available for four species, Atlantic mackerel, haddock, Atlantic herring, and northern pike, that growth was logarithmic in character, having a uniform percental rate during the larval period except when there was a change in mode of living (such as yolk-sac absorption). He used length as an index of size because this information was available, although he believed that mass, or volume, would provide a more exact index. For the species that undergo little change in form during early life history, such as mackerel or haddock, he found that a simple logarithmic curve fitted their growth as indicated by length. On reexamining the data on growth of herring larvae in Marshall, Nicholls, and Orr (1937), Sette concluded that logarithmic curves with a change in slope at 30 days of age, or length of 19 mm., provided a better fit for the observation than the straight-line arithmetical relationship proposed by the original investigators. The herring larva, like the sardine, is slender, almost threadlike when young, growing stouter as development proceeds. As a result, length measurements overestimate growth in bulk during the early larval period and underestimate it later. The change in slope at 19 mm. suggests that after this length the herring increases more rapidly in mass than in length.

Because of the similarity in the form of sardine and herring larvae, growth of the sardine prob-

ably follows a pattern similar to the Atlantic herring's. It is likely that the growth of the sardine larva will be found to be logarithmic. Whether growth (based on length as an index of size) over the length range in which we are particularly interested, i.e., larvae between 2.5 and 24 mm. in length, can be expressed by a simple logarithmic curve without a change in slope or will require a more complex expression, can be determined only when sufficient data are at hand. For the present, I am assuming that the growth of sardine larvae can be represented by a simple logarithmic curve.

The growth rate of sardine larvae cannot be determined adequately from present survey data. Duration of the embryonic period, which can be determined with a fair degree of accuracy, has been found to average about 3 days, but it can be as short as 1 day or as long as 5 days, depending on the temperature at which development has taken place. For example, sardine eggs developing at 12.6° C. require approximately 4 days from fertilization to hatching, while eggs developing at 18° C. require only 2 days. Our information on the length of time needed to complete the yolk-sac stage is not as precise as for the embryonic period. Living larvae have been observed to absorb the yolk sac completely in 3 to 5 days. Although the relation to temperature has not been determined, 3½ days is probably a fair estimate of the average duration of the yolk-sac stage. Hence, a sardine larva developing under average conditions would be about 6.5 days old at the time it completed the yolk-sac stage, and would measure about 4.5 to 5 mm. in length (the range of this size class is 4.26 to 5.25 mm.).

From an inspection of seasonal curves of abundance of sardine larvae, grouped by size categories, it appears that between 1 and 2 months are required for a sardine to develop to 24 mm. length ("zero" age at fertilization). Two series of seasonal curves of larval abundance are illustrated in figure 30. One of the series is based on collections made off southern California during 1941 (data from Ahlstrom 1948), the other from collections obtained from the central Baja California spawning center during 1951. In both, the season of maximum abundance of larvae of 19.25-mm. size class is not more than a month later than the season of maximum abundance of larvae of the 5.25-mm. group. It is interesting to note that the peaks of abundance during 1941 off southern California occurred slightly earlier in the year than corresponding peaks off central Baja California during 1951.

The seasonal curve of egg abundance in the 1951 series appears to be out of phase with the curves of larval abundance for that year. The peak month for egg abundance in 1951 was March, a month earlier than in 1950. The seasonal curves of larval abundance are similar for the 2 years in the central Baja California area, however, with the peak month for most stages occurring in May.

Only a rough estimate of the growth rate of sardine larvae can be obtained from the foregoing and similar series.[4] It is difficult to refine further the rough estimate of between 1 and 2 months as the time required to complete the planktonic phase of the life history. Until more exact data are available I feel justified in using the midpoint of this estimate, 45 days, as an approximation of the average age of a sardine larva 24 mm. in length. Inasmuch as the embryonic and yolk-sac stages would take approximately 6.5 days, 38.5 days would be left for a larva to grow from 4.5 to 24 mm. in length. Assuming that the growth is logarithmic, the logarithm of the increase per day would be a constant 0.01916.

The duration of each size category can be computed from the following formula, modified from that given by Sette (1943 : 179) :

$$\text{Duration of size category (in days)} = \frac{\log 1'' - \log 1'}{0.01916}$$

in which $1'$ is the lower boundary of the size-class interval in millimeters and $1''$ is the upper boundary.

Determination of the average age of the larvae in each size category can be computed from the formula:

$$\text{Age (in days)} = 6.50 + \frac{\log 1'' - \log 1'}{0.01916}$$

where $1''$ is the midvalue of the size-class interval and $1'$ is 4.26 mm., the lower boundary of the first larval size category following yolk-sac absorption. Values for the duration of all size classes routinely used in tabulations of sardine larvae are given in table 11. The estimate of duration of the

[4] One of the chief limitations on the use of survey data for determining growth rate of sardine larvae arises from infrequency of sampling. Cruises are spaced at monthly intervals. With such wide spacing in time, it is nearly impossible to follow homologous modes from cruise to cruise.

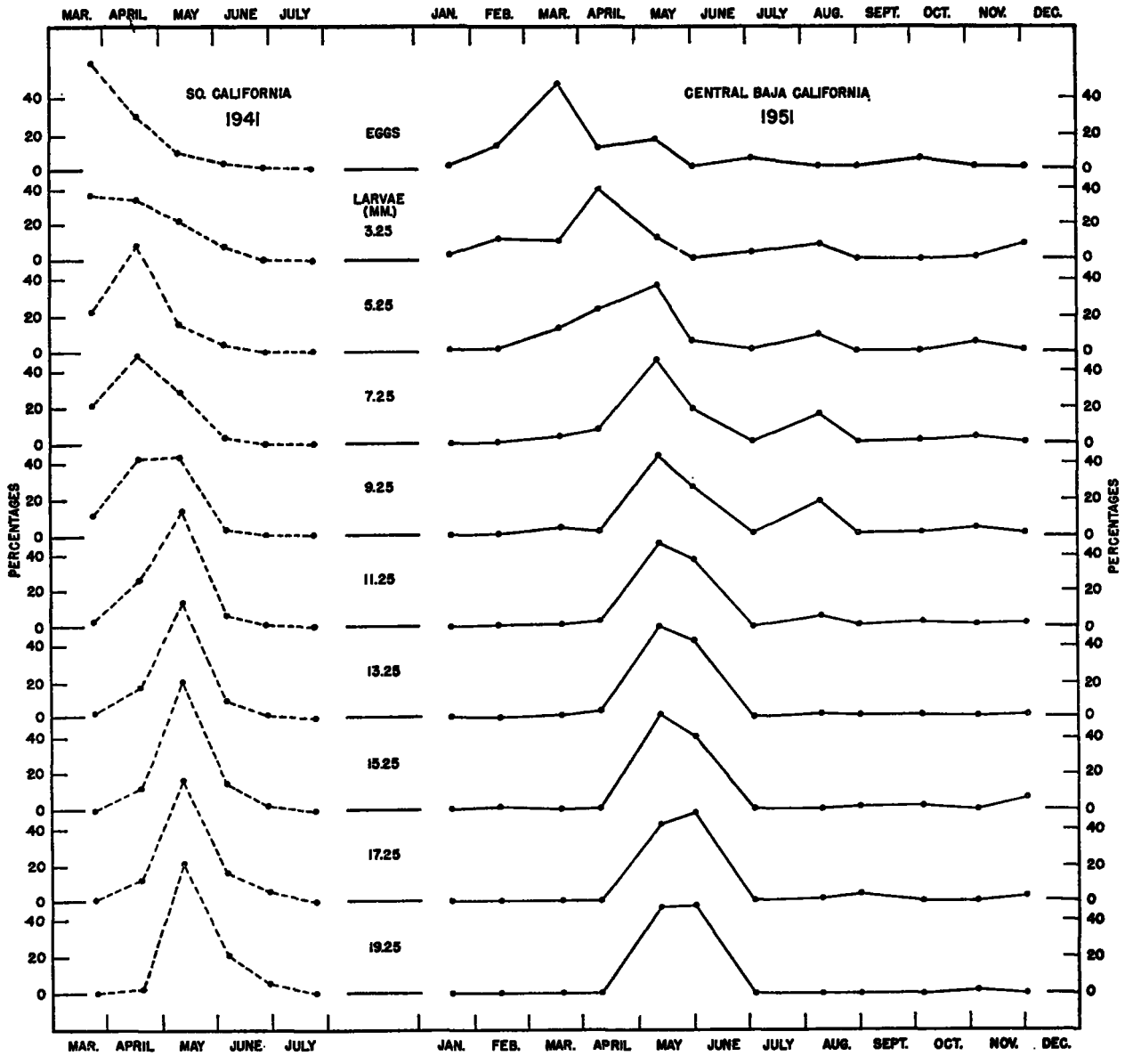

FIGURE 30.—Two series of diagrams illustrating season of maximum occurrence of sardine eggs and of nine stages of sardine larvae (grouped by 2-mm. intervals). The series on the left is based on collections made off southern California during 1941, that on the right on material collected off central Baja California during 1951. In the 10 separate diagrams comprising each series, the vertical scale represents the percentage of the season's total for the category that was taken on each cruise; the horizontal axis indicates the distributions of the observations in time.

smallest size class of larvae, 4.26 to 5.25 mm. in length, is 4.75 days, while it is estimated that less than 1 day would be required for a larva to grow from 23.26 to 24.25 mm. in length.[5] Also included in this table are estimates of the age in days to the midpoint of each size class. As indicated previously, these determinations are rough approximations. Since age estimates are essential in determinations of the abundance of size categories of larvae, I believe that the best present estimates should be used, even though they might introduce errors of as much as 25 percent.

[5] Obviously, this accelerated growth cannot continue indefinitely. There probably is a change in rate before the larva reaches 24 mm. in length. However, more exact data are needed before this can be determined.

TABLE 11.—*Survival of young stages of sardine, 1950 and 1951*

Category	Size range	Duration	Average age	1950		1951	
				Estimated abundance	Survival per 100,000 eggs	Estimated abundance	Survival per 100,000 eggs
	Mm.	*Days*	*Days*	*Billions*		*Billions*	
Egg		3.0	1.5	285,676		610,847	
Yolk-sac larvae	2.26–4.25	3.5	4.8	11,850	4,148	12,083	1,978
Larvae 4.75 mm	4.26–5.25	4.8	8.9	10,778	3,772	9,327	1,527
Larvae 5.75 mm	5.26–6.25	3.9	13.2	5,590	1,957	7,153	1,171
Larvae 6.75 mm	6.26–7.25	3.3	16.8	6,197	2,169	6,853	1,122
Larvae 7.75 mm	7.26–8.25	2.9	20.0	5,931	2,076	7,979	1,306
Larvae 8.75 mm	8.26–9.25	2.6	22.7	4,834	1,692	6,233	1,020
Larvae 9.75 mm	9.26–10.25	2.3	25.1	3,738	1,308	7,015	1,148
Larvae 10.75 mm	10.26–11.25	2.1	27.3	2,880	1,008	5,938	972
Larvae 11.75 mm	11.26–12.25	1.9	29.3	1,942	680	6,152	1,007
Larvae 12.75 mm	12.26–13.25	1.8	31.2	2,214	775	4,600	753
Larvae 13.75 mm	13.26–14.25	1.6	32.8	1,701	595	4,281	701
Larvae 14.75 mm	14.26–15.25	1.5	34.4	1,198	419	4,676	765
Larvae 15.75 mm	15.26–16.25	1.4	35.9	1,046	366	1,509	247
Larvae 17.25 mm	16.26–18.25	2.6	37.9	750	262	1,128	185
Larvae 19.25 mm	18.26–20.25	2.4	40.4	337	118	550	90
Larvae 21.25 mm	20.26–22.25	2.1	42.6	253	88	688	113
Larvae 23.25 mm	22.26–24.25	1.9	44.7	18	6	354	58

DETERMINING ABUNDANCE OF LARVAE

The simplest kind of estimate of abundance is based on total numbers of larvae. This type of estimate can be made even when the size composition of the samples of larvae has not been determined. Except for certain limited uses, as in comparisons of the relative abundance of larvae of different species in the survey area, such an estimate has little value. It cannot be used in determinations of larval survival, for these require a knowledge of the size composition of the larval population. Furthermore, unless size measurements were recorded it would be impossible to make necessary adjustments for day escapement, for net selectivity, or for differences in growth rate.

Another complicating factor is that homologous groups of larvae may be sampled on two or more cruises, depending on frequency of sampling and rate of growth. If larvae require approximately a month and a half to grow from 2.5 to 24 mm. in length and cruises are spaced at monthly intervals, approximately one-half of the larvae would be sampled on two successive cruises, one-half would be sampled on one cruise only. If cruises are spaced at weekly intervals, however, homologous groups of larvae would be sampled on a minimum of five successive cruises. Sampling the same population of larvae at several stages during the larval period, although desirable from the standpoint of mortality determinations, must be taken into account in determinations of abundance. This is difficult to do in determinations of abundance based on total numbers of larvae, but the problem would cease to exist if determinations of abundance were based on sufficiently fine size groupings of larvae. The requirement that would have to be met is that the growth period from the lower to the upper limit of size categories should not exceed the time interval between successive cruises.

Sardine larvae have been grouped into a number of size categories, usually by 1-mm. intervals. Estimates can be obtained of the magnitude of the sardine population at each of these different stages of the larval period. Adjustments can be made for the time duration of each category (length of time required to grow from the lower limit to the upper limit of the category), for day escapement, and for net selectivity, all of which are different for each size category. The numbers of larvae can then be integrated over space and time to obtain an estimate of abundance of the larval population at any given size. By comparing the abundance of the different size categories, an estimate can be obtained of the survival rate.

To determine the abundance of larvae of a given size category during a cruise, the following procedure was followed:

1. The standardized number of larvae of the size category taken at each station was divided by d_c, the estimated duration of the size category in days.

2. The samples were then divided into two groups, those collected by day and those obtained at night. The day hauls were adjusted for daytime escapement.

3. The adjusted number of larvae of the size category taken at each station was integrated over area and time in the manner already described for eggs.

4. The cruise total was obtained by summing the values for the individual stations.

Estimates of the several cruises were added together to obtain an estimate of the abundance of the size category for the year. The estimated abundance of larvae in all size categories from 3.25 to 23.25 mm. during 1950 and 1951 is given in tables 11, 12, and 13.

TABLE 12.—*Abundance of sardine larvae, by month and area, 1950*

[In billions]

Month and area	Size in millimeters																	Disintegrated [1]	Total
	3.25	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	17.25	19.25	21.25	23.25	27.25	
Area north of Point Conception:																			
June	29	52	24	0	0	0	0	200	0	0	0	0	0	0	0	0	0	0	305
July	12	0	0	10	0	13	14	0	0	149	0	19	407	248	0	0	0	0	872
August	0	8	10	6	34	0	0	10	0	0	0	0	0	0	0	0	18	0	86
Total	41	60	34	16	34	13	14	210	0	149	0	19	407	248	0	0	0	18	0	1,263
Southern California area:																			
March	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
April	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	1,039	452	52	8	15	0	0	0	0	0	0	0	0	0	0	0	0	29	1,595
June	567	395	715	684	883	717	797	418	549	946	551	388	0	94	68	0	0	30	7,802
July	0	0	0	0	0	0	0	0	0	0	15	0	17	25	55	148	0	0	260
Total	1,606	849	767	692	898	717	797	418	549	946	566	388	17	119	123	148	0	59	9,659
Northern Baja California area:																			
April	186	281	53	13	0	9	0	0	0	0	27	0	0	0	0	0	0	0	569
May	612	1,133	762	567	442	657	520	506	227	483	128	159	364	163	31	53	0	32	6,839
June	58	237	441	895	763	1,151	136	264	109	55	40	22	0	16	4	15	0	0	4,206
July	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
Total	856	1,679	1,256	1,475	1,205	1,817	656	770	336	538	195	181	364	179	35	68	0	0	32	11,642
Central Baja California area:																			
February	246	673	112	312	332	170	292	112	41	0	17	15	0	0	0	0	0	0	22	2,344
March	368	707	259	170	165	131	202	163	58	67	37	11	0	0	0	0	0	0	144	2,482
April	2,466	4,246	1,595	1,182	1,162	543	838	517	550	171	474	488	0	0	14	0	0	0	204	14,440
May	6,183	2,522	1,541	2,337	2,115	1,431	939	678	389	312	379	96	258	189	82	37	0	0	163	19,651
June	6	17	6	13	0	0	0	0	13	0	15	0	0	6	73	0	0	0	0	149
July	14	25	30	0	20	12	0	0	0	17	18	0	0	9	10	0	0	0	0	155
August																				
September	64	0	0	0	0	0	0	12	6	14	0	0	0	0	0	0	0	0	0	96
Total	9,347	8,190	3,533	4,014	3,794	2,287	2,271	1,482	1,057	581	940	610	258	204	179	37	0	0	533	39,317
Aggregate, all areas:																			
February	246	673	112	312	332	170	292	112	41	0	17	15	0	0	0	0	0	0	22	2,344
March	368	709	259	170	165	131	202	163	58	67	37	11	0	0	0	0	0	0	144	2,484
April	2,652	4,527	1,638	1,195	1,162	552	838	517	550	171	501	488	0	0	14	0	0	0	204	15,009
May	7,834	4,107	2,355	2,912	2,572	2,088	1,459	1,184	616	795	507	255	622	352	113	90	0	0	224	28,085
June	660	701	1,186	1,592	1,646	1,868	933	882	671	1,001	606	410	0	116	145	15	0	0	30	12,462
July	26	53	30	10	20	25	14	0	0	166	33	19	424	282	65	148	0	0	0	1,315
August	0	8	10	6	34	0	0	10	0	0	0	0	0	0	0	0	0	18	0	86
September	64	0	0	0	0	0	0	12	6	14	0	0	0	0	0	0	0	0	0	96
Grand total	11,850	10,778	5,590	6,197	5,931	4,834	3,738	2,880	1,942	2,214	1,701	1,198	1,046	750	337	253	0	18	624	61,881

[1] In too poor condition to be measured.

How adequate are these abundance determinations? It should be noted that no adjustment has been made for net selectivity. As a result, the abundance of the smaller-sized groups is underestimated by an undetermined amount.

The 1950 estimates of larger-sized sardine larvae are probably too low, because of incomplete coverage of the distributional range of the larvae off central Baja California. The lowermost line occupied routinely during 1950 was off Point Abreojos. Although very few sardine eggs have been taken south of this point, during the 1951 and 1952 surveys a considerable proportion of the larvae had drifted to the south of this area. During 1951, for example, only 0.66 percent of the eggs and 0.65 percent of the larvae 2.5 to 5 mm. in length taken off central Baja California occurred to the south of Point Abreojos (lines 133 and 137). But 6 percent of the larvae 5.5 to 10 mm. in length, over 39 percent of the larvae 10.5 to 15 mm. in

TABLE 13.—*Abundance of sardine larvae, by month and area, 1951*

[In billions]

Month and area	Size in millimeters																	Disintegrated [1]	Total
	3.25	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	17.25	19.25	21.25	23.25	27.25	
Area north of Point Conception: June	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	0	48
Southern California area:																				
February	16	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29
March	0	6	0	0	6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	18
April	8	100	146	16	158	126	66	43	0	0	0	147	0	0	13	0	0	0	0	823
May	62	98	42	41	0	80	0	0	0	0	19	0	0	0	0	0	0	0	0	342
June	96	39	0	6	25	0	0	0	0	0	419	0	0	51	12	13	0	0	0	661
July	14	15	12	14	16	37	0	0	0	0	23	0	0	0	0	0	0	0	0	131
Total	196	271	200	77	205	243	66	43	0	0	461	147	0	57	25	13	0	0	0	2,004
Northern Baja California area:																				
February	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
March	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
April	140	162	47	8	0	11	0	89	16	17	0	21	230	0	0	0	0	0	0	741
May	944	684	188	331	115	54	92	53	150	10	22	24	38	21	8	0	0	0	0	2,734
June	103	165	230	76	74	0	63	0	10	0	0	164	0	0	158	181	15	0	0	1,239
Total	1,187	1,024	465	424	189	65	155	142	176	27	22	209	268	21	166	181	15	0	0	4,736
Central Baja California area:																				
January	270	89	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	400
February	1,281	98	44	0	23	29	0	16	35	0	0	24	0	0	0	9	0	0	0	1,559
March	1,131	959	716	157	249	273	256	189	106	347	0	0	0	0	0	0	0	0	0	4,383
April	4,162	2,350	1,239	635	511	225	264	138	697	371	173	21	0	0	0	0	0	0	0	10,776
May	1,300	3,051	2,476	3,734	4,481	3,168	4,136	3,673	2,839	2,373	2,553	2,865	835	559	298	15	0	0	0	38,356
June	6	144	447	507	1,017	1,033	824	930	1,272	1,055	896	731	320	334	61	452	119	34	296	10,408
July	419	276	76	50	139	78	63	0	0	0	0	0	0	0	0	0	0	0	0	1,101
August	870	458	832	771	759	788	528	294	162	54	20	0	0	15	0	0	0	0	0	5,551
September	50	12	41	38	26	23	9	26	0	25	0	0	15	21	0	0	0	0	0	286
October	7	19	43	55	44	7	375	379	708	279	12	197	0	0	0	18	48	0	0	2,191
November	249	396	357	233	245	287	233	62	17	3	8	0	0	81	0	0	0	0	0	2,171
December	930	140	92	38	73	14	32	7	113	8	27	128	35	19	0	0	0	0	0	1,656
Total	10,665	7,992	6,404	6,218	7,567	5,925	6,720	5,704	5,949	4,515	3,689	3,966	1,205	1,029	359	494	167	34	296	78,898
Southern Baja California area:																				
April	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	15
June	25	29	64	133	18	0	74	49	27	58	94	354	36	21	0	0	173	0	0	1,154
September	10	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
Total	35	40	84	133	18	0	74	49	27	58	109	354	36	21	0	0	172	0	0	1,210
Grand total	12,083	9,327	7,153	6,852	7,979	6,233	7,015	5,938	6,152	4,600	4,281	4,676	1,509	1,128	550	688	354	82	296	86,896

[1] In too poor condition to be measured.

length, and about 53 percent of the larvae 15.5 mm. and over were taken to the south of Point Abreojos.

There is good reason to assume that an even larger proportion of the larvae would have occurred to the south of Point Abreojos in 1950 than in 1951. More spawning occurred in the southern part of the area that year, as is shown by the following tabulation, summarizing the percent of

	1950	1951
	Percent	*Percent*
Lines 110–117	3.6	8.0
Line 120	28.2	36.4
Line 123	33.7	46.9
Line 127	.4	6.8
Line 130	34.1	1.2
Line 133	----------	.7
Line 137	----------	0
Total	100.0	100.0

spawning in the central Baja California center taken on different station lines.

A third of the spawning occurred off Point Abreojos in 1950, and we can assume that nearly all of the larvae from this spawning would have drifted to the south of the area being sampled. Hence, at the very least, the abundance of larvae off central Baja California would have been underestimated by one-third; also, many of the larvae resulting from spawning off Point San Eugenio would have drifted south of the area. In 1951, when spawning was centered off Point San Eugenio, more than 50 percent of the larvae over 15.5 mm. in length were collected to the south of Point Abreojos. For these sizes of larvae the underestimation of their abundance may be as much as two-thirds.

The rate of drift in this area can be shown from a special study made during late April 1952. It was determined by following a buoy fitted with a drag at a depth of 10 meters, that this water mass moved southward in the area between Point San Eugenio and Point Abreojos at the rate of about 15 miles a day. This study was made during a period of heavy sardine spawning. Even though the water mass would be moving more slowly at the levels where most of the sardine larvae occur, still the larvae would be transported southward at a fairly rapid rate.

Other lines of evidence tend to support the foregoing conclusions relative to this southward drift. The two major spawning centers contributed the following percentages of eggs and larvae in 1950 and 1951:

	1950		1951	
	Southern California and adjacent Baja California	Central Baja California	Southern California and adjacent Baja California	Central Baja California
	Percent	*Percent*	*Percent*	*Percent*
Eggs	17.3	82.7	5.6	94.4
Larvae to 5.0 mm	22.4	77.6	13.3	86.7
Larvae 5.5 to 10.0 mm	37.1	62.9	6.8	93.2
Larvae 10.5 to 15.0 mm	49.9	51.1	3.7	96.3
Larvae 15.5 mm. and larger	66.8	33.2	10.4	89.6

About one-half of the larvae 10.5 to 15 mm. in length, and two-thirds of the larvae 15.5 mm. and larger were taken in the northern spawning center, despite the fact that less than one-fifth of the spawning occurred in this area during 1950. The following explanations could account for this: (1) Markedly better survival in the northern spawning center in 1950 as compared with the southern center, (2) undersampling of the larvae in the southern center, or (3) a combination of both. In view of the evidence previously presented, there is little doubt that much of the discrepancy in regard to abundance of older larvae in the northern and southern spawnings centers in 1950 must have resulted from the southward drift of larvae out of the survey area off central Baja California.

DETERMINING LARVAL SURVIVAL

The initial strength of a year class is dependent on the amount of spawning; its subsequent strength, on survival after spawning. In actual numbers of individuals, a year class at its inception is many times as large as the total adult population. If an average-sized adult female sardine spawned 100,000 eggs per year,[6] and if the sexes were equally divided, a year class at the embryonic, or egg, stage would be 5×10^4 times as abundant as the total adult population. Consequently, the history of each year class is one of rapid decrease in numbers.

Much of the decline in abundance occurs during the first month or two of life. This can be shown graphically by plotting the estimated abundance of a year class at various stages during its planktonic existence (fig. 31). The decline is quite precipitous, so instead of plotting actual numbers, logarithms of the estimated abundance at each stage are used. The stages are based on size (standard length) groupings, for each of which an approximation of the average age (in days) has been derived (*cf.* table 11).

The plots of population abundance during the early history of the 1950 and 1951 year classes (fig. 31) are, in effect, survival curves. The actual survival rate is better shown in a somewhat different diagram, as illustrated in figure 32. I am calling the latter diagram a survival curve, the former (shown in fig. 31) a graph of population abundance. The survival curves are based on the estimated survival per 100,000 eggs spawned, and the data used in constructing them for 1950 and 1951 are summarized in table 11. Survival to 21.25 mm. was about 1 in 1,000 in both 1950 and 1951.

The survival curves for 1950 and 1951 are fairly similar—in both there is an abrupt decline between egg and yolk-sac stages. This may be a real decline due to very high mortality during the critical period immediately following yolk-sac absorption, or it may be an artifact resulting from net selectivity (loss of larvae through the apertures of the nets used). I favor the latter explanation. The survival curve for 1951 levels off in the section based on larvae between 5.75 to 11.75 mm. in length.[7] This means, interpreted literally, that mortality during this period of life was negligible, after having been precipitous im-

[6] This estimate is based on the data presented by Clark (1934). She estimated that the Pacific sardine would spawn from 30,000 to 65,000 eggs in a batch, depending on the size of the fish, and as many as three batches a season.

[7] The survival curve for 1941 (southern California area) is nearly flat for the section based on larvae between 6.75 to 12.75 mm. in length.

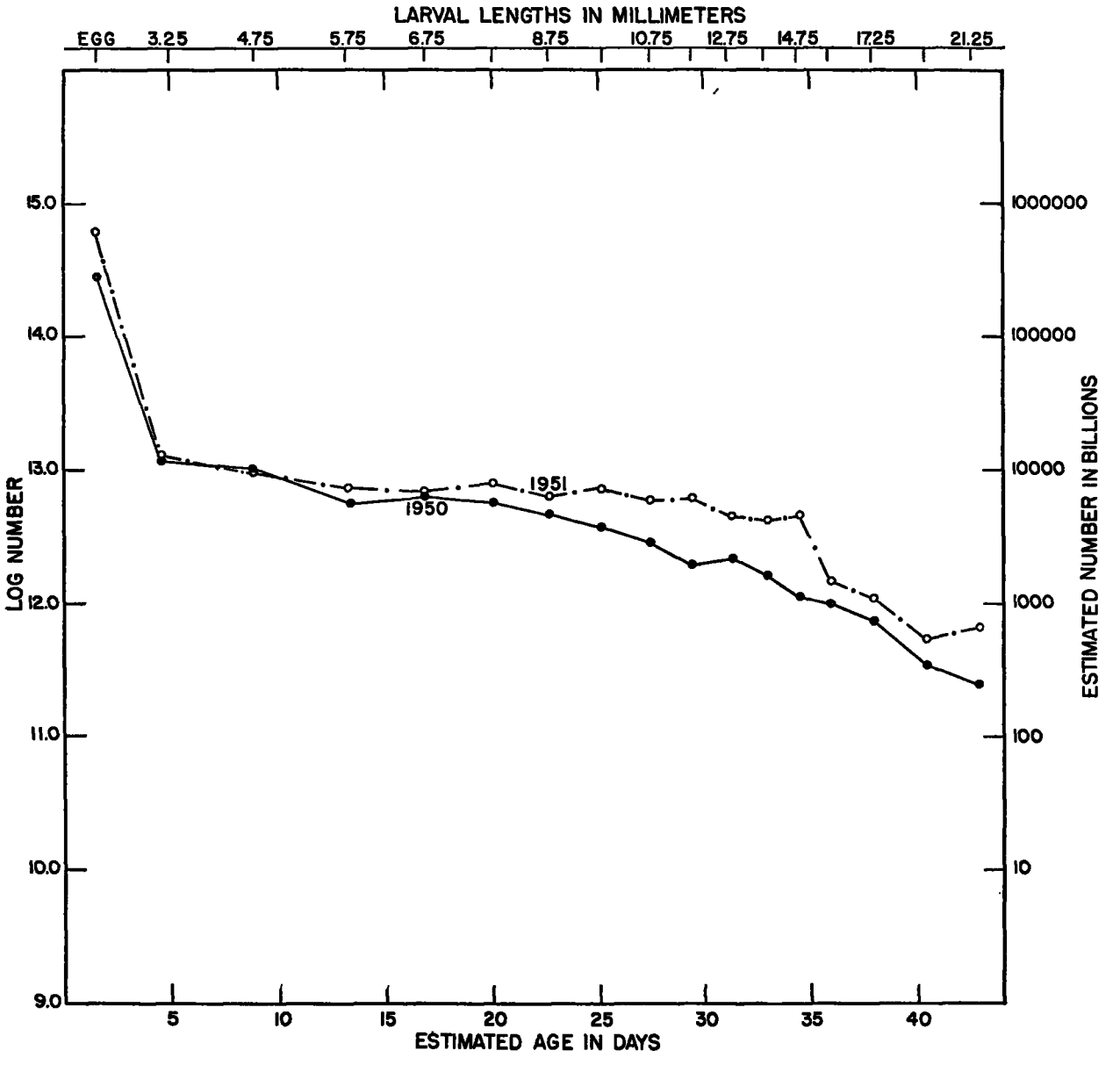

FIGURE 31.—Curves of population abundance during the planktonic phase of 1950 and 1951 year classes.

mediately following hatching. This does not seem reasonable. Net selectivity, severest on newly hatched larvae and becoming progressively less severe with increase in larval size, could produce the flat section of the curve. If the latter interpretation is correct, selectivity of standard nets is considerable. The extent of such loss will be determined and taken into account in future work.

The terminal slopes in the survival curves are probably the result of larvae dodging the nets, rather than of an increase in mortality in larvae of 15.75 mm. and larger. The decline would be even more precipitous if the curves had been extended to include the few larvae larger than 21.25 mm. taken each season.

A survival curve is no more reliable than the data on which it is based, and I have already indicated some of the limitations of the 1950 data. The larger sizes are probably underestimated by as much as 50 percent, due to the inadequacy of our "southern" coverage in 1950. The collections of 1951 appear to have covered the distributional

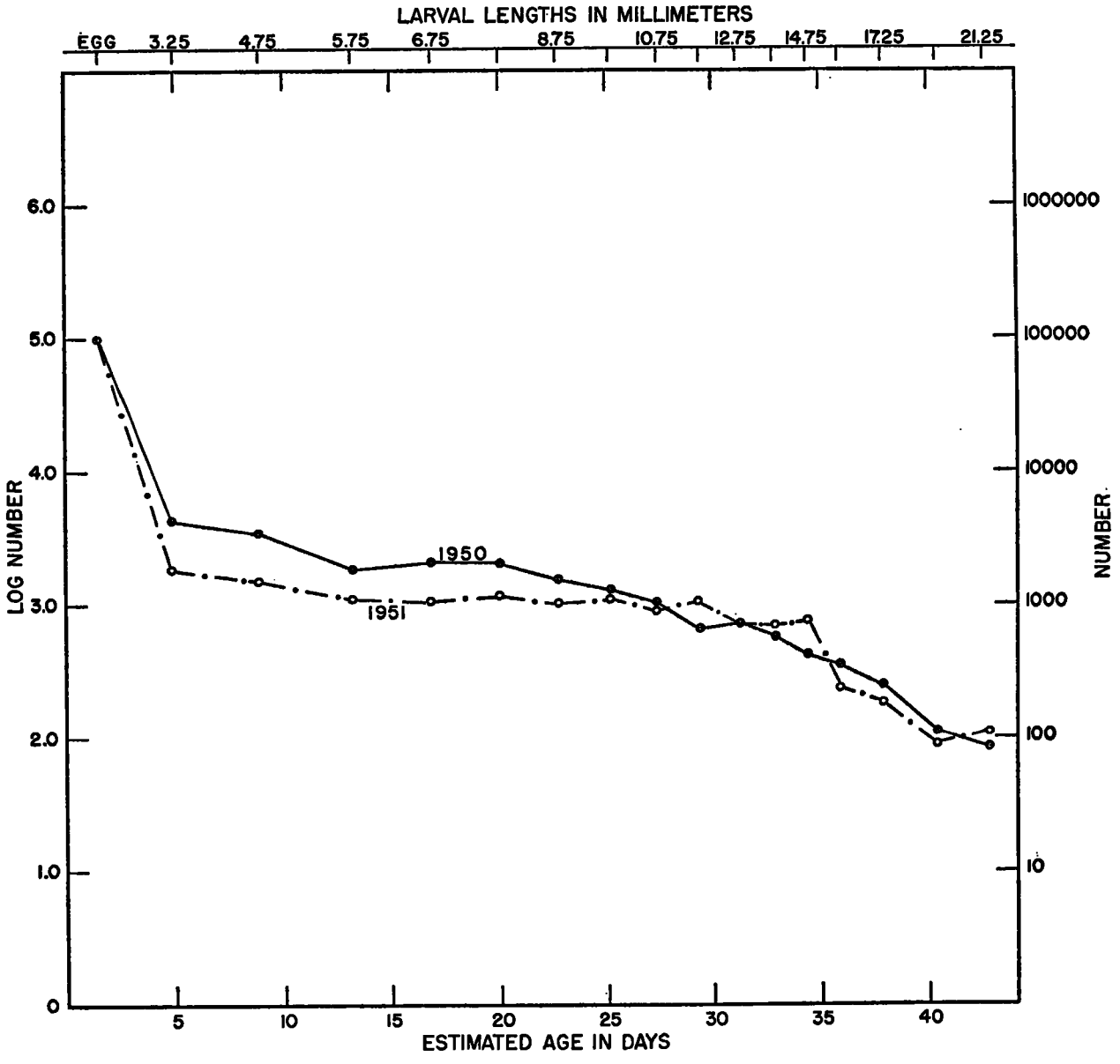

FIGURE 32.—Survival of young stages of sardines per 100,000 eggs spawned during 1950 and 1951.

range of the larvae adequately, and the 1951 estimates are probably as reliable as can be obtained with present methods of sampling.

SUMMARY

1. Distribution and abundance of egg and larval populations of the Pacific sardine, or pilchard, are being determined by means of quantitative plankton hauls taken at regular intervals over an extensive grid of stations off California and Baja California. The results of 3 years of surveys, 1949 through 1951, are presented.

2. Distribution of sardine eggs affords, at present, the only reliable information on the distribution of the sardine spawning stock during the spawning season. An estimate of the total number of eggs spawned during a year is one of the values needed in determining the survival rate of larvae. When used in conjunction with data on fecundity, an estimate of egg abundance can be

translated into an estimate of the size of the spawning stock.

3. The method followed in estimating the total abundance of sardine eggs is similar to that described by Sette and Ahlstrom (1948). The number of eggs taken in any given haul has been made comparable with other samples by referring all collections to a common basis, the number of eggs under a standard area of 10 square meters, and by determining for each sample the average number of sardine eggs spawned per day. The data from each cruise have been treated as a problem of integration over space, the combining of the monthly cruises as a problem of integration on time.

4. Estimates of the number of sardine eggs spawned during 1950 and 1951 were 286×10^{12} and 611×10^{12}, respectively.

5. There are, at present, two major areas of sardine spawning, a compact area of intense spawning off central Baja California, and a larger area of diffuse spawning off southern California and adjacent Baja California. In 1950, approximately 82 percent of sardine spawning occurred off central Baja California, 17 percent in the area off southern California and adjacent Baja California, and 1 percent off central California. In 1951, 94 percent of all eggs taken were obtained off central Baja California, the remaining 6 percent were from southern California and adjacent Baja California.

6. Most sardine spawning has been found to occur within a 4-degree temperature range, 12.5° to 16.5° C. Only negligible amounts of spawning have been found at temperatures lower than this. The upper temperature limit does not appear to be so sharply defined, since some off-season spawning has been obtained at temperatures exceeding 20° C.

7. Sardine eggs have been collected during every month of the year off central Baja California, although the period of major abundance has been limited to the months of February through May. Off-season spawning, especially that occurring from August through December, has been largely confined to Sebastian Viscaino Bay. In the waters off southern California and adjacent Baja California, most spawning (over 98 percent) has occurred during a 3-month period, April through June.

8. A basic reason for conducting sardine larval studies is to test the assumption that the early postembryonic period is probably the most critical in regard to mortality, hence the period during which the success or failure of a year class probably is determined.

9. In the quantitative sampling of sardine larvae, several difficulties have been encountered, important among which are (1) net selectivity, i. e., the loss of smaller larvae through the mesh openings of plankton nets, and (2) a marked undersampling of the larger larvae during daylight hours.

10. Exact data on the rate of growth of sardine larvae are not available. Sardine larvae taken in plankton hauls are between 3 mm. (the size at hatching) and 24 mm. in length. From an inspection of seasonal curves of abundance of sardine larvae, grouped by size categories, it appears that between 1 and 2 months are required for a newly fertilized egg to develop into a larva 24 mm. in length. Growth during the larval period is assumed to be logarithmic. Based on a total time period of 45 days between fertilization of the egg and attainment of a larval length of 24 mm., values for the time duration of all size classes routinely used in tabulation of sardine larvae have been determined.

11. Estimates have been obtained of the magnitude of the sardine population at a number of different larval stages. The survival rate of sardine larvae has been determined per 100,000 eggs spawned. During both 1950 and 1951, the minimal estimate of survival to 21 mm. was about 1 in 1,000.

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METHOD OF ESTIMATING FISH POPULATIONS, WITH APPLICATION TO PACIFIC SARDINE

BY T. M. WIDRIG

FISHERY BULLETIN 94

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

A method is presented of estimating size of fish populations from data on catch, fishing effort, and age composition. It employs the regression of observed (or apparent) instantaneous total-mortality rate on the number of effective effort units. This regression is linear under certain conditions of natural mortality and of distribution of fishing effort with reference to distribution of the fish.

Variation in observed total-mortality rate for a given amount of fishing effort must be due to variation in the rate of natural mortality, in the level of availability, or in both. Therefore, lacking information about rate of natural mortality and level of availability, estimates of population size can be made only under given conditions of these two factors.

Application of the method to the Pacific sardine, or pilchard (data from California landings), yields estimates of population size for each year from 1932 through 1937 and 1941 through 1950. Under the hypothesis of constant level of availability, the average population during these years was estimated to be 23 billion fish. Under the hypothesis of constant rate of natural mortality, the average minimum population was estimated to be 6 to 11 billion fish. The average annual catch for these years was 2.7 billion fish.

It is unlikely that either the rate of natural mortality or the level of availability is constant in nature. At least some of the observed variations must be attributed to availability changes.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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METHOD OF ESTIMATING FISH POPULATIONS WITH APPLICATION TO PACIFIC SARDINE

By T. M. WIDRIG, *Statistician*

THEORY OF THE METHOD

INTRODUCTION

One of the most pressing and perplexing problems of fishery biology is that of securing reliable estimates of population sizes. Apart from complete counts of fish, which are impractical for marine species, the tag-and-recapture method of estimating the fraction of the population that is caught in a period of time by a fishery is one that has been commonly practiced on large populations (see Ricker 1948 and Schaefer 1951, for example). This method is both difficult and expensive, as is the one based on annual egg censuses and information on fecundity.

DeLury (1947) has suggested a method of estimating population size using catch and effort data. An assumption necessary to his method is that there be no natural mortality. When catch data are measured over long periods, as annually, natural mortality conceivably could be large with respect to fishing mortality.

The method of estimating population size described in this paper is an elaboration of the method developed by Silliman (1943). It requires data on the age composition of the catch and on fishing effort. The necessary assumptions are more easily satisfied than those required by DeLury (1947).

Since methods of estimating population sizes are difficult and since the estimates are subject to error (the magnitude of which it is often impossible to assess), it is desirable that, whenever possible, two independent methods be used.

GENERAL STATEMENT OF THE METHOD

In attempting to estimate the size of a population, the fishery worker generally knows, first of all, the size of the catch from that population. The problem might then be stated: *What is the ratio between this catch which I observe and the total stock from which it came?* I wish to compute the ratio between the catch and the size of the population from which it came by subtracting the natural mortality rate from the total mortality rate to get the fishing mortality rate. The latter, of course, is the ratio of the catch to the initial stock.

The rate of total mortality can be computed from estimates of the ratio of the stock size in one year to the size of that stock in the following year. For this purpose, information on the age composition of the total catch per unit-of-effort is usually sufficient.

Having computed the total-mortality rate from the catch data, all that remains is to find the natural-mortality rate, so that it can be subtracted from the total-mortality rate to give the rate of fishing mortality.

Under certain conditions, the rate of natural mortality can be derived from two series of data—

1. The number of fishing effort units expended to obtain the given catch.

2. The total annual-mortality rate that the total stock experienced while yielding the given catch.

Briefly, the method of estimating the natural-mortality rate is as follows:

In a fishery that has experienced a wide range of fishing effort between years, and therefore in fishing mortality between years, the total-mortality rate will vary as well. But if natural mortality is constant, a given percentage change in fishing effort should produce a smaller percentage change in total-mortality rate. If natural mortality is large, one expects fishing effort to affect total mortality less than if natural mortality is small.

By examining the past sequence of total-mortality rate and the corresponding fishing effort, one should be able to compute a constant rate of natural mortality necessary to give the observed relation between total mortality and fishing effort.

To examine the relation between fishing effort and the attendant total mortality, I consider a regression of the total-mortality coefficient on the

number of fishing effort units. I show that this relation should be linear, if my assumptions are granted. When fishing effort is extrapolated to zero, the total-mortality rate will be equal to the rate of natural mortality.

DEVELOPMENT OF THE METHOD

If fishing acts so that the catch of a standard unit of gear in a moment of time is proportional to the population size at that moment, then the rate of fishing mortality referred to above will be p (see Notation, p. 163) in

$$\frac{dC}{dt}=pN_t \tag{1}$$

where $\frac{dC}{dt}$ is the rate of catch on time and N_t is population size during time dt. If natural mortality behaves in a similar fashion, that is, q, in

$$\frac{dn}{dt}=qN_t \tag{2}$$

where $\frac{dn}{dt}$ is the rate of natural death on time and q is its coefficient, then the instantaneous rate of total death, say, i, can be expressed as

$$i=p+q \tag{3}$$

Further, under certain assumptions concerning the time and space distribution of p and q, the annual total death rate, expressed as a fraction of the initial population for a unit time period, may be written as a in

$$a=1-e^{-(p+q)} \tag{4}$$

or

$$a=1-e^{-i}$$

since, of course, the total rate of death is the sum of the two rates, when expressed as instantaneous rates. (See Baranov 1918 and Ricker 1940 and 1944, for detailed derivations.) Now u, or the rate of exploitation, can, under certain conditions, be written simply in the above notation as

$$u=p\frac{a}{i} \tag{5}$$

Since a, the seasonal rate of total mortality, often can be estimated from age-composition data, and since i is related to a as

$$a=1-e^{-i}$$

the ratio of a to i is fairly easy to compute from age-catch data. The problem remains to compute p, in order to find u, and hence the population size, given the catch.

Under certain conditions (see appendix, p. 164), fishing effort may be considered as directly proportional to p, say

$$p=Qf \tag{6}$$

where Q is the constant factor of proportionality, and f is number of fishing effort units.

Now only a constant, Q, remains to be estimated, to estimate population size. Recall the relation between Q and the various mortality rates:

$$i=p+q$$

or

$$i=Qf+q$$

If q is constant, and one has measures of i and f, Q will be the slope coefficient in a linear regression of several such relationships, say, one from each season for which data on age-composition and effort are available.

Silliman (1943) solved two similar equations:

$$a_1=m_1+n-nm_1 \tag{7}$$

$$a_2=m_2+n-nm_2$$

where $m=1-e^{-p}$ and $n=1-e^{-q}$ and where

$$\frac{f_1}{f_2}=\frac{\log(1-m_1)}{\log(1-m_2)}. \tag{8}$$

It can be shown that equations 7 and 8 are equivalent to

$$i_1=Qf_1+q \tag{9}$$

$$i_2=Qf_2+q$$

Silliman used sardine total-mortality and effort data that he took to represent an average for two periods of years, 1925–33 and 1937–42. His method is equivalent to fitting a regression line to all his yearly data by the method of semi-averages. The method described in this paper is one of fitting a regression line to all the yearly data by the method of continuous averages, or least squares.

A HYPOTHETICAL EXAMPLE

Suppose that data on the total-annual-mortality rate, a, and effective fishing effort, f, are available for some fishery over a period of several years, as follows (see fig. 1):

TABLE 1.—*Hypothetical mortality and effort data*

	a	f	i		a	f	
		Boat-days				*Boat-days*	
Year 1	0.50	101	0.69	Year 4	0.71	208	1.24
Year 2	.63	153	.99	Year 5	.76	246	1.43
Year 3	.62	161	.97	Year 6	.78	249	1.51

The regression (slope) coefficient is $Q=0.005318$, and the i intercept is $i=0.147$. Thus, with no fishing effort, the data lead one to infer that the total-mortality rate would be $i=0.147$, or 13.7 percent annually. This would be the average natural-mortality rate of the population. And for every 100 boat-days of effort during a season, one would infer that the total-mortality rate would be increased over the natural rate, 0.147, by 0.5318 units. Thus, if there were 100 boat-days in some particular season, one would infer that the fishing-mortality coefficient that those boats generated was $p=0.5318$, and that the total-mortality coefficient during that season was $p+q=0.5318+0.147=0.6788$. This i corresponds to an a of 49.3 percent per year. Of this 49.3 percent, one would infer that the fraction p/i was that part of the initial population that was caught during the season, or $0.5318/0.6788=0.7834$. So, the fraction caught, or rate of exploitation, is 0.7834 times 49.3 percent, or 38.6 percent, with the remainder of total mortality representing the fraction that died naturally, or 10.7 percent. The initial population for that year, of fish that were fully recruited and therefore sustaining these various rates of mortality, would be estimated by dividing the catch for that year by the rate of exploitation, since,

$$u=\frac{C}{N} \tag{10}$$

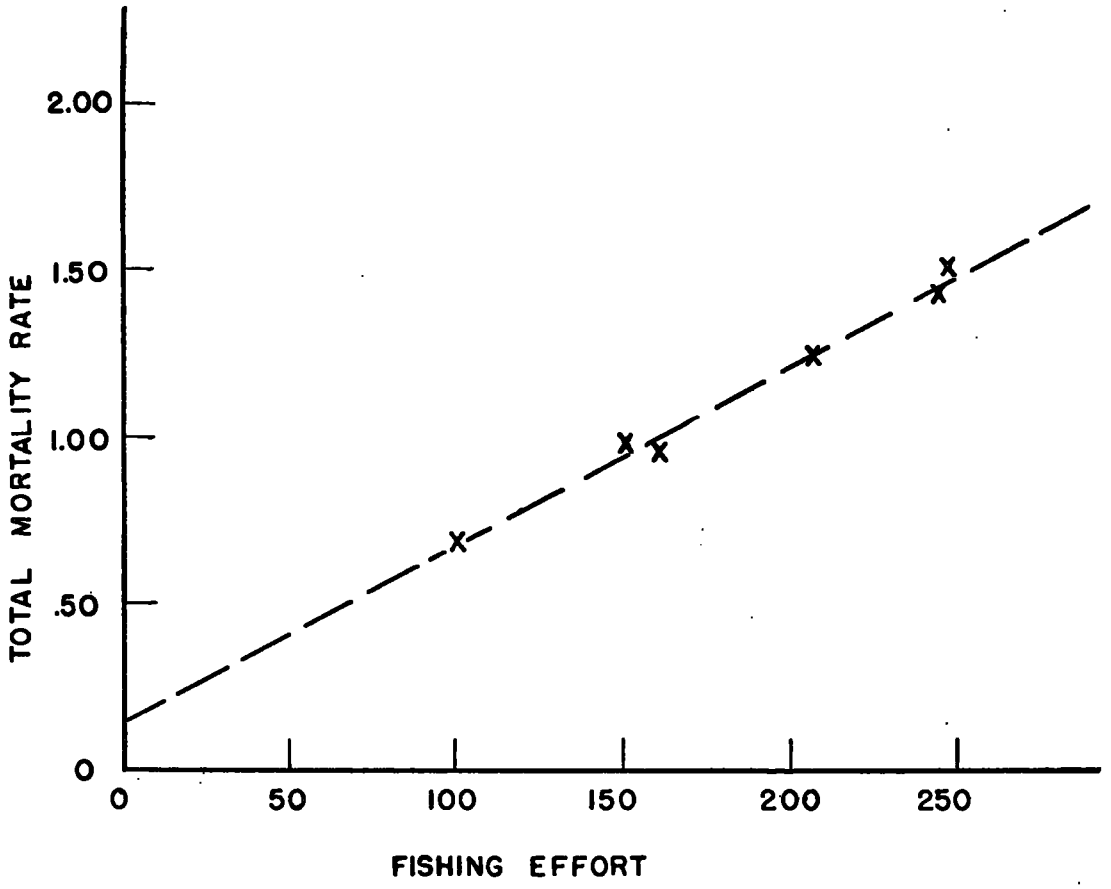

FIGURE 1.—Instantaneous total-mortality rate and fishing effort in an example. Data from table 1 in text.

and therefore

$$N=\frac{C}{u} \tag{11}$$

That is, N, the initial population, would be estimated at 1/.386, or 2.6 times the catch in that season.

ASSUMPTIONS OF THE METHOD

The method, just described, of estimating population size from age-composition data and effort data involves four assumptions, as follows:

1. Fishing effort: Must be equally distributed over the area of the fishery and during the unit time period considered.
2. Natural mortality: Must be either constant or uncorrelated with fishing effort.
3. Fishing efficiency: Effort is directly proportional to p, i. e., Q is constant.
4. Area of the fishery: Encompasses range of the fish.

To summarize, the regression analysis gives the means of computing, for each year, the instantaneous rate of fishing. If one then takes the seasonal total-mortality rate for that year, and its corresponding instantaneous total-mortality rate, the percentage that the instantaneous fishing rate is of the instantaneous total-mortality rate will be the fraction of the total seasonal-mortality rate that is due to fishing. This percentage, by definition, is the ratio between the catch during that season and the total stock on hand at the start of the season. If the catch is known, one may estimate the initial stock by dividing the catch by that percentage.

Methods of treating the catch data to satisfy the assumptions listed above will be given in the next section.

SATISFYING THE ASSUMPTIONS

The assumption that fishing effort is uniformly distributed in space is seldom fulfilled by a commercial fishery. Where fish are more dense, fishermen generally make better catches, with the result that fishing effort usually follows the fish population density. Also, the relative distances of different areas of the fishing grounds from a port of landing very often contribute to a nonuniform distribution of fishing effort.

If one has measures of catch per unit-of-effort from several of the component areas of the fishery, any differences in effort among these several subareas may be easily adjusted to yield an effort and catch per unit-of-effort measure that will not violate the above assumption. A method for doing this has been developed by Beverton and Holt (in press), and is as follows:

Let fishing effort be defined as the ratio between the total catch from an area and the average catch per standard unit-of-effort in that area, for a given interval of time. If one is concerned with the effort measure over several areas, he need only divide the total catch of the several areas by the sum of the average catch per unit-of-effort from the several areas. Since catch per unit-of-effort is really a measure of the relative average population density over a given period of time in a given area, a relative average population size index, $(C/f)_t$, in several given areas over a given period of time would simply be the sum of the average population density in each of the component areas, weighted to the respective area sizes. That is

$$(C/f)_t=\sum_{i=1}^{N}(\overline{C/f})_i \tag{12}$$

where t refers to the total area, there are N subareas of equal size, and $(\overline{C/f})_i$ refers to average catch per unit-of-effort in the i^{th} area. Under the definition of fishing effort given above, generally let

$$f=\frac{C}{(\overline{C/f})} \tag{13}$$

where $(\overline{C/f})$ is the average observed catch per unit-of-effort, and f is the effective total effort, i. e., the effective number of effort units. Note that $(C/f)_t$ is a single observed quantity (from a single unit-of-effort), while C/f would be the ratio of two different quantities. Since the $(\overline{C/f})$ measure is an average, it need not necessarily be observed from an entire fleet. Indeed, only one unit-of-effort need be observed to obtain an estimate of the average catch per unit-of-effort that the total-fishing effort experiences during a season. Of course, such an estimate would be more accurate if it were taken as the average of as many units-of-effort as possible. Further, each such unit-of-effort should be equivalent in efficiency.

We can now easily define the effective fishing effort over any number (N) of areas at once:

$$f_t=\frac{\sum_{i=1}^{N}C_i}{\sum_{i=1}^{N}(\overline{C/f})_i} \tag{14}$$

where f_i is again the effective fishing effort for N areas. This effort measure, f_i, will be one which, if applied uniformly to each area of the fishery, would yield the observed total catch and observed sum of average catch per unit-of-effort.

In other words, this effective effort is a weighted average of the effort in the several subareas, the weights being proportional to the observed average catch per unit-of-effort measure in each subarea as follows:

Let the average catch per unit-of-effort in N areas be

$$(\overline{C/f})=\frac{\sum_{i=1}^{N}(C/f)_i}{N} \tag{15}$$

and recall that

$$C_i=(\overline{C/f})_i f_i \tag{16}$$

Substituting these in (14), we have

$$f_i=\frac{\sum_{i=1}^{N} C_i}{\sum_{i=1}^{N}(\overline{C/f})_i}$$

$$=\frac{\sum_{i=1}^{N}(C/f)_i f_i}{(\overline{C/f})N}$$

$$=\frac{\sum_{i=1}^{N}\left[\frac{(C/f)_i}{(\overline{C/f})}\right]f_i}{N} \tag{17}$$

The ratio $\frac{(C/f)_i}{(\overline{C/f})}$ is the weight factor. Of course, if the population density in each subarea is equal, this weight factor is unity, and in that case,

$$f_i=\frac{\sum_{i=1}^{N} f_i}{N}$$

That is, the total effective effort in that case is simply the arithmetic mean of the effort in each subarea.

Of course, if the effort in each subarea is equal, then the total effective effort is the same as this constant effort, regardless of differences in population density among the subareas. Let $f_i=f'$, a constant.

Then

$$f_i=\frac{\Sigma f_i\frac{(\overline{C/f})_i}{(\overline{C/f})}}{N}$$

$$=\frac{f'\Sigma\frac{(\overline{C/f})_i}{(\overline{C/f})}}{N}$$

$$=f'\frac{\frac{N(\overline{C/f})}{(\overline{C/f})}}{N}$$

$$=f'$$

A practical definition of the necessary subareas, then, is that they be those within which fishing effort is more nearly uniform. Fishing effort between the subareas need not be uniform. In many coastal fisheries, the within-season change in the number of boats fishing from an individual port is not nearly as great as the difference, during the season, between the fleet sizes at the several ports of landing. Where the fishing grounds are near these ports of landing, it would be convenient to define subareas as those that are fished by the fleet operating out of each port of landing.

If the density measure (catch per unit-of-effort) is to be taken as a population measure, then each subarea must be equal in size. Otherwise, the density measures must be weighted by the size of their respective areas, to yield a population estimate. Since the range of operation of units of fishing effort is usually not very variable, the units of gear generally will fish areas of similar size. A careful selection of a unit of effort can sometimes be made such that each unit can be assigned specifically to a certain area.

No treatment of catch data can satisfy the assumption regarding natural mortality. In application, one should consider the effect of various reasonable natural-mortality rates.

The necessity for the assumption on the constancy of the efficiency of a unit of gear can be relieved by a careful measurement of fishing effort, with the objective of the assumption in mind. See the appendix, p. 165 for a detailed definition of this constant.

The fourth assumption is one that can only be directly satisfied by fishing outside the normal

fishing area. The problem of assessing the degree to which this assumption is violated will occupy a major part of this paper.

COMPUTING AN INITIAL-POPULATION INDEX

The catch per unit-of-effort index one usually has from a fishery is an estimate of relative average population size during the time period that the fishing effort has accumulated the observed catch. This period is usually a year or a fishing season.

To compute total-mortality rates, it will be necessary to have an estimate of the initial population, or the population at the beginning of the time unit, rather than the average population being fished, which would occur at some time between the beginning and the end of the season.

If we describe the population at any time, t, as

$$N_t = Ne^{-it} \tag{18}$$

where N is the initial population, and i is a constant rate of instantaneous decrease, then the average population during time t, from 0 to 1, is

$$\overline{N} = N\int_0^1 e^{-it}dt$$

$$= (N)\frac{1-e^{-i}}{i} = (N)\frac{a}{i}, \tag{19}$$

since, if i is constant, the annual or seasonal total-mortality fraction, a, is related to i as

$$a = 1-e^{-i}$$

and the survival fraction s, as

$$s = e^{-i}$$

If we desire an index of initial population, and are given an index of average population (the catch per unit-of-effort index) we may convert the average population to the initial population by multiplying the average population by the ratio i/a.

This has been noted by Ricker (1948) and by Beverton and Holt (in press). The latter authors effect the conversion of average- to initial-population-size estimates simultaneously with an estimate of the rate of exploitation for a series of years, through a process of iteration of a regression equation. Iteration is necessary, since one must have a first estimate of i as derived from some estimate of the survival fraction s. Of course, the only estimate of s one has to begin with is the ratio of average populations in successive seasons of a single year class or group of tagged fish. This first estimate of s enables one to approximate the correction term i/a, and the corrected population-size estimates yield a second and more accurate estimate of s, and so on.

EFFECT OF CHANGING AVAILABILITY ON TOTAL-MORTALITY ESTIMATES

Let a population of fish be those members of a stock of fish that are potentially capable of being fished by a fishery. This population would include fish which in a given season are not within the range of (available to) the fishery, but which are potentially available to the fishery by virtue of the possible movement of the fish into and out of the range of fishing operations, or by movement of fishermen into and out of the range of the population of fish. This population would not be barred by any land barrier from entering the area of fishing and some part of them would be in the area of fishing, while all would be capable of moving in and about the fishing area. Let the ratio of the number of fish in the population that are within the scope of fishing operations during a season to the number of fish in the total population be termed the availability level, or availability (Marr 1951 and Sette 1950).

This definition of availability is somewhat general, but it has real intuitive meaning to any fisherman. Sometimes the fisherman is able, by his scouting, to fish so that most of the population is available to him, but this is not often the case. Most fishing gear is limited to certain depths, areas, or sea conditions, and the population is generally not bounded by these same factors. Thus one often finds that some part of a population is unavailable to a fishery, because of limitations in the physical capacity of the gear to fish the entire habitat or range of the population.

The condition of a population being less than fully available is seldom measured directly. Fishermen's records are of little direct help, since they measure only that portion of the population that is within their range; however, if the availability level were to change, the fishermen's catches of a given year class would immediately change accordingly. The result observed by the fishermen would be an apparent change in the efficiency of a

unit of standard gear. If the physical efficiency of the gear had not changed, an apparent change in the efficiency could only be due to a change in availability. That is, the population range or behavior would have changed relative to the fishery. Such a change is not difficult to observe in catch data, but the absolute level of availability is impossible to compute from catch data alone. Supplementary observations would be required to estimate directly the level of availability of a population to a fishery. This would involve fishing outside the area of the fishery.

Since a fishery yields data only on the fished, or available, population, an estimate of total-survival rate from the fishery would be an estimate of the total-survival rate of the population only if the availability ratio in two adjacent seasons were the same, as follows:

Let N_a be the initial available population. Then the availability level would be r in

$$r=\frac{N_a}{N} \tag{20}$$

Let N_1 be the initial total population in a given year, and N_2 the initial total population in the succeeding year. Then the total-population survival rate would be s, in

$$s=\frac{N_2}{N_1}$$

$$=\frac{\frac{N_{a2}}{r_2}}{\frac{N_{a1}}{r_1}}$$

$$=\frac{N_{a2}}{N_{a1}}\left(\frac{r_1}{r_2}\right)$$

So, if $r_1=r_2$, then

$$s=\frac{N_{a2}}{N_{a1}}$$

That is, if the availability level is constant, this estimate of the total-population survival rate from the fishery is an unbiased estimate of the total-population survival rate, even though the survival rate in the available population may be much lower.

If, on the other hand, $r_1 \neq r_2$, we have

$$s=\left(\frac{r_1}{r_2}\right)\frac{N_{a2}}{N_{a1}} \tag{21}$$

$$=\left(\frac{r_1}{r_2}\right)s^*$$

where s^* is the survival rate computed from the fishery data, N_{a1} and N_{a2}.

Large changes in the availability ratio can render estimates of s^* unreal, if s^* is interpreted as survival rate in the entire population, since survival rate in the unavailable population will nearly always be greater than that in the available population. If all causes of death other than fishing are the same for all fish in the population, survival rate in the available population will always be less than that in the unavailable population, and in the total population. In terms of the total population, this means that the total-mortality rate of the entire population, as a maximum, can be no greater than that of the unfished population, plus that resulting from the fished population being taken entirely each year. The initial stock on the fishing grounds in a given year would then be the survivors of the previous year's unfished population. Of course, the lower the level of availability, the lower is this limit of total-mortality rate of the total population. With availability very low, the population initially on the fishing grounds could be fished out entirely each year, yet in succeeding years the ground could continue to supply fish that annually move onto the fishing grounds from the unfished areas. In this case the total-mortality rate of the fished population would be very high indeed, yet for the total population it could be low.

Closing certain parts of the fishing grounds to fishing has the same effect: No matter how hard the remaining grounds are fished, the total population can suffer only a limited total mortality, depending on the level of availability. (How limited this total mortality will be is influenced, of course, by the ratio of size of the closed area to the total area inhabited by the fish.) This procedure is not as efficient, for fishermen, as the alternative procedure of limiting effective fishing effort so that a desired (for whatever reason) total

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mortality of the total population occurs. The effect in this latter instance is to fish a higher average density of fish (catch per unit-of-effort is higher) than in the closed-area procedure, even with the same catch. Limiting the fishing effort is in most cases made practical only by setting a bag limit, and to set a bag limit so that a certain total mortality results, one must have good knowledge of the absolute size of the initial total population each year. Such information about marine fishes is at best extremely rare, but nevertheless important, if the bag limit is used to control total-mortality rate and rate of exploitation.

ESTIMATING AVAILABILITY AND TOTAL MORTALITY

If variation in r is random, an average s^* is an unbiased estimate of s, the total-survival rate. If all mortality but that resulting from fishing is constant, then from a given fishing effort one can compute an "expected," or "normal," survival rate for a population if availability is constant. If availability changes, the observed s^* will depart from the true survival rate accordingly.

A regression of i^*, computed from s^*, on fishing effort, f, will yield a system of s's which would be expected if availability does not change from the average availability of the years to which the regression was fitted. Similarly, Q, or the effort-unit efficiency, computed from the regression, will not be that pertaining to the fished population, but to the total population at the average level of availability. Accordingly, the instantaneous rate of fishing mortality to be expected from a given number of fishing-effort units would be Q times that number of units, and would obtain only if those units fished a population whose availability was the same as the average availability when Q was computed. The efficiency of fishing, then, depends on the level of availability. If availability varies, so will the efficiency of a unit of gear.

It is this variation in the apparent efficiency of a unit of gear that will enable one to estimate the ratio of availability in successive seasons. A rough approximation to availability can be easily obtained by assuming that s', the value of s estimated from the regression, is always equal to s for any year, and then taking the ratio s'/s^* as an estimate of r_1/r_2 for each pair of years for which one has the necessary data. A maximum availability measure can then be computed from the series of r_1/r_2. Of course, this measure of availability is not exact, since s' will seldom be exactly equal to s for a given year. The direction of the change will be different, depending upon whether s was greater or less than s' for a given year.

Although the estimated ratios, r_1/r_2, are not biased, the mean of the resulting availability estimates is a maximum. The s' measures are those pertaining to the condition of average availability over the period of the data to which the regression is applied. If the rate of average natural mortality, estimated from the regression, is at all precise (depending on the extent of variation in availability in the data) one can estimate the survival rate in the available population under the condition of average availability. The relationships between the several mortality rates and availability are as follows:

Let

$$D=D_a+D_u \tag{22}$$

where D is deaths in numbers from all causes, D_a in the available population, and D_u in the unavailable population, so that $S=S_a+S_u$, where S is number of survivors from all causes of death, S_a in the available population, and S_u in the unavailable population. Then $S=N-D$. Now

$$s=\frac{S}{N}$$

$$=\frac{S_a+S_u}{N}$$

$$=\frac{s_aN_a+s_uN_u}{N}$$

So

$$s=s_ar+s_u\,(1-r) \tag{23}$$

Taking

$$s'=s_a\bar{r}+s_u\,(1-\bar{r})$$

Then

$$s_a=\frac{s'-s_u\,(1-\bar{r})}{\bar{r}}$$

If s_a were known, one could interpret the slope, Q_a, of the resulting regression of i_a on f as the efficiency of fishing, and the product, Q_a times f, as p_a.

Then

$$u=\left(\frac{p_a}{i_a}\right)a_a$$

and

$$N_a=\frac{C}{u}$$

Now, s_a is seldom known. But there is another, although less precise, procedure for estimating Q_a, with only s^* and f known.

The general expression for the total-population total-instantaneous-mortality rate, in terms of natural mortality, fishing effort, and the level of availability, can be developed as follows:

$$s=rs_a+(1-r)s_u$$

or

$$\begin{aligned}e^{-i}&=r(e^{-i_a})+(1-r)e^{-q}\\&=r(e^{-Q_af})e^{-q}+(1-r)e^{-q}\\&=e^{-q}[r(e^{-Q_af})+(1-r)]\end{aligned}$$

so that

$$(24)\qquad i=q-\log_e[re^{-Q_af}+(1-r)]$$

Of course, if $r=1.00$, this becomes

$$\begin{aligned}i&=q-\log_e e^{-Q_af}\\&=q+Q_af\end{aligned}$$

as before, since $Q_a=Q$, when $r=1.00$, and $i_a=i$. Also, when $f=0$,

$$\begin{aligned}i&=q-\log_e[re^{-0}+(1-r)]\\&=q-\log_e[1]=q, \text{ as before.}\end{aligned}$$

But for $f>0$, and $r<1.00$, i is less than i_a. Further, when $f=\infty$, i is not ∞, but is limited. That is, i has an asymptote, with respect to f, when $r<1.00$. It is

$$\begin{aligned}i&=q-\log_e[re^{-\infty}+(1-r)]\\&=q-\log_e[1-r]\end{aligned}$$

Thus, the locus of total mortality on effort, with less than full availability, will be curved—the slope decreasing as effort gets larger. The fitted straight line, then, is not entirely without bias, especially for higher effort levels. The true total-mortality curve will be an exponential with negative exponent, as in formula 24, and therefore the higher the effort, the more rapidly the slope decreases. One can substantially reduce this bias by transforming the fitted straight line to a curve of the type of equation 24. One might take an estimate of $\bar{r}$ and $\bar{q}$, to approximate the transformation. The straight line gives a fairly accurate measure of $\bar{r}$ and $\bar{q}$, and by taking the mean i and the mean f as coordinates of a point that is common to both the curve and the fitted straight line, one simply solves equation 24 for Q_a.

$$Q_a=\frac{\log_e\left[\frac{\bar{s}-s_u(1-\bar{r})}{\bar{r}s_u}\right]}{\bar{f}}$$

The population size would be estimated as previously outlined, taking Q_a and q to get u_a and N_a, and taking the estimates obtained above to get r and hence N.

This estimate is not necessarily unbiased or consistent. In an example to follow, where r is variable, it will turn out to be slightly biased.

SOME HYPOTHETICAL EXAMPLES WITH LESS THAN FULL AVAILABILITY

In the foregoing hypothetical example, I assumed that there was full availability—that the entire range of the population was sampled by the commercial fleet. These samples would render possible the easy computation of total-population relative size, and the total-mortality rate of the population. Further, the fishing effort was directed at least to some degree over the entire population.

With less than full availability, only part of the total population is fished and the unavailable remainder suffers only natural mortality. With a migratory-fish population, the magnitude of the fished part can be expected to vary, both with the habits of the fish and of the fishermen that pursue them.

Estimates of total mortality from the fished population alone are far worse than estimates from a regression of total mortality on fishing effort. Even these estimates are not exact, but if availability is constant, they are very close. If availability varies, they depart somewhat from the true total-population total-mortality rate. Estimation of the ratio of pairs of successive-years' availability is fairly accurate, but computing the fished-population size is more difficult. The total-population size, of course, would follow from knowledge of the fished-population size and the corresponding availability level.

Estimation of the mortality rates in the fished population can be accomplished in the manner outlined in the preceding section, but they are not entirely unbiased. Further, their reliability is difficult to ascertain, since one has no assurance that availability is varying at random.

Some hypothetical examples will illustrate the magnitude of variation of i^* from i, for various given conditions of availability. The examples assume fishing effort to be increasing throughout the period of years considered.

Example 1 (see table 2 and fig. 2):

(a) Availability constant at beginning of each year=50 percent.

(b) Natural mortality=0.

The regression of i_a on f is straight, but i on f is curved down; i is always less than i_a, as expected. The limit of i is 0.69, or a=50 percent, of course.

TABLE 2.—*Computation of mortality rates, for given fishing effort, with constant natural-mortality rate, availability level, and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ r=50 \text{ percent} \\ q=0 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: s_a=survival rate, annual, in unfished population=e^{-q}
i=instantaneous total-mortality rate in total population=$-\log_e(s)$

	f	p_a	i_a	s_a	s	i
Year 1	10	0.1	0.1	0.90	0.95	0.05
Year 2	20	.2	.2	.82	.91	.09
Year 3	30	.3	.3	.74	.87	.13
Year 4	40	.4	.4	.67	.84	.17
Year 5	50	.5	.5	.61	.80	.22
Year 6	60	.6	.6	.55	.77	.26
Year 7	70	.7	.7	.50	.75	.28
Year 8	80	.8	.8	.45	.72	.32
Year 9	90	.9	.9	.41	.70	.35
Year 10	100	1.0	1.0	.37	.68	.38
	∞	∞	∞	0	.50	.69

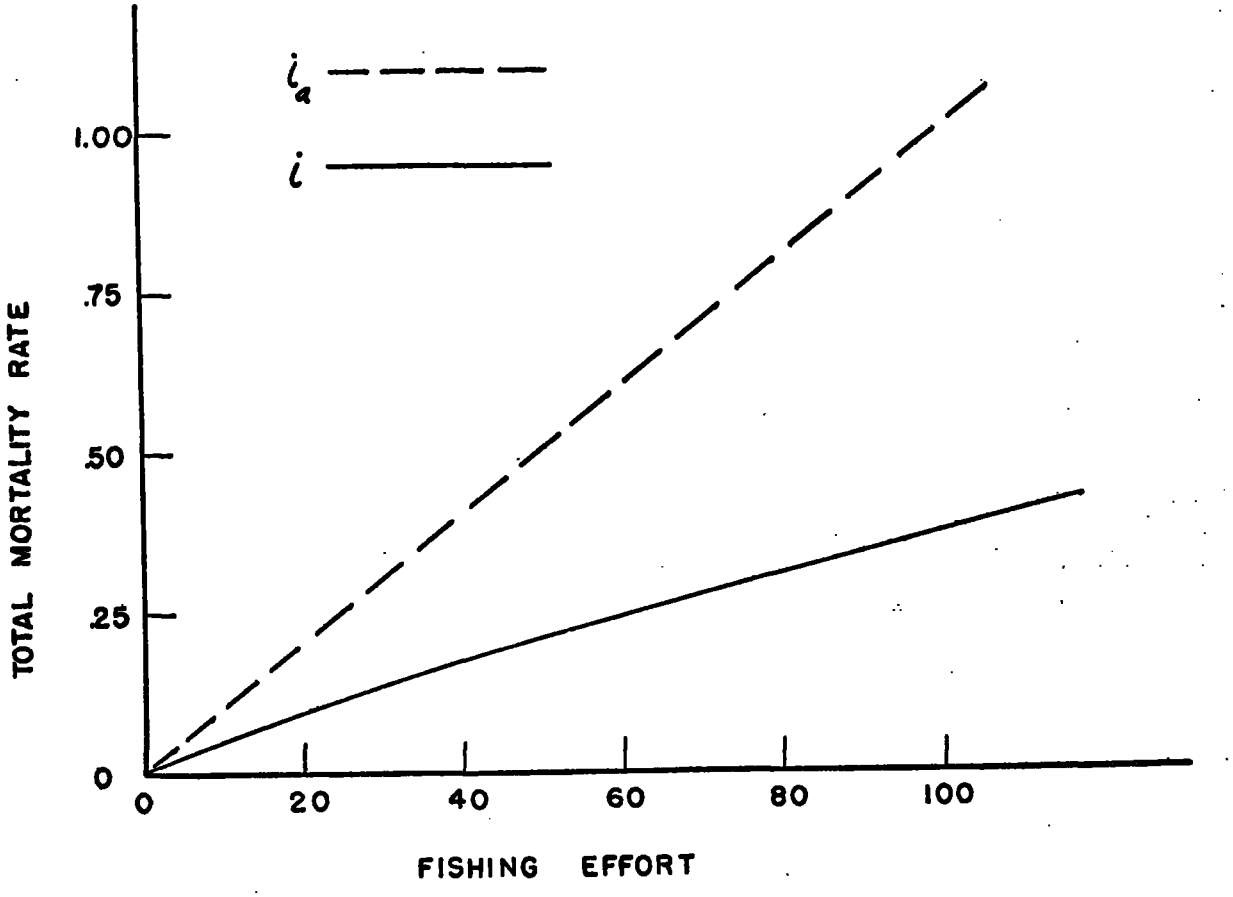

FIGURE 2.—Instantaneous total-mortality rate and effort, from example 1 in text.

Example 2 (see table 3 and fig. 3):

(a) Availability constant at beginning of each year=50 percent.

(b) Natural mortality: $q=0.2$, or $a=18$ percent in unfished population.

Again, i_a on f is straight, while i on f is curved down. Both regressions originate at $i=0.2$, and i is always less than i_a. The limit of i is 0.89, as expected (=0.69+0.2), or $a=59$ percent.

TABLE 3.—*Computation of mortality rates, for given fishing effort, with constant natural-mortality rate, availability level, and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ r=50 \text{ percent} \\ q=0.2 \end{cases}$

f=fishing effort
p_a=instantaneous fishing mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: s_a=survival rate, annual, in unfished population=e^{-q}
i=instantaneous total-mortality rate in total population=$-\log_e(s)$

	f	p_a	i_a	s_a	s	i
Year 1	10	0.1	0.3	0.74	0.78	0.25
Year 2	20	.2	.4	.67	.74	.30
Year 3	30	.3	.5	.61	.71	.34
Year 4	40	.4	.6	.55	.68	.38
Year 5	50	.5	.7	.50	.66	.41
Year 6	60	.6	.8	.45	.63	.46
Year 7	70	.7	.9	.41	.61	.49
Year 8	80	.8	1.0	.37	.59	.53
Year 9	90	.9	1.1	.33	.57	.56
Year 10	100	1.0	1.2	.30	.56	.58
	∞	∞	∞	0	.41	.89

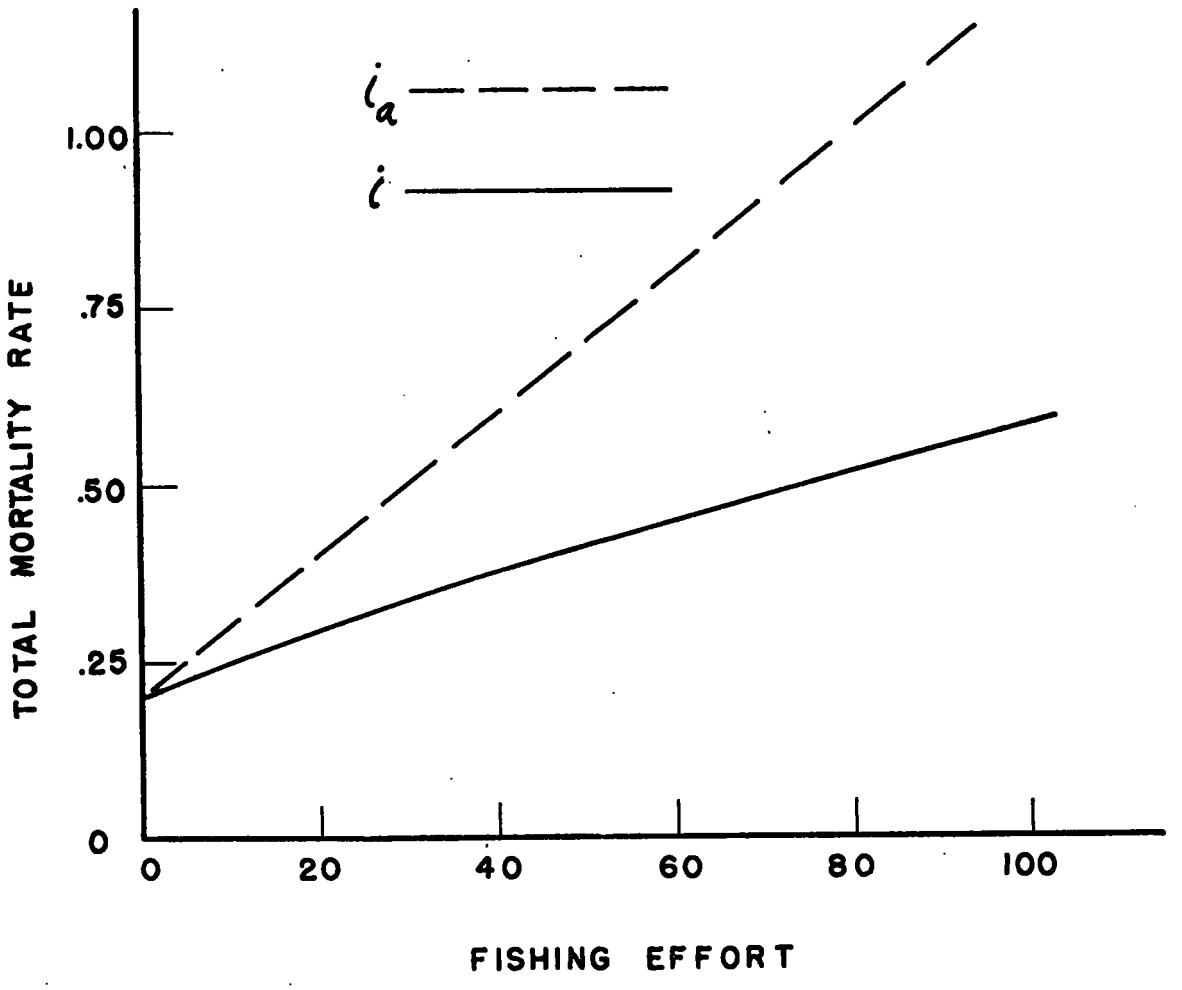

FIGURE 3.—Instantaneous total-mortality rate and effort, from example 2 in text.

Example 3 (see table 4 and fig. 4):

(a) Availability at beginning of each year varying-alternating from 40 to 60 percent in successive years.

(b) No natural mortality.

The limit of a is 50 percent, although it would vary from 60 to 40 percent each year when $f=+\infty$.

In this example I have computed the s^* series: these figures are those that one would obtain if he had only the catch data from which to estimate total mortality. Note that i^* goes from minus values to plus values, while of course i does not. The variation in i is around ± 0.1, but the variation in i^* is around ± 0.5! Note that although the variation in i^* is about five times greater than the variation in i, the regression of i^* on f, even though straight, falls very nearly on what a regression i on f would be. In fact, using i' (the regression of i^* on f) as estimates of i, when processed to yield estimates of r_1/r_2, give rather accurate measures of this ratio.

TABLE 4a.—*Computation of mortality rates for given fishing effort and availability level, with constant natural-mortality rate and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ q=0 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
r=availability level
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: $_a$=survival rate, annual, in unfished population=e^{-q}
s^*=available population survival rate, annual,=$s\left(\frac{r_2}{r_1}\right)$
i=instantaneous total-mortality rate in total population=$-\log_e(s)$
i^*=instantaneous total-mortality rate in available population=$-\log_e(s^*)$

	f	p_a	i_a	s_a	r	$1-r$	s	s^*	i	i^*
Year 1	10	0.1	0.1	0.90	40	60	0.960	1.44	0.04	−0.37
Year 2	20	.2	.2	.82	60	40	.892	.59	.12	.53
Year 3	30	.3	.3	.74	40	60	.896	1.34	.11	−.29
Year 4	40	.4	.4	.67	60	40	.802	.54	.22	.61
Year 5	50	.5	.5	.61	40	60	.844	1.27	.17	−.24
Year 6	60	.6	.6	.55	60	40	.730	.49	.31	.71
Year 7	70	.7	.7	.50	40	60	.800	1.20	.22	−.18
Year 8	80	.8	.8	.45	60	40	.670	.45	.40	.80
Year 9	90	.9	.9	.41	40	60	.764	1.15	.27	−.14
Year 10	100	1.0	1.0	.37	60	40	.632	.41	.47	.89

TABLE 4b.—*Estimation of the change in availability level from regression of* i* *on* f

i'=points on regression line corresponding to given f, and assuming q to be zero
s'=estimate of s (from regression)=$e^{-i'}$
$(r_2/r_1)^*$=estimate of $(r_2/r_1)=s^*/s'$
(r_2/r_1)=actual availability level ratio

	i'	s'	$(r_2/r_1)^*$	(r_2/r_1)
Year 1	0.04	0.961	1.50	1.50
Year 2	.08	.923	.64	.67
Year 3	.13	.878	1.53	1.50
Year 4	.17	.844	.64	.67
Year 5	.21	.811	1.57	1.50
Year 6	.25	.779	.63	.67
Year 7	.30	.741	1.62	1.50
Year 8	.34	.712	.63	.67
Year 9	.38	.684	1.68	1.50
Year 10	.42	.657	.62	.67

Example 4 (see table 5 and fig. 5):

(a) Availability variable. No regular pattern to the variation in availability. Average availability is 73 percent.

(b) Natural mortality: $q=.2$, or total mortality of 18 percent per year in the unfished population. The limit of total mortality of the total population at average availability is 88 percent per year. Note the wide variation in i^*, while i is much less variable. Table 5a and figure 5 illustrate this situation.

In table 5b the availability ratios and a set of maximum-availability estimates from s^* are computed for comparison with the true availability levels. The true average availability is 73 percent, while the estimated maximum-availability average is 75 percent, in this example. The availability ratios are unbiased (expected to average neither greater nor less than the true average). An example of estimating the availability levels and Q_a is contained in table 5b.

A linear regression of i^* on f yields a q of .245, and a Q of .00511. The true q is .2, and if the mean i is taken as the $\bar{i}^*$, or .526, Q is .00593.

The estimates $q^*=.245$, $\bar{i}^*=.526$, $\bar{r}^*=.75$, and $\bar{f}=55$, yield an estimate of Q_a of .00720. The true Q_a was .01000. Note, however, that the true $q=.2$, $\bar{i}=.513$, $\bar{r}=.73$, and $f=55$, yield a Q_a of only .00800!

The actual i corresponding to a constant r of 73 percent, with $q=.2$, at $f=55$, is $i=.57$. That is, the process of taking $\bar{i}$ and $\bar{f}$ as coordinates of a point on the locus of i with r constant at 73 percent, does not give the exact Q_a that was used with the r not constant, even though its mean was 73 percent. This implies that the procedure of estimating Q_a suggested above is biased. In this example r was fluctuating widely, yet the estimates of it were not far wrong. I have not attempted to get an unbiased estimate of Q_a, but the procedure I chose gave fairly close estimation. In applying these procedures to observational data, then, one should keep in mind that the tolerance of the estimates of such things as $\bar{r}$, Q_a, and q cannot be computed from the theory given in this paper. The accuracy of estimation in the preceding example has been shown to be fairly good, and, in this example, r was varying a great deal. One can expect similar accuracy of estimate in problems where r is varying over a similar range. If there

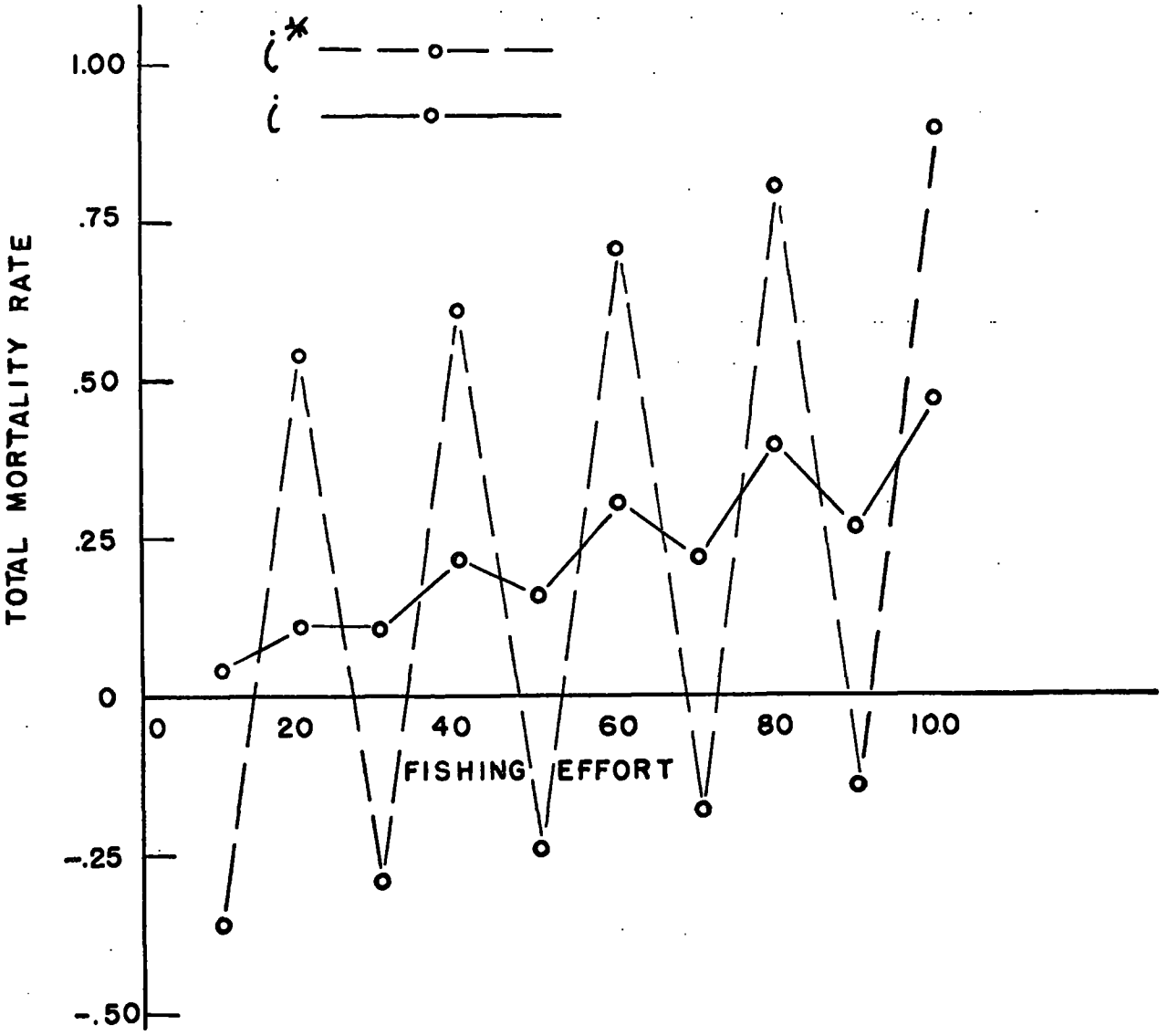

FIGURE 4.—Instantaneous total-mortality rate and effort, from example 3 in text.

is a trend of r on f, the estimation will be less accurate than if r is varying at random with f.

Briefly, with less than full availability the regression of s^* on f will not be linear, but a curve—an exponential with negative exponent—and will have an asymptote (limit). The intercept will, as with full availability, be an average rate of natural mortality. Varying availability will produce extreme variation in s^*, but the locus of average s^* for given effort will yield an unbiased estimate of the average natural-mortality rate, as well as an estimate of the efficiency of a unit of gear as applied to the total population, with average availability.

A first approximation to availability can be obtained from a straight-line regression to the data from which a second and better estimate can be obtained, both of a series of maximum-availability levels and the efficiency (assumed constant) of a unit of gear, on the available population. Knowing this constant, estimates of the size of the available population can easily be computed.

It is only necessary to divide the available population by the availability level, to obtain the total population. Since the availability estimates are maximums, the resulting total population-size estimates are minimums.

TABLE 5a.—*Computation of mortality rates for given fishing effort and availability level, with constant natural-mortality rate and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ q=0.2 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
r=availability level
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: s_a=survival rate, annual, in unfished population=e^{-i_a}
s^*=available population survival rate, annual,=$s\left(\frac{r_2}{r_1}\right)$
i=instantaneous total-mortality rate in total population=$-\log_e(s)$
i^*=instantaneous total-mortality rate in available population=$-\log_e(s^*)$

	f	p_a	i_a	s_a	r	$1-r$	$s_a r$	$s_a(1-r)$	s	s^*	i	i^*
Year 1	10	0.1	0.3	0.74	70	30	0.52	0.25	0.77	0.82	0.26	0.20
Year 2	20	.2	.4	.67	75	25	.50	.20	.70	.75	.36	.29
Year 3	30	.3	.5	.61	80	20	.49	.16	.65	.49	.43	.71
Year 4	40	.4	.6	.55	60	40	.33	.33	.66	.61	.41	.49
Year 5	50	.5	.7	.50	55	45	.28	.37	.65	.59	.43	.53
Year 6	60	.6	.4	.45	50	50	.23	.41	.64	1.02	.45	−.02
Year 7	70	.7	.9	.41	80	20	.33	.16	.49	.49	.71	.71
Year 8	80	.8	1.0	.37	80	20	.30	.16	.46	.35	.78	1.05
Year 9	90	.9	1.1	.33	60	40	.20	.33	.53	.53	.63	.63
Year 10	100	1.0	1.2	.30	60	40	.18	.33	.51	.51	.67	.67

TABLE 5b.—*Estimation of the change in availability level from regression of* i* *on* f

i'=points on regression line corresponding to given f, assuming $q=0.2$
s'=estimate of s (from regression)=$e^{-i'}$
$(r_2/r_1)^*$=estimate of $(r_2/r_1)=s^*/s'$
(r_2/r_1)=actual availability level ratio
r^*=estimation of r, from $(r_2/r_1)^*$. Necessary to assume year of maximum r^* is an r^* of 100 percent (full availability). The several r^*'s are therefore maximal
r=actual r

	i'	s'	$(r_2/r_1)^*$	(r_2/r_1)	r^*	r
Year 1	0.26	0.77	1.06	1.07	78	70
Year 2	.32	.73	1.03	1.07	83	75
Year 3	.38	.68	.72	.75	86	80
Year 4	.44	.64	.95	.92	62	60
Year 5	.50	.61	.97	.91	59	55
Year 6	.56	.57	1.79	1.60	56	50
Year 7	.62	.54	.91	1.00	100	80
Year 8	.67	.51	.69	.75	91	80
Year 9	.73	.48	0.10	1.00	63	60
Year 10	.79	.45	1.13	1.00	69 78	60 60

SUMMARY

The basis for a method of estimating population size has been developed from four assumptions on the nature of fishing and natural mortality. Those concerning fishing can, if the reporting of catches is sufficiently detailed, be relieved. The assumption that natural mortality is constant is not crucial, since it has been shown that, for the levels of fishing intensity considered, variation in level of natural mortality has little effect on estimates of availability and therefore of population size. One cannot ignore variation in natural mortality, of course, but it is not difficult to explore the consequences of its variation in applied examples.

The extent of the range of fishing effort in the data to which one would apply this method is important. The greater the range, the more accurate will be the population estimates. If the range of effort is small, but at a high level (total mortality high), then one can still apply the method, by assuming several different, though reasonable, rates of natural mortality. This results in a range of population estimates that would be as likely to be true as the assumed natural-mortality rates are likely to be true.

The effect of availability, and how to recognize it, has been developed and illustrated.

THE METHOD APPLIED TO THE SARDINE FISHERY

SOURCE OF DATA

Clark and Daugherty (1950 and 1952) give catch per unit-of-effort data for the three major ports of sardine landings in California. To arrive at a catch per unit-of-effort figure that will represent the total population fished at all three ports, these data must be pooled. Since the fishery of two northern ports, San Francisco and Monterey, occupies an area similar to that of the operation out of the southern port, San Pedro, I have divided the entire fishery into two parts that are approximately equal in area. The catch per unit-of-effort from the two northern ports, then, measure one unit of the population jointly. That is, the catch per unit-of-effort from either of the northern California fleets should measure the relative

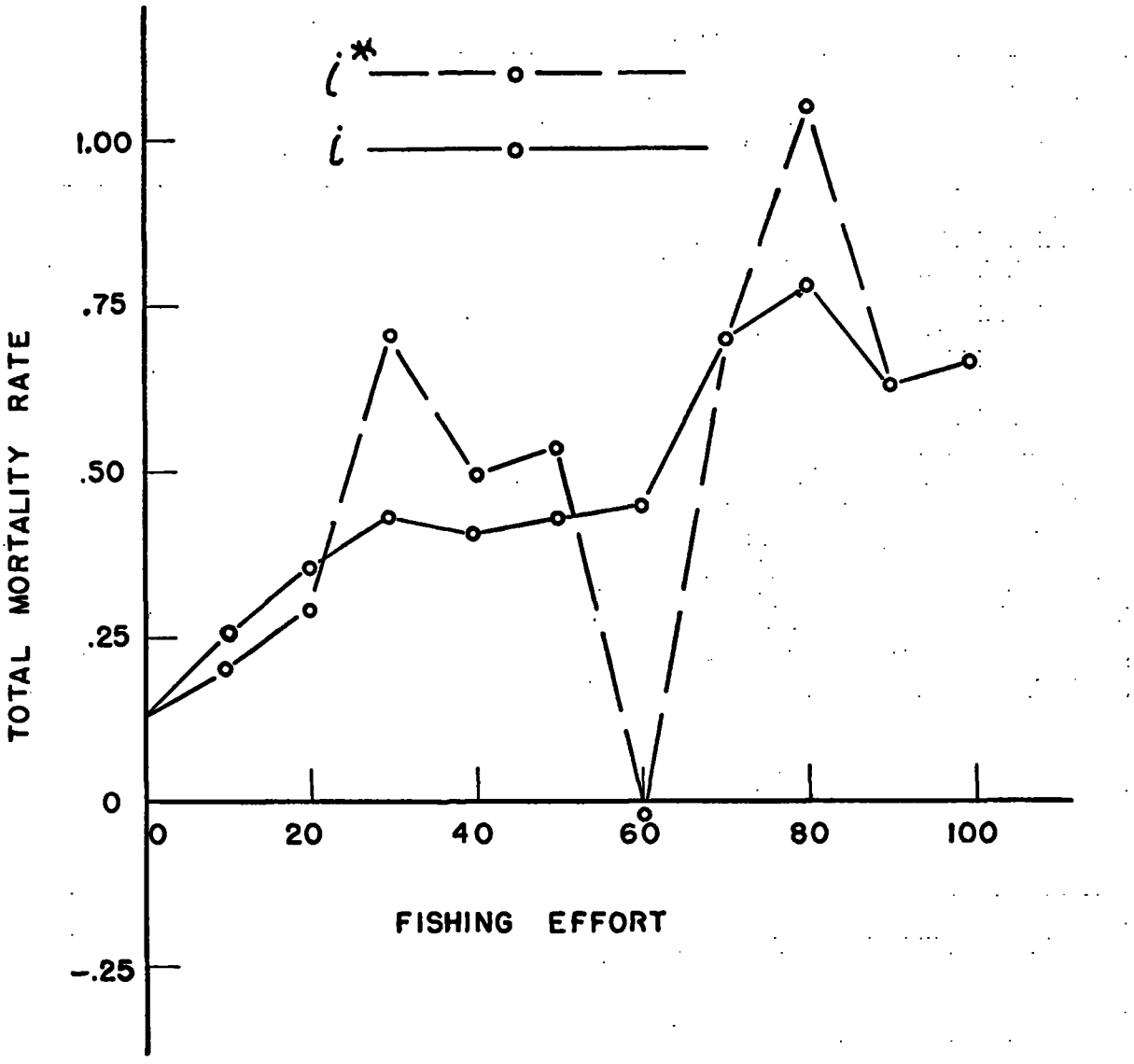

FIGURE 5.—Instantaneous total-mortality rate and fishing effort, with variable level of availability. See text, example 4.

average-population size in the northern area. Therefore, I have averaged the catch per unit-of-effort from these two ports, taking the ratio of the sum of the catches at the two ports to the sum of the efforts at the two ports. The resulting figure should be added, unweighted, to the catch per unit-of-effort at San Pedro to give a catch per unit-of-effort figure for the combined ports that is pertinent to this population study.

Table 6 contains the data necessary to the derivation of the total catch per unit-of-effort figure, which appears in column 11. The total catch is in column 12, and the effective effort for use in a population model is in column 13.

To compute a measure of total mortality, one must know the relative population size of a specific group of fish in at least 2 periods—in this fishery, 2 successive years. A specific group of fish would be an individual year class or a group of year classes. The catch per unit-of-effort of each of the year classes aged as 1 ring (second year of life) through 6 rings, for each of the two areas, and their total, is contained in table 7. The total catch per unit-of-effort for all year classes (column 9, table 7) was separated into that for the individual year classes by reference to the age composition of the sardine catch off

TABLE 6.—*Computation of California catch per unit-of-effort*

(1)	Effort			Catch				Catch per unit-of-effort			(12)	(13)
Season	(2) Monterey	(3) San Francisco	(4) Northern California	(5) Monterey	(6) San Francisco	(7) Northern California	(8) Southern California	(9) Northern California	(10) Southern California	(11) Total California	Total California catch	Total California effective effort
1932–33	205.2	133.4	338.6	496	366	862	509	2,546	2,045	4,591	1,371	299
1933–34	351.3	165.6	516.9	830	490	1,320	790	2,554	2,829	5,383	2,110	392
1934–35	343.0	209.1	552.1	1,345	927	2,272	1,225	4,115	3,239	7,354	3,497	476
1935–36	389.3	277.3	666.6	1,118	1,237	2,355	1,053	3,533	2,441	5,974	3,408	570
1936–37	410.2	518.0	928.2	1,273	2,232	3,505	937	3,776	1,725	5,501	4,442	807
1937–38	447.5	542.0	989.5	725	1,196	1,921	867	1,941	1,276	3,217	2,789	867
1938–39	497.7	620.3	1,118.0	1,513	1,732	3,245	1,437	2,903	1,983	4,886	4,683	958
1939–40	603.6	440.2	1,043.8	1,721	1,544	3,265	863	3,128	1,487	4,615	4,128	894
1940–41	563.8	226.8	790.6	1,424	886	2,310	1,712	2,923	2,350	5,272	4,022	763
1941–42	706.5	294.0	1,000.5	2,378	1,441	3,819	1,524	3,817	1,984	5,801	5,344	921
1942–43	538.7	213.1	751.8	1,337	732	2,069	1,920	2,752	2,622	5,374	3,988	742
1943–44	588.8	234.0	822.8	1,496	717	2,213	1,241	2,690	1,498	4,188	3,453	824
1944–45	701.2	437.0	1,138.2	1,652	692	2,344	1,466	2,059	2,147	4,206	3,810	906
1945–46	733.2	353.7	1,086.9	895	454	1,349	1,444	1,241	1,930	3,171	2,793	881
1946–47	639.1	----------	639.1	187	----------	187	1,688	293	1,269	1,562	1,893	1,212
1947–48	639.9	----------	639.9	131	----------	131	792	205	558	763	927	1,215
1948–49	539.2	----------	539.2	475	----------	475	1,004	890	1,221	2,101	1,493	711
1949–50	461.2	----------	461.2	937	----------	937	1,698	2,055	2,172	4,227	2,757	652
1950–51	774.3	----------	774.3	271	----------	271	2,319	350	1,378	1,728	2,590	1,499

the Pacific coast for the seasons 1941–42 through 1951–52, as given by Felin and Phillips (1948); Mosher, Felin, and Phillips (1949); Felin, Phillips, and Daugherty (1949); Felin, Daugherty, and Pinkas (1950 and 1951); Felin, Anas, Daugherty, and Pinkas (1952). I used the seasons' total "age composition of the catch" from the ports concerned. For the seasons 1932–33 through 1937–38, I used the season's total age composition from the ports of Monterey and San Pedro, as reported by Eckles (1954). Age data for the three seasons, 1938–39, 1939–40, and 1940–41, are not available.

TABLE 7.—*Age composition of California catch per unit-of-effort, 1932–33 to 1950–51*

[The sum of the catch per unit-of-effort in the two separate areas, northern California and southern California]

(1) Season	(2) 0-ring	(3) 1-ring	(4) 2-ring	(5) 3-ring	(6) 4-ring	(7) 5-ring	(8) 6-ring	(9) Total catch per unit-of-effort
1932–33:								
North	----------	----------	187.5	670.0	706.5	424.5	223.2	2,546
South	----------	26.3	141.0	867.5	761.9	176.5	49.2	2,045
Total	----------	26.3	328.5	1,546.5	1,468.4	601.0	272.4	4,591
1933–34:								
North	----------	31.9	439.1	408.8	463.2	426.5	291.5	2,554
South	----------	268.1	472.5	320.3	436.4	499.9	329.4	2,829
Total	----------	300.0	911.6	729.1	899.6	926.4	620.9	5,383
1934–35:								
North	----------	87.7	1,003.1	1,478.9	565.9	334.8	304.7	4,115
South	----------	19.3	800.9	1,015.2	466.5	259.7	280.6	3,239
Total	----------	107.0	1,804.0	2,494.1	1,032.4	594.5	585.3	7,354
1935–36:								
North	----------	66.8	510.1	1,596.8	730.9	229.7	334.6	3,533
South	----------	----------	479.3	1,575.0	276.8	78.0	10.9	2,441
Total	----------	66.8	989.4	3,171.8	1,007.7	307.7	345.5	5,974
1936–37:								
North	----------	28.7	567.2	863.4	1,283.9	675.0	197.8	3,776
South	----------	----------	26.4	361.0	972.0	329.5	19.3	1,725
Total	----------	28.7	593.6	1,224.4	2,255.9	1,004.5	217.1	5,501
1937–38:								
North	2.7	146.2	779.1	365.7	252.6	238.3	68.4	1,941
South	2.2	68.4	488.8	198.0	310.2	162.8	39.6	1,276
Total	4.9	214.6	1,267.9	563.7	562.8	401.1	108.0	3,217
1941–42:								
North	----------	266.1	2,170.6	1,091.5	225.1	52.2	7.0	3,817
South	----------	246.0	1,028.6	607.5	74.7	22.2	4.8	1,984
Total	----------	512.1	3,199.2	1,699.0	299.8	74.4	11.8	5,801

TABLE 7.—*Age composition of California catch per unit-of-effort, 1932-33 to 1950-51*—Continued

[The sum of the catch per unit-of-effort in the two separate areas, northern California and southern California]

(1) Season	(2) 0-ring	(3) 1-ring	(4) 2-ring	(5) 3-ring	(6) 4-ring	(7) 5-ring	(8) 6-ring	(9) Total catch per unit-of-effort
1942-43:								
North		65.5	419.1	1,392.3	633.7	172.4	58.6	2,752
South		320.0	987.7	938.9	320.2	42.5	11.1	2,622
Total		385.5	1,406.8	2,331.2	953.9	214.9	69.7	5,374
1943-44:								
North		338.3	150.0	739.9	1,006.2	338.7	89.7	2,690
South		231.3	559.5	421.8	226.3	47.8	10.4	1,498
Total		569.6	709.5	1,161.7	1,232.5	386.5	100.1	4,188
1944-45:								
North		201.6	686.0	191.7	342.8	421.6	156.3	2,059
South		284.3	676.5	775.6	281.9	104.9	18.4	2,147
Total		485.9	1,362.5	967.3	624.7	526.5	174.7	4,206
1945-46:								
North		50.4	351.3	431.7	191.5	109.1	72.1	1,241
South		252.9	698.6	488.9	359.1	104.5	20.8	1,930
Total		303.3	1,049.9	920.6	550.6	214.6	72.9	3,171
1946-47:								
North	3.4	123.8	39.5	56.1	32.8	18.7	8.6	293
South	.5	519.2	378.6	251.6	87.0	28.3	2.2	1,269
Total	3.9	643.0	418.1	307.7	119.8	47.0	10.8	1,562
1947-48:								
North		102.3	59.1	20.4	11.5	7.9	3.0	205
South	20.0	134.5	193.8	111.1	57.3	31.0	7.6	558
Total	20.0	236.8	252.9	131.5	68.8	38.9	10.6	763
1948-49:								
North	1.3	719.0	125.9	24.1	7.4	2.0	.3	880
South		121.5	832.8	181.4	65.0	18.0	2.4	1,221
Total	1.3	840.5	958.7	205.5	72.4	20.0	2.7	2,101
1949-50:								
North		36.1	1,360.6	430.7	134.7	69.4	16.7	2,055
South		252.2	916.7	699.9	200.4	96.5	5.5	2,172
Total		288.3	2,277.3	1,130.6	335.1	165.9	22.2	4,227
1950-51:								
North			56.9	150.1	113.1	19.1	10.3	350
South			640.5	519.2	178.7	55.1	4.5	1,378
Total			697.4	669.3	291.8	74.2	14.8	1,728

APPLICATION AND RESULTS

The first approximations (using catch per unit-of-effort) to s^* are in column 4 of table 8, using a weighted mean of the survival rate of three year classes in each pair of successive seasons as follows:

$$s^* = \frac{A_4 + B_5 + C_6}{A_3 + B_4 + C_5}$$

where A, B, and C are the catch per unit-of-effort measures of the three year classes. The subscripts refer to the age of each year class. This estimate is a weighted mean—weighted to the catch per unit-of-effort of the year classes as 3-, 4-, and 5-ring fish. This procedure gives more emphasis to the younger fish, whose sample size is usually larger. The variance of these age-composition estimates is usually inversely proportional to their sample size, so the more reliable measures have greater emphasis in this computation.

The correction factors, a/i, are computed from the s' (the survival rates from the regression line), and the corrected s^* is in column 10.

In figure 6, the i^*'s are plotted as ordinates, and California effective effort as abscissae. Clearly, the apparent efficiency, or effectiveness, of a unit-of-effort varies widely. The physical characteristics of the effort have been standardized in the process of computing catch per unit-of-effort (see Clark and Daugherty 1950). Any variation in the total-mortality rate, then, must be ascribed to variation in natural mortality or in availability, or both. I shall describe the variation in the one, holding the other constant, that

TABLE 8.—*Estimation of total-mortality rate from the California catch per unit-of-effort in the available population*

N_2=sum of year class catch per unit of effort for 4-, 5-, and 6-ring fish
N_1=sum of year class catch per unit of effort for 3-, 4-, and 5- ring fish
s_1^*=estimate of $s_1=\frac{N_2}{N_1}$
i^*=estimate of $i=-\log_e s^*$
f=fishing effort
i'=estimated i from regression of i^* on f
$(i'/a)=(i'/1-e^{-i'})$
Ratio=ratio of (i/a): $\frac{(i/a)'_2}{(i/a)'_1}$
$s^{**}=s^*$ corrected for changing fishing effort—after the first iteration

(1) Season	(2) N_2	(3) N_1	(4) s^*	(5) i^*	(6) f	(7) i'	(8) (i'/a)	(9) Ratio	(10) s^{**}
1932–33		3,615.9	0.677	0.390	299	0.343	1.183	1.046	0.708
1933–34	2,446.9	2,555.1	.866	.147	392	.439	1.237	1.042	.902
1934–35	2,212.2	4,121.0	.403	.910	476	.527	1.289	1.043	.420
1935–36	1,660.9	4,487.2	.775	.252	570	.634	1.345	1.113	.863
1936–37	3,477.5	4,484.8	.239	1.430	807	.870	1.497	1.029	.246
1937–38	1,071.9				867	.933	1.540		
1938–39					958	1.027			
1939–40					894	.961			
1940–41					763	.825			
1941–42		2,073.2	.597	.514	921	.989	1.577	.924	.552
1942–43	1,238.5	3,500.0	.491	.711	742	.803	1.457	1.036	.509
1943–44	1,719.1	2,780.7	.477	.740	824	.888	1.510	1.034	.493
1944–45	1,325.9	2,118.5	.396	.923	906	.973	1.562	.990	.392
1945–46	839.1	1,685.8	.105	2.250	881	.947	1.547	1.151	.121
1946–47	177.6	474.5	.249	1.390	1,212	1.291	1.781	1.002	.249
1947–48	118.3	239.2	.398	.922	1,215	1.294	1.785	.803	.320
1948–49	95.1	297.9	1.756	−.563	711	.771	1.433	.974	1.710
1949–50	523.2	1,631.6	.233	1.453	652	.709	1.396	1.431	.333
1950–51	380.8				1,499	1.590	1.997		

is necessary to produce the observed variation in estimated total-mortality rate. The corresponding population estimates will then be possibilities, rather than estimates with known probability of accuracy. The selection of any given set can only be based on an individual's judgment of which conditions most nearly describe the true history of the population as regards its availability and natural mortality.

POPULATION SIZE ASSUMING CONSTANT AVAILABILITY

If the entire population is available to the effort of the fishing fleet, then any variation in total-mortality rate, for given level of effort, must be due to variation in the rate of natural mortality. Or if the level of availability is assumed constant, variation in total-mortality rate must again be interpreted as due only to variation in natural-mortality rate. If one assumes full availability, then the relation of instantaneous fishing mortality, p, to fishing effort, f, is one of direct proportion:

$$p=Qf$$

If availability is assumed constant, at some given level, say r_o, then the relation of instantaneous fishing mortality to fishing effort is nearly proportional—p being a little less than directly proportional to f as f increases:

$$p=-\log_e [r_o e^{-q_o f}+(1-r_o)]$$

In either case, the difference between the total-mortality rate, i, and the fishing-mortality rate, p, must be interpreted as the rate of natural mortality, q. And in either case, variation in i, for given f (with r assumed full or constant), implies variation in q.

Table 9 contains the minimum natural-mortality rates, under the hypothesis of full, or 100 percent, availability (column 5). These rates are minimal because the season of lowest relative natural mortality, 1935–36, was taken as zero natural mortality, and it could be no less. The corresponding total-population estimates (column 9) are therefore also minimal. The seasonal, or percentage, natural-mortality rate, if there were no fishing, n, corresponding to q, is contained in column 10. Since the estimated total-mortality rate for the season 1948–49 is negative, there must have been a change in availability between the seasons 1948–49 and 1949–50—the availability level in the later season being higher than in the earlier. Under the hypothesis of no change in availability, then, the season 1948–49 must be omitted.

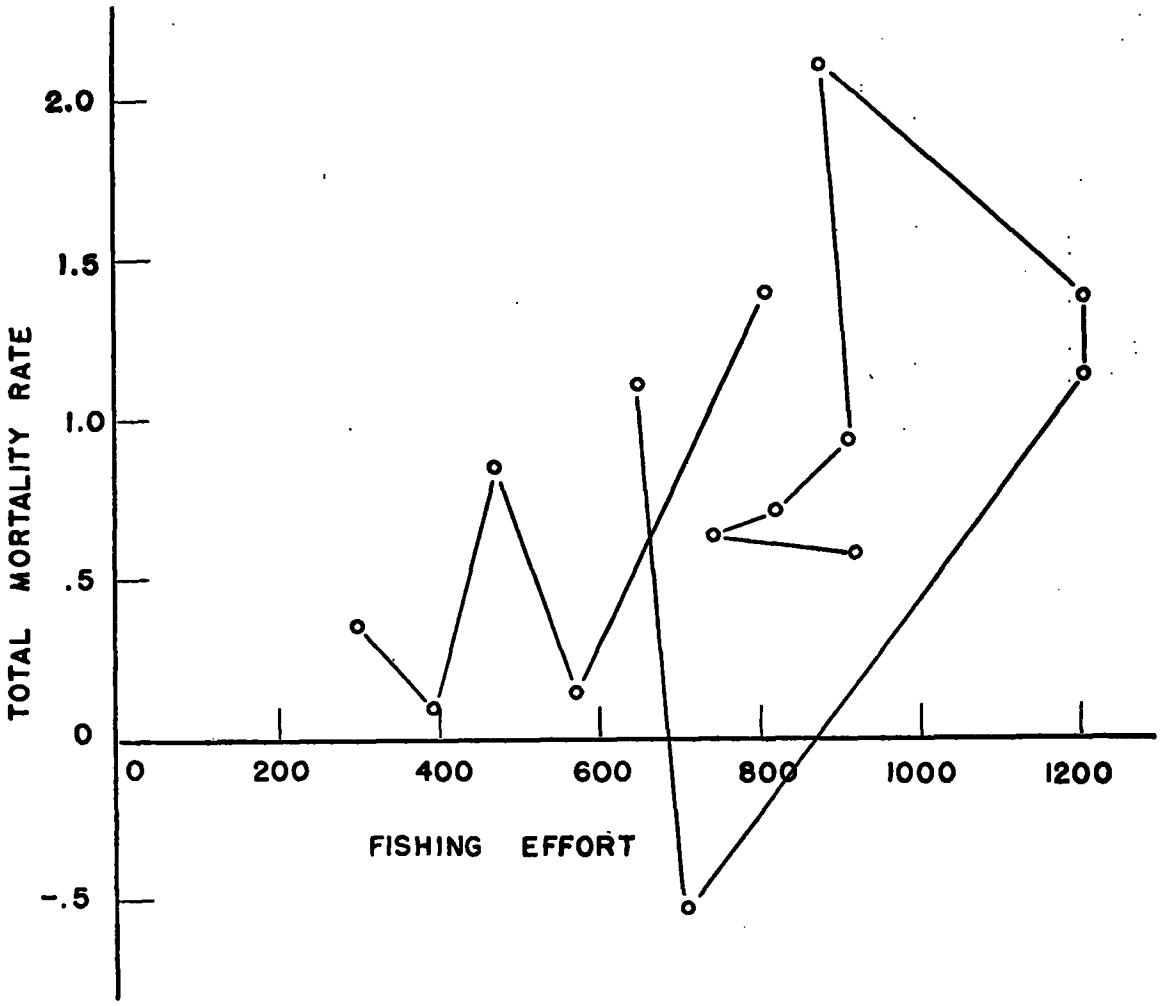

FIGURE 6.—California fishing effort and the apparent instantaneous total-mortality rate.

If the availability level is taken as constant, but less than 100 percent, the necessary natural mortality to produce the observed estimated total-mortality rate can easily be computed, for any given level of availability. Table 10 contains the necessary natural-mortality rates, under the hypothesis of constant availability at 50 percent. Table 11 contains the corresponding population sizes: the available population, N_a, in column 9, and the total-population size, N, in column 10. Again, natural mortality was assumed zero in the year of relative minimum natural mortality, 1935–36. The only major difference in the two situations—full availability or not—is that with less than full availability, the exploitation rate, u, is necessarily greater. The resulting natural-mortality rates, even under two such different conditions of constant availability, are nearly the same. The population sizes resulting from the two situations are also nearly the same.

The possibility of some or all of the variation in total-mortality rate being due simply to variation in the availability level can be explored. Between 1948 and 1949 some change in availability must have taken place. A change from high availability to low would result in an apparent abnormally high total-mortality rate. So an increase in total-mortality rate as computed here could result either from an increase in natural-mortality rate or from a decrease in the availability level between the two seasons from which the total-mortality rate was computed. Without an independent measure of the natural-mortality rate, and without a direct estimate of the avail-

TABLE 9.—*Estimated minimum-population size of fish, 2 rings and older, under the hypothesis of full availability, 1932–33 to 1950–51*

(1) Season	(2) f	(3) Qf	(4) i	(5) Minimum q	(6) a	(7) u	(8) C	(9) N	(10) n
							Billions	*Billions*	*Percent*
1932–33	299	0.077	0.345	0.268	0.292	0.065	1.3	20.0	23
1933–34	392	.101	.103	.002	.098	.096	2.0	20.8	0
1934–35	476	.123	.868	.745	.580	.082	3.5	42.7	53
1935–36	570	.147	.147	0	.137	.137	3.4	24.8	0
1936–37	807	.208	1.407	1.199	.754	.112	4.4	39.3	70
1937–38	867	.224	------	------	------	------	------	------	------
1938–39	958	.247	------	------	------	------	------	------	------
1939–40	894	.231	------	------	------	------	------	------	------
1940–41	763	.197	------	------	------	------	------	------	------
1941–42	921	.238	.595	.356	.448	.180	4.8	26.7	30
1942–43	742	.191	.675	.484	.491	.139	3.7	26.6	38
1943–44	824	.213	.707	.494	.507	.153	3.0	19.6	39
1944–45	906	.234	.936	.702	.608	.152	3.4	22.4	50
1945–46	881	.227	2.112	1.885	.879	.094	2.6	27.7	85
1946–47	1,212	.313	1.390	1.077	.751	.169	1.1	6.5	66
1947–48	1,215	.313	1.139	.826	.680	.187	.6	3.2	56
1948–49	711	.183	------	------	------	------	1.0	------	"0"
1949–50	652	.168	1.100	.932	.667	.102	2.5	24.5	61
1950–51	1,499	.387	------	------	------	------	2.6	------	------

TABLE 10.—*Computation natural-mortality rate under the hypothesis of constant availability at 50 percent, 1932–33 to 1950–51*

(1) Season	(2) f	(3) p	(4) i	(5) Minimum q	(6) n
					Percent
1932–33	299	0.081	0.345	0.264	23
1933–34	392	.099	.103	.004	0
1934–35	476	.124	.868	.744	52
1935–36	570	.147	.147	0	0
1936–37	807	.201	1.407	1.206	70
1937–38	867	.214	----------	----------	----------
1938–39	958	.233	----------	----------	----------
1939–40	894	.221	----------	----------	----------
1940–41	763	.191	----------	----------	----------
1941–42	921	.226	.595	.369	31
1942–43	742	.188	.675	.487	39
1943–44	824	.206	.707	.501	39
1944–45	906	.223	.936	.713	51
1945–46	881	.217	2.112	1.895	85
1946–47	1,212	.284	1.390	1.106	67
1947–48	1,215	.284	1.139	.855	57
1948–49	711	.180	----------	----------	"0"
1949–50	652	.167	1.100	.933	61
1950–51	1,499	.335	----------	----------	----------

TABLE 11.—*Estimated minimum-population size of fish 2 rings and older, under the hypothesis of constant availability at 50 percent, 1932–33 to 1949–50*

(1) Season	(2) f	(3) p_a	(4) Minimum q	(5) i_a	(6) a_a	(7) u_a	(8) C	(9) N_a	(10) N
							Billions	*Billions*	*Billions*
1932–33	299	0.168	0.264	0.432	0.351	0.137	1.3	9.5	19.0
1933–34	392	.220	.004	.224	.201	.197	2.0	10.2	20.4
1934–35	476	.267	.744	1.011	.636	.168	3.5	20.8	41.6
1935–36	570	.320	0	.320	.274	.274	3.4	12.4	24.8
1936–37	807	.453	1.206	1.659	.810	.221	4.4	19.9	a9.8
1937–38	867	.487	------	------	------	------	------	------	------
1938–39	958	.538	------	------	------	------	------	------	------
1939–40	894	.502	------	------	------	------	------	------	------
1940–41	763	.428	------	------	------	------	------	------	------
1941–42	921	.517	.369	.886	.588	.343	4.8	14.0	28.0
1942–43	742	.417	.487	.904	.595	.274	3.7	13.5	27.0
1943–44	824	.463	.501	.964	.619	.297	3.0	10.1	20.2
1944–45	906	.509	.713	1.222	.705	.294	3.4	11.6	23.2
1945–46	881	.495	1.895	1.390	.751	.267	2.6	9.7	19.4
1946–47	1,212	.680	1.106	1.786	.832	.317	1.1	3.5	7.0
1947–48	1,215	.682	.855	1.537	.785	.348	.6	1.7	3.4
1948–49	711	.399	------	------	------	------	1.0	------	------
1949–50	652	.366	.933	1.299	.727	.205	2.5	12.2	24.4
1950–51	1,499	.842	------	------	------	------	2.6	------	------

ability change, one must ascribe the variation in total-mortality rate to a change in either or both of these factors.

Having described the necessary change in natural mortality under the hypothesis of constant availability, I shall now consider the necessary changes in availability level, under the hypothesis of constant natural mortality.

Population Size Assuming Constant Natural-Mortality Rate

I would expect the distribution of a fish population, relative to a fishery, to change more readily than the natural mortality in that population. Having no really direct evidence of the level or variability of natural mortality, one must keep its possible influence in mind in interpreting computed availability measures. For example, I would place more significance in an estimated large change in availability than in a small one, when natural mortality was assumed constant. This is, of course, a subjective qualification—an opinion—and not evidence.

Since the rate of natural mortality is unknown, I have computed several sets of availability measures, each based on a different but possible constant rate of natural mortality. Generally, the higher the true average rate of natural mortality, the less variable are the computed availability measures. That is, the possible range of percentage variation in i to be expected from a given change in availability is less, the higher the level of natural mortality assumed. The reason for this, intuitively, is that natural mortality takes place in both the available and unavailable population, and the higher it is, the less will be the effect of the fishing mortality on the total-mortality rate, regardless of the level of availability.

The following computations will rest on the assumption that natural mortality is constant. The procedure has been outlined in previous sections.

First estimates of the ratio of the availability level between successive pairs of years for three assumed constant natural-mortality rates are in columns 5, 8, and 11 of table 12. Taking these ratios, a series of maximum-availability levels is in columns 6, 9, and 12. These are maximal, since it is necessary, of course, to assume that in some one year the entire population is available. In these data, there are two periods where this assumption

TABLE 12.—*Estimation of availability level, for various assumed rates of natural mortality and corresponding estimated total mortality in the total population*

For $\begin{cases} q=0,\ Q=.001036 \\ q=0.2,\ Q=.000772 \\ q=0.4,\ Q=.000508 \end{cases}$

$s^*=s^{**}$ from previous tables
f=fishing effort
$s'=e^{Qf-q}$.
s'/s^*=estimate of (r_1/r_2)
r^*=maximum estimate of the availability level, r

(1) Season	(2) s^*	(3) f	$q=0$ (4) s'	$q=0$ (5) s'/s^*	$q=0$ (6) r^*	$q=0.2$ (7) s'	$q=0.2$ (8) s'/s^*	$q=0.2$ (9) r^*	$q=0.4$ (10) s'	$q=0.4$ (11) s'/s^*	$q=0.4$ (12) r^*
1932–33	0.708	299	0.734	1.037	71.4	0.650	0.918	50.9	0.576	0.814	36.1
1933–34	.902	392	.666	.738	68.9	.605	.671	55.4	.549	.609	44.4
1934–35	.420	476	.611	1.455	93.3	.567	1.350	82.5	.526	1.252	72.9
1935–36	.863	570	.553	.641	64.1	.527	.611	61.1	.502	.582	58.2
1936–37	.246	807	.434	1.764	100.0	.439	1.785	100.0	.445	1.809	100.0
1937–38		867			53.6	.419		56.0	.432		55.3
1938–39		958				.391			.412		
1939–40		894				.411			.426		
1940–41		763				.454			.455		
1941–42	.552	921	.385	.697	51.4	.402	.728	58.0	.420	.761	61.6
1942–43	.509	742	.463	.910	73.8	.462	.908	79.7	.460	.904	80.9
1943–44	.493	824	.425	.862	81.1	.433	.878	87.8	.441	.895	89.5
1944–45	.392	906	.391	.997	94.1	.407	1.038	100.0	.423	1.079	100.0
1945–46	.121	881	.401	3.314	94.4	.415	3.430	96.3	.428	3.537	92.7
1946–47	.249	1,212	.285	1.145	28.5	.321	1.289	28.1	.362	1.454	26.2
1947–48	.320	1,215	.284	.888	24.9	.320	1.000	21.8	.362	1.131	18.0
1948–49	1.710	711	.479	.280	28.0	.473	.277	21.8	.467	.273	15.9
1949–50	.333	652	.509	1.529	100.0	.495	1.486	78.7	.481	1.444	58.2
1950–51		1,499			65.4	.257		53.0	.313		40.3
				$\bar{r}$=68.3			$\bar{r}$=64.4			$\bar{r}$=59.4	

is necessary, since the series is broken from 1937–38 to 1941–42.

Now the value of Q_a can be computed by

$$Q_a=\frac{\log_e\left[\dfrac{\bar{s}-\bar{s}_u(1-\bar{r})}{\bar{r}\,\bar{s}_u}\right]}{f}$$

I have assumed several different possible values for $\bar{q}$ and shall compute the stock-size series for each as being possible. If $\bar{q}$ be taken as 0.2, and with $\bar{i}$=.785 and $\bar{f}$=758, and $\bar{r}$=65 percent, Q_a takes the value 0.00151. Computation of Q_a for the three levels of natural mortality are in table 13. The computation, from previous sections, of the adjusted r, is in table 14, and the computation of the available and total stock-size series is in table 15. These total-stock-size estimates are minimums, but have considerable possible variance, since the estimates of availability are not precise. They simply suggest the general order of the stock size in the past, under the hypothesis of constant natural mortality.

TABLE 13.—*Computation of* Q_a *for various assumed natural-mortality rates* (q), *and the corresponding average fishing effort, average total-mortality rate, and average maximum estimate-of-availability level*

Constants $\begin{cases} \bar{f}=758 \\ \bar{i}^*=.785,\ \bar{s}^*=.456 \end{cases}$

$\bar{r}^*$=estimate of $\bar{r}$, from previous tables

Q_a^*=estimated constant fishing effort unit efficiency=$\dfrac{-\log_e\left[\dfrac{\bar{s}^*-(1-\bar{r}^*)s_u}{\bar{r}^*\,s_u}\right]}{\bar{f}}$

	$q=0$	q=0.2	q=0.4
Q^*	0.001036	0.000772	0.000508
$\bar{r}^*$	.683	.644	.594
Q_a^*	.002098	.001533	.001018
s_u	1.000	.8187	.6703

SUMMARY

Estimates of the total-population survival rate were computed from data on the age composition of the commercial catch of Pacific sardines in California and from the catch per unit-of-effort of the fleet, for the period 1932–33 through 1950–51.

TABLE 14.—*Estimation of availability level, from availability-corrected estimates of survival rate, corresponding to various assumed natural-mortality rates*

$$s' = e^{-q+\log_e [F(1-e^{-Q_a f})-1]}$$

(1) Season	$q=0$			$q=0.2$			$q=0.4$		
	(2) s'	(3) s'/s^*	(4) Maximum r	(5) s'	(6) s'/s^*	(7) Maximum r	(8) s'	(9) s'/s^*	(10) Maximum r
1932–33	0.682	0.963	53.9	0.624	0.881	43.6	0.566	0.799	33.9
1933–34	.618	.685	56.0	.580	.643	49.5	.540	.599	42.4
1934–35	.567	1.350	81.8	.545	1.298	77.0	.517	1.231	70.8
1935–36	.523	.606	60.6	.512	.593	59.3	.496	.575	57.5
1936–37	.443	1.801	100.0	.444	1.805	100.0	.447	1.817	100.0
1937–38	.428	----------	55.5	.431	----------	55.4	.437	----------	55.0
1938–39	.409	----------	----------	.413	----------	----------	.422	----------	----------
1939–40	.421	----------	----------	.426	----------	----------	.432	----------	----------
1940–41	.455	----------	----------	.455	----------	----------	.455	----------	----------
1941–42	.416	.754	60.8	.420	.761	61.5	.428	.775	63.0
1942–43	.461	.906	80.6	.461	.906	80.8	.459	.902	81.3
1943–44	.439	.890	89.0	.440	.892	89.2	.444	.901	90.1
1944–45	.419	1.069	100.0	.422	1.077	100.0	.430	1.097	100.0
1945–46	.425	3.512	93.5	.428	3.537	92.9	.434	3.587	91.2
1946–47	.370	1.486	26.6	.373	1.498	26.3	.388	1.558	25.4
1947–48	.370	1.156	17.9	.373	1.166	17.6	.387	1.209	16.3
1948–49	.471	.275	15.5	.468	.274	15.1	.465	.272	13.5
1949–50	.491	1.474	56.4	.485	1.456	55.1	.477	1.432	49.6
1950–51	.346	----------	38.3	.344	----------	37.8	.359	----------	34.6
			$\bar{r}=61.7$			$\bar{r}=60.1$			$\bar{r}=57.8$

TABLE 15.—*Minimal estimates of population size, available and total, for various assumed rates of natural mortality*

C=California catch in billions of fish 2 rings and older

u_a=estimated rate of exploitation in available population=$Q_a f\left(\frac{a}{i}\right)_a$

N_a=California available population size in billions of fish

N=minimal estimate of total population in billions of fish

(1) Season	(2) C	$q=0$				$q=0.2$				$q=0.4$			
		(3) u_a	(4) N_a	(5) Maximum r	(6) Minimum N	(7) u_a	(8) N_a	(9) Maximum r	(10) Minimum N	(11) u_a	(12) N_a	(13) Maximum r	(14) Minimum N
1932–33	1.3	0.465	2.8	53.9	5.2	0.336	3.9	43.6	8.9	.219	5.9	33.9	17.4
1933–34	2.0	.560	3.6	56.0	6.4	.413	4.8	49.5	9.7	.275	7.3	42.4	17.2
1934–35	3.5	.632	5.5	81.8	6.7	.475	7.4	77.0	9.6	.321	10.9	70.8	15.4
1935–36	3.4	.698	4.9	60.6	8.1	.536	6.3	59.3	10.6	.369	9.2	57.5	16.0
1936–37	4.4	.816	5.4	100.0	5.4	.656	6.7	100.0	6.7	.478	9.2	100.0	9.2
1937–38	2.6	.838	3.1	55.5	5.6	.680	3.8	55.4	6.9	.498	5.2	55.0	9.5
1938–39	----------	.866	----------	----------	----------	.714	----------	----------	----------	.529	----------	----------	----------
1939–40	----------	.847	----------	----------	----------	.691	----------	----------	----------	.507	----------	----------	----------
1940–41	----------	.798	----------	----------	----------	.636	----------	----------	----------	.456	----------	----------	----------
1941–42	4.8	.855	5.6	60.8	9.2	.702	6.8	61.5	11.1	.518	9.3	63.0	14.8
1942–43	3.7	.789	4.7	80.6	5.8	.628	5.9	80.8	7.3	.448	8.3	81.3	10.2
1943–44	3.0	.822	3.6	89.0	4.0	.633	4.5	89.2	5.0	.481	6.2	90.1	6.9
1944–45	3.4	.850	4.0	100.0	4.0	.696	4.9	100.0	4.9	.512	6.6	100.0	6.6
1945–46	2.6	.842	3.1	93.5	3.3	.686	3.8	92.9	4.1	.501	5.2	91.2	5.7
1946–47	1.1	.922	1.2	26.6	4.5	.788	1.4	26.3	5.3	.608	1.8	25.4	7.1
1947–48	.6	.922	.7	17.9	3.9	.788	.8	17.6	4.5	.609	1.0	16.3	6.1
1948–49	1.0	.775	1.3	15.5	8.4	.613	1.6	15.1	10.6	.435	2.3	13.5	17.0
1949–50	2.5	.745	3.4	56.4	6.0	.582	4.3	55.1	7.8	.409	6.1	49.6	12.3
1950–51	2.6	.957	2.7	38.3	7.0	.843	3.1	37.8	8.2	.676	3.8	34.6	11.0
1951–52	.9	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------

The total-population size for each year was estimated from the survival-rate data, under the hypothesis of constant availability level. Variation in estimated-survival rate for a given level of fishing effort was therefore ascribed to the necessary change in natural mortality. The population-size estimates are nearly the same for either the assumed full level of availability, or for the assumed 50-percent level of availability.

The total-population size for each year was also estimated from the survival-rate data under the hypothesis of constant natural-mortality rate. Variation in estimated-survival rate for a given level of fishing effort was therefore ascribed to the necessary change in the level of availability between successive seasons. The computation was carried through for each of several possible rates of natural mortality.

NOTATION

Population numbers:
- N_____ initial population.
- C_____ catch.
- D_____ deaths from all causes.

Annual mortality rates:
- u_____ catch fraction (rate of exploitation).
- v_____ natural death fraction.
- a_____ total mortality fraction.
- s_____ total survival fraction.
- m_____ fishing mortality (in absence of natural mortality).
- n_____ natural mortality (in absence of fishing).

Instantaneous mortality rates:
- p_____ fishing.
- q_____ natural.
- i_____ total.
- f_____ effective fishing effort.

Miscellaneous:
- Q_____ fishing effort efficiency, or constant of proportionality between p and f.
- r_____ availability fraction.

Subscripts:
- a_____ available population (in fished area).
- u_____ unavailable population (in unfished area).
- t_____ total population.

Superscripts:
- $*$_____ a statistic: Estimate of a parameter.
- $'$_____ a statistic: Estimate of a parameter.

APPENDIX

USING CATCH PER UNIT-OF-EFFORT TO MEASURE POPULATION SIZE

Let a unit-of-effort be the operation of a unit of fishing gear (net, hook, or trap) for a certain period of time (hour, day, or month). If the gear chosen is standard (constant), then the area of the fish's habitat that the unit of gear fishes (or scouts) in a fixed interval of time should be a constant area. Further, if the gear strains or otherwise attracts fish to it, and catches fish if they are within this area, let us describe this catching power quantitatively by noting that, for most gear, the more fish in the area, the greater will be the catch, and the fewer fish in the area, the smaller the catch. However, if fish are extremely numerous, as they may be, let us admit that the gear may become filled with fish and stop being effective in catching more. If the time during which the gear is thus not fishing is recognized, that time could be deducted from the total fishing time and saturation would not affect the reliability of the reported catching time. Some gear, such as longlines and gill nets, may vary in effectiveness with varying densities of fish in the area fished.

To be entirely general, let us say that a unit-of-effort becomes fully saturated when the catch is some contant, say C_s. When the gear contains no fish, but is being fished, let us say the gear is capable of taking some constant fraction of the fish in the area that is being fished—that is, some fraction of the population in an area fished is caught, and the remainder is not caught. Let the ratio of those caught, to the total before fishing took place, be E. This fraction might be termed the efficiency of fishing. Now as the gear becomes filled with fish, let us say (a) the efficiency of the gear stays constant, or (b) it decreases, in direct proportion as the ratio of catch to the saturated catch.

If n is the population in the fished area during a very short period of time, dt, let the rate of catch be:

$$\frac{dC}{dt}=En \tag{1}$$

for the fished area, say α, in time dt. Note that the catch, dC, is directly proportional to the number of fish in the area α. From this it follows that the instantaneous density of catch, $\frac{dC}{\alpha}$, is directly proportional to the density of fish in the area, $\frac{n}{\alpha}$, and that the constant of proportionality is E. These relations form the basis of using fishery statistics to estimate fish-population size.

ESTIMATION

If a unit-of-effort operates within an area larger than α, and wherein density of fish is uniform

(equal), then the catch of that unit-of-effort constitutes a sample—usually a random one—of the density of fish in that larger area. If we denote by A the large area within which density is uniform, and by N the population size in that area, then:

$$\frac{N}{A}=\frac{n}{\alpha}$$

$$=\frac{dC}{\alpha}\left(\frac{1}{E}\right)$$

So, if α and E are constant, then the instantaneous catch (per unit-of-effort) is directly proportional to the standing population density. Of course, if the area A is known, the product of dC and A gives a measure of the relative size of the population that is sampled in the area A:

$$N=dC\left[\left(\frac{1}{\alpha E}\right)A\right]$$

where $\left[\left(\frac{1}{\alpha E}\right)A\right]$ is the constant of direct proportionality.

Now fishery data yield not measures of dC, but of its integral, over some finite period of time, such as a day, a week, or a year.

Taking some unit of time as a standard unit that can be reported upon, the catch over that unit of time, say C, is often easily determined for a fishery.

Now if several, say f, units of fishing effort are operating in the area A at the same time, then in the instant dt they are all fishing the same population density, or size, in that area, if each unit's efficiency is the same. This may be written

$$\frac{dC}{dt}=f(En)$$

where each unit's E and α are equal.

Since

$$\frac{n}{\alpha}=\frac{N}{A}$$

$$n=\frac{\alpha}{A}N$$

so

$$\frac{dC}{dt}=f\,E\,\frac{\alpha}{A}N$$

Let us write Q for the constant of proportionality of each unit of effort to its instantaneous catch and the standing population size. That is, let

$$Q=E\left(\frac{\alpha}{A}\right)$$

We then have

$$\frac{dC}{dt}=(Qf)N$$

Following Ricker's (1944) notation, we may observe that the proportion of N that is caught, instantaneously, by a given number of effort units, has been called p, in

$$\frac{dC}{dt}=pN$$

Here, then, $p=Qf$, and Q is taken to be constant. It is easy to show that if other causes of death, termed natural, by q, are equal for any fish in the population in an instant, then the total deaths, D, occurring instantaneously are

$$\frac{dD}{dt}=(p+q)N$$

$$=(i)N$$

where

$$i=p+q$$

Whereupon

$$C=p\,\frac{a}{i}N_o$$

where N_o is the population size at the beginning of the period during which C is accumulated, and a is $(1-e^{-i})$.

Further,

$$C=p\bar{N}$$

where $\bar{N}$ is the average population during the period of time that C is accumulated, if p and q are constant.

Recall that

$$p=Qf,$$

so

$$C=Qf\bar{N}$$

or

$$\frac{C}{f}=Q\bar{N} \qquad (2)$$

or

$$\frac{C}{f}=QN_o\left(\frac{a}{i}\right) \qquad (3)$$

In equation 2 the catch per unit-of-effort is directly proportional to the average population during the period, while application of the factor $\left(\frac{a}{i}\right)$ gives equation 3, which states how catch per unit-of-effort can be directly proportional to the initial population of the time period.

Note that here Q is constant and does not vary even if f changes; however, if f changes from one period to another, the factor (a/i) will change, although a lesser percentage amount. To summarize, if f changes from one period to another, C/f is directly proportional to $\overline{N}$, while C/f is nearly proportional to N_o and is directly proportional to it if C/f be multiplied by $\left(\frac{i}{a}\right)$.

Of course, if Q is known, C/f can be made to measure the true population size. It is a major problem of population-dynamics studies to determine the value of Q. Now consider the alternative to situation (1) in the opening section:

$$\frac{dC}{dt}=E\left[\frac{C_s-C}{C_s}\right]n \qquad (4)$$

Ordinarily, fishing gear will be operated such that the factor $\left[\frac{C_s-C}{C_s}\right]$ is close to unity. With such gear as trawls, it would probably always be unity, but with gear such as longlines or gill nets, it would probably vary directly with the abundance of fish (fish density). Generally such gear is emptied as often as necessary to maintain its maximum efficiency—that is, to keep $\left[\frac{C_s-C}{C_s}\right]$ very close to unity.

If $\left[\frac{C_s-C}{C_s}\right]$ is maintained merely constant, on the average, one may regard, say, E' as simply the product of $\left[\frac{C_s-C}{C_s}\right]$ and E, and consider E' as constant, just as E is considered constant. Then the results for equation 1 are the same as for equation 4.

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INTERTIDAL SPAWNING OF PINK SALMON

BY MITCHELL G. HANAVAN AND BERNARD EINAR SKUD

FISHERY BULLETIN 95

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Extensive spawning of the pink salmon (*Oncorhynchus gorbuscha*) in the parts of streams subject to tidal action has been observed in Southeastern Alaska. A series of experiments at Lover's Cove stream on Baranof Island was set up to determine the success of this spawning in terms of numbers of fry produced from eggs deposited in the intertidal zone. The experiments used rectangular wire-mesh pens whose lower parts were buried in the stream gravel. Adult salmon were confined in these pens and allowed to spawn; pens remained in the gravel during the incubation period, and fry were counted as they emerged.

Survival rates, calculated as number of fry produced in relation to estimated number of eggs contained in the females, were 20.9, 3.2, and 19.8 percent for 1949, 1950, and 1951, respectively, at the 8- to 9-foot tidal level. Somewhat higher survival rates were noted at the intermediate tidal levels in 1950 than at the extremes, and this was attributed to the winter-tempering effect of water of moderate salinity and temperature.

The effect of crowding was studied by pairing pens at identical tidal levels and doubling the number of females placed in one of the members of the pair. Observations of survival rates and of the adult fish after completion of spawning indicated that the chief effect of crowding was increased egg retention by the more crowded females.

Detailed observations were made of salinities prevailing in the spawning gravels during the tidal cycle. Water was pumped from a pipe driven into the gravel, and its salinity measured with a hydrometer. Salinity was found to increase with each increase in depth of tidal inundation, until a salinity similar to that of open coastal water was reached. Accuracy of hydrometer observations was verified by comparison with titration and conductance measurements.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

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SURVIVAL OF PINK-SALMON SPAWN IN AN INTERTIDAL AREA WITH SPECIAL REFERENCE TO INFLUENCE OF CROWDING

By MITCHELL G. HANAVAN, *Fishery Research Biologist*

Pink salmon (*Oncorhynchus gorbuscha*) are taken commercially from Puget Sound to Western Alaska but occur in greatest abundance in Southeastern Alaska, the approximate midpoint of their geographical distribution on the west coast of North America. Collectively, the hundreds of streams of the Alexander Archipelago and of the mainland provide a great expanse of spawning gravel suitable for pink salmon. Individually, many of these streams are short with steep gradients that provide few or no accessible spawning areas above the high-tide level. As a consequence the pink salmon, which spawn in large numbers in streams of the latter type, are limited to riffles within the intertidal zone, i. e., the stream sections between the lower low-tide and higher high-tide levels. Many of the nests made in the gravels of the intertidal zone are covered with salt water for a substantial part of the fall and winter incubation period.

The survival and contribution to the pink-salmon populations of spawn deposited in intertidal areas are of current interest because of the damage to these areas that may result from logging operations. Development of the woodpulp industry in Southeastern Alaska will result in increased logging in the near future and experience proves that logging can be detrimental to salmon-producing streams. Unstable streams are particularly vulnerable to such damage, as a change in the equilibrium of the stream channel at one point may be followed by the shifting of riffles and channels farther downstream with a resulting loss of eggs or alevins in the gravels. Intertidal-stream sections, flowing over barren alluvial deposits, frequently are less stable than stream channels above high-tide level, and consequently are likely to sustain the greater damage from an upset in the equilibrium of the stream.

Presented in this report are measurements of the survival of pink-salmon spawn in an intertidal area as determined by impounding spawners within screened pens and counting the fry produced. Measurements obtained by this method are compared with survival rates in a natural stream, the latter measured by the upstream-downstream counting weir used since 1940 to determine annual fresh-water survival rates in Sashin Creek at Little Port Walter (fig. 1).

A comparison of survival rates under two levels of spawning density is presented as a secondary subject of this report, in part because the pens used in the intertidal study presented an opportunity to obtain a direct comparison under otherwise similar conditions. The technique is better suited to provide information on the manner in which crowding affects survival than to define the most productive distribution of spawners under natural conditions.

Bernard Skud and Willard Brewington of the Seattle Laboratory staff and Jerrold Olson, foreman of the Little Port Walter Station, assisted with the experiments.

THE INTERTIDAL STUDY AREA

We selected Lover's Cove stream near the Little Port Walter field station for our intertidal-zone spawning study. It is typical of many small streams in the southern part of Baranof Island: steep, flood-washed, and unstable. The average annual precipitation at the Little Port Walter station from 1940 to 1951 was 214.07 inches. Undoubtedly, the Cove stream, 2½ miles distant and lying deeper in the mountains, receives even greater rainfall. Frequent floods produce sharp fluctuations in stream level, particularly during the fall months, and result in a shifting of gravel bars and stream channels, and undoubtedly they destroy many eggs deposited in the less stable parts of the stream.

The intertidal zone of the study stream extends approximately 1,500 feet—from high-tide level to

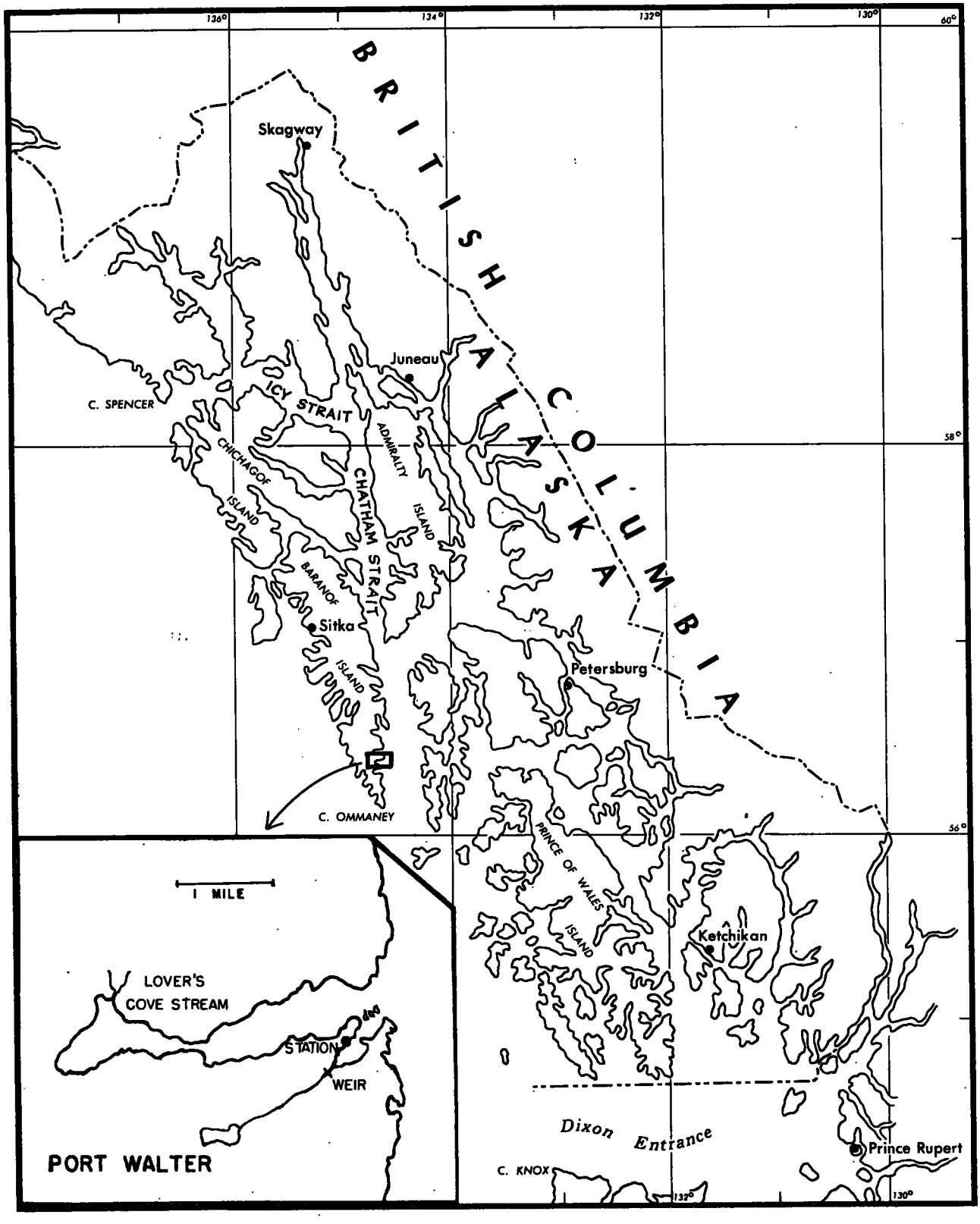

FIGURE 1.—Southeastern Alaska, with insert showing Port Walter.

mean low tide. Through virtually all of this distance the stream traverses a delta which drops abruptly to depths of 20 fathoms and more a short distance below mean low tide. The intertidal zone provides a stream section of moderate gradient with extensive gravel riffles. It is within the upper portion of this section that most of the pink salmon are observed to spawn—roughly, from the plus-4-foot tide level to the higher high-tide mark, plus-11.5 feet.

MEASUREMENT OF SURVIVAL

To measure survival rates in the intertidal zone at Lover's Cove, screened pens were designed to enclose both spawners and fry. A pen constructed for this purpose (shown in fig. 2) measured 8 feet in length and 4 feet in width, and was 2 feet deep. The bottom of the pen was open since the sides extended to a depth of 18 inches in the gravel—10 inches below the level of the deposited eggs. Materials used were $\frac{3}{16}$-inch angle iron, $\frac{1}{8}$-inch strap iron, and 18-gage 6-mesh-per-inch galvanized wire cloth. Corner bolts held the removable lid in place. Heavy construction provided weight and strength to resist damage from flood, ice flow, and the inquisitive Alaska brown bear. A clearance of 6 to 10 inches between the enclosed gravel and the lid of the pen provided a low profile and minimum resistance to the current. Figure 3 shows pens in position in the stream.

Calculation of survival rates in the pens conformed to the method used at Sashin Creek weir (U. S. Fish and Wildlife Service 1941). This method describes the success of a pink-salmon brood from the count of spawners as they enter the stream in the fall to the count of fry as they enter the sea in the spring. Each mature female, on the basis of repeated sampling contains approximately 2,000 eggs. The 1951 sample, for example, included 77 females, average fork length 21.50 inches, average egg count 2,074.2, standard deviation 239.28 eggs. With 2,000 eggs per female as the basis of calculation, the estimate of the survival rate is determined by the following equation:

$$\text{Survival rate} = \frac{\text{number of fry} \times 100}{\text{number of females} \times 2{,}000}$$

THE 1949 IMPOUNDMENTS

Lover's Cove stream enters the intertidal zone in two main branches which join in a large pool at the plus-4-foot tide level. Four pens were used in the 1949 experiment, two in each branch of the stream at the plus-8-foot tide level, the approximate midpoint of the intertidal area used by spawning salmon.

The pink-salmon populations of lower Chatham Strait, including those of the Cove stream and Sashin Creek, are "late" races that spawn in September and October. Small numbers of pink salmon are observed near the mouth of the Cove stream early in August, but few enter the stream to spawn until mid-September after which spawning activity increases rapidly and declines to completion early in October.

During the second week in September, a movement into the stream with the rising tide and a retreat to the bay with the receding tide characterized the behavior of the pink-salmon schools. Meanwhile the number of active spawners steadily increased, particularly in the upper section of the intertidal zone. On September 11 the behavior pattern changed and a large school of fish remained in the pool at the 4-foot level. We seined these fish, examined them, and selected individuals that appeared to be unspawned. These were measured and placed in the pens. The average fork length of the 18 females used in the experiment was 21.25 inches, standard deviation 1.06 inches.

To determine the effects of crowding on the survival rate, 1 of each pair of pens received 3 females and the other, 6. Pens with 3 females provided approximately 1 square yard for each female while 6 females doubled this concentration. We released 2 males in the pens with 3 females, 5 males in the pens with 6 females, and secured the lids. Fewer males than females, we believed, might reduce the competition between males for partners but later observations indicated that this was an unnecessary precaution. In one instance the impounded males appeared particularly battered about the snout and an additional male was added to the pen to ensure attendance of a male to the end of the spawning period.

In the following history of the impoundment pens those in the west branch of the stream are referred to as 3a and 6a, in the east branch 3b and 6b, in accordance with the number of females held. All pens were stocked on September 11 and table 1 lists the dates on which the dead fish were removed.

TABLE 1.—*Removal of pink salmon from the impoundment pens, 1949*

[M=male; F=female]

Date	Number of adults removed from pen No. —							
	3a		6a		3b		6b	
	M	F	M	F	M	F	M	F
Sept. 26	0	1	0	1	0	2	0	1
29	0	0	0	0	1	0	0	0
Oct. 6	2	2	3	4	2	1	5	5
11	0	0	2	1	0	0	0	0

Ice covered the cove and adjacent inner bay of Port Walter from late November until the latter part of April. The pens were not visited during this period but the first inspection on May 1 revealed them to be in good condition. Fifteen visits were made in May and June to remove and count the fry as they emerged from the gravel (table 2).

Visits to the pens were too infrequent to completely define the periods of spawning and of emergence of the fry from the gravel. Tables 1 and 2 indicate that while the spawning period did not exceed 20 days, the period of emergence was more than 45 days. Later-than-average spawning occurred in pen 6a, possibly accounting for a delay in time of emergence in this pen. The 50-percent-of-emergence date fell on May 19 in pen 6a and on May 8 in 3a. May 12 was the 50-percent-of-emergence date in both 3b and 6b. The later time of emergence in pen 6a is in conformity with the general rule that late-spawning fish produce late-emerging fry.

TABLE 2.—*Removal of pink-salmon fry from impoundment pens, spring 1950*

Date	Number of fry removed from pen No.—			
	3a	6a	3b	6b
May 1	221	95	35	133
3	85	22	6	116
8	195	0	309	122
10	175	0	237	158
12	(1)	18	277	270
15	26	48	135	148
17	14	187	43	100
19	59	373	15	38
22	23	212	45	62
24	21	115	23	63
29	3	9	5	14
June 4	8	16	58	48
10	5	9	49	40
18	(1)	(1)	11	24
30	(1)	0	4	6
Total	835	1,104	1,252	1,342

[1] High water prevented removal of fry.

Summarized results of the 1949 impoundments, with survival rates, are presented in table 3.

Table 3 describes (1) the degree of spawning success achieved by the individual females in each pen, (2) the count and estimated percentage of eggs retained, (3) an estimate of the number of eggs loose in the pens at the conclusion of spawning, (4) the number of fry produced in each pen, and (5) the resulting survival rates.

Comparison of the number of eggs loose in the pens with the number retained in the spent females shows that retention was by far the more important factor in reducing the survival rates. The greater egg retention in the more crowded pens, 6a and 6b, is highly significant by chi-square test but the number of eggs loose in the pens was not clearly related to crowding.

Survival rates were significantly higher in the less-crowded pens, 3a and 3b, although the higher survival in 3b coincided with the largest accountable loss of eggs. The death of a female in 3b shortly after the pens were stocked left only 2 females during the spawning period. This reduction in the effect of crowding apparently favored survival and more than compensated for the larger accountable loss of eggs. Lack of a direct ratio between the accountable loss of eggs and survival rates suggests that crowding may adversely affect survival in some obscure manner—possibly as a result of repeated disturbance of the gravels after they have received the initial deposit of eggs.

TABLE 3.—*Lover's Cove impoundment pens, 1949–50*

Item	Pen No.—			
	3a	6a	3b	6b
Females:				
With 1,800 eggs or more (unspawned)	0	0	1	0
With fewer than 1,800 eggs but more than 100	1	4	1	3
With 100 eggs or less (spent)	2	2	1	3
Eggs:				
Total number	6,000	12,000	6,000	12,000
Number retained by females	174	4,224	3,212	3,455
Retained (percent)	2	35	54	29
Loose in pens	15	300	300	125
Fry:				
Number removed from pens	835	1,104	1,252	1,342
Survival (percent)	13.9	9.2	20.9	11.2

THE 1950 IMPOUNDMENTS

To explore variations in survival related to levels in the intertidal zone, and to obtain additional data on the effect of crowding on survival, we added 6 pens to the experiment in 1950 and

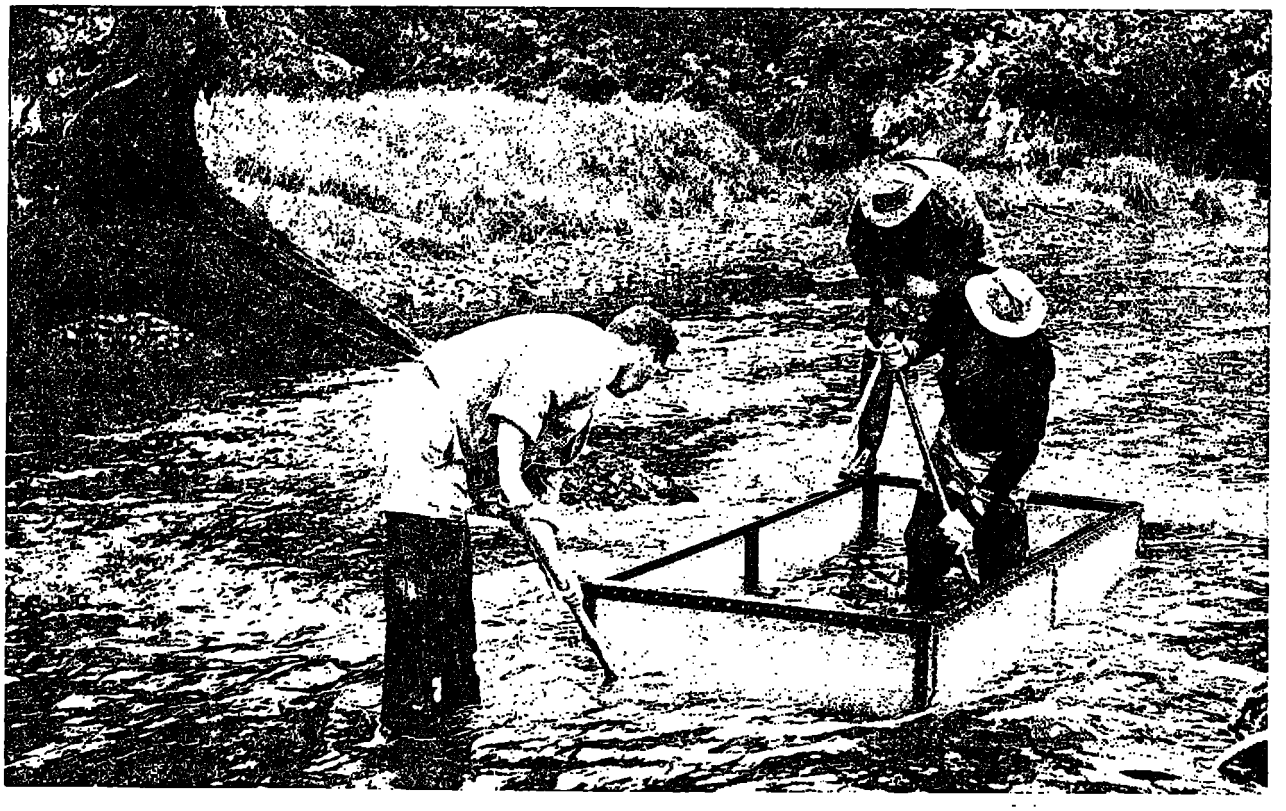

FIGURE 2.—Impoundment pen; setting pen in the gravel of Lover's Cove stream.

FIGURE 3.—Impoundment pens; in place in stream with tops closed.

placed them in pairs at the plus-4-, plus-7-, and plus-11-foot tide levels, while retaining pens 3b and 6b at the plus-8-foot level.

The behavior pattern of the pink salmon in 1950 was similar to that of the previous year, and on the ebb tide of September 13 a large school of salmon remained in the pool at the plus-4-foot tide level. We seined these fish, selected and measured the females to be used in the experiment, and placed them in those pens located between the 4- and 8-foot levels. The fish placed in pens at the plus-11-foot tide level were caught in small pools in the upper intertidal zone. The average fork length of the 35 females used was 21.97 inches, standard deviation 1.12 inches.

Three pairs of pink salmon were placed in 1 of each of the paired pens and 6 pairs in the other. In the following tables each pen is described by 2 numbers, the first indicating elevation above mean low tide (0-foot tide level) and the second the number of female pink salmon held in it; for example, 7–6, 7–3, designate pens at the 7-foot tide level, one of which contains 6 females and the other 3.

Table 4 gives the schedule of removal of dead fish from the pens listed in their upstream order. High water on September 20 and October 2 prevented inspection of pens 4–5 and 4–3 on those dates. On October 8, following a week of continuous rainfall, we found the lids of 4–5, 4–3, and 7–6 dislodged, and the pens empty. High waters obscured conditions in the other pens on this date. In view of the subsequent history of 7–6 it is probable that all three of these pens received a fairly complete deposition of eggs. As a general rule, in any well-defined spawning area, there is a downstream progression of spawning

TABLE 4.—*Removal of pink salmon from the impoundment pens, 1950*

[M = male; F = female]

Date	Number of adults removed from pen No.—															
	4-5		4-3		7-3		7-6		8-3		8-6		11-6		11-3	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Sept. 16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	(1)	(1)	(1)	(1)	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Oct. 2	(1)	(1)	(1)	(1)	0	2	1	4	1	1	1	2	5	5	2	2
8	(2)	(2)	(2)	(2)	(1)	(1)	(2)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
14	(2)	(2)	(2)	(2)	3	1	(2)	(2)	2	2	5	4	0	0	0	0

[1] Obscured by high water.
[2] Pen cover dislodged by high water.

TABLE 5.—*Removal of pink-salmon fry from impoundment pens, 1951*

Date	Number of fry removed from pen No.—							
	4-5	4-3	7-3	7-6	8-3	8-6	11-6	11-3
Apr. 29	0	0	24	85	123	114	0	0
May 7	0	0	243	480	34	98	(1)	181
9	0	0	114	196	23	27	(1)	52
14	(1)	0	0	0	5	(1)	(1)	(1)
16	0	0	83	191	4	(1)	(1)	(1)
25	0	1	10	13	0	(1)	(1)	(1)
28	1	0	1	2	0	33	(1)	31
31	0	0	0	1	0	3	(1)	3
June 4	0	0	0	0	0	2	(1)	0
8	0	0	1	0	0	(1)	(1)	(1)
Total	1	1	476	968	189	277	0	267

[1] High water prevented removal of fry.

activity during the course of the season—a tendency for early arrivals to spawn in the upper and late arrivals in the lower reaches of the spawning gravels. This is true even in a relatively short intertidal-zone stream section, and, as a result, the fish seined in the upper part of the intertidal zone and held in pens 11–6 and 11–3 spawned shortly before those in the other pens.

Ice covered Big Port Walter Bay, preventing access to the pens from November 15 until April 28. Between April 28 and June 8 the pens were visited 10 times to remove and count the fry as shown in table 5.

In general, the periods of spawning and emergence in 1950–51 were similar to those of 1949–50. A notable difference, seen by comparing tables 2 and 5, was the rapid decline in the numbers of emerging fry in the spring of 1951, after what appeared to be a productive start, in contrast with the more prolonged period of emergence in 1950.

The cause of the failure of pen 11–6 to produce fry was not determined. High water submerged the pen through the entire period of the emergence of the fry and, although visibility through the screen was believed adequate to permit observation of fry, were any present, none was observed nor was any means of escape detected.

Results of the 1950 impoundment are summarized in table 6. Fifty percent of the females removed from the pens in 1950 were completely spawned, a slight increase over the 1949 percentage, and one entirely attributable to the spawning success of the more mature females placed in the pens at the 11-foot tide level.

Retention of eggs resulted in a substantial loss during the spawning period and, as in 1949, it was

TABLE 6.—*Lover's Cove impoundment pens, 1950–51*

Item	Pen No.—							
	4–5	4–3	7–3	7–6	8–3	8–6	11–6	11–3
Females:								
With 1,800 eggs or more (unspawned)	(1)	(1)	0		0	0	1	0
With fewer than 1,800 eggs but more than 100			2	3	1	4	1	0
With 100 eggs or less (spent)			1	1	2	2	4	3
Eggs:								
Total number	10,000	6,000	6,000	12,000	6,000	12,000	12,000	6,000
Number retained by females			1,624	4,658	1,116	2,646	2,846	16
Retained (percent)			27	39	19	22	24	0
Loose in pens			100	125	1,000	1,000	425	150
Fry:								
Number removed from pens	1	1	476	968	189	277	(2)	267
Survival (percent)			7.9	8.1	3.2	2.3		4.5
Percentage of time covered by tide	65	65	35	35	25	25	2	2
Maximum salinity in gravel (‰)	30.7	30.7	29.7	29.7	7.6	7.6	.0	.0

[1] Record incomplete as noted in table 4.
[2] Record incomplete as noted in table 5.

significantly greater in the more crowded pens. The estimate of eggs loose in impoundment pens at the conclusion of the spawning period again indicated that this source of loss not only was less than the loss of eggs by retention, but it also was less clearly related to crowding than was egg retention.

The level of survival in the impoundment pens during the winter of 1950–51 was well below that of the previous year. In 1949–50, survival rates in pens 3b and 6b were 20.9 and 11.2 percent. The same pens, identified as 8–3 and 8–6 in 1950–51, had survivals of 3.2 and 2.3 percent.

Table 6 includes two categories of measurements not contained in table 3. These are (1) percentage of the incubation period during which nests were exposed to tidal inundation, and (2) maximum salinities measured at high tide at a point 8 inches deep in the stream gravel. The methods used in obtaining these measurements and the hydrodynamics of the intertidal zone are discussed in Salinity gradients in the intertidal zone of an Alaskan pink-salmon stream, page 177.

THE 1951 IMPOUNDMENTS

In 1951, the pen locations remained as they were in 1950 with the exception that pens at the 11-foot level were moved to more stable and accessible locations at the 9-foot level. Pens at the 4-foot level were washed several hundred feet downstream by heavy rains September 8 and 9, and as further shifting of the stream channel appeared imminent they were not replaced.

Flood damage to the stream channel and continuing high water prevented effective use of the seine; however, on September 15, fish were taken to stock all pens with the exception of one at the 9-foot level. Average fork length of the 21 females was 21.79 inches, standard deviation 0.99 inches.

Big Port Walter remained frozen from mid-December until mid-April and on April 28 the first fry were counted from the pens. Production was well below expectations in the pens at the 7- and 8-foot levels, and when water levels permitted, a close inspection revealed holes in the screens caused by corrosion and abrasive action of sand. An unknown number of fry escaped through these openings, and as a result data were incomplete from 4 of the 5 pens.

Results of the 1951 impoundments follow in table 7.

Table 7 shows fewer females in the completely spawned category than occurred in previous impoundment trials, but the percentages of eggs retained were similar to those of previous experiments—a significantly greater retention of eggs occurring in the more crowded pens.

Contrary to previous experience, the number of eggs loose in the pens at the conclusion of spawning

TABLE 7.—*Lover's Cove impoundment pens, 1951–52*

Item	Pen No.—				
	7–3	7–6	8–6	8–3	9–3
Females:					
With 1,800 eggs or more (unspawned)	0	1	1	0	0
With fewer than 1,800 eggs but more than 100	1	3	5	2	2
With 100 eggs or less (spent)	2	2	0	1	1
Eggs:					
Total number	6,000	12,000	12,000	6,000	6,000
Number retained by females	843	4,228	6,127	1,678	672
Retained (percent)	14	35	51	28	11
Loose in pens	43	500	225	10	7
Fry:					
Number removed from pens	(1)	(1)	(1)	(1)	1,185
Survival (percent)	(1)	(1)	(1)	(1)	19.8

[1] Corroded screens allowed fry to escape.

was positively and significantly correlated with the number of females held ($r=0.883$, $P<.05$). This loss of eggs again was of minor significance compared with the loss by retention.

Fortunately, one of the 5 pens (9–3) survived the rigors of the winter and produced 1,185 fry from the spawning of 3 females. The high survival rate, 19.8 percent, was similar to the 20.9 percent survival of pen 3b at the 8-foot tide level, during the successful winter of 1949–50.

DISCUSSION

The use of screened enclosures in the intertidal experiments imposed limitations on the interpretation of results. Measurements obtained by this method are not directly comparable to those obtained by weir counts in a natural stream area, such as Sashin Creek (fig. 4), nor do they measure spawning success and survival in intertidal areas other than those within the pens. The handling of adult fish and the restricted space available for them within the pens were factors that did not favor spawning success or the survival rate. On the other hand, both adults and fry were protected from predators, a condition favoring survival.

The interplay of natural and imposed conditions on the intertidal experiments for the years 1949, 1950, and 1951 resulted in survival rates of 20.9, 3.2, and 19.8 percent in pens that contained 3 females located at the 8- and 9-foot tide levels. Survival rates in Sashin Creek for these years were 3.7, 0.1, and 9.3 percent. The average for the 12-year period 1940–51 was 2.54 percent. The similarity in the years of occurrence of the high- and low-survival rates in the intertidal and fresh-water areas suggests a response to common environmental factors and specifically to those factors related to the fresh-water environment.

It may be significant in this regard that the winter of 1950–51 was unusually cold with the greatest departure from normal temperatures occurring in November. In the 12-year period 1940–51, the four lowest survival rates in Sashin Creek coincided with the four coldest Novembers suggesting that abnormally low stream temperatures occurring early in the incubation period (between the 6th and 10th weeks) may be particularly damaging to the developing eggs. The average Sashin Creek stream temperature for November in 1949 was 43.3° F., in 1950 it was 36.9° F., and in 1951 it was 39.4° F.

If the abnormal drop in stream temperatures in November 1950 was, in fact, the cause of low survival rates in the pens and in Sashin Creek, and if low temperatures proved particularly damaging to eggs deposited during the latter part of the spawning period (those in an early stage of development), this factor could account for both the low survival rates and the brief period of emergence shown in table 5.

Differences in the survival rate related to the 4-, 7-, 8-, and 11-foot tide levels are shown in table 6. Pens 4–5 and 4–3, located near the lower limit of the intertidal area used by spawning pink salmon, produced one fry each. Similarities in the histories of these pens and of pen 7–6 during the spawning period indicate that seeding occurred at the 4-foot level. It may therefore be inferred that the low survival resulted from exposure of eggs to salinities which reached concentrations approaching those of open coastal sea water, 30.7 p. p. th. Thus, during periods of tidal inundation, which totaled 65 percent of the October–April incubation period, eggs at the 4-foot level were subjected to high salinities for extended periods of time.

The eggs in pens 7–3 and 7–6 were exposed to maximum salinities (only slightly lower than those at the 4-foot level) but with much shorter intervals of exposure; periods of tidal inundation totaled 35 percent of the incubation period. Apparently this was an optimum level during the adverse winter of 1950–51, as the pens at the 7-foot level were more productive than those at higher elevations.

Frequency of exposure to salt water of moderate temperature may have favored survival at the 7-foot level, as all high tides of November and December exceeded 7 feet, although several successive lower high tides failed to reach the 8-foot level. Thus the 8-foot level and those above it were exposed to more prolonged periods of untempered stream flow. The tempering effect of the tides continues through the incubation period, as marine temperatures exceed stream temperatures from October through April. In November 1950, the mean Sashin Creek temperature was 36.9° F., while the marine temperature at Sitka was 44.5° F. (U. S. Coast Geodetic Survey 1952). April 1951 temperatures were 34.2° and 41.4° F., respectively. Temperatures measured in the bay at Little Port Walter in February 1951 are probably more indicative of differences existing in water temperatures at the Cove and in the sea. Bay tem-

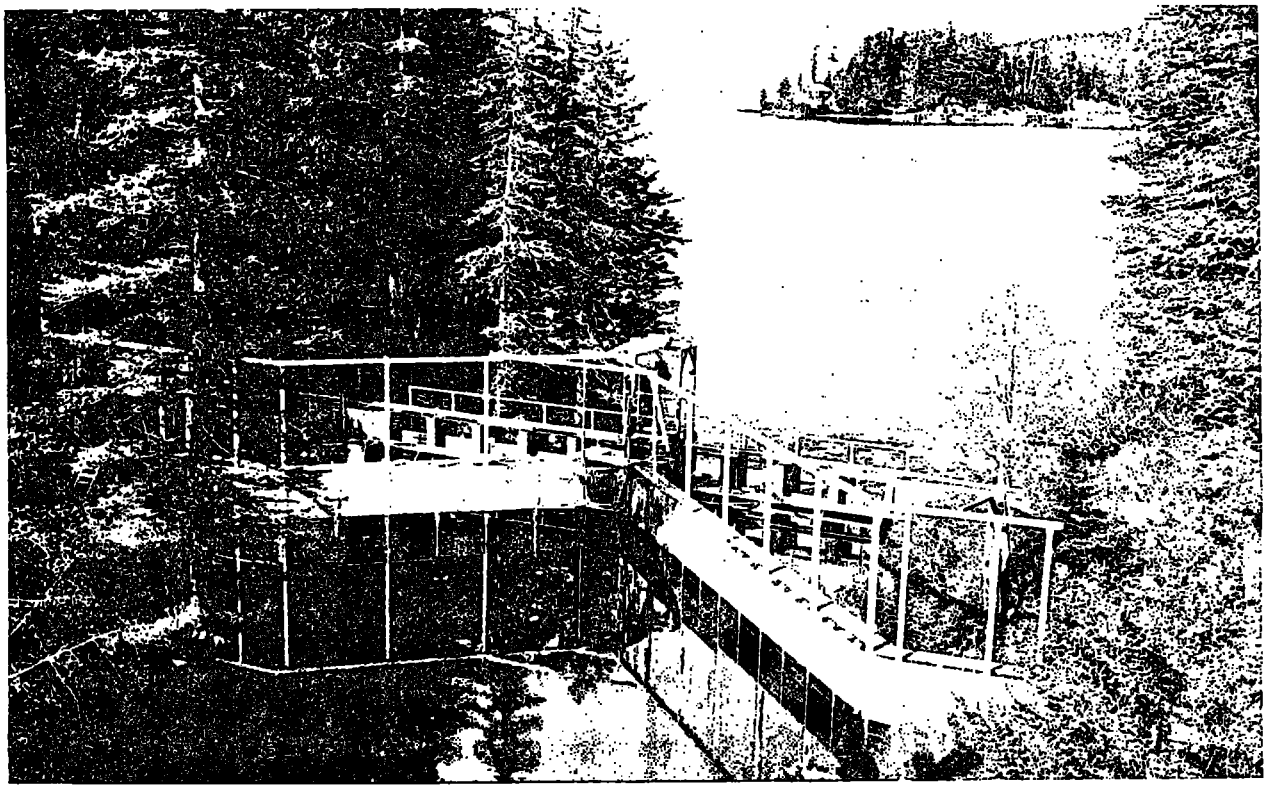

FIGURE 4.—Sashin Creek weir, Little Port Walter, Alaska.

peratures averaged 34.6° F. in the brackish surface layer and 39.1° F., 20 feet below the surface. Appendix table B–1, p. 185, shows the warming in the stream gravel that accompanied a rising tide in August 1951.

While the periods of immersion in salt water at the 7-foot level favored survival they did not favor earlier emergence of the fry from the gravel which, as table 5 shows, occurred at the 8-foot level. As previously noted, low-survival rates during the 1950–51 season apparently were related to an unfavorable fall stream-temperature gradient. In contrast, emergence and downstream migration of the fry are related more closely to the spring stream-temperature gradient. On the basis of 10 annual measurements, the time of the seaward migration of fry in Sashin Creek shows a correla tion of $r=-0.215$ with the November–December stream temperatures; while the correlation with March–April stream temperatures is $r=-0.881$, a highly significant correlation.

Crowding, as an influence on successful spawning and survival, was measured by the device of pairing the pens and stocking one with twice as many females as the other. The levels of crowding arbitrarily selected approximated 1 and 2 females per square yard. There is evidence in past escapement records that under natural conditions crowding may be an influence in reducing the survival rate. Egg retention, failure to deposit in the gravel, and mechanical shock caused by repeated stirring of the gravel may all result from crowding and contribute to this loss. The first of these, increased egg retention, was the only factor consistently in evidence in pen experiments.

SUMMARY

Pink salmon spawn in large numbers in many of the intertidal areas of Southeastern Alaska streams. To obtain information on the productivity of intertidal spawning, a series of experiments using wire-screen enclosures was undertaken in an intertidal area near the Little Port Walter station during the years 1949, 1950, and 1951. The experiments were designed to show differences in the survival rate, from spawning to the emergence of fry, related to periods of inundation at various tidal levels.

Crowding as an influence on successful spawning and survival was measured by the device of pairing the pens and stocking one with twice as many females as the other. The levels of crowding arbitrarily selected approximated 1 and 2 females per square yard. Results of the experiments indicated the following:

1. The lower limit of the intertidal area in which pink salmon spawn, approximately 4 feet above mean low tide, may be unproductive but above this level the survival of spawn is comparable to if not greater than survival in fresh-water stream areas.

2. Abnormally cold stream temperatures, resulting in a low fresh-water survival rate, may be modified by warmer tidewater to create conditions most favorable for survival at some intermediate level in the intertidal zone.

3. Crowding reduces the survival rate by increasing the retention of eggs and possibly by increasing the incidence of mechanical shock to eggs previously deposited in the gravel. The loss of eggs by failure to deposit in the gravel was secondary to retention as a cause for lower survival rates and was less clearly related to crowding.

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SALINITY GRADIENTS IN THE INTERTIDAL ZONE OF AN ALASKAN PINK SALMON STREAM

By BERNARD EINAR SKUD, *Fishery Research Biologist*

This study [1] was carried out to supplement fresh-water survival data which have been gathered in Southeastern Alaska on the pink salmon (*Oncorhynchus gorbuscha*), a species known to utilize spawning areas in the intertidal zone of some streams. Environmental differences between intertidal and fresh-water zones of a stream have led fishery biologists to question whether intertidal spawning by pink salmon is detrimental to the survival of their eggs and fry. To interpret the effects of tidal inundation on survival of spawn, it is necessary to understand the physical characteristics of the intertidal zone. The purpose of this investigation was to determine the degree of salinity in the water within the gravel beds of known intertidal spawning grounds.

In recent years, the physical and biotic characteristics of waters in the intertidal zone have drawn the attention of numerous ecologists and oceanographers. Whether their studies dealt with the hydrobiology of organisms or hydrological features in relation to pollution, the investigations have readily exhibited the complexity of the factors involved.

In the literature there is a noted discrepancy in the interpretation of different types of saline waters and it is, therefore, appropriate to qualify and define the estuarine area referred to in this paper. It is not the intent to evaluate previously proposed definitions, but only to present, for the sake of clarity, descriptions best suited for the study. Rochford (1951) distinguishes estuarine from brackish waters on a principle of variability based on time; that is, estuarine suggests a daily as well as a seasonal fluctuation in salinity, whereas brackish implies only a seasonal salinity change. It is necessary to submit only two divisions of the estuarine waters—those of the inlet up to the mouth of the stream and those of the intertidal zone from the mouth to the farthest reaches of the highest tide. The mouth, in this instance, is considered as the equivalent of the zero tide level. Further classification is not necessary for the purposes of this paper.

[1] The author was assisted by Jerrold Olson and Willard Brewington, of the Fish and Wildlife Service.

SAMPLING PROCEDURES

In conjunction with a series of experimental spawning pens at Lover's Cove stream sampling of the water within the stream bed was initiated during the summer of 1951 (see fig. 1, p. 168). The spawning pens were set at selected distances upstream from the mouth to subject them to varying degrees of inundation by tidal waters. The pens were stocked each fall with a given number of male and female pink salmon and the fry were counted out each spring so that the survival could be determined. A sampling station for measuring salinity was set up at four of the pen locations so that salinity sampling results could be correlated with fry survival (see p. 173).

At each location, a galvanized pipe with an outside diameter of 1 inch was set in the gravel of the stream bed to a depth of 6 to 8 inches, corresponding to the average depth of pink-salmon nests. A 10-foot length of pipe was used at the set of pens closest to the creek mouth (station A) to permit sampling at flood tide, and a 5-foot section of pipe was placed beside it at the same depth, to facilitate sampling at ebb tide. The pipe was open at both ends and the pipe end in the gravel was perforated with 12 ⅜-inch holes to ensure maximum exchange of water within the pipe and in the area immediately surrounding the pipe.

Actual sampling was accomplished by using a hand pump and a length of ½-inch rubber tubing which could be inserted into the pipe. Water was pumped into sampling jars at the approximate rate of 1 quart in 15 seconds, and each sample was held for density determinations with a hydrometer. This method was devised to obtain preliminary information on the changes that take place under the influence of tidal inundation. Though neces-

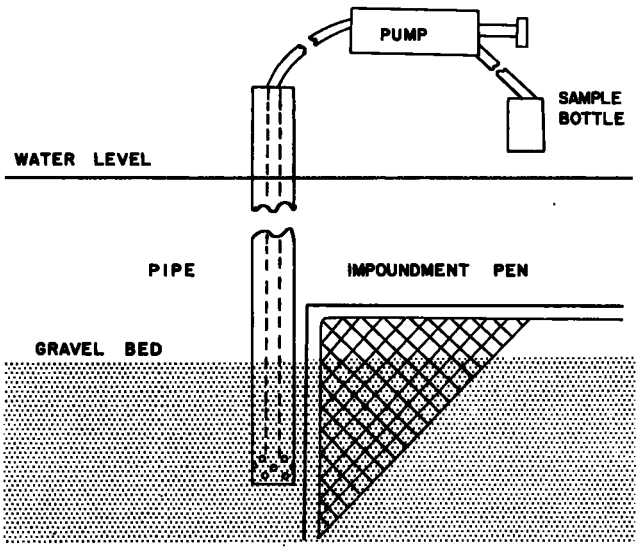


FIGURE 1.—Diagrammatic section of sampling station at high tide.

sarily crude, this initial procedure for taking samples from within the gravel of the stream bed was carried on at the other stations (fig. 1). Table 1 gives the location of the stations and their relation to the tides (based on astronomical predictions from mean lower-low water).

TABLE 1.—*Location of stations and tidal influence*

Approximate distance upstream from zero tide level	Tidal level at station, from mean lower-low water	Approximate time covered by the tide in a 7-month period
	Feet	*Percent*
Station A: 400 feet	4	65
Station B: 800 feet	7	35
Station C: 950 feet	8	25
Station D: 1,300 feet	11	2

The pipes used at each station were wired to the steel impoundment pens so that they would not be subject to any movement that might disturb the gravel surrounding the openings at the bottom of the pipe. These permanent stations could be sampled repeatedly during various tidal cycles. When the height of the water permitted, sampling was done by standing on top of the pens which were approximately level with the normal stream height. When the incoming tide raised the water level too high, samples were taken from a small skiff. The following data were recorded: Time sample was drawn, height of water, air and water temperatures, and maximum tidal height.

To facilitate recording the progressive rise of tidal waters at each station, the sampling pipes were marked in inches, the zero mark being equivalent to the level of the impoundment pen cover. Samples were originally drawn at 1-foot and ½-foot intervals, but in an effort to determine more accurately the stage at time of the change from fresh to salt water, samples were drawn at 1-inch and 2-inch intervals. Samples were drawn at a number of different stations during the same tidal cycle to compare the resulting salinities as the tidal water progressed upstream. Continuous sampling sequences were attempted at two of the stations during both flood and ebb tides; however, it was not possible to attain complete sequences on different days with similar tidal cycles.

SALINITY DETERMINATIONS

The positions of the pens were such that station A was reached at a tidal level of 4 feet, station B at 7 feet, and station C at 8 feet. The depth of tidal water at which a given degree of salinity occurred within the gravel bed varied at these three stations during the same tidal cycle, and also varied at any one of the stations during different tidal cycles (fig. 2). Stations B and C, located on the left-hand tributary of the stream, were exposed to an equal volume of fresh-water discharge. During a particular tidal cycle, under 25 inches of tidal inundation, station B reached a saline content of 27 parts per thousand, whereas, at the same depth station C registered a salinity of less than 5 parts per thousand. This progressive salinity decrease upstream represents the

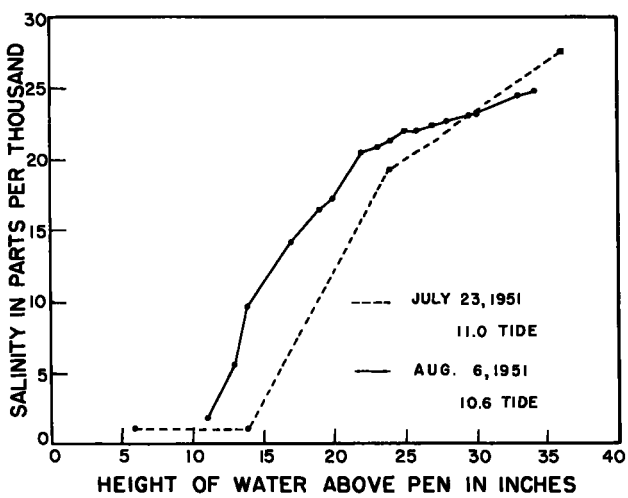


FIGURE 2.—Samples from station A on days with comparable tidal heights.

longitudinal salinity gradient, and is brought about by the continual dilution and mixing of fresh and sea water. Station A, which was located below both the left and right branches of the stream, was subject to washing by a greater volume of fresh water than the other stations. This fact introduced a variable which prevented an exact comparison among all of the stations during a tidal cycle.

Station D was reached by only the highest tidal waters which were subject to continuous mixing and hence to the greatest dilution. Sampling was soon discontinued at this station, since no substantial increase in salinity was recorded.

The method of testing for salinity, by use of a set of hydrometers, necessitated drawing off as much as a quart of water for each sample. At the outset of the work, the amount of water sampled was considered a means of ensuring complete circulation of the ambient water with that in the pipe. At a later date it was suggested that such quantities for each sample might tend to draw water, by suction, from areas above the gravel of the stream bed. This possibility, later tested and compared by the conductivity method, is discussed in appendix A, p. 182. Salinity determinations in the tidal zone required the use of three hydrometers to provide density readings for the entire range—one with a scale ranging from 0.996 to 1.011, a second with a scale 1.010 to 1.021, and a third with a scale from 1.020 to 1.031. The hydrometers were floated in the sample water contained in quart mason jars (the best available containers). The temperature of each sample was taken to correct for differences of density arising from reading the hydrometer at temperatures other than its calibration temperature of 15° C.; such corrections and the conversion of density to salinity were made from tables in the Manual of Tide Observations (U. S. Coast and Geodetic Survey 1941). These data are recorded in appendix B, p. 183.

Specific conductance determinations were made on the model RC–1B conductivity bridge manu factured by Industrial Instruments, Inc. The conductivity cell was a dipcell, type Cel–1A, supplied by the same manufacturer. The accuracy of this a.-c. unit is somewhat limited, depending on the scale used and the ability and care exercised in using the instrument. Personal error may be present either in reading the scale or in setting the null indicator. Compensation for differences in conductance due to temperature was necessary. Before use, the conductivity cell was replatinized, and the cell constant was determined and checked after each series of observations.

The table presented by Thomas, Thompson, and Utterback (1934) was used to determine chlorinity and the established empirical relation (salinity equals 0.03 plus 1.805 [chlorinity]) between salinity and chlorinity provided the salinity readings in parts per thousand. Redfield (1948) points out that the concentration of various constituents of sea water mixed with river water cannot be precisely estimated from chlorinity because of the relatively richer composition of dissolved solids in river water. For this reason, salinity is not exactly proportional to chlorinity.

Approximately 200 samples were taken from the creek at Lover's Cove. Some 40 of these were retested at the Seattle laboratory of the Fish and Wildlife Service by the conductivity method of determining salinity. As a further check of the accuracy of the determinations, the salinity of a number of the samples was tested by the titration method at the oceanographic laboratories of the University of Washington. The results of the three methods were compared and the hydrometer, or density, method found sufficiently accurate for the purposes of this work.

The conductance method was also used in the field for testing the sampling method and warrants further explanation and discussion of the procedure followed. Comparisons of the accuracy of the three methods showed that the original values obtained with the hydrometer differ by less than 10 percent from the values found by titration and conductance (table 2). This method

TABLE 2.—*Comparison of salinity determinations by 3 methods of samples from Lover's Cove stream, 1951*

Sample	Salinity (°/₀₀) determined by—		
	Titration	Conductance	Hydrometer
No. 698	2.8	2.9	2.9
No. 702	12.6	11.8	12.9
No. 703	10.7	10.0	10.8
No. 704	8.7	8.5	8.8
No. 713	5.4	5.1	5.1
No. 714	26.8	25.7	27.7
No. 716	4.0	3.8	3.9
No. 718	3.6	3.3	3.4
No. 3268	17.8	17.2	17.5
No. 3273	21.9	20.8	22.6
No. 3283	18.9	19.0	20.9
No. 3285	22.3	21.7	22.7

also has many distinct advantages in the field. In areas of comparatively small ranges of density, the common form of stem hydrometer is generally not sufficiently accurate but it is applicable in estuarine waters, where greater ranges in density are encountered.

HYDROLOGY OF THE INTERTIDAL ZONE

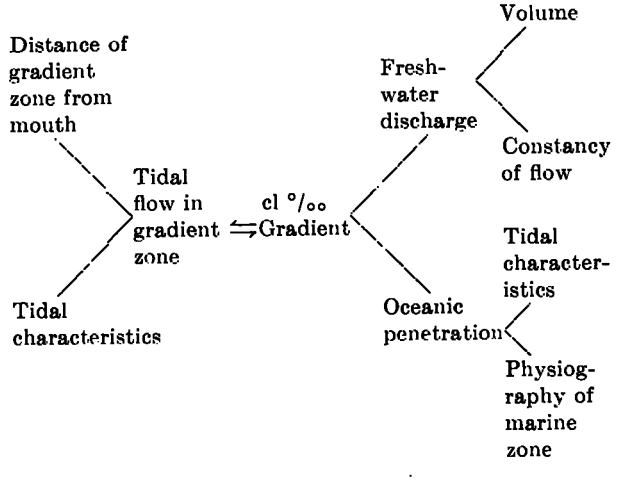
Consideration of the physical changes in the intertidal zone, brought about by the mixing of fresh and salt waters, is essential in an analysis of the sampling results. The variables most significant in this study include density, salinity, tidal forces, stream discharge, and turbulence. The density of inshore sea water is, for the most part, dependent on salinity. Density and salinity gradients may, therefore, be regarded as essentially the same. The forces exerted by tidal waters and stream discharge produce the turbulence and, in effect, the mixing of the fresh and saline waters. These components and their relation to density contribute to the production of the three zones of oceanographic structure of a water mass described by Tully (1949). The upper zone is formed by fresh water entering the tidal body and mixing with the underlying sea water, and its lower limit is marked by an inflexion in the salinity gradient. The seaward movement of fresh water and the reciprocal movement of the tide produce a middle, or circulatory, zone bounded by a threshold, which separates it from the third, or deep, zone.

For the most part, Tully's work was limited to that area of an inlet up to the creek mouth. The results obtained in sampling the Lover's Cove stream during tidal inundation showed that the phenomena of salinity gradients continue upstream. Some distinction should be made, however, between the differences encountered in a restricted channel of a stream and in the wider scope of an inlet or bay. A stream of fresh water entering the inlet has a tendency to spread, more or less fan shaped, over the underlying saline water. In this process, some mixing of fresh and salt waters is in evidence and results in the formation of lateral salinity gradients, the water becoming more saline as the distance from the mouth increases. On the other hand, when tidal waters have progressed upstream into a comparatively small channel, fresh water entering the system is limited to the same channel and lateral gradients are less significant.

The dispersion of fresh-water runoff as it enters estuarine waters during flood tide is described concisely by Tully:

> It is reasoned from the principle of isostacy that when fresh water is being supplied continually in one part of the system and sea water is supplied in another there will be a constant isostatic head inducing a surface seaward flow. It is remarked that both the upper and middle zones become more saline to seaward, from which it is reasoned that all the fresh, and at least some of the sea water leaves the inlet through the upper zone . . . any fresh water accumulating in the middle zone would tend to join with the upper zone, and a compensatory inflow of sea water in the middle zone would result.

It follows, then, that the mixing process is largely a horizontal exchange across the salinity gradients, and the extent and manner of mixing largely determine the degree of zonation in estuarine waters. A composite picture of the components and their contribution to the development of the salinity gradient is found in the following diagram (after Rochford 1951):



During an ebbing tide, the tidal flow decreases and eventually reverses its movement so as to be flowing in the same direction as the overlying fresh water. As the estuarine waters in the intertidal zone decrease in depth to include only the upper zone of density stratification, the process of recovery begins as the churning fresh water enters the system uninhibited by an incoming tide.

During the early stages or at the upper limits of an incoming tide, the depth of tidal inundation in the stream is not great enough to establish the

three zones of density stratification. Depending on the depth of the tidal waters, either the lower zone or both lower and middle zones may be lacking. Nevertheless, where the depth of sea water is sufficient, the upper and middle zones in the open waters of the inlet should appear in the stream. Sampling data from the surface to the stream bottom confirmed that this was true for Lover's Cove stream. Furthermore, the same stratification was present when sampling was done from the surface to varying depths within the gravel. By sampling at short intervals, it was possible to follow the progress from the upper zone to the presence of the inflected boundary and then to the middle, or circulatory, zone (fig. 3). There is also adequate evidence of the longitudinal stratification which was present in the intertidal zone. As mentioned before, this stratification proceeds to an approximate nil salinity at or near the tidal limit for any given instant.

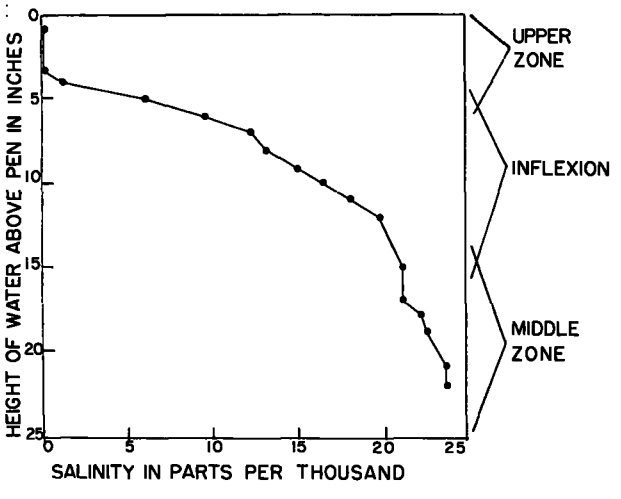


FIGURE 3.—Lover's Cove, station B, depicting oceanographic structure of the salinity gradient, August 7, 1951.

The stratification revealed by sampling indicates that the gravel bottom did not essentially impede either the exchange of fresh and sea water or the forces exerted by an incoming tide. This brings to light an interesting comparison of bottom types and their tendency to obstruct the transfer of fluids of varying density. The texture, shape, and sorting of the materials composing the stream bottom are important factors to be considered in the porosity, hence the water content, of a particular deposit. Permeability of a sediment which is related to porosity, is of particular concern and is a measure of the ability of water to circulate through the sediment.

Reid (1930) and W. B. Alexander et al. (1932) found considerable retention of saline water in intertidal sand after the tide had receded. A gravel bottom undoubtedly has similar tendencies toward retention, but is more permeable than sand and permits thorough washing by fresh water. In a few instances, a lag occurred in the recovery to fresh water and also in the establishment of saline water within the gravel. This tendency, possibly effected by interstitial water, occurred in areas of less-coarse gravel. In general, however, the recovery to fresh water within the stream bed at Lover's Cove during an ebb flow exhibited a very slight distinction, if any, from the recovery in the layer of water just above the stream bed (table 3).

To predict the threshold of change from the upper to the middle zone during any tidal cycle, stream discharge, local runoff, wind, and seasonal salinity changes must be considered. Stream discharge and runoff are of particular concern in this part of Southeastern Alaska which annually records over 200 inches of rainfall. Wind can bring about changes in the degree of mixing in estuarine waters, in addition to influencing the tidal cycle itself. Seasonal changes in salinity are likewise of some consequence. The salinities of these waters are the highest in the months preceding the spring thaw and the lowest in the summer months.

TABLE 3.—*Data sheet showing recovery to fresh water during an ebbing tide at station B, July 31, 1951*

[High water—8.7 feet at 1323; low water—3.9 feet at 1829]

Sample	Height of water above pen	Time	Tide height	Temperature	Hydrometer reading	Density corrected to 15° C.	Salinity
	Inches		*Feet*	*° C.*			*°/₀₀*
No. 6	12	1401	8.5	15.5	1.0114	1.0115	16.1
No. 8	11	1409		15.5	1.0100	1.0101	14.2
No. 10	10	1418		15.5	1.0100	1.0101	14.2
No. 12	9	1425		15.5	1.0094	1.0095	13.5
No. 13	8	1430		15.5	1.0090	1.0091	12.9
No. 14	7	1437		15.5	1.0074	1.0075	10.8
No. 15	6	1442	8.0	15.5	1.0058	1.0059	8.8
No. 16	5	1448		15.5	1.0034	1.0034	5.5
No. 17	4	1452		15.5	1.0018	1.0018	3.4
No. 18	3	1456		15.5	1.0008	1.0008	2.1
No. 19	2	1500		15.5	1.0002	1.0002	1.3
No. 20	1	1505		15.5	1.0000	1.0000	1.1
No. 21	0	1509	7.5	15.5	<1.0000	<1.0000	<1.0
No. 22	0	1514		15.5	<1.0000	<1.0000	<1.0

CONCLUSIONS

Pink salmon utilize spawning areas in the intertidal zone of some streams in Southeastern Alaska.

To evaluate the survival of spawn in an intertidal area it is necessary to ascertain and understand the physical components of such an environment. The purpose of this study was to determine the degree of salinity reached in the water within the gravel bed of a known pink-salmon spawning area. The conclusions are as follows:

1. The three zones of oceanographic structure of waters in the inlet are found in the intertidal zone of the stream when exposed to tidal inundation.

2. The saline content of the water within the gravel of the spawning beds is dependent on the salinity of the overlying waters.

3. When tidal waters have increased the water depth of the stream to include the middle zone of the salinity gradients, the water within the gravel is of a salinity similar to that of the coastal waters open to the ocean.

4. The coarse gravel of the spawning bed showed no appreciable tendency to hold the denser saline water and allowed thorough washing by fresh water during ebb tide.

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APPENDIX A

TEST OF SALINITY-SAMPLING METHOD

A means of testing the original sampling method was devised to determine the possibility of drawing water from areas of lesser or greater density than that in which the sampling pipe was situated. This work was done in the State of Washington on a small stream which enters Puget Sound a few miles south of Three Tree Point. The method made use of a conductivity cell and required a source of electricity which was supplied by a property owner in the vicinity. Essentially, the procedure used at Lover's Cove was repeated. The sampling pipe, however, was larger—of 2-inch outside diameter—to enable use of the conductivity unit. Procedure of pumping the samples was the same, except that the cell was lowered in the pipe first and was then followed by the tube for pumping. The sensitivity of the instrument could distinguish changes of approximately 0.5 of a unit of salinity at constant temperature, and therefore, any amount of water drawn into the pipe at the sampling level which was of different density than that which existed originally could be noted on the conductivity bridge scale.

Repeated tests failed to show any change in salinity due to pumping. That is to say, while pumping was in progress, no noticeable change in conductance was recorded, indicating that any ambient water drawn into the pipe at sampling level was of the same characteristics as that already in the pipe. This may be explained on a purely physical basis, as water of less density forced downward into a region of greater density would tend to return to its original position, and vice versa. Undoubtedly, enough suction could be applied to counteract this tendency, but the opening of the tubing was less than one-half inch in diameter and even extremely rapid pumping did not result in changes that could be detected on the conductance bridge. With such evidence, it was assumed that the method of pumping water samples from within the gravel of the stream bed provided a substantially accurate means of sampling. If any contamination occurred from

areas of different densities, it could be regarded as negligible in view of the large range of density and the comparatively rapid changes.

APPENDIX B

TABLE OF OBSERVATIONS

July 17: Experimental sampling was carried on to design a system for future sampling. Samples 2 and 3 were taken in the open water of the stream to test differences of the water at the surface and at the stream bottom.

July 19: Experimental sampling; samples 4 and 6 were taken in open water rather than from within the pipe.

July 23: The procedure used to obtain the data presented under this date was used for all samples taken subsequently.

July 26 and 28: Two sections of pipe, station A(1) and station A(2), were set in the gravel to depths of 12 and 4 inches, respectively, and pipe A remained at the 6- to 8-inch depth. This experiment was designed to show the progressive change of salinity at various depths within the gravel bed of the stream.

August 20: Samples 1, 2, 3, and 4 were drawn from the top 6 inches of water within the pipe to determine any difference in samples drawn from the bottom of the pipe in the gravel. On the same date, samples 6, 7, and 8 were drawn in open water at varying distances below the surface.

The salinity-sampling results at Lover's Cove stream, Alaska, from all stations are presented in appendix table B–1. The temperatures recorded in the table were measured for density correction and do not represent field conditions.

APPENDIX TABLE B–1.—*Salinities recorded at all stations, Lover's Cove stream, Alaska, 1951*

Date and sample	Station	Height of water above pen	Time	Tide height	Temperature	Hydrometer reading	Density corrected to 15° C.	Salinity
July 17 (High water, 12.5 feet at 0018):				*Feet*	° *C.*			°/₀₀
No. 1	A		2345	12.5	14.5	1.0222	1.0221	29.9
No. 2	A	Surface sample			14.5	1.0000	<1.0000	<1.0
No. 3	A	Stream bottom			14.5	1.0222	1.0221	29.9
No. 4	A		0030		14.5	1.0220	1.0219	29.7
July 19 (High water, 10.5 feet at 1436):								
No. 1	A		1400	10.5	14.5	1.0212	1.0211	38.6
No. 2	B				14.5	1.0212	1.0211	28.6
No. 3	B				14.5	1.0212	1.0211	28.6
No. 4	B	Surface sample			13.5	1.0000	<1.0000	<1.0
No. 5	D	0 inch	1530		13.0	<1.0000	<1.0000	<1.0
No. 6	B	Stream bottom			14.0	1.0212	1.0210	28.5
July 23 (High water, 11.0 feet at 1717):								
No. 1	A	6 inches	1400		16.0	<1.0000	<1.0000	<1.0
No. 2	A	14 inches	1415		16.0	<1.0000	<1.0000	<1.0
No. 3	A	24 inches	1435	6.5	16.0	1.0136	1.0138	19.1
No. 4	B	0 inch	1450		16.0	<1.0000	<1.0000	<1.0
No. 5	A	36 inches	1456		15.5	1.0200	1.0201	27.3
No. 6	C	0 inch	1510	8.0	15.5	<1.0000	<1.0000	<1.0
No. 7	B	12 inches	1517		16.0	<1.0000	<1.0000	<1.0
No. 8	A	48 inches	1521		16.0	1.0212	1.0214	29.0
No. 9	C	12 inches	1539	9.0	16.0	<1.0000	<1.0000	<1.0
No. 10	A	59 inches	1545		16.0	1.0216	1.0218	29.5
No. 11	B	26 inches	1549		15.5	1.0200	1.0201	27.3
No. 12	C	24 inches	1614	10.0	15.5	1.0016	1.0016	3.2
No. 13	B	37 inches	1619		15.5	1.0210	1.0211	28.6
No. 14	A	72 inches	1626		15.5	1.0226	1.0227	30.7
No. 15	D	4 inches	1717	11.0	16.0	<1.0000	<1.0000	<1.0
No. 16	C	36 inches	1725		16.0	1.0048	1.0050	7.6
July 26 (High water, 9.7 feet at 1931):								
No. 1	A(1)	12 inches	1536	5.5	14.5	1.0132	1.0131	18.2
No. 2	A(2)	12 inches			14.5	1.0156	1.0155	21.3
No. 3	A(1)	13 inches	1539		14.5	1.0132	1.0131	18.2
No. 4	A(2)	13 inches			14.5	1.0158	1.0157	21.6
No. 5	A(2)	14 inches	1542		14.5	1.0162	1.0161	22.1
No. 6	A(1)	14 inches			14.5	1.0144	1.0143	19.7
No. 7	A(2)	15 inches	1545		14.5	1.0162	1.0161	22.1
No. 8	A(1)	15 inches			14.5	1.0144	1.0143	19.7
No. 9	A	17 inches	1550		14.5	1.0148	1.0147	20.3
No. 10	A	18 inches	1557	6.0	14.5	1.0150	1.0149	20.5
No. 11	A	19 inches	1600		14.5	1.0150	1.0149	20.5
No. 12	A	20 inches	1604		14.5	1.0150	1.0149	20.5
No. 13	A	21 inches	1606		14.5	1.0152	1.0151	20.8
No. 14	A	22 inches	1609		14.5	1.0152	1.0151	20.8
No. 15	A	23 inches	1612		14.5	1.0152	1.0151	20.8
No. 16	A	24 inches	1617	6.5	14.5	1.0152	1.0151	20.8

APPENDIX TABLE B–1.—*Salinities recorded at all stations, Lover's Cove stream, Alaska, 1951*—Continued

Date and sample	Station	Height of water above pen	Time	Tide height	Temperature	Hydrometer reading	Density corrected to 15° C.	Salinity
				Feet	° *C.*			°/₀₀
July 28 (High water, 9.8 feet at 2129):								
No. 1	A	15 inches	1400	5.8	15.0	1.0224	1.0224	30.3
No. 2	A	13 inches	1415		15.0	1.0224	1.0224	30.3
No. 3	A	12 inches	1424		15.0	1.0222	1.0222	30.0
No. 4	A(1)	12 inches	1435		15.0	1.0212	1.0212	28.8
No. 5	A(2)	12 inches	1437	5.5	15.0	1.0212	1.0212	28.8
No. 6	A	11 inches	1442		15.0	1.0214	1.0214	29.0
No. 7	A	10 inches	1500		15.0	1.0210	1.0210	28.5
No. 8	A(2)	10 inches	1506		15.0	1.0210	1.0210	28.5
No. 9	A(1)	10 inches	1509		15.0	1.0208	1.0208	28.2
No. 10	A	9 inches	1515	5.2	15.0	1.0204	1.0204	27.7
No. 11	A(1)	9 inches	1520		15.0	1.0210	1.0210	28.5
No. 12	A(2)	9 inches	1523		15.0	1.0208	1.0208	28.2
No. 13	A	9 inches	1535		15.0	1.0196	1.0196	26.7
No. 14	A(1)	9 inches	1543		15.0	1.0206	1.0206	28.0
No. 15	A(2)	9 inches	1545		15.0	1.0202	1.0202	27.4
No. 16	A	9 inches	1600		15.0	1.0184	1.0184	25.1
July 30 (High water, 8.2 feet at 1239):								
No. 1	A	45 inches	1239		20.5	1.0192	1.0204	27.7
No. 2	B	11 inches	1245	8.5	20.5	1.0148	1.0159	21.8
No. 3	C	2 inches	1249		19.5	<1.0000	<1.0000	<1.0
No. 4	B	10 inches	1320		19.5	1.0112	1.0120	16.7
No. 5	C	0 inch	1326		19.5	<1.0000	<1.0000	<1.0
No. 6	C	0 inch	1339		19.5	<1.0000	<1.0000	<1.0
No. 7	B	7 inches	1344		19.5	1.0130	1.0139	19.2
No. 8	C	0 inch	1347		21.0	<1.0000	<1.0000	<1.0
No. 9	B	6 inches	1351	8.0	19.5	1.0014	1.0021	3.8
No. 10	C	0 inch	1355		20.5	<1.0000	<1.0000	<1.0
No. 11	B	5 inches	1400		19.5	1.0000	1.0007	2.0
No. 12	C	0 inch	1404		19.5	<1.0000	<1.0000	<1.0
No. 13	B	3 inches	1408		19.5	<1.0000	<1.0000	1.0
No. 14	B	2 inches	1417		19.5	<1.0000	<1.0000	<1.0
No. 15	B	1 inch	1422		19.5	<1.0000	<1.0000	<1.0
No. 16	B	0 inch	1428	7.5	20.5	<1.0000	<1.0000	<1.0
No. 17	B	Creek bottom	1430		20.5	<1.0000	<1.0000	<1.0
No. 18	B	0 inch	1435		20.5	<1.0000	<1.0000	<1.0
No. 19	B	0 inch	1440		21.0	<1.0000	<1.0000	<1.0
No. 20	B	0 inch	1445		21.0	<1.0000	<1.0000	<1.0
No. 21	B	0 inch	1450		21.0	<1.0000	<1.0000	<1.0
No. 22	B	0 inch	1457		21.0	<1.0000	<1.0000	<1.0
No. 23	A	25 inches	1504		21.0	1.0192	1.0205	27.8
July 31 (High water, 8.7 feet at 1313):								
No. 1	C	5 inches	1330		15.5	<1.0000	<1.0000	<1.0
No. 2	B	14 inches	1337		15.5	1.0104	1.0105	14.8
No. 3	C	4 inches	1341		15.5	<1.0000	<1.0000	<1.0
No. 4	B	13 inches	1355		15.5	1.0102	1.0103	14.5
No. 5	C	3 inches	1358		15.5	<1.0000	<1.0000	<1.0
No. 6	B	12 inches	1401	8.5	15.5	1.0114	1.0115	16.1
No. 7	C	2 inches	1405		15.5	<1.0000	<1.0000	<1.0
No. 8	B	11 inches	1409		15.5	1.0100	1.0101	14.2
No. 9	C	1 inch	1413		15.5	<1.0000	<1.0000	<1.0
No. 10	B	10 inches	1418		15.5	1.0100	1.0101	14.2
No. 11	C	0 inch	1421		15.5	<1.0000	<1.0000	<1.0
No. 12	B	9 inches	1425		15.5	1.0094	1.0095	13.5
No. 13	B	8 inches	1430		15.5	1.0090	1.0091	12.9
No. 14	B	7 inches	1437		15.5	1.0074	1.0075	10.8
No. 15	B	6 inches	1442	8.0	15.5	1.0058	1.0059	8.8
No. 16	B	5 inches	1448		15.5	1.0034	1.0034	5.5
No. 17	B	4 inches	1452		15.5	1.0018	1.0018	3.4
No. 18	B	3 inches	1456		15.5	1.0008	1.0008	2.1
No. 19	B	2 inches	1500		15.5	1.0002	1.0002	1.3
No. 20	B	1 inch	1505		15.5	1.0000	1.0000	1.1
No. 21	B	0 inch	1509		15.5	<1.0000	<1.0000	<1.0
No. 22	B	0 inch	1514	7.5	15.5	<1.0000	<1.0000	<1.0
No. 23	A	30 inches	1520		15.5	1.0212	1.0213	28.9
Aug. 2 (High water, 9.6 feet at 1413):								
No. 1	C	18 inches	1415		16.5	1.0008	1.0010	2.4
No. 2	B	27 inches	1423	9.5	16.0	1.0194	1.0196	26.7
No. 3	C	17 inches	1435		16.0	1.0022	1.0023	4.1
No. 4	C	16 inches	1453		16.0	1.0030	1.0031	5.1
No. 5	B	25 inches	1457		16.0	1.0202	1.0204	27.7
No. 6	C	14 inches	1502		16.0	1.0030	1.0031	5.1
No. 7	C	13 inches	1511		16.0	1.0030	1.0031	5.1
No. 8	C	12 inches	1515	9.0	16.0	1.0030	1.0031	5.1
No. 9	C	11 inches	1519		16.0	1.0030	1.0031	5.1
No. 10	C	10 inches	1524		16.0	1.0030	1.0031	5.1
No. 11	B	19 inches	1526		16.0	1.0202	1.0204	27.7
No. 12	C	9 inches	1530		16.0	1.0030	1.0031	5.1
No. 13	C	8 inches	1535		16.0	1.0030	1.0031	5.1
No. 14	C	7 inches	1538		16.0	1.0028	1.0029	4.8
No. 15	C	6 inches	1542	8.5	15.5	1.0028	1.0028	4.7
No. 16	C	5 inches	1545		15.5	1.0028	1.0028	4.7
No. 17	B	13 inches	1550		16.0	1.0202	1.0204	27.7
No. 18	C	3 inches	1555		15.5	1.0022	1.0022	3.9
No. 19	C	2 inches	1559		15.5	1.0018	1.0018	3.4
No. 20	C	1 inch	1602		15.5	1.0018	1.0018	3.4
No. 21	C	0 inch	1605	8.0	15.5	1.0016	1.0016	3.2
No. 22	C	0 inch	1609		15.5	1.0014	1.0014	2.9
No. 23	B	6 inches	1615		16.0	1.0136	1.0138	19.1

APPENDIX TABLE B–1.—*Salinities recorded at all stations, Lover's Cove stream, Alaska, 1951*—Continued

Date and sample	Station	Height of water above pen	Time	Tide height	Temperature	Hydrometer reading	Density corrected to 15° C.	Salinity
				Feet	° *C.*			°/₀₀
Aug. 6 (High water, 10.6 feet at 1559):								
No. 1	A	11 inches	1300	5.2	11.5	1.0010	1.0006	1.8
No. 2	A	13 inches	1305		11.5	1.0040	1.0036	5.6
No. 3	A	14 inches	1306		11.5	1.0072	1.0067	9.8
No. 4	A	15 inches	1308		11.5	1.0084	1.0079	11.4
No. 5	A	16 inches	1310	5.7	11.5	1.0096	1.0091	12.9
No. 6	A	17 inches	1312		11.5	1.0108	1.0103	14.5
No. 7	A	18 inches	1315		12.0	1.0114	1.0110	15.4
No. 8	A	19 inches	1316		12.0	1.0122	1.0118	16.5
No. 9	A	20 inches	1318		12.0	1.0130	1.0126	17.5
No. 10	A	21 inches	1320		12.0	1.0144	1.0140	19.4
No. 11	A	22 inches	1321		14.5	1.0150	1.0149	20.5
No. 12	A	23 inches	1323	6.2	14.5	1.0152	1.0151	20.8
No. 13	A	24 inches	1326		14.5	1.0156	1.0155	21.3
No. 14	A	25 inches	1328		14.5	1.0162	1.0161	22.1
No. 15	A	26 inches	1330		13.0	1.0164	1.0161	22.1
No. 16	A	27 inches	1332		13.0	1.0166	1.0163	22.4
No. 17	A	28 inches	1334		13.0	1.0168	1.0165	22.6
No. 18	A	29 inches	1336	6.7	14.0	1.0170	1.0168	23.0
No. 19	A	30 inches	1338		14.0	1.0172	1.0170	23.3
No. 20	A	31 inches	1340		14.0	1.0174	1.0172	23.5
No. 21	A	33 inches	1344		14.0	1.0180	0.0178	24.3
No. 22	A	34 inches	1346		14.0	1.0182	1.0180	24.6
Aug. 7 (High water, 10.7 feet at 1626):								
No. 1	B	1 inch	1411	4.5	16.0	<1.0000	<1.0000	<1.0
No. 2	B	2 inches	1412		16.0	<1.0000	<1.0000	<1.0
No. 3	B	3 inches	1414		16.0	<1.0000	<1.0000	<1.0
No. 4	B	4 inches	1416		16.0	1.0000	1.0001	1.2
No. 5	B	5 inches	1418		16.0	1.0038	1.0039	6.2
No. 6	B	6 inches	1420	5.0	16.0	1.0064	1.0066	9.7
No. 7	B	7 inches	1422		16.0	1.0080	1.0082	11.8
No. 8	B	8 inches	1424		16.0	1.0092	1.0094	13.3
No. 9	B	9 inches	1426		16.0	1.0106	1.0108	15.2
No. 10	B	10 inches	1430		16.0	1.0120	1.0122	17.0
No. 11	B	11 inches	1432		16.0	1.0126	1.0128	17.8
No. 12	B	12 inches	1434	5.5	16.0	1.0138	1.0140	19.4
No. 13	B	13 inches	1436		16.0	1.0144	1.0146	20.1
No. 14	B	14 inches	1438		16.0	1.0148	1.0150	20.6
No. 15	B	15 inches	1440		16.0	1.0150	1.0152	20.9
No. 16	B	16 inches	1442		16.0	1.0150	1.0152	20.9
No. 17	B	17 inches	1444		16.0	1.0150	1.0152	20.9
No. 18	B	18 inches	1446	6.0	16.0	1.0158	1.0160	22.0
No. 19	B	19 inches	1448		16.0	1.0160	1.0162	22.2
No. 20	B	20 inches	1451		16.0	1.0164	1.0166	22.7
No. 21	B	21 inches	1455		16.0	1.0170	1.0172	23.5
No. 22	B	22 inches	1457		16.0	1.0170	1.0172	23.5
Aug. 20 (High water, 11.7 feet at 1554):								
No. 1	C	34 inches	1455	10.9	15.0	1.0002	1.0002	1.3
No. 2	C	35 inches	1459		15.0	1.0006	1.0006	1.8
No. 3	C	36 inches	1501		15.0	1.0014	1.0014	2.9
No. 4	C	37 inches	1503		15.0	1.0018	1.0018	3.4
No. 5	C	38 inches	1506	11.1	15.0	1.0026	1.0026	4.5
No. 6	C	2 inches below surface			15.0	<1.0000	<1.0000	<1.0
No. 7	C	12 inches below surface			15.0	<1.0000	<1.0000	<1.0
No. 8	C	24 inches below surface			15.0	1.0002	1.0002	1.3

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WHITINGS ON THE COASTS OF THE AMERICAN CONTINENTS

By ISAAC GINSBURG

FISHERY BULLETIN 96

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Fishes of the genus *Merluccius*, often designated by the common name whiting, are of much economic importance. A number of different species in various parts of the world are taken and marketed in large quantities. On the Atlantic coast of the United States, about 80 million pounds of whitings were marketed annually during postwar years, according to statistics of the United States Fish and Wildlife Service. This constitutes a considerable item in the economy of the country's fisheries. Hitherto, this large catch was generally believed to consist of one species, *Merluccius bilinearis*. A comparative study of the whitings of the western Atlantic to determine the particular species occurring in the Gulf of Mexico, revealed that two common and easily distinguishable species occur on the Atlantic coast of the United States—that is, two distinct species occur where only one was hitherto supposed to exist. This discovery is important to the study and understanding of these fishes.

Information previously published on the life history, biology, and economics of the common east-coast whitings is based on the assumption that only one species lives in this region. The discovery that two species are there necessitates a reexamination and reappraisal of published accounts and a new approach to the study of our common commercial whitings, both biologically and economically. The objective of this paper is to prove that the two common east-coast species are distinct and to show how they may be distinguished and identified. For comparative purposes and to advance the study of these common food fishes occurring on the coasts of the American continents, all the species found on the Atlantic and Pacific coasts of North and South America are here included. Based on the specimens examined, this paper distinguishes eight American species, one of which is divided into two subspecies.

Hitherto, the commercial catch of whiting in the waters of the United States was taken mostly on the Atlantic coast, and nearly all of it along the coast of the New England States. During the last few years, the Fish and Wildlife Service vessel *Oregon*, in the course of experimental fishing operations, found that whitings are common in the Gulf of Mexico also, offshore in rather deep water. The Gulf of Mexico whitings belong to a hitherto unknown species, which is here distinguished and described. Whether a profitable fishery for this offshore species could be developed on the coast of the Gulf States remains to be determined.

One new species is here described from the coast of Chile, and one new subspecies from the coast of Peru.

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

FISHERY BULLETIN 96

(Fishery Bulletin of the Fish and Wildlife Service,
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CORRECTION

The first paragraph of the second column on page 197 should read as follows:

Comparison.—This species from the Atlantic coast of South America, in common with *polylepis* from the Pacific coast, has its gill raker count rather intermediate between the two primary groups of species separated in the key, but nearer the second group that includes species with the greater number of gill rakers. It is compared above with *polylepis* under the account of that species.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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WHITINGS ON THE COASTS OF THE AMERICAN CONTINENTS

By Isaac Ginsburg, *Fishery Research Biologist*

Fishes belonging to the genus *Merluccius* are commercial species of much economic importance in the aggregate, in the coastal waters of the United States, in other American countries, and in other parts of the world. Notwithstanding the relative abundance of these fishes a remarkable misapprehension exists regarding the species that make up the considerable catch in the northwestern Atlantic. It is now generally assumed that only one species of *Merluccius* occurs on the east coast of the United States, and conclusions in earlier studies of these fishes have been based on this assumption. However, two distinct species occur in this region. The two species are well-divergent, and single specimens are easily separable, and identifiable with the species to which they belong.

In view of the existence of two very different species in this region, it is to be expected that many of the conclusions regarding the bionomics and economics that were made as a result of studies of the supposedly single species, will now become obsolete. A reappraisal of existing data is needed to accord with this newly discovered fact. Bibliographies of the whitings need to be segregated by species. Some of the published observations and data, based on a composite of two distinct species, may now have to be reconsidered. It may be impossible to segregate some published records by species, and such references will have to be considered as applying to a mixture of two species.

The primary objective of this study is the determination of the species of *Merluccius* in the northwestern Atlantic, including the Gulf of Mexico; specimens of other species available in the National Museum have been studied also, for comparative purposes. The northwestern Atlantic species are best considered in relation to the other American species; the eight American species, including two new species, are therefore treated here. Since a comparative world-wide study of the species of *Merluccius* is one of the desiderata of fish taxonomy, a secondary purpose of this report is to present data toward such a revision.

Merluccius Rafinesque

Merluccius Rafinesque, Caratteri di alcuni nuovi generi e nuove specie di animali e pianti della Sicilia, p. 25, 1810 (genotype *Gadus merlucius* Linnaeus by later designation).

Jordan and Gilbert, Bull. U. S. Nat. Mus. 16: 808 (1882), 1883 (*Gadus merlucius* Linnaeus designated as genotype).

Characters common to the American species.—Elongate; well-compressed; rather spindle-shaped, but posterior taper more pronounced than anterior one. Top of head flat; interorbital broad, wider than eye or subequal to it, and only a little less than length of snout. Eyes large to notably large. Snout depressed, broad, rounded, moderately longer than eye to twice as long as its diameter. Mouth moderately large, angle of gape under anterior margin of eye or a little behind, articulation of mandible under posterior margin of eye or a little behind; moderately inclined, a horizontal through anterior part of gape passing nearly through middle of eye, varying moderately both ways; terminal or subterminal, lower jaw subequal to or usually a little longer than upper jaw. Maxillary reaching to under posterior margin of pupil, varying a little both ways, its distal outline characteristically concave asymmetrically, the lower distal angle somewhat projecting. Teeth well-developed, sharp, in two irregular rows in jaws and on vomer; outer teeth fixed, widely or moderately spaced, inner teeth larger and depressible, moderately spaced; teeth in jaws larger at anterior part, considerably smaller at their articulated end; in upper jaw a small area at symphysis without teeth; no palatine teeth. Opercle subtriangular in outline its posterior part flexible, merging almost imperceptibly with soft membranous border, without spines. Gill opening rather wide, gill membranes united at a point variably under eye.

Pseudobranchiae absent. Gill rakers well-developed, rather few or in moderate numbers, usually abruptly separable from the low tubercle-like outgrowths at both ends of arch. Barbels absent.

Scales cycloid, small, in about 112–186 oblique rows over lateral line, from a point over upper anterior corner of gill opening to end of hypural; body all scaled, including chest and fleshy pectoral base; dorsal aspect of head and antedorsal area scaled, except an irregular small or moderate area at anterior end of snout; opercle scaled; lateral aspect of snout continuously to a variable point under eye, and maxillary scaleless, except side of snout with a lengthwise strip of scales in individual variants of *albidus;* cheek, preopercle and interopercle only partly scaled, scaleless in moderate or greater part, except in *albidus* (p. 192) and *magnoculus* (p. 194); ventral aspect of head scaleless; scales on head smaller than those on body, those on anterior part of head minute; caudal scaled for a variable area at its base, scaleless distally; pelvic and pectoral almost scaleless, with only a small scaled area at base; dorsal and anal fins scaleless, except a small anterior portion of posterior part of second dorsal and anal partly scaled or scaleless. (The scalation is incompletely preserved in most specimens examined and the foregoing statements might need some modification. See also following discussion).

Lateral line begins over gill opening and continues nearly straight all the way, or slightly and broadly curved anteriorly, to base of caudal. Two well-separated dorsal fins; first dorsal roughly triangular with 10–14 rays, anterior three rays unevenly graduated, the third longest, the first subequal to sixth or fifth, the second moderately shorter than third or subequal to it, the fourth a little shorter than third or subequal to it, thence decreasing in length backward, the decrease being slow to fifth or sixth ray, thence becoming rapid, last ray short; second dorsal with 36–45 rays, incompletely divided by an emargination into two parts, the number of rays in the two parts equal, varying to posterior part having a few more rays (the relative numbers not accurately determinable, the two parts of the fin not delimitable definitely, with the great majority of available specimens having the fins damaged), the rays in anterior part rather widely spaced, those in posterior part somewhat crowded in comparison, especially in its anterior portion; anal also with 36–45 rays, but its counts for a given species, anyway for most species examined, averaging slightly higher than those of dorsal, its structure similar to that of second dorsal; rays in the three fins segmented and branched, except first ray of first dorsal unsegmented and unbranched and first one or two anal rays and last one to four rays in all three fins segmented but not branched. Pectoral with 12–18 rays, notably narrow. Pelvic inserted at a moderate distance in advance of pectoral, normally with 7 rays. (Of 167 specimens of all species counted, on right side, all but 3 have 7 rays, the 3 variants having 6 rays on right side and 7 on left.) Caudal short, rounded in the smaller specimens becoming emarginate with growth; tail moderately isocercal, posterior part of vertebral column moderately tapering, its end well-rounded; outer caudal rays growing progressively shorter anteriorly, extending symmetrically for some distance above and below end of caudal peduncle.

The palate and the inner walls of the gill chamber are very dark to black. The peritoneum is solid black, or dark or silvery stippled and spotted with black, depending on the species and growth changes within the species. Externally it is difficult to determine specific color differences, if any, in preserved specimens of *Merluccius.* In general, preserved specimens have silvery, golden, brownish, dusky or dark shades. The fins are dusky or dark in part. There are no definite distinctive specific color marks.

Characters useful in distinguishing the species.—The preceding description outlines some external taxonomic characters that are more or less common to the eight American species here considered. The characters that are of greater or lesser utility in distinguishing the species are hereafter discussed in some detail. The species of *Merluccius* by and large are very closely related; but they are not too difficult to distinguish when the species-characters are accurately determined, and tabulated for ease of comparison.

Gill rakers.—The number of gill rakers constitutes an important character in distinguishing the species of *Merluccius.* It is the chief character that may be used in separating the two common, sympatric species on the Atlantic coast of the United States, and is useful in other species as well. It is therefore important to consider in

some detail the structure of the gill rakers and the method of counting them used during this investigation.

As in many other fishes the outer gill arch in *Merluccius*, in addition to the well-developed gill rakers, has outgrowths at both ends that may be described as low spinulose tubercles, sometimes designated "rudiments" by authors. In the species of *Merluccius* examined, the tubercles number 0–3 on the upper limb and 2–12 on the lower limb. The tubercles are usually fairly separated in the small specimens, but they differ considerably in size or, rather, extent. In the larger specimens some of the tubercles on the lower limb tend to coalesce, and their number cannot be determined with precision. To a lesser extent coalescense also occurs sometimes in small specimens. Because of the latter difficulty combined with the considerable individual variability in their number, the tubercle count is not well-adapted to be used as a character in separating the species. On the other hand, in the great majority of specimens of these species, the change from the gill rakers to the tubercles is abrupt and usually the former are readily countable with precision, although the gill rakers decrease in size from the angle outward both ways. Therefore, the numbers of gill rakers here given do not include the tubercles.

In some individual variants, the change from the gill rakers to the tubercles is not so abrupt. The outgrowth standing next to the tubercles on one or both limbs of the arch is very short approaching the size of a tubercle. In many such variants the outgrowth though very short is rather tapering and somewhat conical and was included in the count. Very few of the many specimens examined presented doubt in my mind whether to include such an outgrowth near the border line in the gill raker count. Because of the latter variants the count is apt to differ slightly with the individual observer, or seldom in successive counts of the same specimen made by the same observer. Nevertheless, while this method of counting is not precise, it approaches precision more nearly than that of other methods of counting. When the gill raker count is based on numbers of specimens, such possible differences are negligible, especially where the difference in the gill raker count of the species is pronounced.

There might be a slight growth change in the gill raker count. That is, in variants in which the end gill raker is very short, it might change to a tubercle with growth. However, I was unable to determine this point definitely. While the counts on which the tables are based have been determined with large and small specimens, I did not have a sufficient number of specimens in a graded size-range from any one locality to determine growth changes. As far as my observations go, possible growth changes in the gill raker count, if any, are negligible.

The frequency distributions in the number of gill rakers are given in tables 1–3. As the number of available specimens of *polylepis*, *productus*, *angustimanus*, *peruanus*, and *gayi* are relatively few, the gill raker count was made on both sides of each specimen and entered in the tables independently. The count often differs on both sides. In the other species the count was made on one side only, generally on the right side unless, rarely, for some reason an accurate count on that side was not possible when the gill rakers on the other side were counted.

Scalation.—The scales are arranged with fair regularity and the number of rows above the lateral line, is fairly determinable in any one specimen that has the scalation complete, or nearly so. When so determined, the number of scales seems to constitute a species character in some instances. However, the application of this character is difficult, and except for *polylepis*, it is only of minor practical value, because the scalation is more or less incompletely retained in the great majority of preserved specimens, and the number of rows is not accurately determinable in such specimens.

The number of oblique rows of scales over the lateral line, from a point over the upper anterior angle of the gill opening to the end of the hypural, is stated under the account of every species. The given range of the count for each species has been determined on a few specimens (the number of which is stated in parenthesis) that were best preserved for this purpose. In some species, however, the best specimens examined were none too good for this purpose. Consequently, the given ranges of the scale counts are only roughly approximate, probably by a rather wide margin in some instances.

The extent of scalation is described under the genus (p. 188). The statements made there seem to apply in general to the genus as a whole, but the finer details cannot be elaborated now. Because the scalation is incompletely or very poorly preserved in the great majority of specimens examined, it is not possible to determine intraspecific individual variability or average specific differences, if any, in the extent of scalation, especially on the fins. Also, it is not possible to determine from the available specimens, growth changes in the scalation. Consequently, statements made under the genus and species headings might need some modification on examination of better-preserved specimens.

The extent of scalation of the side of the head might form a basis for the division of the species of *Merluccius* into two major groups, perhaps of subgeneric importance, as it is correlated with another character. In *albidus* and *magnoculus*, the side of the head, excluding the snout and maxillary, is almost completely scaled, and correlated with this the number of gill rakers is relatively few. (The same combination of characters was observed in one large specimen from Norway, 17372, see p. 193.) The other American species, on the other hand, have the cheek, preopercle, and interopercle incompletely scaled in combination with a greater number of gill rakers. However, because the scalation is defective, poorly preserved in the great majority of specimens, this character is not easy to use in practice. Moreover, the taxonomic value of this character may best be judged by a study and comparison of all the species on a world-wide basis.

Fin rays.—The number of rays in the second dorsal and anal is of considerable importance as taxonomic characters in some instances, as in the separation of *angustimanus* from *productus*, the distinction of the two subspecies of *gayi*, and the proper distinction of *polylepis*. In other instances, the numbers of these rays show lesser and variable degrees of divergence. The number of rays in the first dorsal and pectoral generally show divergences of subspecies magnitude or less when related species are compared for these numbers. Species differences in these numbers are shown in tables 4–7 and discussed under the accounts of the species. The rather narrow spread of the distribution for each species in the number of dorsal and anal rays is noteworthy considering the comparatively numerous rays. The anal count averages slightly higher, at least in most species.

Measurements.—Some proportional measurements are of considerable importance in distinguishing the species as follows. Measurements here given in the text and tables are expressed as percentages of the standard length, that is, the distance from the tip of the snout to the end of the hypural as determined externally by flexing the caudal fin, the decimal point being omitted in the tables for brevity. Because measurements of the same species differ with the size of the fish, changing with growth, sometimes considerably so, the data are segregated in the tables by size groups. In general, judged by the specimens examined the greatest diverence in proportional measurements in *Merluccius* seems to be shown by the smaller size groups. With growth the extent of divergence appears to become lessened and perhaps disappears in some instances.

The head length is of value in separating some of the species and is used in the key for this purpose. It is long in *angustimanus* and *gayi*, especially in the subspecies *peruanus*, and short or of medium length in *polylepis*, *hubbsi*, *bilinearis*, and *productus*. It is also rather long in *magnoculus* as compared with its nearest relative, *albidus*. The head length differs moderately with size, becoming shorter, on the average, with growth. Hence it is necessary to compare specimens of approximately like size. The head ends in a soft membranous border. In well-preserved specimens the hard part of the opercle usually thins out gradually to the soft border so that no definite line of demarcation marks off the latter. Consequently, this measurement was made to the margin of the membranous border.

The pelvic fin was measured from the point of articulation of the outer rays as determined on the outside by flexing the rays, to the tip of the ray extending farthest backward. It is relatively long in *albidus*, *hubbsi*, and *bilinearis*, and short in *magnoculus*, *productus*, *angustimanus*, and *gayi*. This measurement also differs with growth, and specimens of approximately like size are best compared. The difference in this measurement between *bilinearis* and *productus* is such that even when those of all sizes are lumped together, as in

table 9 (p. 205), the distributions of the two species are separated by a gap.

The pectoral length was measured from the point of articulation of the upper rays as determined externally by flexing, to the tip of the ray extending farthest backward. It is especially useful in distinguishing *magnoculus* from *albidus* and *hubbsi* from *gayi*. The pectoral appears to increase in length moderately with growth in some species and to scarcely change in proportion with growth in others.

The other measurements tabulated, namely those of the maxillary, eye, snout, depth and caudal, perhaps named in order of importance, are of secondary or of minor importance. In general, species differences in these measurements are overlapping and expressible in terms of averages only; although in some instances the divergence is considerable, such as the difference in the length of the maxillary or the snout between *albidus* and *magnoculus*.

The snout was measured from its tip to the anterior soft border of the eye; the eye between its soft borders; the depth at the origin of the first dorsal.

The fin rays including those of the pelvic, pectoral, and caudal are often more or less damaged, hence these measurements are not altogether satisfactory characters to use; but those of the pectoral and pelvic are of considerable value in distinguishing the species. In making up the tables an attempt was made to exclude specimens with damaged fins, but this is not always evident, and hence the tables might be slightly lacking in precision.

Caudal shape and its measurement.—In the smaller specimens the posterior margin of the caudal is rounded with the middle rays longest. With growth it becomes emarginate, and the rays near the upper and lower margin are then longest. The approximate size at which the change takes place evidently differs with the species; but this could not be definitely determined, because sufficiently graded size ranges are unavailable for the several species, moreover the caudals are damaged in most preserved specimens examined. The approximate size at which the change takes place, as far as determinable by the specimens examined is stated in the accounts of the several species. It appears that in *peruanus* the change takes place at a smaller size and in *hubbsi* at a larger size than in other species for which specimens in graded size ranges are available. In two species at least, *albidus* and *bilinearis*, the size at which the caudal becomes emarginate appears to vary greatly with the individual.

Judged by the poor material examined, that is, poor from the viewpoint of studying this development, it seems that the main successive stages are as follows: First, the middle rays become shortened in relation to the adjacent rays and the posterior margin of the fin becomes approximately truncate. Then, two rays near the upper margin become slightly longer than those below them, and a moderate extent of the upper part of the fin becomes slightly emarginate while the rest is still truncate. Finally, the entire caudal becomes moderately or well-emarginate in the larger specimens of the several species.

Because of its change with growth, it is difficult to state properly the caudal length in *Merluccius* and to determine the species differences in that length, if any. The best way is to compare growth changes between the species of those rays that undergo the greatest growth change, namely, those near the middle and those near the upper or lower margin. However, this ideal way was not possible of attainment because of the incompleteness of the material examined. On account of the difficulties, the caudal measurements here recorded were made from the end of the hypural on the midline to the end of the longest rays, which are generally situated at the middle of the fin in the smaller specimens and near the upper margin in the larger fish. Consequently, these measurements do not express the change with growth of the particular rays. Also, measurements of the several species are not strictly comparable; because at a given standard length the longest ray in one species may be the one at the middle, and in another species of the same length it may be at the upper margin. Although not strictly comparable, the given measurements present the approximate caudal length in the several species.

Measurement of intergradation and divergence.—In the following accounts of the species and subspecies, the sections headed Comparison are devoted to a discussion of the distinguishing characters between the several species or subspe-

cies. The statements made regarding degrees of intergradation or divergence, whether of species, of subspecies, or less than subspecies magnitude are based on criteria previously established by me in another paper (1938). In tables 1–7 presenting counts of gill rakers and fin rays in the form of frequency distributions, one line for each species gives the distribution in the number of specimens, and a second line immediately underneath gives the distribution in percentages. The latter numbers enable the reader to make a quick determination of the indices of intergradation and divergence between any two species compared as proposed in the paper cited.

KEY TO THE AMERICAN SPECIES OF MERLUCCIUS

1a. Total number of gill rakers on outer arch (not counting tubercles, see discussion in text) 9–11. Side of head almost completely scaled.
2a. In 11 specimens 173–293 mm. in standard length, head 27.4–30.1, pelvic 15.5–17.7, pectoral 18.3–20.9 (for measurements of other lengths see tables 8–10). Pectoral rays modally 15, varying 13–16. Atlantic coast of the United States ..... *albidus* (p. 192)
2b. In 20 specimens 189–290 mm. in standard length, head 29.6–31.3, pelvic 13.4–15.9, pectoral 15.8–19.2. Pectoral rays modally 13, varying 12–15. Gulf of Mexico ..... *magnoculus* (p. 194)
1b. Total number of gill rakers on outer arch 13–25. Side of head incompletely scaled.
3a. Total number of gill rakers on outer gill arch 13–15, when 16, in about 12 percent of specimens of *hubbsi*, head 27.6–30.7. Atlantic and Pacific coasts of South America.
4a. Rays in second dorsal 43–45. Anal rays 42–45. Scales in about 182–186 oblique rows over lateral line from upper angle of gill opening to end of hypural. Chile ..... *polylepis* (p. 195)
4b. Rays in second dorsal and anal 37–40. Scales in about 138–144 rows. Argentina ..... *hubbsi* (p. 197)
3b. Total number of gill rakers on outer gill arch 17–25, except 15–16 in about 5 percent of the specimens of *bilinearis* on Atlantic Coast of United States and Canada, or 16 in about half the specimens of *angustimanus* from the Pacific coast of Central and North America, the latter having the head 31.0–33.3.
5a. Head 26.8–29.2 in specimens 113–158 mm. in standard length; 25.4–28.6 in specimens 181–294 mm.; 26.1–28.4 in specimens 318–367 mm.; 25.5–27.6 in specimens 409–459 mm. East and west coasts of United States and Canada.
6a. Pelvic 14.8–20.5 in specimens 66–442 mm. in standard length (for its change with growth see table 9). Atlantic coast of United States and Canada ..... *bilinearis* (p. 198)
6b. Pelvic 10.8–14.1 in specimens 113–459 mm. Pacific coast of United States and Canada ..... *productus* (p. 199)
5b. Head 32.1–33.5 in specimens 138–161 mm. in standard length; 30.6–32.8 in specimens 235–289 mm.; 28.4–31.5 in specimens 308–389 mm.; 28.0–30.1 in specimens 402–478 mm. Pacific coast of Southern California to Chile.
7a. Total number of gill rakers on first arch 16–17, except 18 in about 6 percent of the specimens. Southern California to Panama ..... *angustimanus* (p. 200)
7b. Total number of gill rakers on first arch 18–25, except 17 in about 5 percent of specimens of *peruanus*. Pacific coast of South America ..... *gayi* sensu lato (p. 201)
8a. Anal rays 36–39. Second dorsal rays 36–40. Peru ..... *gayi peruanus* (p. 202)
8b. Anal rays 39–42. Second dorsal rays 37–42. Chile ..... *gayi gayi* (p. 202)

Merluccius albidus (Mitchill)

Gadus albidus Mitchill, Jour. Acad. Nat. Sci. Philadelphia 1 (2) : 409, 1818 (New York)

Description.—Gill rakers 1−3+8−9 or 9–11 in combined number. Dorsal 11–13, 37–40. Anal 37–41. Pectoral rays modally 15, varying 13–16. Proportional measurements about medium, on the whole; head 27.4–30.1, pelvic 15.5–17.7, pectoral 18.3–20.9 (measurments here given referring to same 11 specimens 173–293 mm., standard length; for other measurements and growth changes see tables 8–15). Scales about 129–144 (in 6 specimens). Cheek, preopercle, and interopercle almost wholly scaled; lateral aspect of snout naked or with a lengthwise strip of scales, narrow or of moderate width. Peritoneum solid dark brown or black in the larger specimens; in the smaller fish dark brown or almost black stippled with dots of a more intensely dark color.

The normal size at which the caudal shape changes could not be definitely determined because the caudal is more or less damaged in the great majority of the specimens examined. It appears to have been rounded on one specimen 115 mm. in standard length, truncate in 5 specimens 124–210 mm., and emarginate in 17 specimens 237–626 mm.; but in one specimen 293 mm. it is truncate. Tentatively, then it may be stated in round figures, that in *albidus* the caudal usually becomes truncate at about 125 mm. in standard length and emarginate at about 240 mm., but the change with growth appears to vary much with the individual, sometimes it remains truncate up to about 295 mm. in standard length.

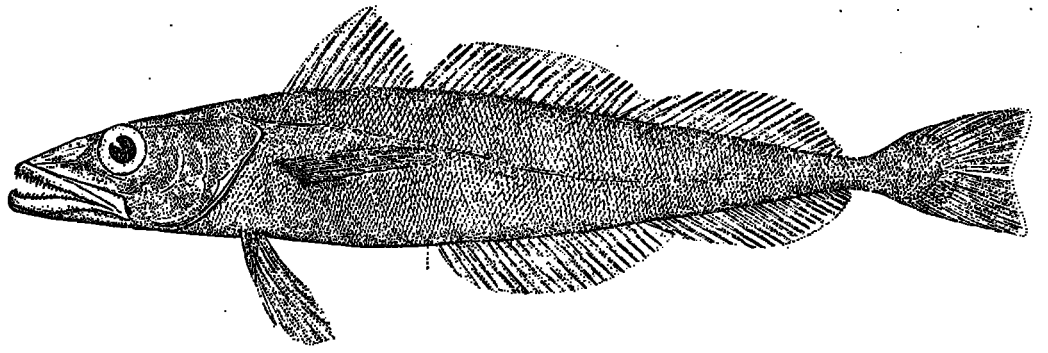

FIGURE 1.—*Merluccius albidus;* U. S. Nat. Mus. 31844; off Long Island, N. Y.; 125 fathoms (39°58'30" N., 70°37' W.); 492 mm. Drawn by Mildred H. Carrington.

Neotype.—As two common sympatric species of *Merluccius* are here distinguished where recently only one species was supposed to exist, and Mitchill's early names are applied to both for reasons stated below, while Mitchill's original specimens are presumably not in existence now, it seems desirable to set up neotypes for these two species in order to fix their names definitely. Accordingly, the following specimen is hereby designated as neotype of *albidus*: U. S. Nat. Mus. 31630; Fish Hawk Station 1096; lat. 39°53' N., long. 69°47' W.; off Long Island, N. Y.; 317 fathoms; August 11, 1882; 325 mm., 293 mm. in standard length.

Other specimens examined.—Off Long Island, N. Y., 19 constituent samples comprising 29 specimens 33–626 mm. in standard length, taken between latitudes 39°48'30" and 40°15'30" and longitudes 71°43' and 68°54' (25769, 26049, 26061, 26073, 26190, 28826, 31677, 31686, 31739, 31741, 31822, 31842, 31844, 31863, 44264, 45963–4, 157755–6). Also, one constituent sample each from off the following localities: Cape May, N. J. (39259, 2 specimens 115–124 mm.). Cape Charles (33032, 237 mm.) and Cape Henry (32791, 278 mm.), Va. Savannah (155475, 2 specimens 252–280 mm.), Ga. Cape Canaveral (45920, 445 mm.) and Tortugas (92066, 138 mm.), Fla. Total examined, including the neotype, 38 specimens about 36–691 mm. in 26 constituent samples. Depth records, available for all except 2 constituent samples, range 58–640 fathoms.

The 3 specimens 252–445 mm. in standard length from off Savannah and Cape Canaveral fit in readily in their measurements and counts with the other northern specimens of *albidus* rather than with the Gulf of Mexico *magnoculus*. The single specimen 138 mm., from off Tortugas is in poor condition, and no Gulf specimens of comparable size are available for comparison. Hence its proper placement is not altogether certain. However, its determinable characters agree well with similar-sized specimens of *albidus* and it is included in its account.

This species evidently has a different vertical distribution, living in deeper water than the other common species (*bilinearis*) that occurs in its geographic range. However, their vertical ranges overlap and two of the constituent samples of *albidus* examined (157755–6) were separated from containers that included also specimens of *bilinearis*, taken at Albatross Stations 2242 and 2248, off Long Island in 58–67 fathoms. These two composite lots of both species consist of small specimens 36–66 mm.

Comparison.—This species differs sharply from *bilinearis* in the number of gill rakers (tables 1–3). There are no intergrades in the numbers on the lower limb in the many specimens of *bilinearis* examined. The gap between the frequency distributions of the two species becomes wider when the total number on the outer arch is used as the basis of comparison. Other diverging characters that intergrade more or less between those two species are as follows: *albidus* averaging a longer head, larger eye, shorter pectoral and fewer rays in the two dorsals and anal.

This species is compared with *magnoculus* under the account of the latter (p. 195).

To compare them with *albidus* three European specimens were examined in the U. S. National Museum, with the following standard lengths: Bergen (17372, 730 mm.); Livorno (28471, 351 mm.); Bay of Naples (48446, 111 mm.). The counts and proportional measurements of the

Norwegian specimen are as follows: Dorsal 11; 39. Anal 38; pectoral 14; gill rakers 2+8; scales about 170. Caudal 10.2; pectoral 15, ventral 12.7, head 28.6, maxillary 14.1, snout 10.4, eye 3.9, depth 16.5. The same data for the two Italian specimens, those for the larger specimen stated first and separated by a hyphen where they differ, are as follows: D. 9–10; 39–38. A. 38; P. 14; gill rakers 2+8–9; scales about 153–157. Caudal 11.3–13.1, pectoral 16.1–16.2, ventral 15.6–19.7, head 29.8–32.5, maxillary 15.2–17.1, snout 9.8–12.6, eye 5.8–6.2, depth 17.3–18.4 The gill raker count of the European specimens is therefore about the same as in *albidus;* but the scales in these 3 specimens are more numerous, about 153–170 in the three European specimens and about 129–144 in 6 specimens of *albidus*. The two Italian specimens have fewer rays in the first dorsal and a longer head and shorter pectoral than *albidus*. The first dorsal count of the Norwegian specimen falls at the lower end of the distribution of *albidus;* while in proportional measurements the two nearly comparable specimens, 730 mm. as compared with 626 mm. in standard length of *albidus* (see tables 8–15), do not differ to a notable extent, the Norwegian population perhaps averaging a shorter pectoral, head, and maxillary. While it would be well to compare in detail the European *Merluccius* populations from the Atlantic and Mediterranean coasts, it is evident that the American *albidus* differs in having fewer scales and at least averages more rays in the first dorsal.

Nomenclature.—Now that two common and easily separable species of *Merluccius* are proved to exist on the Atlantic coast of the United States, the question arises of a name to apply to either species.

Mitchill proposed two names, *Stomodon bilinearis*, 1814, and *Gadus albidus*, 1818, for specimens that he presumably thought to represent two distinct species. These two names have been synonymized by later authors and the older name, *bilinearis*, has been applied to what they thought to be a single species of whiting on the coast of New York and adjacent areas in the western Atlantic. However, Mitchill's original accounts contain some clues by which his names may perhaps be identified with the two common species here distinguished.

Mitchill (1914, see citation below), under his account of (*Stomodon*) *Merluccius bilinearis*, states as follows: ". . . a hard featured fish bought in the New York market, Nov. 4, 1813 . . . Eyes large . . ." Under his account of (*Gadus*) *Merluccius albidus* (above citation), he states: "The individual from which I make the present description, was taken in the Atlantic Ocean, a few leagues from Sandy Hook, on what are called the Sea-bass banks . . . Eyes very large . . ." Mitchill's accounts then contrast two factors by which our two species are distinguishable. One is the habitat. A fish bought in the New York market in those days, on which Mitchill based his *bilinearis*, more likely than not was taken inshore, while the specimen on which *albidus* was based was taken offshore. Also, according to the original accounts as quoted, the two species presumably differ in the size of the eye, the offshore species having a larger eye. These two correlated items are the same as characterize in part the two species here distinguished from the Atlantic coast of the United States, and these two species are therefore here designated by Mitchill's names, *bilinearis* and *albidus*, respectively. While the evidence is not conclusive, especially in the absence of gill raker counts, it is about as good as that on which the proper determination of many names by early authors, are based.

Merluccius magnoculus, new species

Description.—Gill rakers 2−3+7−9 or 9–11 in combined number. D. 11–13 ; 36–42. A. 37–41. Pectoral rays modally 13, varying 12–15. Head rather long, 29.6–31.3; pelvic and pectoral rather short, 13.4–15.9 and 15.8–19.2, respectively; eye averaging larger than other species, 6.1–8.2; maxillary and snout long; body rather deep (measurements here given referring to same 20 specimens, 189–290 mm. in standard length; for their changes with growth and other measurements see tables 8–15). Scales about 124–130 (in 2 specimens). Cheek, preopercle, and interopercle probably almost altogether scaled (scalation nearly obliterated or very incompletely preserved in all specimens examined and its extent not altogether certain). Peritoneum solid black; caudal emarginate (peritoneum and caudal shape the same in all specimens examined, including the 2

smallest 210 and 213 mm., 191 and 189 mm. in standard length, respectively).

Holotype.—U. S. Nat. Mus. 157757. Oregon Station 270; lat. 29°23′ N., long. 87°25′ W.; off Pensacola, Fla.; 220 fathoms; 313 mm.

Paratypes.—Off the following localities, all taken by the Oregon, except 3 specimens taken by the Albatross as noted below. Cape San Blas (157760) and Pensacola (144303, 3 specimens 278–305 mm. taken by the Albatross; 157761–2), Florida. Mississippi Delta (157758, 157763), Louisiana. Padre Island (157759), Texas. Total examined 31 paratypes 210–501 mm., taken in 150–305 fathoms.

Comparison.—This species is very near the Atlantic *albidus*, both nearly agreeing in the gill raker count, and the eye is relatively large in both. The two evidently constitute a pair of related allopatric populations. They might possibly be treated as coordinate geographic subspecies. However, the degree of divergence between them is of species rather than subspecies magnitude.

The two species diverge chiefly in 3 characters, *magnoculus* having a longer head and shorter pelvic and pectoral (tables 8–10). The relative length of the head and pelvic changes with growth. When divided into size groups, as in the tables, the determined data are not as extensive as might be desired, as the number of specimens in every size group is rather limited; nevertheless they are fairly sufficient to draw acceptable conclusions. The relative length of the pectoral apparently changes little with growth, if any.

The two species overlap somewhat in all three characters, but the degree of divergence in every one is evidently of species magnitude, even when the data are arranged in wide size groups, as in tables 8–10. The extent of divergence is evidently greater when the comparison is made separately for the several size groups. The degree of divergence also seems to be of nearly the same magnitude in all three characters.

This species also has a longer maxillary (table 11). The degree of divergence also seems to be of species magnitude, although perhaps slightly less than in the three foregoing characters.

Other moderately or slightly diverging characters, perhaps named in order of magnitude of divergence, are as follows: *magnoculus* averaging a longer snout, fewer pectoral rays, a larger eye, more rays in the first dorsal and anal, and fewer rays in the second dorsal. All in all, the treatment of the two diverging allopatric populations as full species seems justified.

On general view the eye in *magnoculus* appears strikingly large. However, after measuring a number of specimens and tabulating the results, as in table 13, it is found that this measurement overlaps rather widely with related species, although the averages appear to be moderately higher in *magnoculus* when compared size for size.

Merluccius polylepis, new species

Merluccius gayi Gunther (not Guichenot), Rept. Voy. *Challenger*, Shore Fishes, p. 22, 1880 (Gray Harbor, Messier Channel, Straits of Magellan)

Merluccius australis Norman (in part), Discovery Rept. 16: 48, 1937 (based in part on specimens recorded by Gunther, as cited above)

Description.—Gill rakers 3−4+10−11, or 13–15 in total number on first gill arch. D. 11–12; 43–45. A. 42–45. Pectoral rays 13–15, the mode possibly at 14. Proportional measurements of head, pelvic, pectoral, and eye rather low in numerical value;

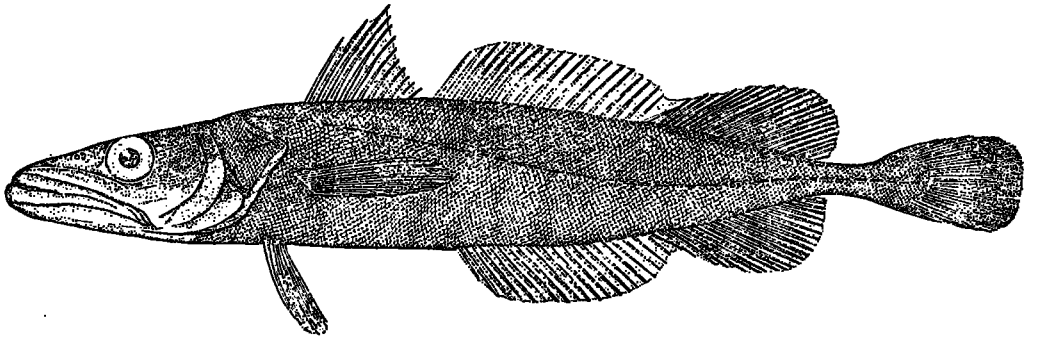

FIGURE 2.—*Merluccius polylepis;* from the holotype; U. S. Nat. Mus. 157764; taken at Castro, Chile (42°29′ S., 72°46′ W.); 314 mm. Drawn by Mildred H. Carrington.

27.5–29.9, 11.6–13.8, 17.4–19.1, and 4.7–5.4, respectively (measurements of 4 specimens 281–325 mm. in standard length; for size differences and other measurements see tables 8–15). Scales about 182–186 (in 4 specimens). Color of peritoneum variable, very dark, moderately dark, or dusky with a silvery wash, speckled profusely with small dots of variable size and of a more intense pigment than ground color, the speckling strongly marked in specimens with a lighter peritoneum, rather faint in those with a dark peritoneum. Caudal rounded in 2 specimens 281–283 mm. in standard length, truncate or nearly so in 2 specimens 323–325 mm.

Holotype.—U. S. Nat. Mus. 157764. Castro, Chile (42°29′ S., 72°46′ W.); M. J. Lobell and others; January 22, 1945; 314 mm., 283 mm. in standard length.

Paratypes.—Castro, Chile; January 20, 1945; 308 mm., 281 mm. in standard length (157765). Puerto Auchemo, Chile (43°01′30″ S., 72°50′ W.); January 24, 1945; 2 specimens 358–359 mm., 323–325 mm. in standard length (157766). The 3 paratypes were obtained by the same collectors as the holotype.

Comparison.—This species about agrees with *hubbsi* in the number of gill rakers, perhaps averaging slightly lower numbers (tables 1–3). It differs from *hubbsi* in having larger numbers of rays in the second dorsal and anal (tables 5–6). It further differs from *hubbsi* in having more numerous scales, about 182–186 in 4 specimens of *polylepis* as compared with about 138–144 in 2 specimens of *hubbsi*. In practice the scale count in *Merluccius* is not an easy character to use with precision as discussed above. However, the difference between the two species in the number of scales is pronounced, and to a certain extent it may be detected on superficial examination without actually making the count. This species possibly will be found to average fewer pectoral rays than *hubbsi*, but the divergence evidently will be of minor degree (table 7). The two species apparently do not differ much in proportional measurements (tables 8–15), possibly some average difference will be found on examination of numbers of specimens in comparable size groups.

In its high number of rays in the second dorsal and anal, and scales, *polylepis* differs, at least on the average from all other species here treated. It is easily distinguished from *gayi*, which occurs in the same region with it, by these characters in combination with its comparatively low gill raker count.

Norman (1937: 48) who examined specimens from the Straits of Magellan that presumably belong to this species, identified them with *australis* of Hutton which was originally described from New Zealand. Regrettably no specimens from New Zealand are available to me for comparison, but the Chilean population evidently differs specifically from that of New Zealand. The fish fauna of New Zealand, by and large, is very different from that of the Pacific coast of South America including Chile. On zoogeographic grounds it is therefore improbable that the two populations are identical, although it is not impossible that both belong to the same species. Furthermore, the Chilean population evidently differs in having a greater number of dorsal and anal rays. The ranges of these two counts given by Hutton (1872: 45) and Waite (1911: 182) are: 36–41 in both fins, whereas the 4 Chilean specimens examined during this study have D. 43–45, A. 42–45.

Gunther (1880: 22) records D. 43–44, A. 43 for his specimens from Gray Harbor, Magellan Straits, which about agrees with our 4 Chilean specimens. That the Chilean population has a notably high second dorsal and anal count is shown by comparing the counts of the 4 specimens examined with the 7 other American species (tables 5–6). The second dorsal count falls out of the range of 6 species, except *productus;* while the anal count falls out of range of 4 species, except *bilinearis*, *productus*, and *gayi*. Even as compared with the 4 exceptional species mentioned the counts in the Chilean specimens average distinctly higher. In sum, judged by our counts compared with those of the three authors discussed, taken in conjunction with the known facts of zoogeography, it is highly probable that the Chilean population is sufficiently divergent to be recognized nomenclatorially, as is done here.

Norman (1937: 49) examined 3 specimens from New Zealand and the Magellan Straits and records the entire range of his counts as D. 36–43 and A. 36–42. However, he does not break down the counts by locality to show any possible population difference, and his account is of no help in deciding the question.

Merluccius hubbsi Marini

Merluccius hubbsi Marini, Rev. Soc. Argentina Cien. Nat. 11: 322, photo., 1933 (Argentina). Norman, Discovery Rept. 16: 45, fig. 20A, 1937 ("Brazil to the Straits of Magellan").

Description.—Gill rakers 3–5+9–12 or 13–16 in combined number. D. 11–14; 37–40. A. 37–40. Pectoral rays modally 15, nearly as often 14, sometimes 16. Measurements rather medium, on the whole: head 28.4–29.0, pelvic 16.7–17.5, pectoral 19.9–20.0 (measurements of 2 specimens 177–209 mm. in standard length; for growth changes and other measurements see tables 8–15). Scales about 138–144 (in 2 specimens). Peritoneum in small specimens with a silvery color densely covered with brown spots of various sizes, small to minute; with growth, the silvery ground color becoming suffused with brownish or changing to brownish, the small spots persisting.

The distal margin of the caudal is rounded in specimens examined up to 209 mm. in standard length. In the next size available, a specimen 412 mm., the margin is somewhat frayed but appears to have been rounded also or truncate. Dr. Robert R. Miller kindly examined at my request a paratype of this species (UMMZ 95461) 750 mm. in standard length. He reports that the caudal in this specimen is somewhat frayed, but that apparently it is, and has been normally, moderately emarginate. Marini (1933) and Norman (1937, above citations) published illustrations showing a moderately or slightly emarginate caudal, but the sizes of the specimens illustrated are not given. The size at which the caudal becomes emarginate in this species still remains to be determined; but it evidently becomes so at a larger size than in the other species here treated with the possible exception of *polyepsis*.

Specimens examined.—Argentina off the following localities: Punta San Roque (103768, 236 mm.; 161491, 452 mm., 52 fathoms). Puerto San Julian, 51 fathoms (77291, 40 specimens, some paratypes of *hubbsi*, about 40–200 mm.). Also, 15 specimens about 90–140 mm., from "Patagonia" without any definite locality (43388). These 15 specimens are in very bad condition. Their data are not included in this account but their gill raker counts about agree with the other specimens of *hubbsi*.

Comparison.—This species from the Atlantic from the Pacific coast, has its gill raker count rather intermediate between the two primary *bilinearis* from the northwestern Atlantic, as the groups of species separated in the key, but nearer the second group that includes species with the greater number of gill rakers. It is compared above with *polylepis* under the account of that species.

While it about agrees with *polylepis* in the number of gill rakers, taking its character pattern as a whole, *hubbsi* is structurally nearest to *bilinearis* from the northwestern Atlantic, as the two species appear to intergrade more or less in every character studied. The greatest divergence between these two species is shown by the gill raker counts (tables 1–3), and though they intergrade in this character also, the degree of divergence is of species magnitude. In the number of rays in the anal and second dorsal (tables 5–6) the degree of divergence between *hubbsi* and *bilinearis* is of subspecies magnitude. This species also averages a longer head, larger eye, and shorter ventral and pectoral than *bilinearis* (tables 8–11 and 13), but the degrees of intergradation in these characters seem to be considerable.

Structurally *hubbsi* is farther removed from *gayi* which lives on the southeastern Pacific coast than from the geographically remoter *bilinearis*. The gill raker count does not intergrade between the two species in the samples examined (tables 2–3), there is even a slight gap as compared with the subspecies *gayi*. In the pectoral count (table 7) *hubbsi* overlaps with both subspecies of *gayi*, but the divergence is about of species magnitude as compared with *peruanus* and subspecies magnitude as compared with the subspecies *gayi*. In the number of rays in the first dorsal (table 4) the degree of divergence appears to be of subspecies magnitude as compared with both subspecies, but it is of greater extent as compared with *peruanus*. In the number of rays in the second dorsal (table 5) the degree of divergence as compared with the subspecies *gayi* appears to be of about subspecies magnitude, but it is considerably less than that as compared with *peruanus*. In the number of anal rays (table 6) *hubbsi* is intermediate between the subspecies *gayi* and *peruanus*, averaging fewer rays than in the former and more than in the latter, but in either case the divergence is less than

of subspecies magnitude. This species also seems to average a shorter head, maxillary, snout, and pectoral, and a longer pelvic, at least in the smaller specimens as compared with *peruanus;* but not enough specimens in the several size groups are available to determine the extent of divergence in proportional measurements.

Merluccius bilinearis (Mitchill)

Stomodon bilinearis Mitchill, Fishes of New York, p. 7, 1814 (original publication not examined; an example of the annotated copy edited and printed by Gill, 1898, examined).

Description.—Gill rakers 2—6+11—17 or 15–22 in total number on first gill arch. D. 11–14; 37–42. A. 39–42. Pectoral rays modally 15, nearly as often 14, varying 13–17. Head short 25.4–28.1; pelvic, pectoral and caudal rather long 16.5–19.6, 19.7–24.1, and 11.6–14.7, respectively; eye averaging smaller than in the other species, 4.9–7.0; snout, maxillary, and depth measurements rather low (given measurements of 26 specimens 181–294 mm. in standard length; for their change with growth and other measurements see tables 8–15). Scales about 112–130 (in 11 specimens). Peritoneum ground color silvery in small specimens, brownish of variable shades of intensity in large fish, at all sizes stippled and finely spotted with black dots.

Of 25 of the larger specimens examined for the caudal that appear to have this fin uninjured or nearly so, 4 specimens 210–238 mm. in standard length have it rounded; in 8 specimens 135–278 mm., it is truncate; in 12 specimens 238–442 mm., it is emarginate. It is evident that the length at which the caudal becomes emarginate differs greatly with the individual. Perhaps it may be said tentatively, that on an average it becomes emarginate at about 260 mm. in standard length.

Neotype.—As discussed on page 193, it seems desirable to designate a neotype for this species. Therefore, the following specimen is hereby set aside as the neotype of *bilinearis:* U. S. Nat. Mus. No. 39935; Oyster Bay, Long Island, N. Y.; E. G. Blackford; January 25, 1889; 265 mm., 236.5 mm. in standard length.

Other specimens examined.—From or off the following localities. Halifax market (21016). Eastport (13888), South Harpswell (70350–1) and Portland (154899), Maine. Georges Bank (21696), Gloucester (83926, 148176), Cape Cod Light (31560, 33431), Nauset Light (31561), Woods Hole (13007, 49231) and Vineyard Sound (37367, 54918, 54924), Mass. Newport (75007–8, 75018) and Narragansett Bay (25806), R. I. Cornfield Light (58508) and Branford Beacon (92634), Conn. Great South Bay (37014) and Long Island (31846, 33033–6 inclusive, 33344, 44265, 45916, 45918), N. Y. Brigantine (118227) and Wildwood (118224–5), N. J. Brandywine (118226), Del. Barren Island (91275) and Cape Henry (91274), Chesapeake Bay. Cape Fear (155474), N. Car. Total examined, including the neotype, 433 specimens 47–487 mm. Depth records, available for 17 of the 40 constituent samples examined, range 13–198 fathoms.

Comparison.—Structurally this species is nearest *productus* from the west coast of the United States, and the differences between them are discussed under that species. The morphological and distributional differences between this species and *albidus*, its common congener that occurs in the same geographic area with it, are discussed under the account of that species. The differences between *bilinearis* and *hubbsi* a closely related species on the Atlantic coast of South America are discussed under the latter.

As compared with *gayi* from the Pacific coast of South America, the extent of divergence differs with the subspecies somewhat as in the comparison between *gayi* sensu lato and *productus* as discussed on page 200. This species differs from both subspecies of *gayi* in having a shorter head and longer pelvic (tables 8–9). The extent of divergence in these two measurements is greater in the smaller specimens and probably greater as compared with *peruanus* than with the subspecies *gayi;* but so far as the specimens measured indicate, it seems to be of species magnitude.

In the number of anal rays (table 6) *bilinearis* diverges from the subspecies *peruanus* to a degree that is about of species magnitude, although they overlap in this character; but the anal rays in the subspecies *gayi* averages only moderately lower than in *bilinearis*. In the number of pectoral rays (table 7) the divergence as compared with *peruanus* is about of species magnitude, although the intergradation is greater than in the anal count; while as compared with the subspecies *gayi*

it is only of subspecies magnitude. In the number of rays in the first dorsal the divergence is of subspecies magnitude as compared with both subspecies of *gayi* sensu lato, but the extent of intergradation is greater as compared with the subspecies *gayi*. In the number of second dorsal rays (table 5) the divergence as compared with *peruanus* is of subspecies magnitude, while as compared with the subspecies *gayi* it is less than subspecies magnitude. On the other hand, in the total number of gill rakers the divergence as compared with the subspecies *gayi* is of subspecies magnitude, while as compared with *peruanus* it is less than that magnitude. This species also averages a shorter pectoral, maxillary and snout than *gayi* sensu lato (tables 10–12). These characters seem to intergrade more or less, especially in the larger size group, and the intergradation is probably greater as compared with the subspecies *gayi*, but the specimens examined are not numerous enough to determine the extent of divergence or intergradation with precision.

A sample with high gill raker count.—One constituent sample examined has a markedly high gill raker count. It is a lot of 277 specimens taken at Wildwood, N. J., U. S. Nat. Mus. 118224. This lot is contrasted in tables 1–3 with the combined count of all other 39 constituent samples taken north and south of Wildwood, comprising 156 specimens, including a smaller lot of 9 specimens from Wildwood. The relatively high count of this constituent sample as compared with the combined data of all other specimens is notable and worthy of special mention for this reason. Treatment of the two sets of data by statistical methods that are often applied to biological data, will likely show a "significant" difference between them. However, the biological significance of this difference is not obvious, and it is doubtful whether it has such a significance.

Merluccius productus (Ayres)

Merlangus productus Ayres, Proc. California Acad. Nat. Sci. 1: 64, 1855 (San Francisco market).

Homalopomus trowbridgii Girard, Proc. Acad. Nat. Sci. Philadelphia 8: 132, 1856 (Astoria, Oregon).

Description.—Gill rakers 4−5+13−18 or 17–22 in total number on first gill arch. D. 10–12; 39–44. A. 41–44. Pectoral rays predominantly 16, often 14 or 15. Head and pelvic rather short, 26.4–28.6 and 12.1–14.1, respectively; pectoral rather long 20.2 (in one specimen); eye, maxillary, snout, and depth measurements rather low (measurements here given of 3 specimens 225–272 mm. in standard length; for their change with growth and other measurements see tables 8–15). Scales about 147–166 (in 7 specimens). Peritoneum in small specimens silvery stippled and finely spotted with dark dots of two general sizes; in the larger fish becoming grayish blotched with brownish or brownish washed with grayish, the small dots rather faint or absent. The caudal is more or less emarginate in 6 specimens 225–446 mm. in standard length; it is damaged in other specimens examined including the smaller fish.

Specimens examined.—Puget Sound (27295), Seattle (26638, 60679), and Chinook (67303), Wash. Astoria (285, type of *trowbridgii;* 37316) and off Seal Rock (54608), Oreg. San Francisco (529, type of *productus*), La Jolla Point (77439; 280 fathoms), San Diego (41863), San Diego Bay (54815) and Point Loma (77440; 241 fathoms), Calif. Total examined 12 specimens about 125–520 mm. in 12 constituent samples, including the holotypes of *productus* and *trowbridgii*. Depth records 241–280 fathoms, are available for only 2 of the constituent samples as indicated above.

Comparison.—Structurally this species is nearest *bilinearis*, most nearly agreeing with it in the gill raker count and the head length. It differs chiefly in having a shorter pelvic fin and a higher scale count. The change with growth in the pelvic and the difference in its length between the two species are shown in table 9. The relative length of the pelvic decreases somewhat with growth; but even when the data for all sizes are lumped, as in table 9, there still remains a gap between the two species for this character. The scale count is not a good character to use, because it cannot be determined with anywhere near precision as discussed above. Nevertheless, the divergence seems to be considerable, about 147–166 rows in 7 specimens of *productus* as compared with 112–130 rows in 11 specimens of *bilinearis*. Other divergent but widely overlapping characters are as follows: *productus* averaging higher gill raker, anal, pectoral, and second dorsal counts and a lower first dorsal count. The head and maxillary seem to average longer and shorter, respectively.

The differences between *productus* and *angustimanus* are discussed under the account of the latter species.

The divergence between *productus* and *gayi*, sensu lato, is not as pronounced as its divergence from *angustimanus*, and it differs with the subspecies, diverging in most characters, excepting the gill raker count, to a greater extent as compared with the subspecies *peruanus* rather than the subspecies *gayi* which occurs farther south. It differs from both subspecies in the following characters, perhaps named roughly in order of extent of divergence: *productus* averaging a greater number of anal and second dorsal rays (tables 5–6) and scales, a shorter head, maxillary, snout, pelvic, and pectoral (tables 8–12). As compared with the subspecies *peruanus* it does not intergrade in the number of anal rays, and the divergence in the head length and the number of rays in the second dorsal is also of species magnitude in the specimens examined. They intergrade to some extent in the number of dorsal rays, but the divergence is still of species magnitude. As compared with the subspecies *gayi* it intergrades in the number of anal rays, but the degree of divergence is of species magnitude; while the extent of divergence in the number of second dorsal rays and the head length is evidently not more than subspecies magnitude, if that much. The divergence in the length of the maxillary and snout seems to be of species magnitude, or nearly so, compared with *peruanus*, and not more than subspecies magnitude, if that much, compared with the subspecies *gayi*. The divergence in the pelvic and pectoral length is moderate or slight; possibly of subspecies magnitude as compared with *peruanus* and less than that magnitude as compared with *gayi*. On the other hand, the number of gill rakers in *productus* is very nearly the same as in the subspecies *peruanus*, and less on the average than in the subspecies *gayi*, although the difference is of very moderate extent.

There appears to be a difference in the scale count: about 147–166 in 7 specimens of *productus* as compared with about 141 in 1 specimen of *peruanus* and about 124–144 in 11 specimens of *gayi;* but the scalation is incompletely preserved in all specimens examined and this character cannot be used with precision as discussed above.

Merluccius angustimanus Garman

Merluccius angustimanus Garman, Mem. Mus. Comp. Zool. 24: 183; pl. 41, figs. 1–1a, pl. 82, fig. 1, 1899 (off Point Mala, Gulf of Panama).

Description.—Gill rakers 3 − 5 + 12 − 14 or 16–18 in total number on first gill arch. D. 11–12; 36–39. A. 37–40. Pectoral rays 15–17. Head and pectoral long, 31.0–32.8 and 21.3–23.3, respectively; pelvic (14.0–14.5) and other measurements about medium (the measurements here given of 4 specimens 235–289 mm. in standard length, for their change with growth and other measurements see tables 8–15. Scales about 130–149 (in 4 specimens). Peritoneum dark brown or brownish with a grayish or silvery cast; stippled and finely spotted with dots, separable approximately into two sizes, darker than ground color, well-marked in specimens with a light peritoneum, faint in those with a dark peritoneum. The caudal is truncate in 1 specimen 161 mm. in standard length and emarginate in 3 specimens 257–289 mm.; it is damaged in the other 4 specimens examined.

Specimens examined.—Del Mar, Calif., 25 miles offshore; approximately 32°57′ N., 117°33′30″ W.; mid-water trawl 640 meters over 580 fathoms (Scripps Institution of Oceanography H50–290). Off Bahia de Ballenas, west coast of Lower California; 48 fathoms; Albatross Station 2834 (46459). Off Santo Domingo, west coast of Lower California; mid-water trawl, 1,040 fathoms over 2,000 fathoms (SIO H51–87). Townsend Expedition, 1911 (87576; 2 specimens 161–162 mm.; no definite locality recorded in catalog, most probably taken in Gulf of California). Off Point Mala, Gulf of Panama (2 cotypes 177 mm.; 57873, 127 fathoms, Albatross Station 3387; 120424, 286 fathoms, Albatross Station 3385). Total examined 8 specimens 161–322 mm., including 2 cotypes; 3 taken by the Albatross in 48–286 fathoms; 2 in the collection of the Scripps Institution of Oceanography taken by mid-water trawls at 350–1,040 fathoms; 2 without definite data.

Comparison.—This species is close to *gayi* from the Pacific coast of South America. They differ chiefly in the numbers of gill rakers (tables 1–3). Although they intergrade in these counts, the divergence judged by the samples examined seems to be of species magnitude. It averages a greater number of rays in the first dorsal (table 4), the degree of divergence being perhaps of subspecies

magnitude. In the number of second dorsal and anal rays (tables 5–6) it diverges from the subspecies *gayi*, perhaps to a subspecific degree of magnitude; but its divergence from *peruanus* in these two counts evidently is slight, if any. It nearly agrees in the number of pectoral rays with both subspecies. It does not differ appreciably in proportional measurements, at least as compared with *peruanus*.

The relationship between *angustimanus*, *peruanus*, and the subspecies *gayi* with respect to the number of gill rakers is similar to that between *Symphurus civitatum*, *S. plagusia*, and *S. tessellata* with respect to the number of fin rays that I treated in another publication (1951). Among the three populations of *Symphurus* the fin ray numbers average lowest in *civitatum*, highest in *tessellata*, and are intermediate on the average in *plagusia*. The frequency distributions of these numbers overlap considerably as between *tessellata* and *plagusia* which are therefore, treated as coordinate subspecies. On the other hand, the change in *civitatum* is more abrupt, the intergradation between it and *plagusia* is of a considerably lesser degree. Therefore, *civitatum* is treated as a full species. With respect to the number of gill rakers a similar situation exists among the three populations of *Merluccius* concerned; but the degrees of divergence differ. Here also *angustimanus* averages the lowest number of gill rakers, the subspecies *gayi* the highest, and the number in *peruanus* is intermediate. The divergence of *angustimanus* from the other two populations is comparatively abrupt, and considering its extent it is properly treated as a full species because of this difference. However, the divergence between *peruanus* and *gayi* in the gill raker count is less than that of subspecies magnitude. In this respect they differ in degree from the relation between *Symphurus plagusia* and *S. tessellata* with respect to the number of dorsal and anal rays. The two *Merluccius* populations are treated as subspecies because of their divergence in other characters than the gill raker numbers, as discussed later under the account of *peruanus;* but this is beside the point in the present connection.

As compared with *productus*, the common species that occurs north of its geographic range, *angustimanus* differs chiefly in four characters that show a divergence of species magnitude, namely it has a smaller number of gill rakers and anal and second dorsal rays and a longer head. The head length (table 8) is 25.5–28.6 in 11 specimens of *productus* 113–459 mm. in standard length and 31.0–33.3 in 8 specimens of *angustimanus* 145–289 mm. In the specimens examined the proportional length of the head does not intergrade even when all measurements for all sizes are lumped together. When the measurements are divided by size groups, as in table 8, the extent of divergence in comparable size groups is increased. In the number of anal rays (table 6) there is no intergradation between the specimens examined. The number of gill rakers on the lower limb and the total number (tables 2–3), as well as the number of dorsal rays (table 5) intergrade slightly between these two species, but the degree of divergence in the samples examined is of species magnitude.

The two species also seem to differ in the number of scales, 147–166 in 7 specimens of *productus* as compared with 130–149 in 4 specimens of *angustimanus;* but this is an unsatisfactory character to use.

This species also has a longer snout, maxillary, pectoral, and pelvic than *productus* (tables 9–12). The extent of divergence in the pectoral and pelvic measurements is not obvious from the few data determined, but it might prove to be considerable Two other characters of less than diverging subspecies magnitude are as follows: *angustimanus* averaging more rays in the first dorsal and pectoral (tables 4 and 7). Altogether *angustimanus* and *productus* constitute two well-divergent species.

Merluccius gayi (Guichenot), sensu lato

Description.—Gill rakers 3−6+13—19 or 17–25 altogether on first gill arch. D. 10–13; 36–42. A. 36–42. Pectoral rays 15–18. Head moderately or notably long (head and other measurements differ to some extent with subspecies; see their accounts and tables 8–15). Scales about 124–144. Peritoneum variable, moderately light to dark, punctate with small dots moderately differing in size.

Comparison.—This species is here subdivided into two subspecies that differ considerably in comparison with the other species of the genus

and with each other. On the one hand *gayi* sensu lato is nearest to the geographically adjacent *angustimanus*, they overlap slightly in the number of gill rakers, the chief character that separates them, and both have a comparatively long head, although the head length in *gayi* possibly also differs with the subspecies, perhaps being shorter in the subspecies *gayi*. On the other hand, *gayi* is near to *bilinearis* which lives in the northwestern Atlantic. It is also near *productus* from the northeastern Pacific. The differences between *gayi* and the above three species are discussed under their accounts. It is also compared above with *polylepis* (p. 196), its more remote congener that lives in the same region with it, and with *hubbsi* from the southwestern Atlantic (p. 197).

The pelvic length in *gayi*, which constitutes the chief character that separates *bilinearis* and *productus*, is intermediate in measurements between those two species.

Merluccius gayi peruanus, new subspecies

Merluccius gayi Evermann and Radcliffe, Bull. U. S. Nat. Mus. 95: 158, 1917 (Paita and Callao, Peru). Hildebrand, ibid. 189: 157, 1946 (account based on same specimens forming basis of present account, see below).

Description.—Gill rakers 4−6+13−17 or 17–23 in total number of first gill arch. D. 11–12; 36–40. A. 36–39. Pectoral rays most predominantly 16–17, varying 15–18. Head and pectoral rather long, 30.6–31.5 and 23.0–23.1, respectively; pelvic (14.6–14.7) and other measurements rather medium (the given measurements of 2 specimens 240–370 mm. in standard length; for their change with growth and other measurements see tables 8–15). Scales about 141 (in 1 specimen). Peritoneum brownish with a grayish cast or grayish with a brownish cast, stippled and finely spotted with dark dots of approximately two sizes. Caudal emarginate in 7 specimens 138–370 mm. in standard length; damaged in the other 4 specimens examined. The caudal in this subspecies apparently becomes emarginate at a smaller size than in the other species examined.

Holotype.—U. S. Nat. Mus. 77727. Paita, Peru; R. E. Coker; 417 mm., 370 mm. in standard length.

Paratypes.—From or off the following localities on the coast of Peru: Chimbote Bay (128181, from stomach of yellowfin tuna), Callao (77525, 77539), Cañete (128180). Total examined, including the holotype, 11 specimens 156–417 mm. in 5 constituent samples. Depth records for the samples examined are unavailable.

Comparison.—The character showing the greatest divergence between the Peruvian and Chilean populations of *gayi* refers to the number of anal rays (table 6). This divergence is about of subspecies magnitude, although the two samples compared are not altogether adequate. Nearly the same degree of divergence is shown by the number of dorsal rays (table 5). The Peruvian population averages lower gill raker counts (tables 1–3), but the divergences are less than subspecies magnitude. A comparison of the measurements of 3 Chilean specimens 308–389 mm. in standard length with a Peruvian specimen 370 mm. (tables 8–15), indicates that the latter population probably averages a longer head and maxillary. Taking everything into consideration it seems that the two populations are best treated as distinct subspecies.

Merluccius gayi gayi (Guichenot)

Merlus gayi Guichenot, *in* Gay, Historia fisica y politica de Chile, vol. 2, p. 32, 1948 (Chile). Guichenot, *in* Gay, Atlas de la historia fisica y politica de Chile, vol. 2, ictiologia pl. 8, fig. 2, 1854 (Chile).

Description.—Gill rakers 3−6+14−19 or 18–25 in total number on first gill arch. D. 10–13; 37–42. A. 39–42. Pectoral rays 15–17. Head and pectoral moderately long, 28.4–29.8 and 19.9–21.0, respectively; pelvic (13.5–14.6) and other measurements medium on the whole (given measurements of the 3 smallest specimens examined 308–389 mm. in standard length; for growth changes and other measurements see tables 8–15; statement regarding proportional measurements is tentative as no smaller specimens of this subspecies are available for comparison). Scales about 124–144 (in 11 specimens). Peritoneum variable, light yellowish to dark brown, rather thickly sprinkled with small dark dots varying moderately in size. Caudal emarginate in all specimens examined, the smallest 341 mm.

Specimens examined.—Collected on the coast of Chile by M. J. Lobell and others, between south latitudes 26°21′ and 45°10′30″ as follows, depth records not available. Chanaral de las Animas Bay (157768), Huasco Bay (157770), Coquimbo Bay (157771), Isla Santa Maria, Norte (157772),

Queule (157773), Puerto Montt (157769), Huichas Island (157767). Total examined, 15 specimens 341–637 mm., 308–581 mm. in standard length.

Comparison.—This subspecies is compared above with *peruanus* under its account.

Nomenclature.—Two species of *Merluccius* occur on the coast of Chile, but it is not possible to tell definitely from Guichenot's accounts which one of the two species he described. His description might apply to both species. His plate taken in connection with the location of the fish shows that his species belongs to *Merluccius;* but the figure is obviously erroneous in detail and does not apply well to either species. Dr. Leon Bertin who very kindly examined the type of *gayi* at the Paris Museum, reports that it is now in bad condition and the number of gill rakers, the most crucial distinguishing character, is not now well determinable. Judged by the specimens examined during this investigation, it seems that the present species is the more common one on the coast of Chile; therefore, I assume that this is the species which Guichenot described, while the other Chilean species is described above under the name of *polylepis.*

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TABLES

TABLE 1.—*Frequency distribution of the number of gill rakers on the upper limb of the first gill arch in American species of* Merluccius

[Tubercles are not included in count. Counts of gill rakers in *polylepis, productus, angustimanus, peruanus,* and *gayi* were made on both sides of each specimen and entered independently in this and the following 2 tables, as though they were taken from 2 specimens. Percentage numbers of the frequencies for every species are given in the second line in this and the following 6 tables for convenience in computing the indices of intergradation and divergence as discussed in the text.]

Species and subspecies	Distribution					
	1	2	3	4	5	6
albidus	4	32	2			
	10.5	84.2	5.3			
magnoculus		31	1			
		96.9	3.1			
polylepis			2	6		
			25.0	75.0		
hubbsi			12	28	2	
			28.6	66.6	4.8	
bilinearis		1	14	261	153	4
		.2	3.2	60.3	35.3	.9
productus				12	12	
				50.0	50.0	
angustimanus			4	11	1	
			25.0	68.8	6.3	
peruanus				9	12	1
				40.9	54.6	4.5
gayi			1	8	18	3
			3.3	26.7	60.0	10.0
bilinearis						
Wildwood U. S. Nat. Mus. 118224			8	158	109	2
			2.9	57.0	39.4	.7
All other samples		1	6	103	44	2
		.6	3.8	66.1	28.2	1.3

TABLE 2.—*Frequency distribution of the number of gill rakers on the lower limb of the outer gill arch in American species of* Merluccius

Species and subspecies	Distribution												
	7	8	9	10	11	12	13	14	15	16	17	18	19
albidus		30	8										
		79.0	21.0										
magnoculus	1	27	4										
	3.1	84.4	12.5										
polylepis				5	3								
				62.5	37.5								
hubbsi			1	10	26	5							
			2.4	23.8	61.9	11.9							
bilinearis					3	13	156	181	67	9	4		
					.7	3.0	36.0	41.8	15.5	2.1	.9		
productus							1	2	5	7	5	3	
							4.4	8.7	21.7	30.4	21.7	13.0	
angustimanus						6	8	2					
						37.5	50.0	12.5					
peruanus							1	4	5	7	5		
							4.5	18.2	22.7	31.8	22.7		
gayi								1	9	9	6	3	2
								3.3	30.0	30.0	20.0	10.0	6.7
bilinearis													
Wildwood U. S. Nat. Mus. 118224						2	76	130	57	8	4		
						0.7	27.4	46.9	20.6	2.9	1.4		
All other samples					3	11	80	51	10	1			
					1.9	7.1	51.3	32.7	6.4	.6			

TABLE 3.—*Frequency distribution of the total number of gill rakers on the outer gill arch in American species of* Merluccius

Species and subspecies	Distribution																
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
albidus	4	24	10														
	10.5	63.2	26.3														
magnoculus	1	26	5														
	3.1	81.3	15.6														
polylepis					1	5	2										
					12.5	62.5	25.0										
hubbsi					6	10	21	5									
					14.3	23.8	50.0	11.9									
bilinearis							4	16	131	128	97	45	9	3			
							0.9	3.7	30.3	29.6	22.4	10.4	2.1	0.7			
productus									1	2	3	4	5	8			
									4.4	8.7	13.0	17.4	21.7	34.8			
angustimanus								8	7	1							
								50.0	43.7	6.3							
peruanus									1	2	4	6	5	3	1		
									4.5	9.1	18.2	27.3	22.7	13.6	4.5		
gayi										1	4	9	6	4	3	2	1
										3.3	13.3	30.0	20.0	13.3	10.0	6.7	3.3
bilinearis																	
Wildwood U. S. Nat. Mus. 118224								6	63	86	73	38	8	3			
								2.2	22.7	31.0	26.4	13.7	2.9	1.1			
All other samples							4	10	68	42	24	7	1				
							2.6	6.4	43.6	26.9	15.4	4.5	0.6				

TABLE 4.—*Frequency distribution of the number of rays in the first dorsal in American species of* Merluccius

Species and subspecies	Distribution				
	10	11	12	13	14
albidus		21	16	1	
		55.3	42.1	2.6	
magnoculus		1	28	3	
		3.1	87.5	9.4	
polylepis		2	2		
		50.0	50.0		
hubbsi		4	10	2	1
		23.5	58.8	11.8	5.9
bilinearis		4	23	14	3
		9.1	52.3	31.8	6.8
productus	2	6	4		
	16.7	50.0	33.3		
angustimanus		2	6		
		25.0	75.0		
peruanus		9	2		
		81.8	18.2		
gayi	2	9	3	1	
	13.3	60.0	20.0	6.7	

TABLE 5.—*Frequency distribution of the number of rays in the second dorsal in American species of* Merluccius

Species and subspecies	Distribution									
	36	37	38	39	40	41	42	43	44	45
albidus		3	14	14	5					
		8.3	38.9	38.9	13.9					
magnoculus	2	6	10	11	2		1			
	6.3	18.8	31.2	34.4	6.3		3.1			
polylepis								2	1	1
								50.0	25.0	25.0
hubbsi		6	8	2	1					
		35.3	47.1	11.8	5.9					
bilinearis		2	3	13	15	9	2			
		4.5	6.8	29.6	34.1	20.5	4.5			
productus				1	4	3	3		1	
				8.3	33.3	25.0	25.0		8.3	
angustimanus	2	3	1	2						
	25.0	37.5	12.5	25.0						
peruanus	2	2	5	1	1					
	18.2	18.2	45.4	9.1	9.1					
gayi		1	2	5	2	3	1			
		7.1	14.3	35.7	14.3	21.4	7.1			

TABLE 6.—*Frequency distribution of the number of anal rays in American species of* Merluccius

Species and subspecies	Distribution									
	36	37	38	39	40	41	42	43	44	45
albidus		5	10	14	5	2				
		13.9	27.8	38.9	13.9	5.6				
magnoculus		1	4	12	11	4				
		3.1	12.5	37.5	34.4	12.5				
polylepis							1	2		1
							25.0	50.0		25.0
hubbsi		3	2	8	4					
		17.6	11.8	47.1	23.5					
bilinearis				5	14	20	5			
				11.4	31.8	45.5	11.4			
productus						5	4	2	1	
						41.7	33.3	16.7	8.3	
angustimanus		2	3	2	1					
		25.0	37.5	25.0	12.5					
peruanus	1	2	4	4						
	9.1	18.2	36.4	36.4						
gayi				6	7	1	1			
				40.0	46.7	6.7	6.7			

TABLE 7.—*Frequency distribution of the number of pectoral rays in American species of* Merluccius

Species and subspecies	Distribution						
	12	13	14	15	16	17	18
albidus		1	7	18	6		
		3.1	21.9	56.2	18.8		
magnoculus	1	19	11	1			
	3.1	59.4	34.4	3.1			
polylepis		1	2	1			
		25.0	50.0	25.0			
hubbsi			7	9	1		
			41.2	52.9	5.9		
bilinearis		4	16	20	3	1	
		9.1	36.4	45.5	6.8	2.3	
productus			1	3	8		
			8.3	25.0	66.7		
angustimanus				1	3	4	
				12.5	37.5	50.0	
peruanus				1	4	5	1
				9.1	36.4	45.4	9.1
gayi				4	5	6	
				26.7	33.3	40.0	

TABLE 8.—*Head length (measurement to distal margin of soft border) in American species of* Merluccius *in thousandths of the standard length, segregated in size groups*

Species and subspecies	Standard length in mm.	Distribution																	
		250	255	260	265	270	275	280	285	290	295	300	305	310	315	320	325	330	335
albidus	75–91											1	1						
hubbsi	62–87							1	1			2	1						
bilinearis	66–93					2	1	1		1									
albidus	114–138							1				1		2	1				
hubbsi	108–160							2	1	1	3	2							
bilinearis	122–158					4				2									
productus	113–134						2												
angustimanus	145–161															1	1	1	1
peruanus	138–148																2	3	4
albidus	173–293						1	2		2	4	2							
magnoculus	189–290										1	3	6	8	2				
polylepis	281–283							1				1							
hubbsi	177–209								1	1									
bilinearis	181–294		3	2	4	8	5	4											
productus	225–272				1		1		1										
angustimanus	235–289													2			1	1	
peruanus	240												1						
albidus	323–376							3	3										
magnoculus	306–378											5	4	2					
polylepis	323–325						1			1									
bilinearis	319–367			1	1	2	1												
productus	318								1										
peruanus	370														1				
gayi	308–389								2			1							
albidus	405–463						2			2									
magnoculus	451													1					
hubbsi	412						1												
bilinearis	413–442				2														
productus	409–459		1			2	2												
gayi	402–478							1	2	3	2	3							
albidus	626												1						
gayi	581								1										
albidus	173–463						3	5	3	4	4	2							
magnoculus	189–451										1	8	10	11	2				

TABLE 9.—*Pelvic fin length in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution																		
		110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205
albidus	75–91															1	1				
hubbsi	62–87												1		1		2		1		
bilinearis	66–93															1	2		1		1
albidus	114–138																1	2	1		
hubbsi	108–160												2	2	3	1	1				
bilinearis	122–158													1			3	2			
productus	113–134				2																
angustimanus	145–161								3	1											
peruanus	138–148							2	3	2	2										
albidus	173–293										1	3	3		3						
magnoculus	189–390						5	3	3	6	2	1									
polylepis	281–283		1					1													
hubbsi	177–209												1		1						
bilinearis	181–294												1	5	7	4	3	3	3		
productus	225–272			1	1			1													
angustimanus	235–289							2	2												
peruanus	240								1												
albidus	323–376									1	3		1		1						
magnoculus	306–378			2		2	4	3													
polylepis	323–325					1	1														
bilinearis	319–367												1	2	1		1				
productus	318						1														
peruanus	370								1												
gayi	308–389						2		1												
albidus	405–463							1		1	1	1									
magnoculus	451			1																	
hubbsi	412						1														
bilinearis	413–442									1		1									
productus	409–459	1	1	1	1	1															
gayi	402–478					4	4	2	1												
albidus	626						1														
gayi	581					1															
albidus	173–376									1	4	3	4		4						
magnoculus	189–378			2		2	9	6	3	6	2	1									
bilinearis	66–442									1		1	2	8	8	5	9	5	4		1
productus	113–459	1	1	2	4	1	1	1													

TABLE 10.—*Pectoral measurements in American species of* Merluccius, *in thousandths of the standard length, segregated in size groups*

Species and subspecies	Standard length in mm.	Distribution																	
		155	160	165	170	175	180	185	190	195	200	205	210	215	220	225	230	235	240
albidus	75- 91							1			1								
hubbsi	85- 87			1	1														
bilinearis	66- 93							1		1	2			1					
albidus	114-138						1	1				2	1						
hubbsi	125-146								1	1		1							
bilinearis	122-148										2		1	1	1				
productus	134												1						
angustimanus	145-161														2			1	1
peruanus	138-148													1	1	3	2	1	1
albidus	173-293							1		1	5	1	1						
magnoculus	189-290		2		5	7	2	1	1										
polylepis	281-283					1		1											
hubbsi	177-209										2								
bilinearis	181-294									1	1	4	3	4	2	4	1	2	1
productus	225										1								
angustimanus	235-289												1	1		1		1	
peruanus	240																1		
albidus	323-376								2	2	1		1						
magnoculus	306-378	1	5	2			1	1											
polylepis	323-325								2										
bilinearis	329-367												2	1			1		
productus	318															1			
peruanus	370																1		
gayi	308-389										2		1						
albidus	405-463							1		1		1		1					
magnoculus	451		1																
hubbsi	412						1												
bilinearis	413-442								1				1						
productus	409-459									1	1		1	1					
gayi	402-478										1	3	2	4	1				
albidus	626							1											
gayi	581													1					
albidus	75-626						1	5	2	4	7	4	3	1					
magnoculus	189-451	1	8	2	5	7	3	2	1										

TABLE 11.—*Maxillary length in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution																	
		124	127	130	133	136	139	142	145	148	151	154	157	160	163	166	169	172	175
albidus	75-91															1			1
hubbsi	62-87							1		1	1			1					
bilinearis	66-93					1	1		2	1									
albidus	114-138										1		1	1	1	1			
hubbsi	108-160			1		4	1			1	2								
bilinearis	122-158				1		2	1	1										
productus	113-134			1		1													
angustimanus	145-161									1	1					1			
peruanus	138-148									1	2	3	2		1				
albidus	173-293			1		3	1	1	2	2	1								
magnoculus	189-290								1		5	6	4	2	2				
polylepis	281-283							1			1								
hubbsi	177-209								1	1									
bilinearis	181-294	1		3	5	10	4	1	1	1									
productus	225-272			1	1	1													
angustimanus	235-289								1		1	2							
peruanus	240								1										
albidus	323-376					1	1	3	1										
magnoculus	306-378									2	3	1	3	2					
polylepis	323-325									2									
bilinearis	319-367				1	2	1	1											
productus	318			1															
peruanus	370										1								
gayi	308-389				2	1													
albidus	405-463						1	1	1		1								
magnoculus	451													1					
hubbsi	412					1													
bilinearis	413-442					2													
productus	409-459		1	1	2	1													
gayi	402-478		1	1	1	5		1	1	1									
albidus	626														1				
gayi	581				1														
albidus	173-463			1		4	3	5	4	2	2								
magnoculus	189-451								1	2	8	7	7	5	2				

TABLE 12.—*Snout length in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution											
		83	86	89	92	95	98	101	104	107	110	113	116
albidus	75–91	---	---	---	---	---	2	---	---	---	---	---	---
hubbsi	62–87	---	---	1	1	3	---	---	---	---	---	---	---
bilinearis	66–93	1	---	1	1	1	1	---	---	---	---	---	---
albidus	114–138	---	---	---	---	---	1	1	1	1	1	---	---
hubbsi	108–160	---	---	---	1	2	6	---	---	---	---	---	---
bilinearis	122–158	---	---	1	3	---	1	1	---	---	---	---	---
productus	113–134	---	---	---	2	---	---	---	---	---	---	---	---
angustimanus	145–161	---	---	---	---	---	---	---	3	1	---	---	---
peruanus	138–148	---	---	---	---	---	1	2	3	3	---	---	---
albidus	173–293	---	---	---	2	2	4	2	1	---	---	---	---
magnoculus	189–290	---	---	---	---	---	2	1	7	2	4	2	2
polylepis	281–283	---	---	---	---	1	---	---	---	1	---	---	---
hubbsi	177–209	---	---	---	---	1	1	---	---	---	---	---	---
bilinearis	181–294	---	2	9	9	4	---	1	1	---	---	---	---
productus	225–272	---	---	1	1	1	---	---	---	---	---	---	---
angustimanus	235–289	---	---	---	---	---	---	---	1	1	2	---	---
peruanus	240	---	---	---	---	---	---	1	---	---	---	---	---
albidus	323–376	---	---	---	3	---	2	1	---	---	---	---	---
magnoculus	306–378	---	---	---	---	1	---	2	---	1	4	2	1
polylepis	323–325	---	---	---	---	---	---	---	1	1	---	---	---
bilinearis	319–367	---	---	1	1	2	---	1	---	---	---	---	---
productus	318	---	---	---	---	---	1	---	---	---	---	---	---
peruanus	370	---	---	---	---	---	---	---	1	---	---	---	---
gayi	308–389	---	---	1	---	1	---	1	---	---	---	---	---
albidus	405–463	---	---	---	---	1	2	1	---	---	---	---	---
magnoculus	451	---	---	---	---	---	---	---	---	1	---	---	---
hubbsi	412	---	---	1	---	---	---	---	---	---	---	---	---
bilinearis	413–442	---	---	1	1	---	---	---	---	---	---	---	---
productus	409–459	1	---	---	2	---	1	1	---	---	---	---	---
gayi	402–478	---	---	---	1	2	4	1	2	1	---	---	---
albidus	626	---	---	---	---	---	---	---	1	---	---	---	---
gayi	581	---	---	---	---	---	1	---	---	---	---	---	---

TABLE 13.—*Eye measurements in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution													
		45	48	51	54	57	60	63	66	69	72	75	78	81	84	87
albidus	75–91	---	---	---	---	---	---	---	---	---	---	---	1	---	1	---
hubbsi	62–87	---	---	---	---	---	---	---	---	---	---	---	1	3	---	1
bilinearis	66–93	---	---	---	---	---	---	---	1	---	1	1	---	1	1	---
albidus	114–138	---	---	---	---	1	---	---	1	1	1	1	---	---	---	---
hubbsi	108–160	---	---	---	---	---	---	---	2	5	2	---	---	---	---	---
bilinearis	122–158	---	---	---	---	---	---	1	3	1	1	---	---	---	---	---
productus	113–134	---	---	---	---	---	---	---	---	1	1	---	---	---	---	---
angustimanus	145–161	---	---	---	---	---	---	1	---	1	1	1	---	---	---	---
peruanus	138–148	---	---	---	---	---	---	2	2	3	2	---	---	---	---	---
albidus	173–293	---	---	---	2	3	1	3	2	---	---	---	---	---	---	---
magnoculus	189–290	---	---	---	---	---	1	3	4	8	2	---	1	1	---	---
polylepis	281–283	---	1	1	---	---	---	---	---	---	---	---	---	---	---	---
hubbsi	177–209	---	---	---	---	---	---	1	---	1	---	---	---	---	---	---
bilinearis	181–294	---	1	1	5	9	3	5	1	1	---	---	---	---	---	---
productus	225–272	---	---	---	1	1	---	---	1	---	---	---	---	---	---	---
angustimanus	235–289	---	---	---	---	---	2	2	---	---	---	---	---	---	---	---
peruanus	240	---	---	---	---	---	---	1	---	---	---	---	---	---	---	---
albidus	323–376	---	---	2	2	1	1	---	---	---	---	---	---	---	---	---
magnoculus	306–378	---	---	---	3	3	---	3	---	1	---	1	---	---	---	---
polylepis	323–325	---	1	---	1	---	---	---	---	---	---	---	---	---	---	---
bilinearis	319–367	1	1	---	1	2	---	---	---	---	---	---	---	---	---	---
productus	318	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---
peruanus	370	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---
gayi	308–389	---	---	---	1	---	---	---	1	1	---	---	---	---	---	---
albidus	405–463	---	1	---	---	3	---	---	---	---	---	---	---	---	---	---
magnoculus	451	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---
hubbsi	412	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---
bilinearis	413–442	---	1	---	1	---	---	---	---	---	---	---	---	---	---	---
productus	409–459	---	1	2	2	---	---	---	---	---	---	---	---	---	---	---
gayi	402–478	---	---	3	4	3	1	---	---	---	---	---	---	---	---	---
albidus	626	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---
gayi	581	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---

TABLE 14.—*Depth of body, measured at origin of first dorsal, in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution													
		135	140	145	150	155	160	165	170	175	180	185	190	195	200
albidus	75–91	---	---	---	---	---	---	---	---	1	1	---	---	---	---
hubbsi	62–87	---	---	---	3	1	---	1	---	---	---	---	---	---	---
bilinearis	66–93	---	---	---	---	---	---	---	1	---	3	1	---	---	---
albidus	114–138	---	---	---	---	---	2	---	---	1	1	---	---	---	---
hubbsi	108–160	---	---	---	---	---	---	4	3	2	---	---	---	---	---
bilinearis	122–158	---	---	---	---	1	---	---	---	2	---	3	---	---	---
productus	113–134	---	---	---	---	2	---	---	---	---	---	---	---	---	---
angustimanus	145–161	---	---	---	---	1	1	2	---	---	---	---	---	---	---
peruanus	138–148	---	---	---	---	---	---	2	3	---	1	1	1	1	---
albidus	173–293	---	1	1	---	1	2	---	2	---	2	2	---	---	---
magnoculus	189–290	---	---	---	2	---	3	1	3	3	2	---	2	1	3
polylepis	281–283	---	1	---	1	---	---	---	---	---	---	---	---	---	---
hubbsi	177–209	---	---	---	1	---	---	---	---	---	1	---	---	---	---
bilinearis	181–294	---	1	2	1	6	6	3	2	4	1	---	---	---	---
productus	225–272	---	---	---	---	1	1	1	---	---	---	---	---	---	---
angustimanus	235–289	---	---	---	---	---	---	1	---	---	2	---	1	---	---
peruanus	240	---	---	---	---	---	1	---	---	---	---	---	---	---	---
albidus	323–376	---	---	---	---	---	---	1	---	---	4	---	---	---	---
magnoculus	306–378	---	---	---	---	---	---	3	1	---	1	2	2	1	1
bilinearis	319–367	1	---	---	1	1	---	1	1	---	---	---	---	---	---
productus	318	---	---	---	1	---	---	---	---	---	---	---	---	---	---
peruanus	370	---	---	---	---	1	---	---	---	---	---	---	---	---	---
gayi	308–389	---	---	---	---	2	---	---	---	1	---	---	---	---	---
albidus	405–463	---	---	---	1	2	---	1	---	---	---	---	---	---	---
magnoculus	451	---	---	---	1	---	---	---	---	---	---	---	---	---	---
hubbsi	412	---	---	---	1	---	---	---	---	---	---	---	---	---	---
bilinearis	413–442	---	---	1	---	1	---	---	---	---	---	---	---	---	---
productus	409–459	---	2	---	---	1	---	---	---	1	1	---	---	---	---
gayi	402–478	---	1	1	---	3	1	2	1	2	---	---	---	---	---
albidus	626	---	---	---	---	---	---	---	1	---	---	---	---	---	---
gayi	581	---	---	---	---	---	---	---	1	---	---	---	---	---	---

TABLE 15.—*Caudal length in American species of* Merluccius, *in thousandths of the standard length, segregated by size groups*

Species and subspecies	Standard length in mm.	Distribution															
		102	105	108	111	114	117	120	123	126	129	132	135	138	141	144	147
albidus	75–91					1			1								
hubbsi	85–87											2					
bilinearis	66–93										1	2		1	1		
albidus	124–137							1		1							
hubbsi	108–160							1		2			1	2	2	1	
bilinearis	122–135							1				1	1				
angustimanus	159–161				1		1										
peruanus	138–148								1	3	1	3	1				
albidus	173–293			1	1		2	1	1								
magnoculus	189–290			1	1	1	3	2	3	3	2	1			1		
polylepis	281–283	1			1												
hubbsi	177–209									1					1		
bilinearis	181–294						2	2	1	4	1	3	1		2		1
angustimanus	257–289						1		1		1						
peruanus	240										1						
albidus	323–371				1		2		2								
magnoculus	306–378			1	1	1	2	1	1	3							
polylepis	323–325						1		1								
bilinearis	329–367								1		1						
productus	318						1										
peruanus	370															1	
gayi	308–389				1			2									
albidus	405–463				1		1		1		1						
magnoculus	451						1										
hubbsi	412				1												
bilinearis	413						1										
productus	446													1			
gayi	402–478				1	1		3		2	2	2					
albidus	626				1												
gayi	581			1													

DESCRIPTION OF EGGS AND LARVAE OF JACK MACKEREL (*Trachurus symmetricus*) AND DISTRIBUTION AND ABUNDANCE OF LARVAE IN 1950 AND 1951

BY ELBERT H. AHLSTROM AND ORVILLE P. BALL

FISHERY BULLETIN 97

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Development of jack mackerel (*Trachurus symmetricus*) is described for the embryonic, larval, and early juvenile stages. The egg is about 1 mm. in diameter, has a single large oil globule, a segmented yolk mass, a rather narrow perivitelline space, and a clear, tough, unsculptured eggshell. Diagnostic characters are given for several stages of embryonic development to aid in the identification of jack-mackerel eggs. The larva, on hatching, is about 2 mm. in length. The oil globule occupies a forward position in the yolk sac. Pigment is mostly confined to the dorsal and ventral margins of the body.

A dynamic approach is followed in discussing larval development. The sequences of fin formation, of ossification, of pigment changes, and of changes in body form are presented. The larval period is considered to end at approximately 16 mm., when fin formation is complete.

The regional and seasonal distributions of jack-mackerel larvae off western North America during 1950 and 1951 are presented. The center of abundance of jack-mackerel larvae lies off southern California, between 80 and 240 miles at sea. Abundance falls off both to the north and to the south of this area. The offshore distribution of jack-mackerel larvae has not been delimited completely. The season of greatest abundance is during the 5-month period, March through July.

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Drawings by GEORGE MATTSON

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DESCRIPTION OF EGGS AND LARVAE OF JACK MACKEREL (*Trachurus symmetricus*) AND DISTRIBUTION AND ABUNDANCE OF LARVAE IN 1950 AND 1951

By ELBERT H. AHLSTROM and ORVILLE P. BALL, *Fishery Research Biologists*

While investigating the distribution and abundance of sardine eggs and the survival of sardine larvae, the younger stages of most of the other fishes in our waters that have pelagic eggs and larvae were collected incidentally. The early stages in the life history of most of these have not been described. Inasmuch as we are interested in the species competing with or preying upon the sardine, we have identified the eggs and larvae of the other species occurring commonly in plankton hauls. Descriptions of the early stages of these other species will be published, this being the first paper in the projected series.

Collections of eggs and larvae of jack mackerel, *Trachurus symmetricus* (Ayres) 1855, were obtained on the monthly survey cruises of the California Cooperative Oceanic Fisheries Investigations. This program is sponsored by the California Marine Research Committee and is being carried out cooperatively by the Scripps Institution of Oceanography of the University of California, the California Department of Fish and Game, the California Academy of Sciences, the Hopkins Marine Station of Stanford University, and the South Pacific Fishery Investigations of the United States Fish and Wildlife Service. Since the spring of 1952, a voluntarily imposed tax of $1 a ton has been paid by California fish processors on all landings of jack mackerel, as well as other species, in support of the research being sponsored by the Marine Research Committee.

The jack-mackerel fishery has shown a most rapid growth since the decline of the sardine and Pacific-mackerel fisheries. Before 1933, the annual catch never reached a million pounds. From 1933 to 1946 the annual catch varied between 1 and 15 million pounds. With the 1947 season, a most rapid expansion of the fishery took place, the catch in that year totaling 129 million pounds. Since then, the annual catch has shown rather marked fluctuations, but it has never dropped below 50 million pounds, and during the 1950 and 1952 seasons it exceeded the amount taken during 1947. The 1952 catch of jack mackerel off California of 146 million pounds, the largest taken to date, was exceeded only by the landings of yellowfin tuna. Hence, the jack-mackerel fishery during the past few years has become one of the most important fisheries on our west coast. Most of the landings are made at San Pedro.

There is but a single species of *Trachurus* known to occur in the eastern Pacific between Baja California and British Columbia. According to Roedel and Fitch (1952), specimens of adult jack mackerel have been taken from central Baja California to British Columbia, and as far offshore as 600 miles (west of Los Angeles). The biology of the jack mackerel had been so incompletely known until recently, that large adults from Oregon and British Columbia were described as a separate species, *Decapterus polyaspis* (Walford and Myers 1944). But, Roedel and Fitch, after examining an extensive collection of jack mackerel obtained between central Baja California and Oregon, were able to show that *D. polyaspis* is a synonym of *Trachurus symmetricus*.

There has been considerable confusion in distinguishing between jack mackerel and Mexican scad. The latter species, *Decapterus hypodus*, occurs off Baja California and is occasionally taken as far north as southern California. It resembles the jack mackerel superficially, but can be separated readily from it on the basis of the following characters: (1) The last ray of both the second dorsal and the anal fin is widely separated from the preceding rays to form a distinct finlet in *Decapterus*, while in *Trachurus* the last ray is not widely separated; (2) *Decapterus* lacks the accessory lateral line present along the first dorsal in *Trachurus;* (3) the lateral line is gently deflexed in *Decapterus*, while it is much more abruptly arched in *Trachurus;* and (4) there are

scutes along only the posterior portion of the lateral line in *Decapterus*, while they extend along the entire length of the lateral line in *Trachurus*. We have taken a number of larvae off central Baja California, that we have tentatively identified as *D. hypodus*. They agree closely with the larvae of *Decapterus punctatus* described by Hildebrand and Cable (1930).

The eggs and larvae of jack mackerel are among the most abundant taken in our plankton collections. The larvae are as numerous as sardine larvae, and have a more widespread distribution. The center of abundance is off southern California. During the spawning season, jack mackerel occur as far seaward as our cruises extend. The largest concentrations of jack-mackerel larvae occur between 80 and 240 miles offshore. If the distribution of adult jack mackerel during the remainder of the year is similar to that found during the spawning period, then the fishery is exploiting only an inshore margin of the jack-mackerel population. However, the fishery takes the younger age groups of jack mackerel, and it may be that they have a more limited distribution, closer to shore, than do the older fish.

In discussing the early stages in the development of jack mackerel, we find it convenient to recognize four categories: (1) Egg stage, (2) yolk-sac larva, (3) larva, and (4) juvenile. The egg stage, or period of embryonic development, scarcely needs defining; it commences at fertilization and ends at hatching. It is convenient to separate the early period of larval development, when the yolk-sac is present, from the subsequent larval period. The larval period is considered to end at the completion of fin formation. Thereafter, young jack mackerel are classed as juveniles. Although the transition to the juvenile stage is considered to occur at about 16 mm. in length, there is no sharp line of demarcation between the larval and juvenile stages of the jack mackerel. There is no well-defined metamorphosis, such as occurs in many kinds of fish larvae.

Some workers have used a separation into three stages during the early postembryonic period: Yolk-sac larva, larva, and postlarva. Hubbs (1943) recommended a broad application of the term "larva" to include all developmental stages between the time of hatching and transformation, which could be subdivided, if desired, into prolarva and postlarva. The term "larva" is here used in such an inclusive sense; however, to designate the early larval period, the term "yolk-sac larva" is substituted for prolarva, and the term "post-larva" is not used.

It is with deep pleasure that the authors acknowledge the cooperation given by the Scripps Institution of Oceanography and the California Department of Fish and Game in the collection of data at sea. The whole staff of the South Pacific Fishery Investigations of the Fish and Wildlife Service has contributed, to a greater or lesser extent, to this study. The authors especially wish to thank John C. Marr, James Böhlke, and Theodore Widrig for helpful advice during the preparation of the paper; James Thrailkill for preparing the charts showing distribution and abundance of jack-mackerel larvae; Robert Counts for his help in the preparation of jack-mackerel material for study; and Dr. Rolf Bolin of Stanford University for critically reading the manuscript.

DEVELOPMENT OF JACK MACKEREL

EGG

(FIGURE 1)

The egg of the jack mackerel is spherical in shape, and of moderate size. It is a pelagic egg that is characterized by a single, fairly large oil globule, a more or less segmented yolk mass, a rather narrow perivitelline space, and a clear, tough, unsculptured eggshell.

The diameter of the jack-mackerel egg, based on measurements of over 500 eggs selected from various parts of the spawning range, averaged about 0.98 mm.; the diameter of the oil globule averaged 0.26 mm.; the diameter of the yolk 0.79 mm.; the width of the perivitelline space 0.09 mm. These measurements are given in more detail in table 1.

The yolk mass appears light yellow to amber in preserved material. It is irregularly segmented. In early developmental stages, the yolk immediately adjacent to the blastodisc often appears much more definitely segmented than the yolk material at the vegetative pole. The membrane around the yolk mass must be quite thin and easily ruptured. In our preserved material, most early-embryonic eggs (before the closure of the blastopore) show a considerable amount of yolk diffusion into the perivitelline space. It is assumed that this is due to

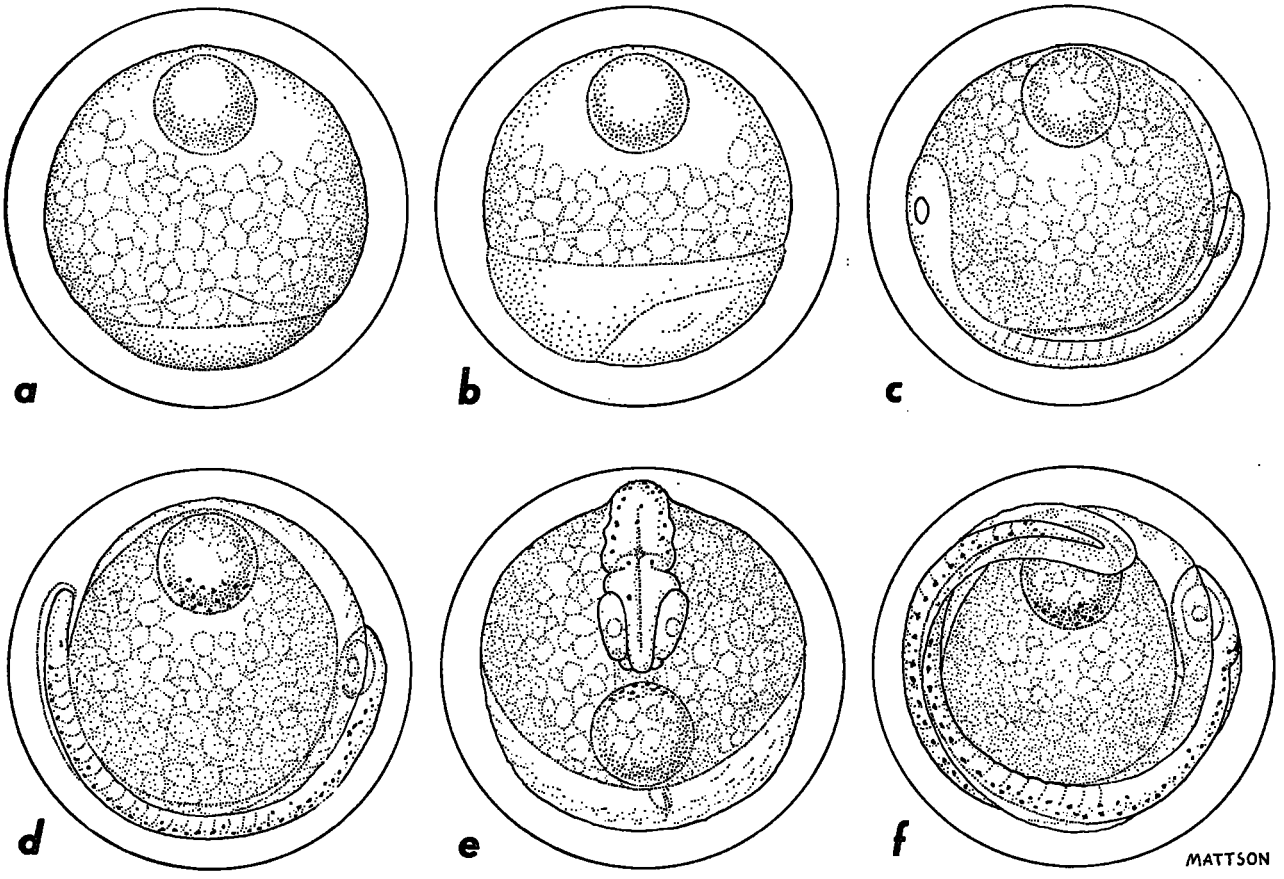

FIGURE 1.—Jack-mackerel eggs in various stages of development. *a*, *b*, and *c*, early embryonic period, *c* being the stage immediately preceding blastopore closure; *d*, intermediate period of embryonic development; *e* and *f*, late-period eggs with advanced embryos; *e* shows an egg as viewed from above; all other figures are lateral views.

TABLE 1.—*Measurements of jack-mackerel eggs, 1950*

Station	Date of collection	Number measured	Diameter in mm. of —					
			Eggshell		Yolk		Oil globule	
			Mean	Range	Mean	Range	Mean	Range
70.100	May 4	49	1.00	(0.92–1.05)	0.78	(0.68–0.85)	0.28	(0.22–0.35)
80.90	May 4	50	.99	(0.92–1.05)	.81	(0.72–0.90)	.26	(0.22–0.30)
83.70	Apr. 11	52	1.02	(0.95–1.08)	.85	(0.75–0.92)	.27	(0.20–0.32)
83.90	May 11	53	.97	(0.92–1.00)	.74	(0.70–0.80)	.26	(0.20–0.30)
87.80	Apr. 10	50	1.01	(0.95–1.08)	.82	(0.72–0.88)	.26	(0.22–0.30)
87.80	May 10	35	.97	(0.92–1.02)	.81	(0.75–0.85)		
90.90	May 6	50	.96	(0.92–1.00)	.79	(0.70–0.82)	.24	(0.18–0.30)
93.60	May 13	49	.99	(0.95–1.05)	.76	(0.68–0.85)	.25	(0.20–0.30)
97.40	May 15	50	1.00	(0.92–1.05)	.79	(0.72–0.85)	.25	(0.18–0.30)
100.60	May 15	50	.96	(0.92–1.00)	.82	(0.75–0.88)	.26	(0.20–0.30)
100.100	May 14	50	.96	(0.90–1.00)	.74	(0.68–0.78)	.24	(0.18–0.30)
Total (average)		538	.98	(0.90–1.08)	.80	(0.68–0.88)	.26	(0.18–0.35)

mechanical rupture of the yolk membrane during collection and preservation of the eggs, inasmuch as eggs in which the germ ring has encircled the yolk mass do not show this damage.

The oil globule is approximately spherical in shape. In some preserved samples, however, the oil globule may be irregularly distorted, occasionally even fractured into several droplets. The oil globule is yellow in preserved material.

During the early stages of development, the oil globule is centered at the vegetative pole, opposite the developing blastodisc. As spherical, pelagic eggs characteristically float with the vegetative pole uppermost, the oil globule is at the top of the

yolk mass. Immediately following the closure of the blastopore, a number of melanophores appear on the underside of the oil globule. During the later stage of embryonic development the oil globule becomes situated rather close to the head (fig. 1*e*), and on hatching is immediately under the forward part of the head (fig. 2). This feature is a reliable diagnostic character in the identification of jack-mackerel eggs, inasmuch as comparatively few species have the oil globule so situated. For example, the eggs of hake, *Merluccius productus* (Ahlstrom and Counts 1954), and Pacific mackerel, *Pneumatophorus diego* (Fry 1936), are similar in size and in superficial appearance to those of the jack mackerel, but in both the oil globule is situated close to the anus, with the result that after hatching, the oil globule is located at the posterior end of the yolk sac.

There is nothing unusual in the embryonic development of jack-mackerel eggs. Most pelagic-fish eggs follow a similar pattern of embryonic differentiation; that of the jack mackerel could be characterized as typical, hence, there seems little point in giving a detailed account. Of more concern to us are diagnostic characters that aid in the identification of jack-mackerel eggs at various stages in their embryonic development. We will list such characters for three embryonic periods: Early (fertilization to blastopore closure), intermediate (from blastopore closure until the separating tail begins to twist out of the plane of the embryonic axis), and late (eggs with advanced embryos).

Fish eggs usually are more difficult to identify during the early stages of development (before blastopore closure), than in later stages. In early stages, diagnostic characters are limited to such features as egg size and shape; number, size, color, and position of oil globules; size of perivitelline space; color and texture of yolk; and the character of the eggshell. However, the degree of development of the embryo before blastopore closure may be a useful diagnostic character. In later stages, when the embryo is better developed, such additional characters as pigmentation, position of the anus, and approximate number of myomeres can be used. In samples containing a number of jack-mackerel eggs there are usually several stages of development represented. In many samples all three periods of embryonic development, early, intermediate, and late, are present. Jack-mackerel eggs, like those of the sardine, seem to require only about 2 to 4 days to complete their embryonic development, the length of time depending on the temperature of the water (*cf.* Ahlstrom 1943). However, a detailed study has not been made of the relation between water temperature and the speed of embryonic development of jack-mackerel eggs.

Characters that aid in identification

1. *During early embryonic development (to closure of blastopore)* (fig. 1, *a*, *b*, and *c*):

Egg size: Approximately 1 mm.

Shell membrane: Unsculptured, clear.

Oil globule: Single, yellow, diameter approximately one-fourth of that of egg; situated at vegetative pole.

Perivitelline space: Rather narrow—about 0.1 mm. wide.

Yolk material: Color tan; probably colorless and translucent in living material; more or less segmented. Segmentation of the yolk material is usual for the eggs of isospondylid fishes, but unusual in those of percomorph fishes. Hence, the segmentation of the yolk is perhaps the most important diagnostic feature of early embryonic jack-mackerel eggs.

Embryo: Myomeres appear behind the head and the optic vesicles form shortly before blastopore closure.

2. *During the intermediate period of embryonic development* (fig. 1*d*).—Most of the characters listed under the early stage, such as egg size, color, size, and position of oil globule, width of perivitelline space, and color and segmentation of yolk mass, apply here. In addition, the following characters are of aid in identifying jack-mackerel eggs during this period of development:

Dorsal body pigmentation: Present on specimens soon after blastopore closure; consists of double row of small melanophores on either side of the notochord, originating behind the eyes and extending along most of the length of the body; arched on back of head. Usually some melanophores scattered over back between the double row.

Oil globule pigmentation: A group of discrete melanophores appears on the underside of the oil globule.

Oil globule position: At the periphery of the yolk in a median position between the head and tail region.

Number of myomeres: About 20 can be counted, and it is quite evident that the number will be low. The number of myomeres will correspond to the number of vertebrae.

3. *During the later part of the embryonic development* (fig. 1, *e* and *f*).—Most of the characters listed under the early and intermediate periods of embryonic development still apply. In addition, the following characters are of aid in identifying late-period jack-mackerel eggs:

Oil globule position: No longer median, but now nearer head than anus.

Pigmentation: In addition to the dorsal pigmentation, which arches anteriorly and ends about eight-tenths of the way back on the body, there is an irregular group of ventral melanophores beginning at the anus and extending as far posteriorly as the dorsal pigmentation. Also, embryos nearly ready to hatch often have a number of small, inconspicuous peritoneal melanophores.

Number of myomeres: Most of the myomeres are differentiated, and it can now be quite definitely determined that the number will not exceed 25.

Fin fold: A fairly wide fin fold develops before hatching. It extends around the body from the back of the head to the yolk sac. It lacks pigmentation.

Yolk mass: Segmentation is still evident in the yolk mass. No pigmentation develops on the yolk membrane. In both respects, jack-mackerel eggs differ from those of the Pacific mackerel and hake.

Length of digestive tract: In late-stage jack-mackerel eggs it can be determined that the digestive tract will extend approximately six-tenths of the way back along the body.

Stage of development at hatching: Jack-mackerel eggs hatch in a relatively undeveloped condition: before the mouth is formed, before the eyes are pigmented, or before any fin formation. These features help to separate the eggs of jack mackerel from those of species that have a more extended embryonic development.

The distribution of pigment (including both its presence and absence) is the most important aid in identifying late-period jack-mackerel eggs.

Fishes differ greatly in the amount of development that takes place during the embryonic period of their life history. As a rule, species with demersal eggs have a more protracted embryonic period and hatch at a more advanced stage of development than species with pelagic eggs. But even among pelagic species there is considerable variation in this regard. The jack mackerel, like the sardine, anchovy, hake, Pacific mackerel and many other pelagic species, begins its postembryonic development in a relatively undeveloped condition. It hatches before the mouth is formed, before the eyes are pigmented, and before the pectorals are formed. In contrast, the saury [1] begins its postembryonic development with a functional mouth, pigmented eyes, functional pectorals, and even a developed caudal fin. There are some species with pelagic eggs, including a number of pleuronectids, which are intermediate between the jack mackerel and saury in the amount of development that takes place during the embryonic period.

Species that complete the embryonic development rapidly and in a relatively undifferentiated condition are usually species that spawn a large number of rather small eggs. Although the fecundity of jack mackerel is not known, the female undoubtedly spawns a very large number of eggs.

[1] The saury is considered to have pelagic eggs, even though the eggs occur in clusters held together by filaments. Saury eggs are commonly taken in plankton hauls.

YOLK-SAC LARVAE

(FIGURES 2 and 3)

Because of the rapid differentiation that occurs during the yolk-sac stage, we are discussing this stage of larval development as a separate category.

Size at hatching

Since all observations were made on preserved material, we have not been able to determine exactly the size at hatching. Measurements were made on yolk-sac larvae that had approximately the same amount of yolk material as eggs about ready to hatch; such larvae had a size range of 1.91 to 2.38 mm., with a mean of 2.07 mm. This mean value may be considered to approximate the average size at hatching as determined from preserved material. Not having studied living material, we cannot estimate the amount of shrinkage due to formalin preservation. However, based on personal experience with other fish larvae at the yolk-sac stage, a significant amount of shrinkage on preservation is to be expected, perhaps as much as 20 percent.

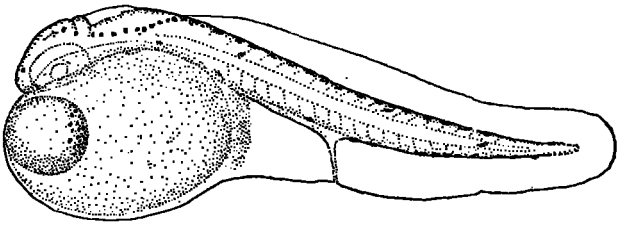

FIGURE 2.—Yolk-sac larva, 2 mm. Soon after hatching.

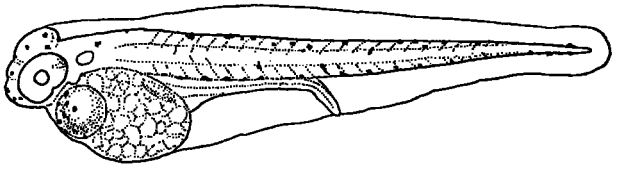

FIGURE 3.—Yolk-sac larva, 2.8 mm.

Size at end of yolk-sac stage

The yolk material has been absorbed by about 75 percent of the larvae by the time they reach 3.25 mm. in length, although one individual 3.8 mm. in length still retained some yolk.

Of the larvae used for measurements, the percentage of larvae retaining yolk material in different size groups was as follows:

Size group	Number examined	Number with yolk	Percentage with yolk
2.00–2.49 mm	8	8	100
2.50–2.99 mm	18	11	61
3.00–3.49 mm	16	4	25
3.50–3.99 mm	15	1	7
4.00–4.49 mm	15	0	0

Oil globule

The oil globule with its associated pigment spots remains fixed in position in the forward part of the yolk sac. In newly hatched larvae it is under the forward part of the head. As the yolk sac contracts, due to absorption of its contents, the oil globule is carried posteriorly to position just forward of, but ventral to, the pectoral bases; however, the globule still retains its anterior position within the yolk sac. It gradually diminishes in size, although a portion of the oil material persists until the end of the yolk-sac stage. The melanophores associated with the oil globule appear to be deposited in the ventral body wall, forming a conspicuous patch just behind the head.

The position of the oil globule within the yolk sac is an aid in the identification of the yolk-sac larva. The forward position of the oil globule has been described in other carangid larvae (Holt 1898, Ehrenbaum 1905, Delsman 1926, Sanzo 1933). The hake and Pacific mackerel are examples of species that have the oil globule in posterior position within the yolk sac. From our observations, the posterior placement of the oil globule is much more common in fish larvae than the anterior position found in most carangids.

Pigmentation at hatching

At hatching, the pigmentation on the jack mackerel larva is mostly confined to the dorsal and ventral margins of the body, and to the peritoneum. The dorsal pigmentation begins in the head region and extends posteriorly for about eight-tenths of the body length. It is similar to the embryonic pigmentation. It consists principally of a double line of dorsal pigment spots, usually parallel, but having a marked lateral arch immediately behind the eyes. There are usually some scattered dorsal melanophores. Peritoneal pigmentation is often present at hatching and soon forms a line of pigment spots along the dorsal surface of the abdominal cavity. The ventral pigmentation, except for that on the oil globule in the yolk sac, occurs behind the anus. It consists of a row of irregularly spaced pigment spots on either side of the body, just above the ventral margin. The ventral pigmentation, like the dorsal, ends some distance before the tip of the notochord. The fin fold neither has pigment at hatching, nor does it acquire any during larval development.

Development during yolk-sac stage

The jack-mackerel larva, on hatching, lacks a mouth, pigment in the eye, and fins of any sort (fig. 2). Other essential organs are in a similarly undeveloped state. Hence the postembryonic differentiation must proceed at a rapid rate during the few days that the yolk-sac larva can subsist on its yolk material.

By the time that the yolk material is absorbed, the development of the structures necessary for seeing, capturing, and utilizing food material has been accomplished, and there has been a similarly rapid differentiation of other essential organs, such as the gills. The eyes may begin to develop pigment in larvae as small as 2.2 mm. Pectoral buds may be observed on larvae about 2.5 mm. in length. These rapidly grow into functional, paired fins with fleshy bases and rather wide fan-shaped membranes without rays. The development of the mouth follows a pattern that we have observed in a number of other pelagic larvae: The lower jaw buds first appear at the posterior corners of the developing mouth and rapidly grow forward.

Ossification begins during the latter part of the yolk-sac stage. Structures containing a high percentage of calcium phosphate stain red with alizarin (Hollister 1934: 94), and we consider ossification to have begun as soon as a bone takes up any amount of alizarin stain. The cleithrum and jawbones are the first structures to ossify. The cleithrum stains with alizarin in some larvae as small as 2.95 mm., and in all larvae over 3.45 mm. in length. The jawbones begin to ossify at about the same time: The upper jaw in larvae between 3 and 3.5 mm. in length, the lower in larvae between 3.2 and 3.8 mm. in length.

LARVAL AND EARLY-JUVENILE STAGES

(FIGURES 4 to 9)

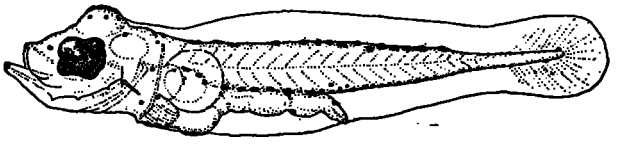

FIGURE 4.—Larva, 3.5 mm.

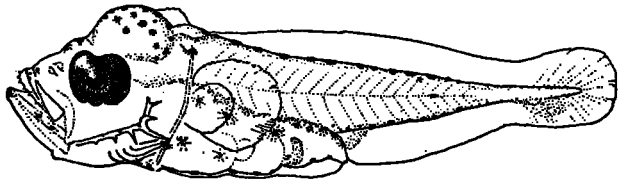

FIGURE 5.—Larva, 4.9 mm., lateral view.

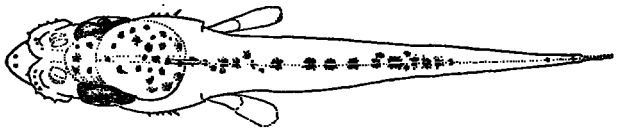

FIGURE 6.—Same specimen as figure 5, dorsal view.

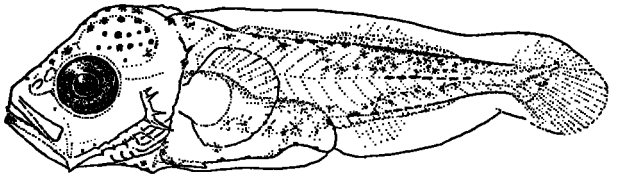

FIGURE 7.—Larva, 7.4 mm.

It has become almost conventional, in papers dealing with larval fish, for the investigator to describe individuals at a few stages in their development. This type of static approach is more or less forced on investigators who are basing their descriptions upon limited material. However, a more systematic investigation of the changes occurring during the larval period can be made when abundant material is at hand. Then, a dynamic approach can be used—the sequence of changes occurring during the larval period can be traced character by character. We have followed the latter approach.

In investigating the changes that occur in development from the time of hatching through the larval period to the early juvenile stage, we have selected at random specimens representative of the size range covered by our material. These specimens have been treated with potassium hydroxide, stained with alizarin and cleared in glycerin. Measurements and counts were made on a total of 182 individuals, and the results are summarized in table 2. The procedures followed in obtaining the measurements and meristic counts are discussed in the Appendix, page 244. An equally large number of unstained specimens were used in studying changes in pigmentation during the larval period.

Larval development will be discussed under the following headings: (1) Pigmentation changes during larval development, (2) changes in body form during larval development, (3) fin formation, and (4) sequence of ossification.

Pigmentation changes during larval development

The only chromatophores that are visible on formalin-preserved eggs and larvae of jack mackerel are melanophores. The pigmentation pattern of jack-mackerel larvae is subject at all sizes to considerable variation in both the amount of pigmentation and the size of individual pigment spots.

Head pigmentation.—There are a few melanophores on the head of the jack-mackerel larva at the end of the yolk-sac stage. The number gradually increases until, on larvae of about 3.5 to 4 mm., a cap of discrete melanophores is present and pigmentation extends forward between the eyes. In addition, a few melanophores are usually present forward of the nostrils and along the lower jaw, with a conspicuous group near the tip of the lower jaw. Pigmentation intensifies during the period of larval development. Lateral pigmentation on

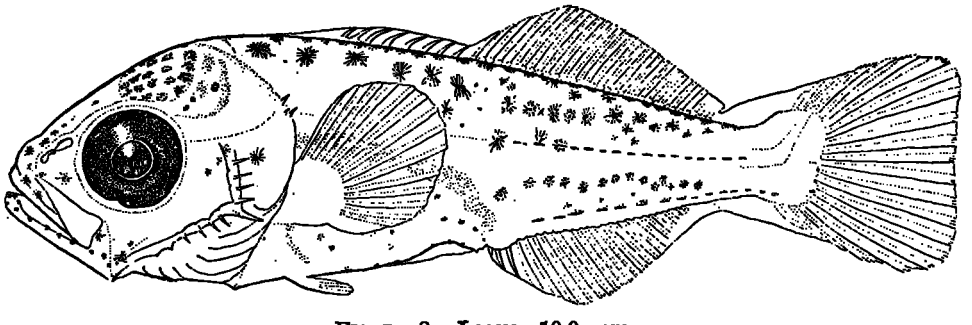

FIGURE 8.—Larva, 10.0 mm.

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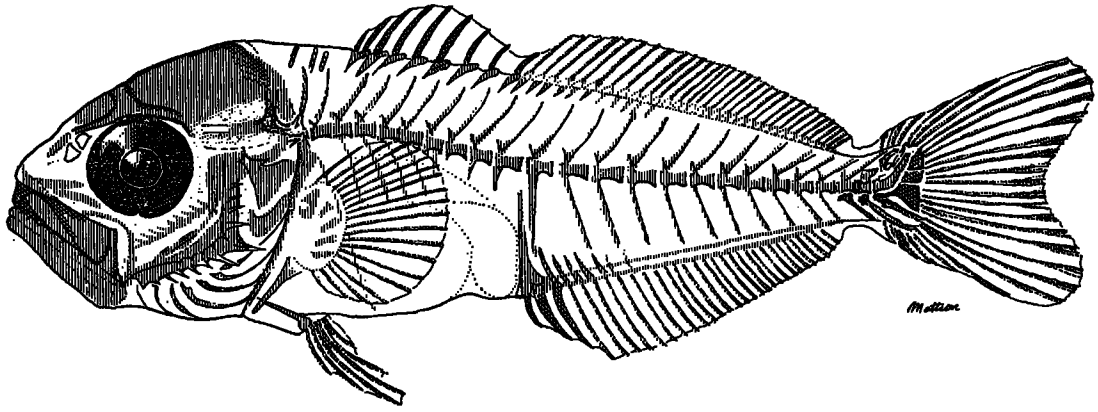

FIGURE 9.—Drawing of a cleared and stained larva, 13.0 mm. in length, showing details of the skeletal structure.

TABLE 2.—*Measurements and meristic counts of 182 jack-mackerel larvae and early juveniles*

[LP=larval pectoral; BF=base forming; F=forming]

Size	Number specimens examined	Average measurements (in mm.)					Meristic counts						
		Standard length	Head	Eye	Snout to anus	Depth	Vertebrae	Caudal [1]	Pectoral	First dorsal	Second dorsal	Anal	Ventral
2.0–2.4 mm	8	2.2		0.19	1.2	Yolk							
2.5–2.9 mm	18	2.8	0.47	.24	1.5	0.46			LP				
3.0–3.4 mm	16	3.2	.66	.30	1.8	.62			LP				
3.5–3.9 mm	15	3.8	.99	.39	2.2	.82			LP				
4.0–4.4 mm	15	4.2	1.25	.46	2.4	1.03		BF	LP				
4.5–4.9 mm	15	4.8	1.52	.54	2.8	1.23		BF	LP		BF	BF	
5.0–5.9 mm	15	5.4	1.65	.60	3.2	1.37	2.6	1.1	LP		BF	BF	
6.0–6.9 mm	15	6.5	2.06	.76	3.8	1.68	17.8	9.2	1.8		BF	[2] 1.4	
7.0–7.9 mm	16	7.5	2.49	.87	4.4	1.93	20.7	15.2	5.6	0 to VI	[2] 6.7	[2] 8.9	Bud.
8.0–8.9 mm	15	8.3	2.82	1.04	5.1	2.32	23.3	16.8	9.8	III to VIII	I, 18.2	[2] 17.8	F.
9.0–9.9 mm	7	9.3	3.23	1.15	5.6	2.58	23.9	17.0	12.2	VI to VIII	I, 22.8	II–I, 18.6	2.2.[2]
10.0–10.9 mm	8	10.6	3.69	1.26	6.3	2.90	24.0	17.0	14.2	VII or VIII	I, 27.3	II–I, 22.6	I, 4.2.
11.0–11.9 mm	2	11.5	4.1	1.40	6.8	3.2	24.0	17.0	15.5	VII or VIII	I, 29.0	II–I, 24.5	I, 5.
12.0–12.9 mm	4	12.2	4.1	1.51	7.0	3.4	24.0	17.0	17.2	VIII	I, 30.8	II–I, 26.5	I, 5.
13.0–13.9 mm	1	13.5	4.8	1.52	8.0	3.6	24.0	17.0	19.0	VIII	I, 30	II–I, 27	I, 5.
14.0–14.9 mm	1	14.4	5.4	1.72	8.6	4.1	24.0	17.0	22.0	VIII	I, 32	II–I, 28	I, 5.
15.0–19.9 mm	4	17.0	5.9	2.09	9.4	4.4	24.0	17.0	20.8	VIII	I, 33.8	II–I, 28.2	I, 5.
20.0–49.9 mm	5	32.1	10.0	3.27	17.4	8.1	24.0	17.0	22.8	VIII	I, 32.8	II–I, 29.4	I, 5.
50.0 mm. and over	2	52.8	14.7	4.50	28.8	12.8	24.0	17.0	21.5	VIII	I, 33.0	II–I, 28.5	I, 5.

[1] Principal caudal rays, i. e., the branched rays and the adjacent unbranched ray on either side.
[2] Spines and rays combined in counts during early differentiation.

the head, however, is usually lacking until the larva reaches about 7 to 8 mm. in length, and is seldom conspicuous even then.

Body pigmentation.—The body pigmentation of jack-mackerel larvae falls naturally into 3 areas:

1. Preanal, including the peritoneal pigmentation, extending from the head to approximately the ninth myomere.

2. Postanal, extending from about the 10th to the 20th myomere, the area of heaviest pigmentation.

3. Caudal peduncle, from about myomere 21 to the tip of the notochord (or base of caudal fin), an area that is inconspicuously pigmented.

Preanal body pigmentation.—At hatching (fig. 2), the pigmentation anterior to a vertical through the anus, which we are calling preanal body pigmentation, is usually confined to the dorsum and to the peritoneal region. Pigment spots do not appear along the median line of the belly until after yolk absorption.

The number of dorsal melanophores decreases soon after hatching. On newly hatched yolk-sac larvae, there is a double line of small melanophores along the back. During the yolk-sac stage, a ventral migration of some of the dorsal melanophores (shown in fig. 3) occurs and probably a coalescence of others. As a result, larvae between 3 and 4.5 mm. (fig. 4) have only 2 to 7 single (not paired) dorsal melanophores in the preanal region. About the time that fin formation commences, there is an increase in the number of dorsal melanophores, and on older larvae the pigmentation spreads laterally (fig. 8). Dorsal pigmentation in the preanal region characteristically is less heavy and

intensifies more slowly than in the region behind the anus.

The peritoneal pigmentation develops most heavily along the dorsal wall. It is present in some embryos before hatching, and is well developed on larvae before the absorption of yolk is completed. Although the peritoneal pigment often gives the impression of forming a solid streak, it is actually made up of discrete melanophores in close contact. The lateral spreading of peritoneal pigments varies markedly from specimen to specimen. Some lateral spreading is found on specimens as small as 4 mm., and at 7 to 8 mm. in length (fig. 7) the lateral melanophores may have spread over most of the abdominal wall. As the larva approaches the juvenile stage, the peritoneal pigmentation becomes less evident, due to the overgrowth of musculature.

Ventral pigmentation along the belly is usually weakly developed. In smaller larvae, ventral pigmentation is often confined to a few melanophores below the pectoral fins. This pigment apparently is derived from the pigment of the oil globule. On older larvae (figs. 5 and 7) a more or less continuous line of pigment spots is present, extending from the isthmus to the anus. There is no tendency toward lateral spreading of the ventral-gut pigment.

Postanal body pigmentation.—The heaviest pigmentation develops in the region posterior to the anus, between approximately the 10th and the 20th myomere. The only ventral pigmentation present at hatching is in this area, and it soon intensifies. The dorsal pigmentation is also more crowded, and there is a more rapid lateral spreading than in the preanal portion of the back (see fig. 7 of 7.4-mm. larva). In larvae about 4 to 4.5 mm. in length, dashes of pigment appear along the lateral midline, at first on only one or two myomeres, but gradually spreading along the length of the body. A somewhat similar pattern of postanal pigmentation, including the lateral-line streak, has been described for several species of carangids, including *Trachurus trachurus* (Ehrenbaum 1905, Schnakenbeck 1931), *Decapterus punctatus* (Hildebrand and Cable 1930), and *Seriola dumerili* (Hildebrand and Cable 1930, Sanzo 1933).

Caudal pigmentation.—The caudal pigment area takes in the posterior portion of the body from approximately the 21st myomere to the tip of the notochord. In older larvae we would term this area the caudal peduncle. Pigmentation is inconspicuous in this area. In fact, unless inspected closely, the caudal area has the appearance of being unpigmented. On closer examination, however, a row of minute, closely spaced melanophores may be seen along the ventral margin and a few scattered melanophores dorsally. After caudal-fin formation, a number of melanophores can be seen along the base of the caudal. Except for the fringe pigmentation, the caudal peduncle remains unpigmented until after fin formation is complete.

During the latter part of the larval period, pigmentation often occurs over most of the head and body of the jack mackerel; however, the melanophores are not uniformly distributed. Dorsal pigmentation is usually better developed than ventral. The areas on which pigment is often sparse or lacking, even on heavily pigmented larvae include: (1) The side of the head, (2) the lower portion of the abdomen just above the ventral pigment line, (3) the sides of the body just above the abdomen, and (4) the caudal peduncle. Except at the base of the caudal, there is no pigmentation on the fins during the larval period.

Pigmentation of juveniles (Figure 10)

In contrast with the pigment areas described for larvae, pigmentation of juveniles is sharply separated into dorsal and ventral areas. The conspicuous line of pigment along the lateral midline of the body separates the heavy dorsal pigmentation from the rather sparse ventral pigmentation. The dorsal melanophores are of several sizes, the larger cells, though scattered, being especially noticeable. The dorsal pigmentation extends from the tip of the snout to the base of the tail. The peritoneal pigmentation can be seen through the overlying musculature, heaviest dorsally, becoming scattered and finally dissipating ventrally.

In addition to the peritoneal markings, there are a number of scattered melanophores over the ventral body surface. Some individuals have very little ventral pigmentation; others have a scattering of large melanophores, most numerous above the anal fin.

The juveniles soon develop pigmentation on the fins, particularly the caudal and dorsal. The caudal membrane develops a line of closely spaced spots which parallel the principal rays. A

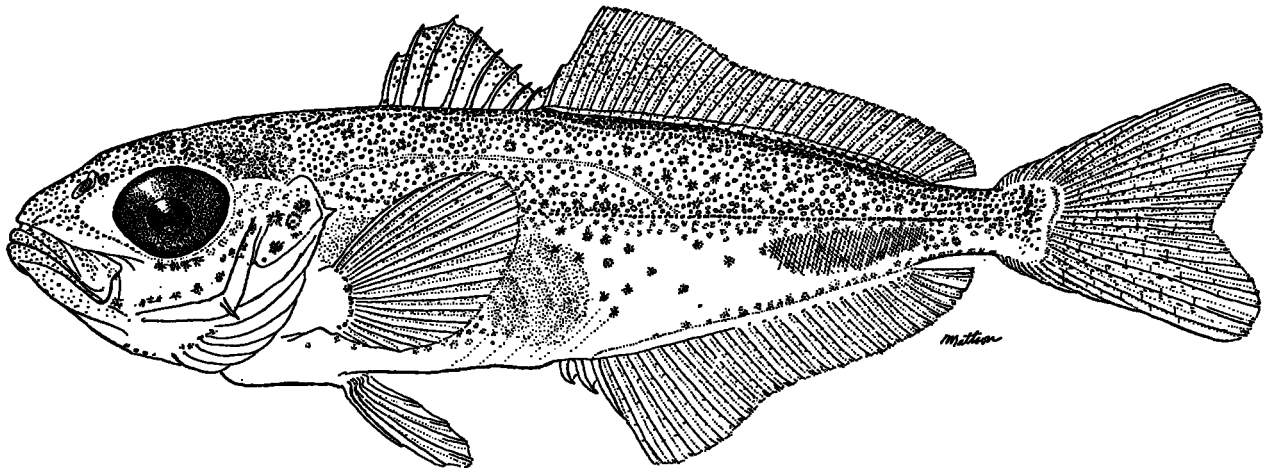

FIGURE 10.—Juvenile, 28 mm.

sprinkling of melanophores appears on the membrane between the spines of the anterior dorsal, especially distally. On the soft dorsal, melanophores first appear on the membrane in the anterior portion, and then spread posteriorly. The anal fin is largely unpigmented, having only a few melanophores near the outer forward margin. The pectorals are lightly pigmented near their dorsal margin. The pelvics are immaculate.

Changes in body form

The most striking changes in body form take place during and soon after the yolk-sac stage of larval development, before the larva attains a length of about 4.2 mm. During this period, the larva changes from the slender-bodied form which it was at hatching to a deep-bodied, stubby form with a large head.

Head.—During the early period of larval development, until approximately 4.2 mm. in length, the head increases in length at a more rapid rate than during later larval development. Two lines can be fitted to a regression of head length on standard length, one applying to larvae up to 4.2 mm. in length, the other to individuals between 4.2 and 17 mm. in length (fig. 11). At 4.2 mm., the head is approximately 1.25 mm. in length. Before attaining this size, the head increases at a rate of 0.56 mm. for each 1-mm. increase in body length; subsequently the head increases at a rate of approximately 0.38 mm. for each 1-mm. increase in body length (see table 3).

Body depth (at pectoral).—There is a correspondingly rapid increase in body depth before a length of 4.2 mm. is attained, and a slower rate of growth thereafter (fig. 12). At 4.2 mm., the body depth (at pectoral) averages 1.03 mm. In individuals smaller than 4.2 mm., the body depth increases at a rate of approximately 0.4 mm. for each 1-mm. increase in body length; subsequently, the depth increases at a rate of approximately 0.28 mm. for each 1-mm. increase in body length (table 3).

TABLE 3.—*Statistics describing regressions of body proportions on standard length for jack-mackerel larvae*

$\bar{x}$=mean of values of x
$\bar{y}$=mean of values of y
N=number of size groups
b=rate of increase of y
a=y-intercept of regression line
$sy{\cdot}x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size of larvae	$\bar{x}$	$\bar{y}$	N	b	a	$sy{\cdot}x$
		Mm.						
Standard length	Head length	2.8–4.2	3.50	0.84	4	0.556	−1.104	0.026
Do	do	4.2–17.0	9.63	3.31	13	.378	−.335	.125
Do	Body depth	2.8–4.2	3.50	.73	4	.400	−.652	.027
Do	do	4.2–17.0	9.63	2.60	13	.278	−.080	.113
Do	Eye diameter	2.2–17.0	8.07	.94	17	.127	−.080	.041
Do	Distance from snout to anus	2.2–17.0	8.07	4.71	17	.581	+.020	.181

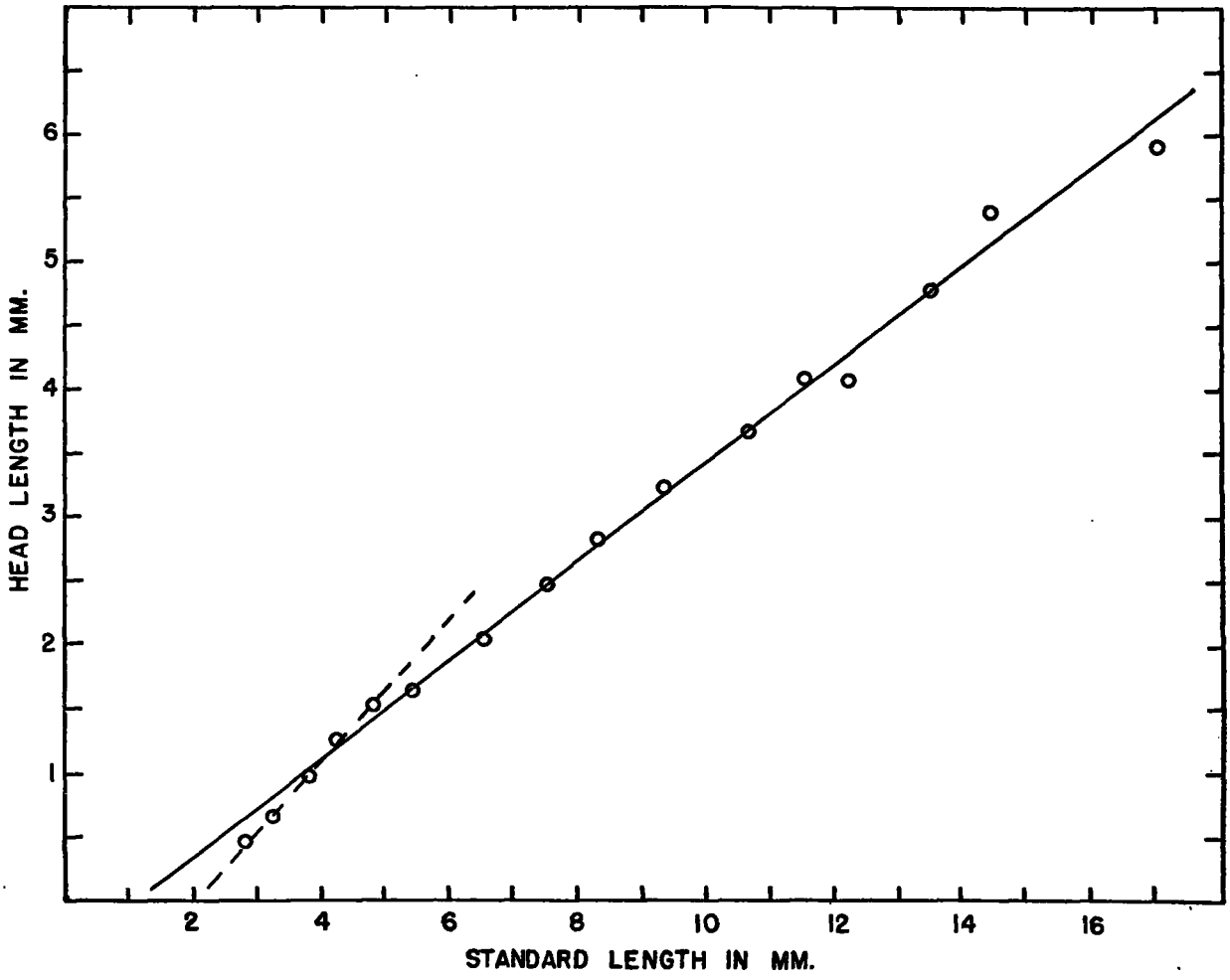

FIGURE 11.—Regression of head length on standard length. Each circle is the average group of measurements, usually 15 (refer to table 2, columns 2, 3, and 4). Two regression lines have been fitted to the data by the method of least squares, one for larvae 2.8 to 4.2 mm. in length, the other for individuals 4.2 to 17 mm. in length. Statistics describing the two lines are given in table 3.

Eye.—Throughout the period of larval development, the rate of increase in eye diameter is proportional to the increase in standard length—the eye increasing 0.127 mm. in length for each 1-mm. increase in standard length. This is shown in figure 13, where eye diameter is plotted against standard length. This relation is obscured by using proportionate measurements, as is so often done in taxonomic and larval studies. For when so expressed, the eye diameter is 8.5 percent of the standard length at hatching, 11 percent of the standard length at 4.2 mm., and over 12 percent of the standard length at 8.3 mm. in length (see table 4). But as we have seen, the eye actually is increasing at a constant increment in relation to standard length, not at a changing rate (some scientists have used such proportions as rates). The difference is due to the circumstance that the y-intercept differs significantly from zero (see in this regard, Marr [in press]). At hatching, the eye is approximately elliptical. Soon after hatching, the eye shape becomes distorted, assuming a somewhat squarish outline. By the time the larva has grown to 5 or 6 mm. in length, the eye usually has assumed the spherical form which it retains throughout its subsequent development. The eye is cleft ventrally.

Distance from snout to anus.—The distance from snout to anus not only increases at a constant rate in relation to standard length (there is an increase of 0.58 mm. in the distance from snout to anus with each 1-mm. increase in standard length) (fig. 14), but a line fitted to the regression of snout to anus on standard length approaches the

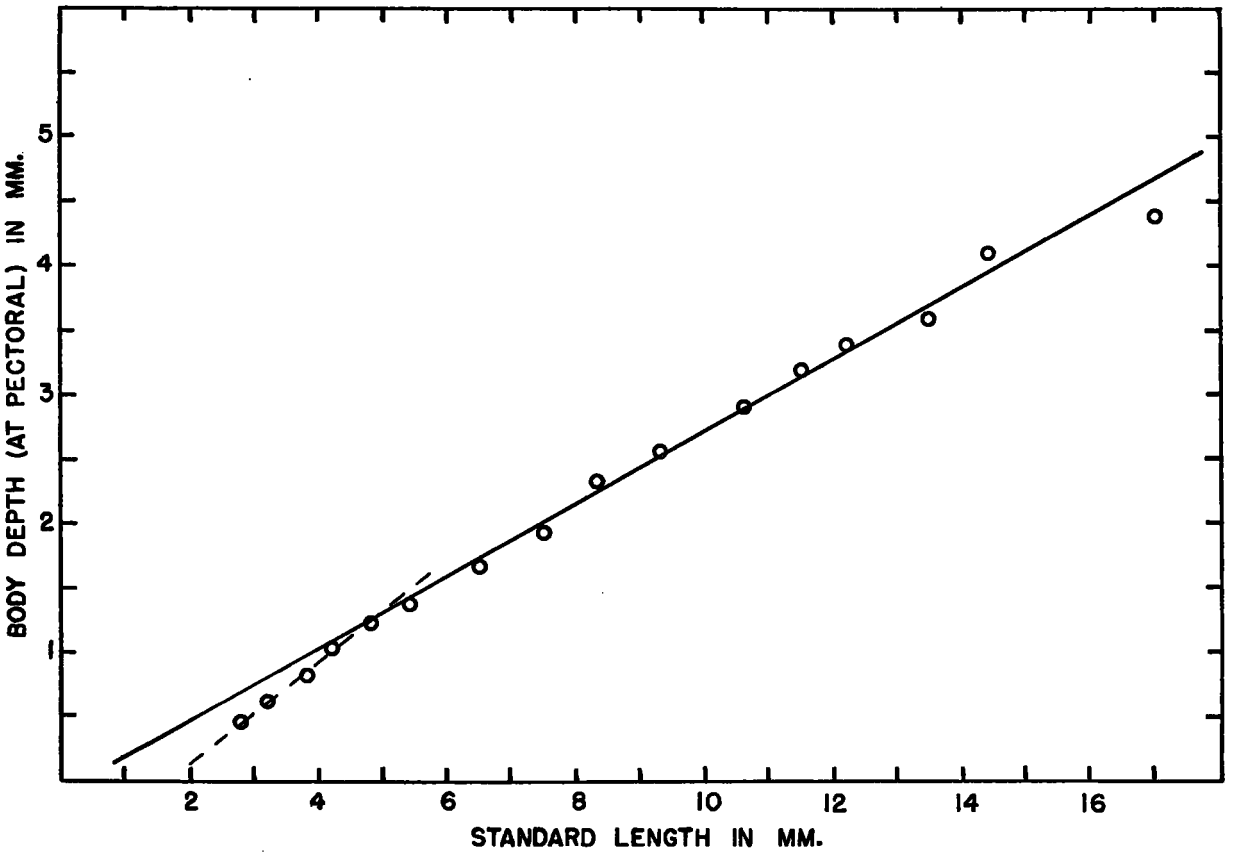

FIGURE 12.—Regression of body depth (at pectoral) on standard length. Each circle is the average of a group of measurements, usually 15 (refer to table 2, columns 2, 3, and 7). Two regression lines have been fitted to the data by the method of least squares, one for larvae 2.8 to 4.2 mm. in length, the other for individuals 4.2 to 17 mm. in length. Statistics describing the two lines are given in table 3.

TABLE 4.—*Body proportions of 182 jack-mackerel larvae and early juveniles*

[Based on values given in table 2, columns 1 through 7]

Size	Standard length	Proportion expressed as percentages of standard length			
		Head	Eye	Pectoral depth	Snout to anus
2.2–2.4 mm	2.2 mm.	----------	8.5	----------	56.1
2.5–2.9 mm	2.8 mm.	16.7	8.8	16.6	52.9
3.0–3.4 mm	3.2 mm.	20.6	9.2	19.3	55.8
3.5–3.9 mm	3.8 mm.	26.1	10.2	21.6	57.0
4.0–4.4 mm	4.2 mm.	29.8	11.0	24.6	58.2
4.5–4.9 mm	4.8 mm.	31.9	11.3	25.8	59.5
5.0–5.9 mm	5.4 mm.	30.3	11.0	25.1	59.6
6.0–6.9 mm	6.5 mm.	31.6	11.6	25.7	58.8
7.0–7.9 mm	7.5 mm.	33.1	11.6	25.7	59.2
8.0–8.9 mm	8.3 mm.	34.1	12.6	28.0	61.1
9.0–9.9 mm	9.3 mm.	34.6	12.3	27.6	59.7
10.0–10.9 mm	10.6 mm.	34.9	11.9	27.5	59.6
11.0–11.9 mm	11.5 mm.	35.5	12.2	27.8	59.1
12.0–12.9 mm	12.2 mm.	33.7	12.4	27.5	57.4
13.0–13.9 mm	13.5 mm.	35.6	11.3	27.0	59.3
14.0–14.9 mm	14.4 mm.	37.5	11.9	28.5	60.1
15.0–19.9 mm	17.0 mm.	34.6	12.3	26.1	55.2
20.0–49.9 mm	32.1 mm.	31.1	10.2	25.1	54.1
50.0 mm. and over	52.8 mm.	27.8	8.5	24.2	54.6

origin (the y-intercept value is only 0.02). Consequently, even proportionate measurements show a constant rate of increase in distance of snout to anus when related to increase in standard length.

The fins are formed in about the position they will retain during life. There is no marked forward movement of the dorsal fin as there is in the sardine and other clupeid larvae. At formation, the origin of the soft dorsal is immediately above the anus, and it retains this relative position during the larval and juvenile stages.

The digestive tract, conspicuous along the ventral portion of the body during the early larval period, is obscured by overlying tissue by the time the larva has attained approximately 10 mm. in length (fig. 8, 10-mm. larva). There is a single loop in the intestine, particularly noticeable in larvae between about 4 and 6 mm. in length. The air bladder is first noticed in larvae about 3.3 to 3.5 mm. in length. It very rapidly grows into a large conspicuous organ which is located just posterior to the pectoral fin, and in larger larvae is partly obscured by that structure. In larvae about 8.5 to 9 mm. in length, the air bladder be-

comes less evident due to intensification of the overlying musculature.

Fin formation

Fin formation follows a definite sequential pattern in jack-mackerel larvae. At hatching, there is no indication of any fin development. The subsequent development of the larval pectoral fin has already been touched upon. In the caudal area, faint traces suggesting rays can be detected shortly after the appearance of the larval pectoral fin (fig. 4, larva 3.5 mm. long). These striations are actinotrichia, rather than true caudal rays. However, the caudal fin is the first to lay down lepidotrichia (true rays or spines), followed in order by the pectoral, anal, soft dorsal, spinous dorsal, and ventral.

Caudal fin.—The fully formed caudal fin of the jack mackerel has 17 principal (15 branched rays and the adjacent unbranched ray on either side) and approximately 18 to 20 secondary rays. The principal rays are divided into two groups, 9 rays above and 8 below the midline of the body. There are 9 or 10 secondary rays on the dorsal margin of the caudal fin, and an equal number on the ventral margin.

The caudal fin forms in much the same manner as the caudal fin of most fish larvae. A ventral thickening can be observed near the posterior end of the notochord in larvae about 4.5 mm. in length (fig. 5). Rays can be distinguished in larvae between 5 and 6 mm. in length. They form at an oblique angle, and usually the first 4 to 6 rays form simultaneously. These are equally distributed between the two sides of what will be the center of the caudal fin (midline) when formed. Differentiation then proceeds in both directions. All principal rays are ventral in origin.

While the principal rays are being laid down, the urostyle goes through the flexion that brings the principal rays into the terminal position they occupy in the fully formed caudal. The princi-

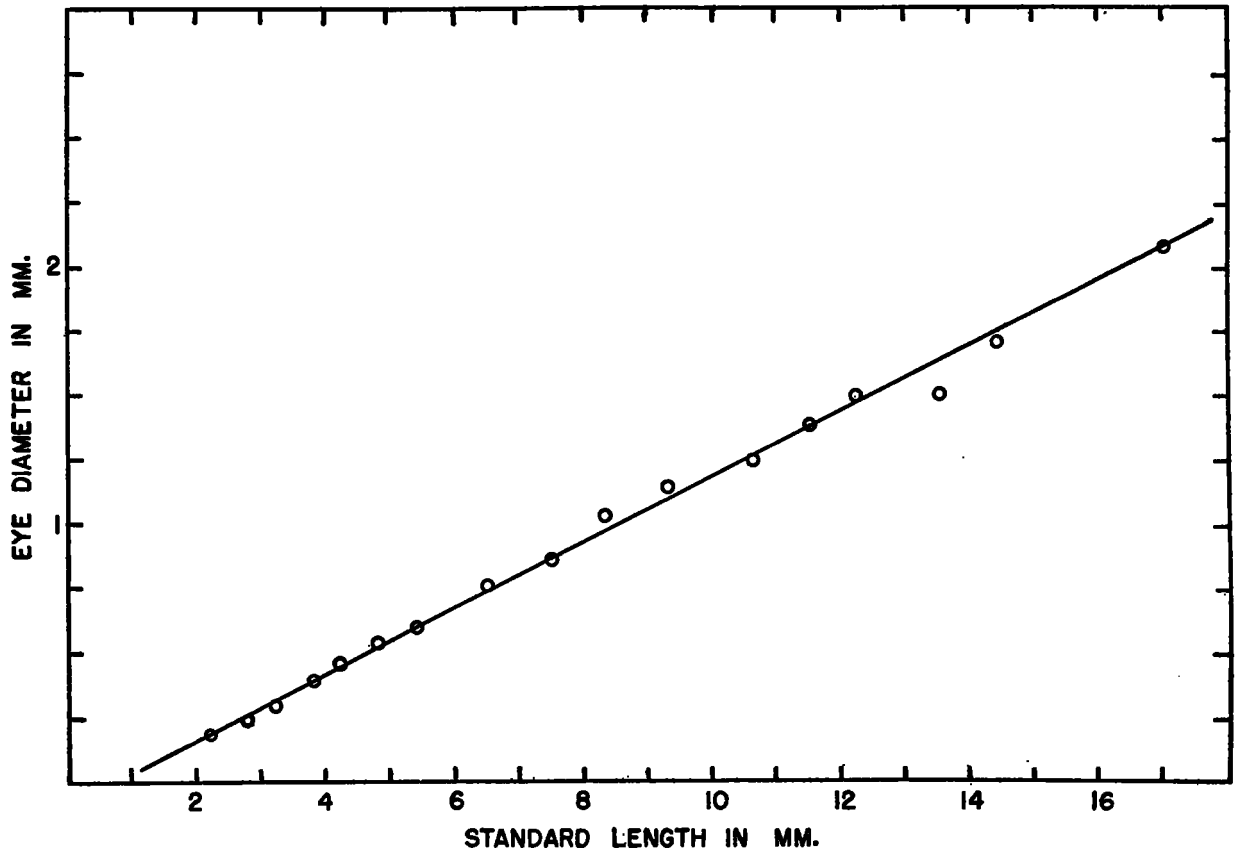

FIGURE 13.—Regression of eye diameter on standard length. Each circle is the average of a group of measurements, usually 15 (refer to table 2, columns 2, 3, and 5). Statistics describing the regression line, fitted by the method of least squares, are given in table 3.

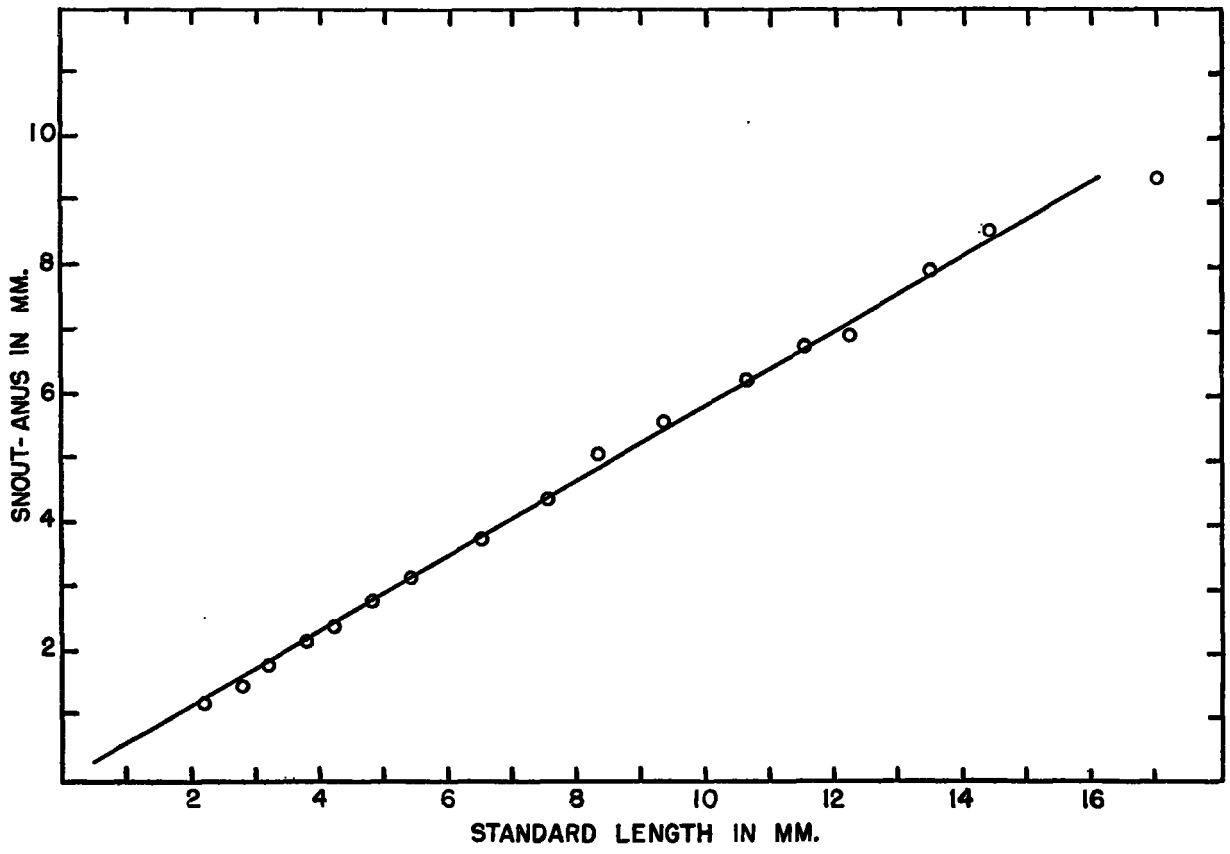

FIGURE 14.—Regression of the distance from snout to anus on standard length. Each circle is the average of a group of measurements, usually 15 (refer to table 2, columns 2, 3, and 6). Statistics describing the regression line, fitted by the method of least squares, are given in table 3.

pal rays are laid down at about 8 mm., but the flexion of the urostyle and development of the hypurals are not completed until about 11 mm. The secondary caudal rays are formed over a longer period, as is shown in the following chart, based on five specimens of selected lengths:

Size of larva	Number secondary dorsal-caudal rays	Principal caudal rays	Number secondary ventral-caudal rays
7.5 mm	0	14	0
8.2 mm	2	17	2
10.6 mm	3	17	4
12.5 mm	6	17	6
15.8 mm	9	17	9

The caudal fin is associated with the last three vertebrae (fig. 15). There are only four dorsal supporting structures, the anterior three being dorsal radials lying above the urostyle.[2] The middle dorsal radial is small and embedded, and does not support secondary caudal fin rays, as do the adjacent dorsal radials. The majority of the secondary fin rays along the dorsal margin are associated with the epural originating from the antepenultimate vertebra. There is no epural originating from the penultimate vertebra; the modified neural spine on this vertebra is expanded at its base but does not extend out for any distance.

There are 6 or 7 hypural elements, one of which would be classed as a ventral radial, and all but two of which are associated with the urostyle. Sixteen of the seventeen principal caudal rays are supported by hypural elements adjacent to the urostyle, and only one by the hypural originating from the penultimate vertebra. All secondary caudal rays along the ventral margin are supported by the anterior two hypurals, which originate from the penultimate and antepenultimate vertebrae.

There is one more hypural element discernible during the larval period than in older jack mack-

[2] We are using the same nomenclature as that given in Whitehouse (1910: 138) and Barrington (1937: 448). It should be noted that this terminology differs from that used by Hollister (1936: 259).

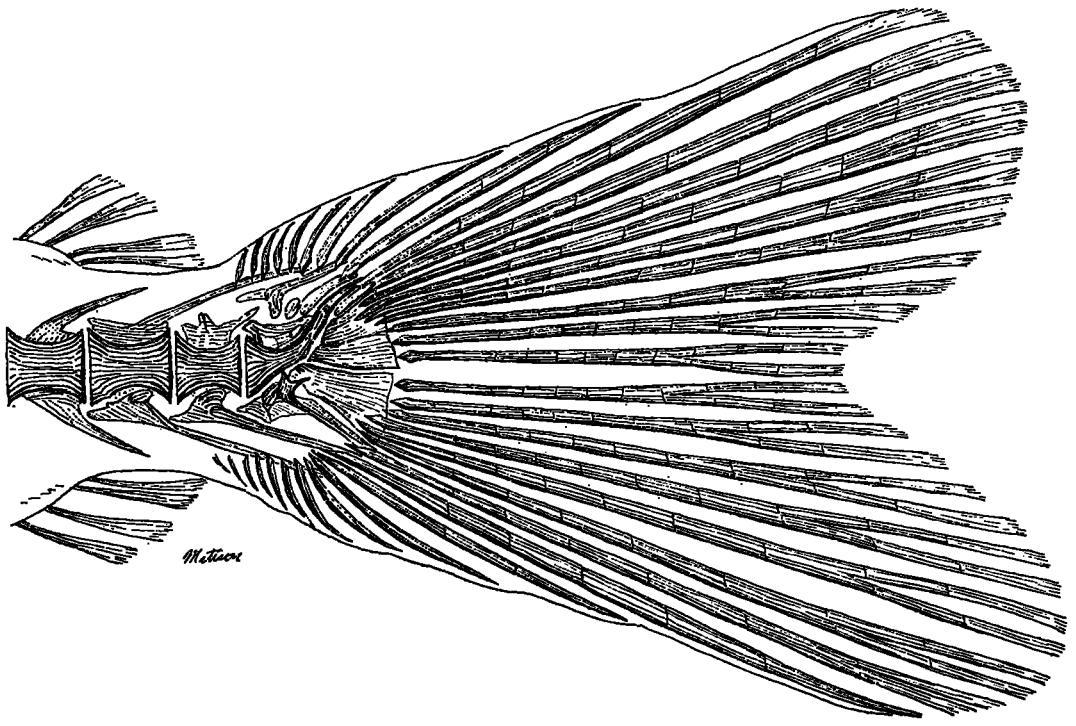

FIGURE 15.—Caudal fin and skeleton of a 24-mm. jack-mackerel larva. The last three rays of the soft dorsal and anal fins also are indicated.

erel. The principal hypural above the midline of the body is formed by the coalescence of two hypural plates, which can be distinguished as separate plates during the larval period.[3] Seven of the nine principal caudal rays above the midline of the body are associated with this hypural. There is a small, inconspicuous hypural located above the hypural just discussed. It is adjacent to the tip of the urostyle, and supports one ray. Six of the eight principal caudal rays below the midline of the body are associated with a single large hypural. A ventral radial completes the complement associated with the urostyle; it supports a single ray. This radial is connected by bony processes to the hypural above and often to the one originating from the penultimate vertebra. There is a bifurcate spine near the base of the radial.

Pectoral fins.—The next fin in which rays form is the pectoral. They are first distinguishable in some specimens about 6 mm. in length. As is usual in pectoral-fin development, the top (dorsal) rays first appear, and then rays are added ventrally. Hence, the bottom ray of the fin is the last to appear. The complete complement of 22 to 24 pectoral rays is usually attained at about 14 mm.

Anal fin.—The base of the anal fin can be observed in some larvae at about 5 mm. in length. Rays first appear in the developing anal fin in larvae between 6.7 and 7.3 mm. in length. The anterior rays take the stain first, then differentiation proceeds posteriorly. The first spine to form is at first indistinguishable from the adjacent rays, but soon differentiates as a spine. All three anal spines may be observed on some larvae as small as 7 mm., and on all larvae 9 mm. and over in length. The anterior of the three anal spines is the last to appear. Ray formation is not complete, however, until the larvae are about 14 mm. long. The full complement of spines and rays in the anal fin is II–I, 28 to 31.

Dorsal fins.—The soft, or second, dorsal fin in the jack mackerel forms before the spinous dorsal. The base of the soft dorsal fin can be seen in some

[3] Schnakenbeck (1931) found a similar sequence in the development of the caudal region of *Trachurus trachurus* (*cf.* his fig. 3). An examination of the caudal region of two other carangids (*Trachinotus* and *Oligoplites*), however, showed that in these species the two hypural plates remained separate in later stages, not coalescing as in the jack mackerel.

larvae of about 5 mm. Rays are evident in specimens about 7 to 7.5 mm. in length. As in the anal fin, the anterior rays appear first, then ray differentiation proceeds posteriorly. By 14 mm., ray formation in the soft dorsal is often complete. The spine at the anterior end of the soft dorsal is at first indistinguishable from the rays, but usually can be distinguished as a spine in specimens of 8 mm. When fully formed, the soft dorsal of our specimens had the formula I, 30 to 35.

The posterior 5 or 6 spines of the spinous, or first, dorsal fin appear almost simultaneously in specimens 7.6 to 8 mm. in length. The anterior 2 or 3 spines develop later, being present in some specimens as small as 10 mm., but not developing in other larvae until 12 mm. or so in length. The spinous dorsal when complete has VIII spines.

Ventral fins.—The bud of the ventral (pelvic) fins can usually be detected under, but slightly posterior to, the pectoral base in larvae 7 mm. in length. The rays may begin to form by 8.5 mm., but in the majority of larvae initial differentiation occurs between 9 and 9.5 mm. The course of differentiation is mesad (toward the midline). By 11 mm., the single spine and 5 rays were present on all specimens examined.

Sequence of ossification

Ossification of skeletal structures, including fin rays and spines, followed approximately the same sequence in all of the jack-mackerel larvae studied. This sequence is summarized in table 5.

Initial ossification has been dealt with briefly in the discussion of larvae in the yolk-sac stage. The cleithrum is the first bone to ossify. This is followed by the upper jawbones (premaxillaries), the lower jawbones, the preopercular spines, and the upper jaw teeth in rapid succession. The branchiostegal rays, branchial arches, and skull bones soon after show ossification. These are followed by the start of vertebral ossification. The beginning of fin-ray differentiation (caudal) occurs at approximately the same time as initial ossification of the vertebral components.

The neural spines of the anterior few vertebrae stain with alizarin in larvae 4.9 to 5.5 mm. in length. Vertebrae ossify progressively posteriorly. The neural spines of abdominal vertebrae and the neural and haemal spines of caudal vertebrae always show ossification before the centra of their respective vertebrae. In specimens 6 to 6.5 mm. in length, the centra of the first 3 or 4 vertebrae will show color, while the remaining 6 or 7 abdominal vertebrae (there are always 10 abdominal vertebrae) will have only their neural spines ossified, and the first 7 or 8 caudal vertebrae (there are almost always 14 caudal vertebrae) will show both neural and haemal spines as being ossified. The centra soon follow, ossifying progressively posteriorly.

TABLE 5.—*Sequence of ossification, exclusive of skull bones*

	Fish size at start	Fish size at finish
	Mm.	*Mm.*
Cleithrum	3–3.5	
Upper jaw	3–3.5	
Lower jaw	3.2–3.8	
Preopercular spines	3.2–3.8	
Teeth (upper jaw)	3.5–4	
Branchiostegals	4.5±	7.
Gill arches	4.5±	7.5–8.
Vertebrae	4.9–5.5	8–9.
Caudal fin	5–6	Approx. 16.
Pectoral fins	6.5–7	Approx. 14.
Anal fin	6.7–7.3	Approx. 14.
Dorsal (soft)	7–7.5	Approx. 14.
Gill rakers	7.5±	>40.
Dorsal (spinous)	7.6–8	10.0–12.
Ventral fins	9–9.5	11.
Teeth (lower jaw)	Approx. 17	
Scales	19–21	35.

The urostyle begins ossifying before the 2 or 3 vertebrae anterior to it. The urostyle first takes stain at its anterior base (at about 7.5 to 7.8 mm. in length) and then ossification progresses toward its distal tip. Simultaneously, the hypurals show evidence of ossification. All vertebrae usually are ossified in specimens 9 mm. in length. Details of skeletal structure are shown in figure 9.

The branchiostegals begin to ossify when the larva is about 4.5 mm. in length, and the process is usually complete by the time the larva reaches 7 mm. When fully formed, the number of branchiostegals is invariably 7 on a side.

The gill arches show ossification at about the same stage in development as the branchiostegals, beginning at approximately 4.5 mm. in length. The initial ossification of the arches is apparently complete at about 7.5 to 8 mm. Gill rakers can be observed on specimens between 7 and 8 mm. in length. The gill-raker counts on 8 specimens of selected sizes were as follows:

Size of specimen	Upper limb of first gill arch	Lower limb of first gill arch
7.0 mm	0	0
7.5 mm	0	10
8.5 mm	0	12
10.0 mm	0	16
15.5 mm	5	23
19.0 mm	7	26
33.5 mm	11	33
40.0 mm	12	35

By the end of the larval period (16 mm.), over 20 gill rakers are developed on the lower limb of the first gill arch, and 5 or 6 on the upper limb. A 40-mm. juvenile had several less rakers on each limb than the full complement, which, according to Roedel and Fitch (1952), should average 15 (13 to 18) on the upper limb, and 41 (37 to 45) on the lower limb of the first gill arch.

Larval armature of the gill cover occurs in a number of teleost groups. In the jack mackerel, the armature consists of spines that form on the rear edge of the preoperculum and on the preopercular crest, a ridge immediately anterior to the edge of the preoperculum. The spines on the edge of the preoperculum are larger, stronger, and more numerous than those on the preopercular crest. At the rear edge of the preoperculum, a corner spine, the largest and strongest, develops at approximately 3.5 mm. in length. Soon after the ossification of this spine, additional spines appear along the ascending and the anterior edges of the preoperculum. The spines increase in size and number during larval development, as many as 4 forming along the ascending edge and 7 along the horizontal edge. On the preopercular crest the spines are usually small and about equal in size; these usually consist of a single spine, rarely 2, on the ascending edge, and 4 to 6 along the horizontal edge. Soon after reaching the juvenile stage (i. e., in individuals more than about 16 mm. in length), the armature becomes less conspicuous. The disappearance of the preopercular spines appears to result from tissue filling in between the spines. In larvae 50 mm. in length, only the corner spine is noticeable.

Two or three small spines form on the upper edge of the operculum at about 5 mm. in length. They are inconspicuous, and may easily be overlooked. They persist until the juvenile stage. A more conspicuous feature, especially in stained material, is a serrated dorsal ridge or crest at the back of the head. It is most noticeable in larvae of about 4 to 8 mm. (figs. 5 and 7).

Teeth are usually observable in specimens of 3.5 to 4 mm. in length, and occasionally on smaller specimens. They first form as a row of minute teeth along the entire length of the upper jaw. By 5 to 6 mm. in length, the larvae have from 16 to 20 teeth in the upper jaw. Teeth do not appear in the lower jaw until the juvenile stage is reached. Individuals of about 17 mm. acquire a group of small teeth near the symphysis of the mandible. By 19 mm., a row of minute teeth is usually present along the lower jaw, similar in size and number to those of the upper jaw. By approximately 35 mm. in length, the dentition of the upper jaw shows signs of disintegrating, and by 50 mm. in length (these sizes are only approximate), the teeth have completely disappeared. The lower jaw teeth still persist in 50-mm. individuals.

The scales that first develop are the small scutes along the lateral line in the caudal peduncle area. These can be observed in juveniles as small as 19 to 21 mm. in length. On specimens 28 mm. long, the scutes along the posterior portion of the lateral line are better developed than those in the forward arched portion, while minute body scales are forming in the caudal peduncle area. On individuals 35 mm. in length, both the lateral-line scutes and body scales are well developed.

LARVAL DISTRIBUTION AND ABUNDANCE, 1950 AND 1951

Inasmuch as the jack-mackerel eggs taken in our samples have not been routinely identified and tabulated, while the larvae have been, the discussion that follows is based entirely on the distribution and abundance of larvae.

The basic data on abundance of jack-mackerel larvae during 1950 and 1951 have been published.[4] Approximately the same area was surveyed during the 2 years (figs. 16 and 17), although the 1951 coverage was somewhat more intensive, especially off Baja California, and was continued over a longer period. A total of 925 plankton hauls was obtained on the 8 routine survey cruises of 1950, distributed as follows: 367 hauls north of Point Conception (lines 20–77), 352 off southern California and adjacent Baja California (between Point Conception and Ensenada, Baja California,

[4] A record of the number of jack-mackerel larvae taken in individual plankton hauls during the 8 survey cruises of 1950 is given in Ahlstrom (1952, pp. 49–51) and a similar tabulation for the 12 survey cruises of 1951 in Ahlstrom (1953, pp. 42–44).

lines 80–100), and 206 off central Baja California (lines 110–130). A total of 1,440 plankton hauls was obtained on the 12 survey cruises of 1951, distributed as follows: 288 hauls north of Point Conception (lines 40–77), 597 hauls off southern California and adjacent Baja California (lines 80–107), 466 off central Baja California (lines 110–137), and 89 off southern Baja California. The difference in coverage during the 2 years should not affect the comparative value of the data. This information is summarized by months in table 6.

TABLE 6.—*Summary of monthly hauls and take of jack-mackerel larvae in survey area, 1950 and 1951*

	1950					1951				
	Number of hauls	Number of hauls taking jack mackerel	Percent of successful hauls	Estimated number of larvae in survey area	Percent of total taken monthly	Number of hauls	Number of hauls taking jack mackerel	Percent of successful hauls	Estimated number of larvae in survey area	Percent of total taken monthly
				Billions					*Billions*	
January						125	1	1	1	<0.1
February	114	4	4	14	0.1	98	12	12	212	1.6
March	111	20	18	1,871	10.4	[1] 107	66	62	3,789	28.0
April	125	50	40	4,880	27.1	138	89	64	4,913	36.3
May	129	74	57	6,996	38.9	127	61	48	1,165	8.6
June	106	49	46	2,020	11.2	[1] 136	85	63	3,137	23.2
July	140	53	38	2,127	11.8	109	37	34	228	1.7
August	93	12	13	56	.3	129	21	16	81	.6
September	107	7	7	21	.1	[1] 112	1	1	5	<.1
October	[2]					116	2	2	2	<.1
November	[2]					89	3	3	8	.1
December						65	0	0	0	0
Total	925	269	29	17,985	99.9	1,351	378	28	13,541	100.1

[1] 89 hauls taken off southern Baja California during March, June, and September, 1951, are not included.
[2] Hauls taken on special cruises made during October and November 1950 are not included.

Although the 1950 survey cruises covered only an 8-month period, February through September, they effectively bracketed the complete spawning season of the jack mackerel. Only 0.09 percent of the larvae collected during 1951 was taken during the 4 months not surveyed in 1950. With regard to the southward extension of coverage during 1951 below Point Abreojos, Baja California, this proved of no importance in the jack-mackerel study, save to show the almost complete absence of jack-mackerel larvae in the area. Although the coverage in some parts of the jack-mackerel spawning range was more intensive during 1951, especially in the area between Ensenada and Cedros Island, Baja California, this has been compensated for by our method of integration in space. Hence, the data of the 2 years should be comparable.

DISTRIBUTION

Jack-mackerel larvae were taken in greatest abundance off southern California and adjacent Baja California (between Point Conception and San Quintin, station lines 80–107). Approximately 80 percent of the jack-mackerel larvae collected during both 1950 and 1951 were taken in this area (figs. 18 and 19). Abundance of larvae falls off sharply both to the north and to the south of this area. The monthly abundance is summarized latitudinally in table 7. The values given in this table constitute an estimate of the total number of jack-mackerel larvae in different portions of the survey area at the time of each cruise, hence are comparable from month to month and year to year. From this table is derived table 8, giving the percent of the season total of jack-mackerel larvae taken in different areas month by month. These data are shown graphically in figure 20.

The center of distribution of jack-mackerel larvae differed somewhat during the 2 years, being more southerly in 1950. The area of greatest abundance of jack mackerel during 1950 centered off San Diego, while in 1951 it was just south of Point Conception. The northward shift in 1951 is shown also by the much larger number of jack-mackerel larvae being taken north of Point Conception—approximately 15 percent of the season total, as compared to 6½ percent during 1950; and by the lower percentage being taken off central Baja California—6⅔ percent of the season total in 1951, as compared to 11⅔ percent in 1950.

An estimate of the number of jack-mackerel larvae in the survey area at the time of each cruise is summarized in tables 6 and 7. The summation of the several cruises gives a comparable figure for the 2 years, although it is not an estimate of the

TABLE 7.—*Estimate of number of jack-mackerel larvae in survey area during each cruise, 1950 and 1951.*

[In billions. Estimates of abundance are monthly census estimates; see Appendix, p. 243, for explanation]

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1950													
North of line 60		0	0	0	0	5	4	0	14				23
Lines 60-67		0	0	0	0	365	42	14	0				421
70-77		0	7	5	142	354	221	8	0	0			737
80-87		1	0	954	2,766	406	255	17					4,399
90-97		12	166	1,575	2,066	879	451	17	2				5,168
100-107		0	1,101	1,289	1,532		1,136		3				5,121
110-117		0	8	884	285	2	7		2				1,188
Line 120 and south		1	589	173	145	9	11		0		0		928
Total		14	1,871	4,880	6,996	2,020	2,127	56	21	0	0		17,085
1951													
North of line 60							0	13					13
Lines 60-67	0			38	0	77	18	0	0	0	0	0	133
70-77	0			86	8	1,748	30	0	0	0	0	0	1,872
80-87	0	99	1,461	2,617	13	845	15	8	0	0	0	0	5,058
90-97	0	113	1,061	1,131	376	320	42	45	0	1	6	0	3,095
100-107	1	0	1,050	522	694	95	79	13	5	1	2	0	2,462
110-117	0	0	125	465	60	30	21	2	0	0	0	0	703
Line 120 and south	0	0	92	54	14	22	23	0	0	0	0	0	205
Total	1	212	3,789	4,913	1,165	3,137	228	81	5	2	8	0	13,541

TABLE 8.—*Monthly take of jack-mackerel larvae by areas expressed as percent of the yearly total, 1950 and 1951*

[Estimates of abundance are monthly census estimates; see Appendix, p. 243, for explanation]

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1950													
North of line 60		0	0	0	0	0.03	0.02	0	0.08				0.13
Lines 60-67		0	0	0	0	2.03	.23	0.08	0				2.34
70-77		0	0.04	0.03	0.79	1.97	1.23	.05	0	0			4.11
80-87		0.01	0	5.31	15.38	2.26	1.42	.09					24.47
90-97		.07	.92	8.76	11.49	4.89	2.51	.10	.01				28.75
100-107		0	6.12	7.17	8.85		6.32		.02				28.48
110-117		0	.04	4.91	1.59	.01	.04		.01				6.60
Line 120 and south		.01	3.23	.96	.81	.05	.06		0		0		5.17
Total		.09	10.40	27.14	38.91	11.24	11.83	.32	.12	0	0		100.05
1951													
North of line 60							0	.10					.10
Lines 60-67	0			.28	0	.57	.13	0	0	0	0	0	.98
70-77	0			.63	.06	12.90	.22	0	0	0	0	0	13.81
80-87	0	.73	10.79	19.32	.10	6.24	.11	.06	0	0	0	0	37.35
90-97	0	.84	7.84	8.35	2.78	2.36	.31	.33	0	0.01	0.05	0	22.87
100-107	.01	0	7.75	3.85	5.13	.70	.58	.10	.04	.01	.01	0	18.18
110-117	0	0	.93	3.43	.44	.23	.16	.01	0	0	0	0	5.18
Line 120 and south	0	0	.68	.40	.10	.16	.17	0	0	0	0	0	1.51
Total	0.01	1.57	27.98	36.27	8.61	23.15	1.68	.60	.04	.02	.06	0	99.99

total number of larvae in the area during the year. The estimate for 1950 is a third higher than for 1951. Inasmuch as there is an undetermined but, undoubtedly, fairly large error of estimate connected with these values, this difference may not be significant.

Jack-mackerel larvae occur at considerable distances from shore; in fact, the center of their abundance appears to be between 80 and 240 miles offshore. Further, the larvae are taken as far seaward as we have gone on survey cruises. A summary of the abundance of jack-mackerel larvae in relation to distance from shore follows:

Distance from shore	1950	1951
	Percent of season's total	Percent of season's total
40 miles or less	2.3	4.0
41-80 miles	4.9	8.6
81-120 miles	7.8	18.9
121-160 miles	18.6	20.0
161-200 miles	32.5	19.6
201-240 miles	11.6	16.1
241-280 miles	9.6	4.1
281-320 miles	9.7	6.6
321-360 miles	2.7	.9
361-400 miles	.3	1.2
Total	100.0	100.0

These data are illustrated graphically in figure 21. A more detailed summary is given in table 9.

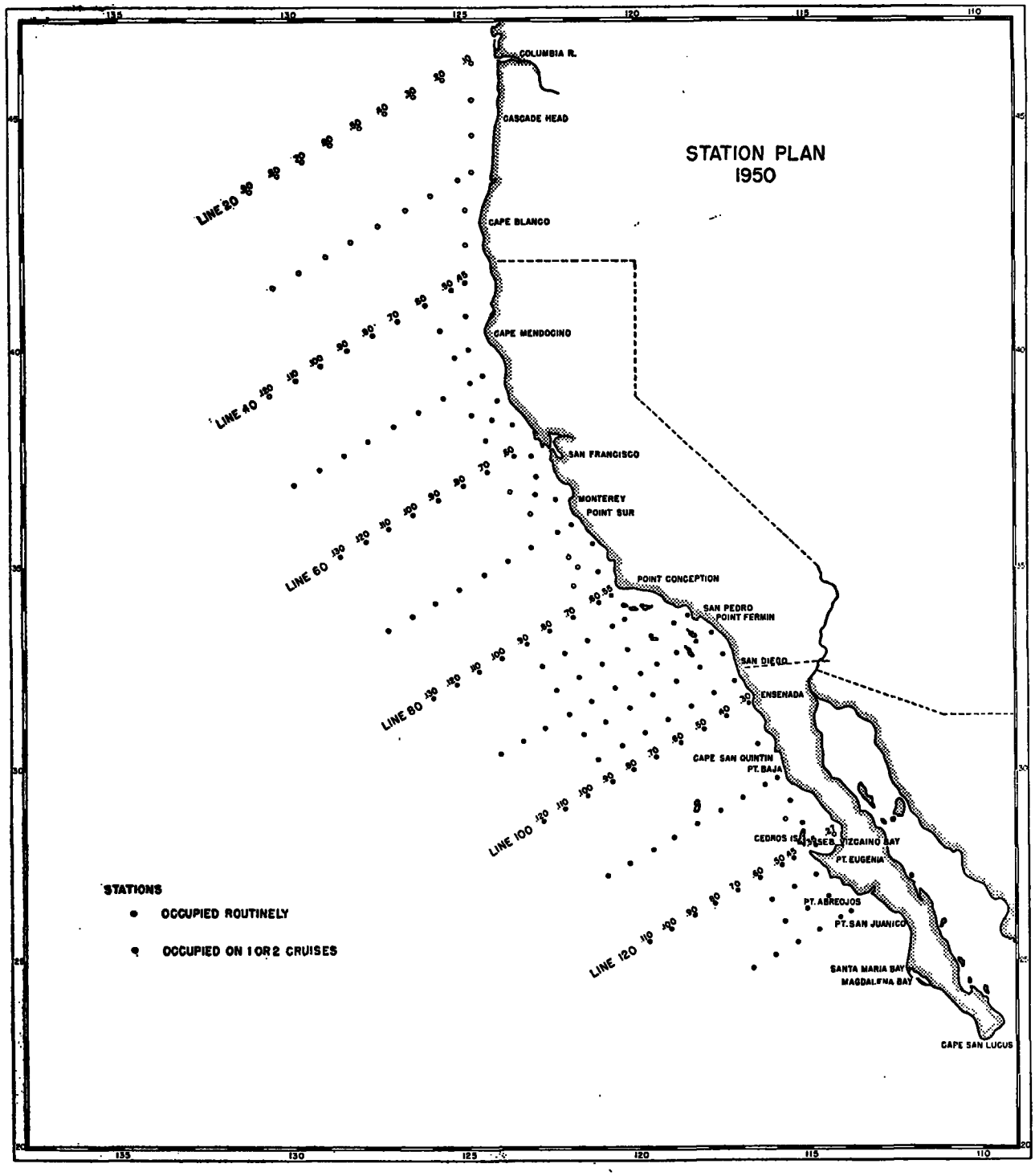

FIGURE 16.—Location of stations occupied during survey cruises made in 1950.

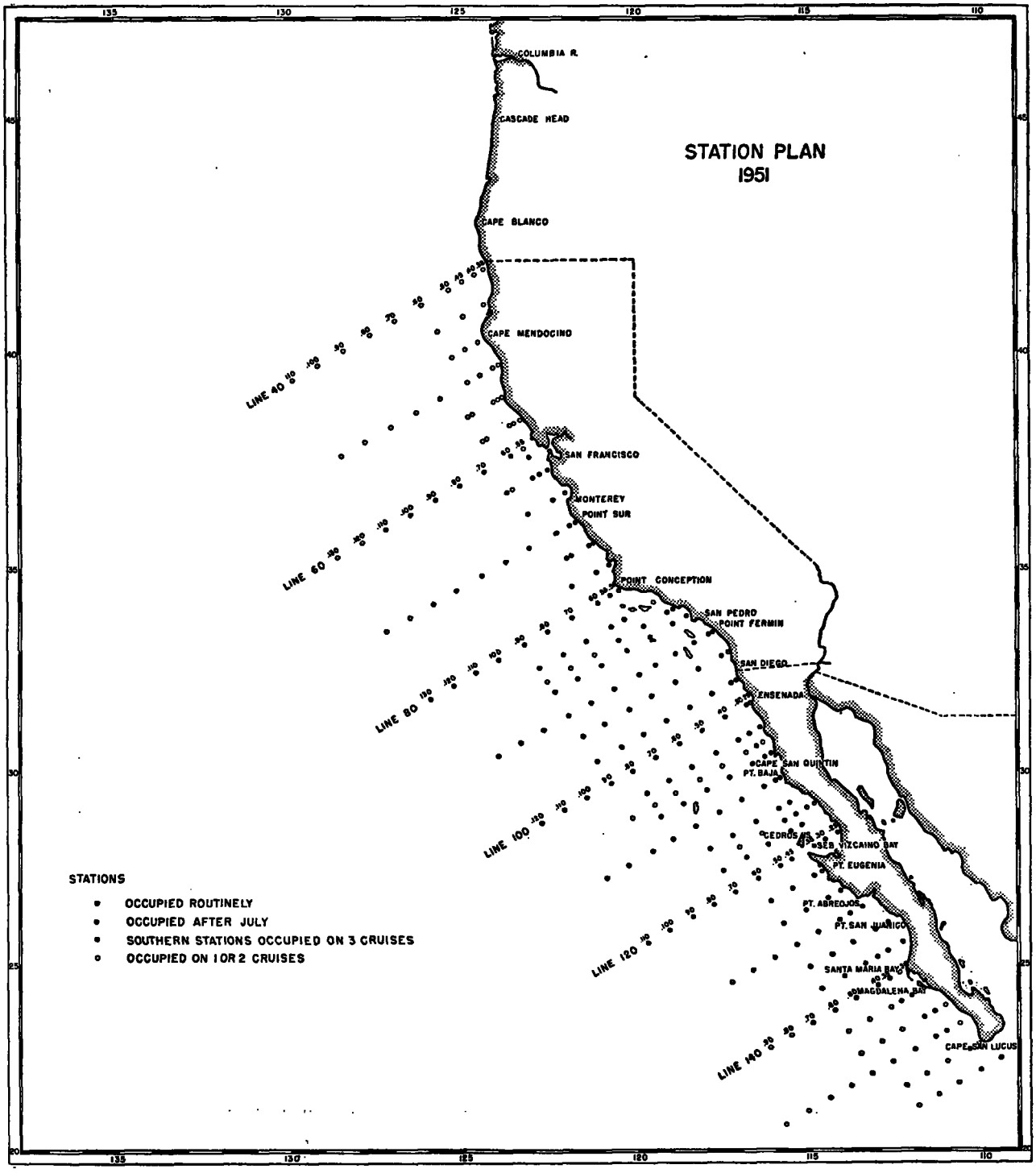

FIGURE 17.—Location of stations occupied during survey cruises made in 1951.

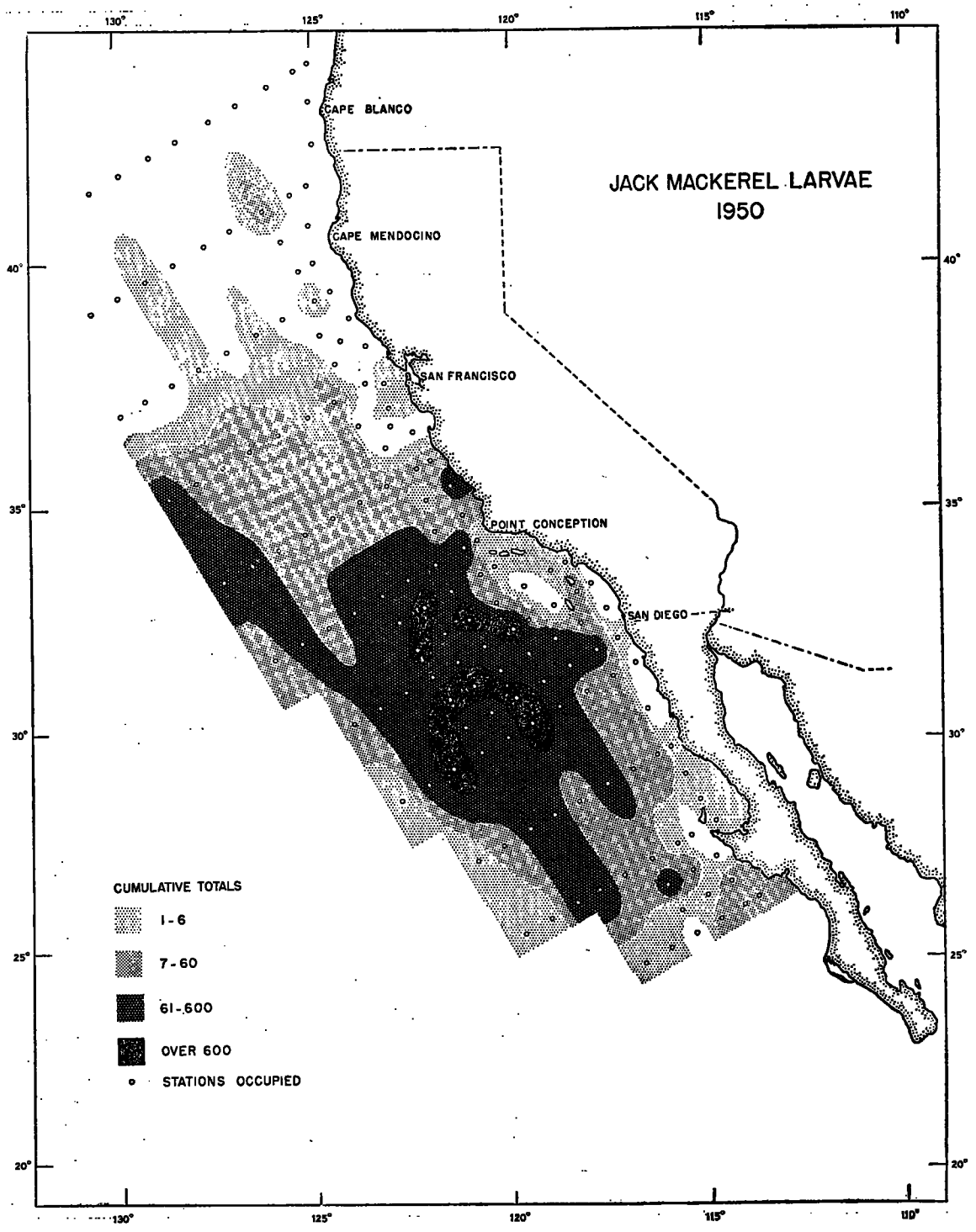

FIGURE 18.—Distribution and abundance of jack-mackerel larvae during 1950.

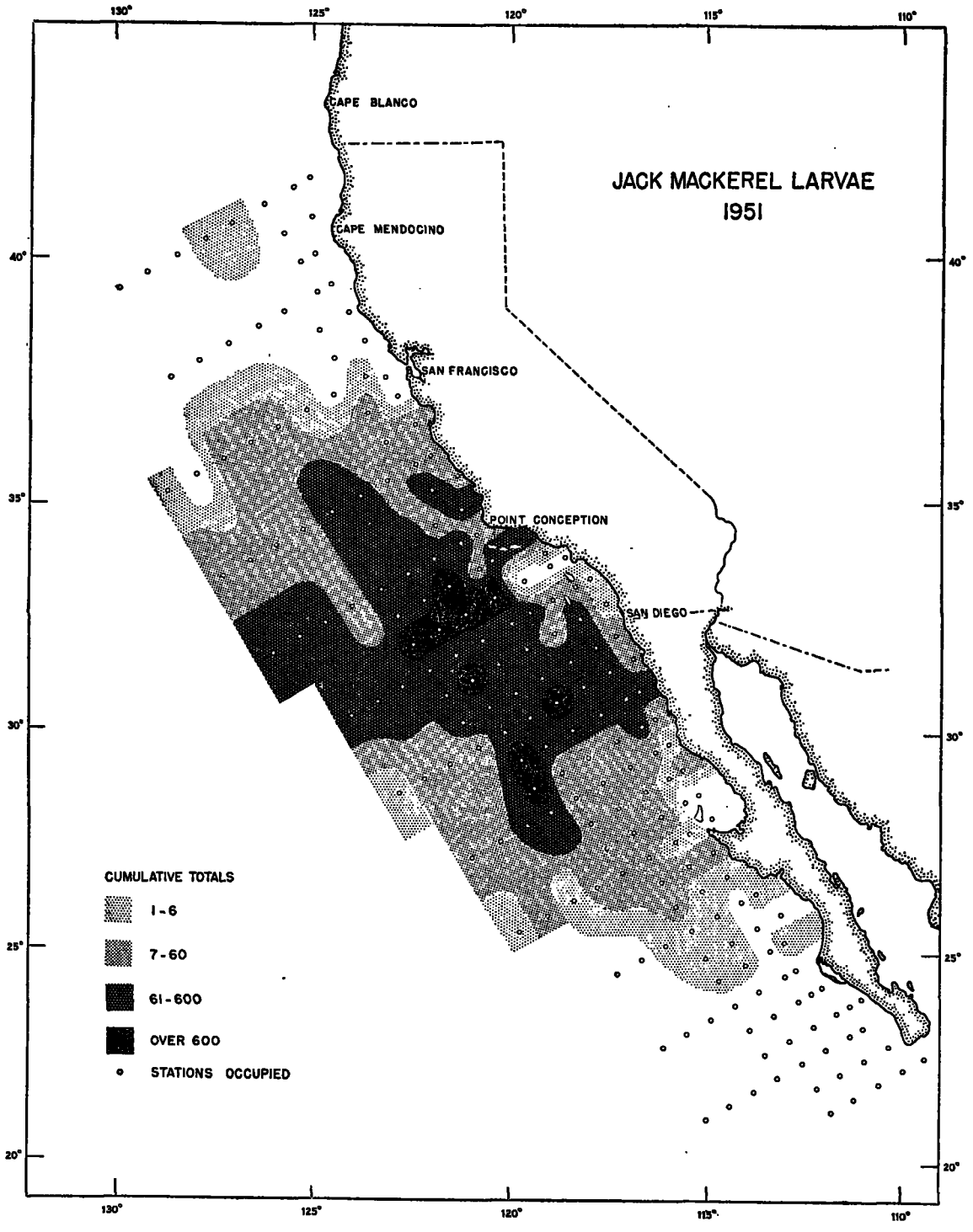

FIGURE 19.—Distribution and abundance of jack-mackerel larvae during 1951.

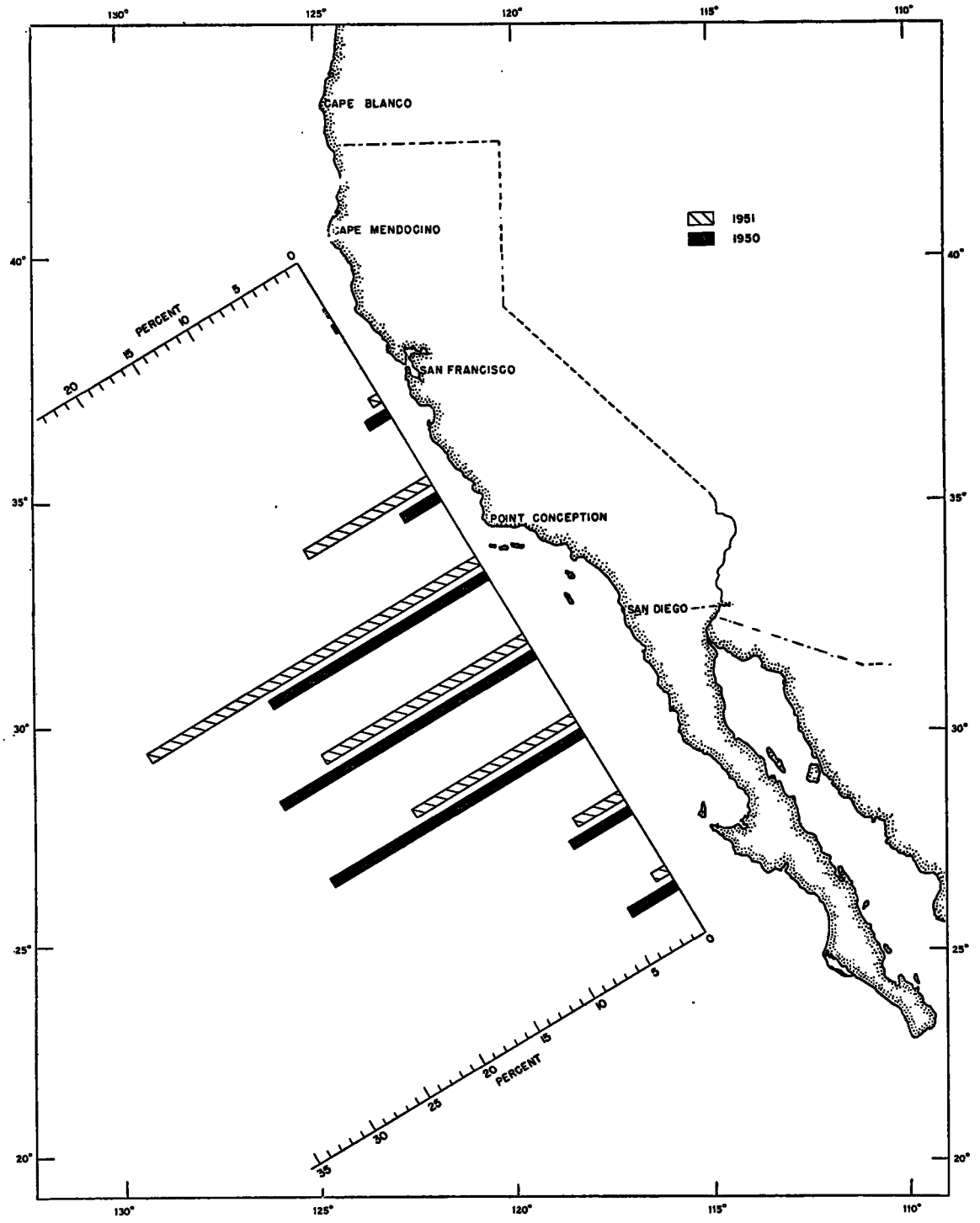

FIGURE 20.—Relative abundance of jack-mackerel larvae in different portions of the survey area during 1950 and 1951, grouped to show north-south distribution. The station lines included in each area are listed in the first column of table 8, the percentage values in the last column of table 8.

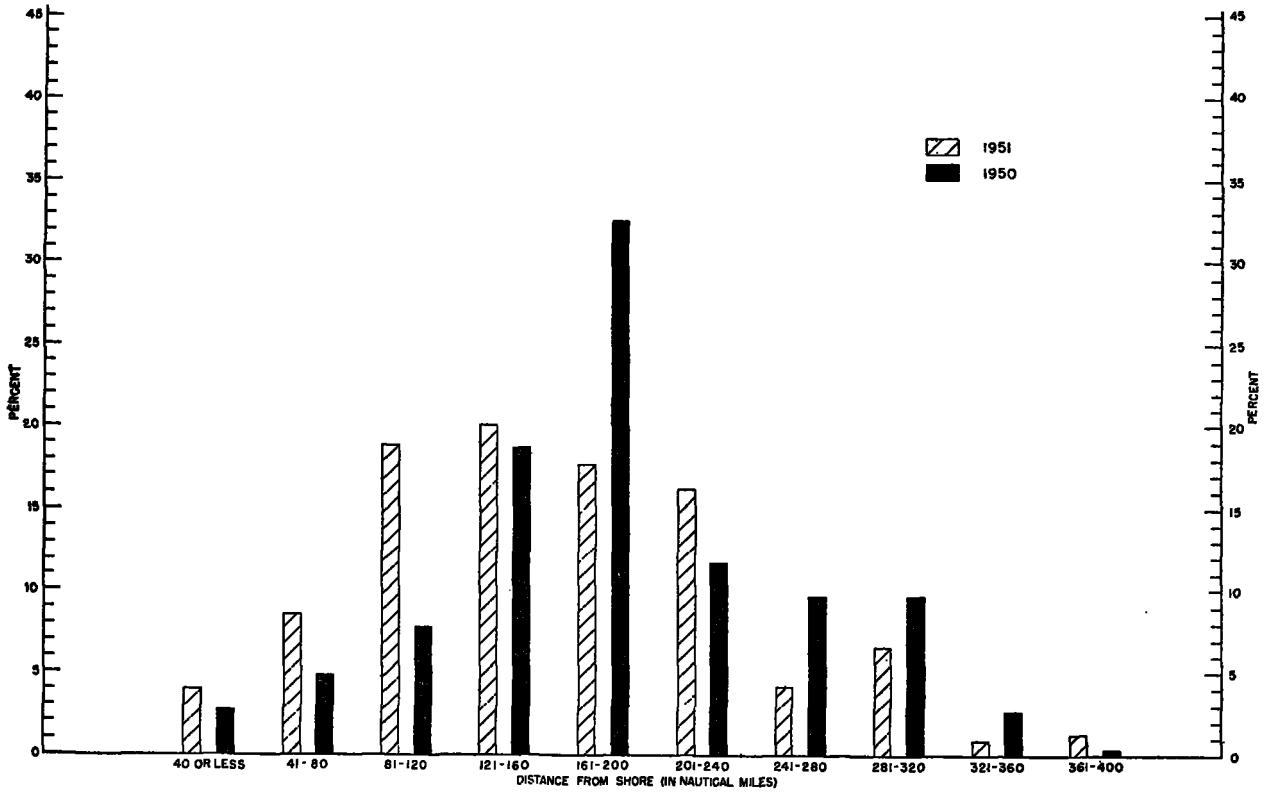

FIGURE 21.—The relative abundance of jack-mackerel larvae in relation to distance from shore, grouped by 40-mile intervals. The percentage values are derived from the data given in table 9.

TABLE 9.—*Abundance of jack-mackerel larvae during survey cruises in relation to distance from shore, 1950 and 1951*

[In billions. Estimates of abundance are monthly census estimates; see Appendix, p. 243, for explanation]

	Number of larvae at a distance from shore of—										Estimated total
	40 or fewer miles	41–80 miles	81–120 miles	121–160 miles	161–200 miles	201–240 miles	241–280 miles	281–320 miles	321–360 miles	361–400 miles	
1950											
January [1]											
February	1	0	0	1	0	12	0	0	0	0	14
March	5	1	2	208	519	147	721	261	7	0	1,871
April	65	192	204	670	2,037	949	272	285	168	38	4,880
May	122	309	982	1,710	1,602	760	488	777	241	5	6,996
June	41	188	144	253	573	142	234	411	35	0	2,020
July	148	154	58	503	1,127	67	3	8	43	16	2,127
August	6	38	3	1	3	5	0	0	0	0	56
September	2	0	9	0	0	3	7	0	0	0	21
October [1]											
November [1]											
December [1]											
Total	390	882	1,402	3,345	5,861	2,085	1,725	1,742	494	59	17,985
1951											
January	0	0	1	0	0	0	0	0	0	0	1
February	2	135	44	6	8	16	1	0	0	0	212
March	301	526	367	372	1,089	406	181	488	41	18	3,789
April	84	164	615	785	1,207	1,432	244	183	56	53	4,913
May	23	59	108	589	57	84	64	74	13	94	1,165
June	112	242	1,387	891	164	182	56	91	12	0	3,137
July	17	24	31	50	21	38	3	41	3	0	228
August	4	12	5	20	12	18	0	10	0	0	81
September	0	0	0	0	5	0	0	0	0	0	5
October	2	0	0	0	0	0	0	0	0	0	2
November	0	6	2	0	0	0	0	0	0	0	8
December	0	0	0	0	0	0	0	0	0	0	0
Total	545	1,168	2,560	2,713	2,653	2,176	549	887	125	165	13,541

[1] No survey cruise during month.

Although the pattern of offshore distribution is similar during the two seasons, there is about as great a difference between the two seasons in this feature as in the latitudinal distribution of the larvae. Jack-mackerel larvae were taken closer to shore in 1951 than in 1950. Over half of the larvae were taken within 160 miles of the coast in 1951; only about one-third during 1950.

SEASON OF OCCURRENCE

Jack-mackerel larvae were taken in greatest abundance during the 5-month period, March through July. In 1950, about 99.5 percent of jack-mackerel larvae were taken during this period, and in 1951 about 98 percent of the larvae. The peak in the abundance of larvae was reached in April of 1951, a month earlier than in 1950 (fig. 24). Whether spawning was actually a whole calendar month earlier during 1951, or only 2 or 3 weeks, cannot be determined from our data, since our sampling is spaced at monthly intervals. Not only jack-mackerel larvae, but hake larvae as well, reached the peak of abundance a month earlier in 1951.

A study of water temperatures off southern California and Baja California during the late winter and early spring months revealed somewhat warmer temperatures in the upper 50 meters in 1951, as compared with 1950. In the area between Point Conception and Point Abreojos, the average temperature of the upper 50-meter stratum was 0.49° C. higher during the 3-month period, February through April, 1951, than during the corresponding period of 1950. This was associated with less intense upwelling during the first third of 1951. The earlier onset of spawning in 1951 was probably related to the warmer conditions prevailing during that season.

The monthly distribution and abundance of jack-mackerel larvae during February through August of each year are shown in figures 22 through 28.

RELATION OF DISTRIBUTION TO TEMPERATURE

Over what temperature range do jack-mackerel larvae occur? Inasmuch as the depth distribution of the larvae is imperfectly known, it is difficult to determine this with any degree of precision. Accepting the data we have on depth distribution as typical, that jack-mackerel larvae occur mostly within the upper 50-meter stratum with the largest concentrations at about 20 meters' depth, we are using temperature values at 20 meters.

Jack-mackerel larvae were taken over a fairly wide temperature range: from 10° to 19.5° C. However, over 70 percent of the larger concentrations of larvae (50 or more larvae per standard haul) occurred within a 2° range: 14° to 16° C. The temperature distribution of jack-mackerel larvae was very similar for successive seasons, 1950 through 1952. The data are summarized in table 10.

TABLE 10.—*Temperature distribution of jack-mackerel larvae, 1950 to 1952*

[Larvae grouped according to abundance per standard haul]

Temperature at 20 meters	Number of samples containing—															
	1–10 larvae				11–50 larvae				51–100 larvae				101 larvae and more			
	1950	1951	1952	Total	1950	1951	1952	Total	1950	1951	1952	Total	1950	1951	1952	Total
° C.																
10.01–10.50	1			1												
10.51–11.00		1		1												
11.01–11.50		2		2												
11.51–12.00	1	1		2	1			1	1			1				
12.01–12.50	3	5		8		4	1	5		1		1				
12.51–13.00	6	3		9	2	4		6		1		1	1			1
13.01–13.50	9	9	3	21	5	7	4	16	3	1	1	5	2	1		3
13.51–14.00	7	8	7	22	6	11	4	21	4	4	1	9	9	6	3	18
14.01–14.50	5	17	6	28	9	8	11	28	2	3		5	12	9	4	25
14.51–15.00	11	12	11	34	10	11	10	31	4	4	6	14	7	8	10	25
15.01–15.50	11	18	10	39	7	12	10	29	7	3	4	14	11	7	3	21
15.51–16.00	9	24	6	39	10	18	17	45	2	3	6	11	8	7	6	21
16.01–16.50	22	26	11	59	11	9	11	31	3	1	4	8			4	4
16.51–17.00	12	20	5	37	1	10	6	17	2		1	3			1	1
17.01–17.50	8	9	2	19	1	3	1	5								
17.51–18.00	8	6	2	16		2		2								
18.01–18.50	4	5		9												
18.51–19.00	3	2		5												
19.01–19.50						1		1								
19.51–20.00																
Total	120	168	63	351	63	100	75	238	28	21	23	72	50	38	31	119

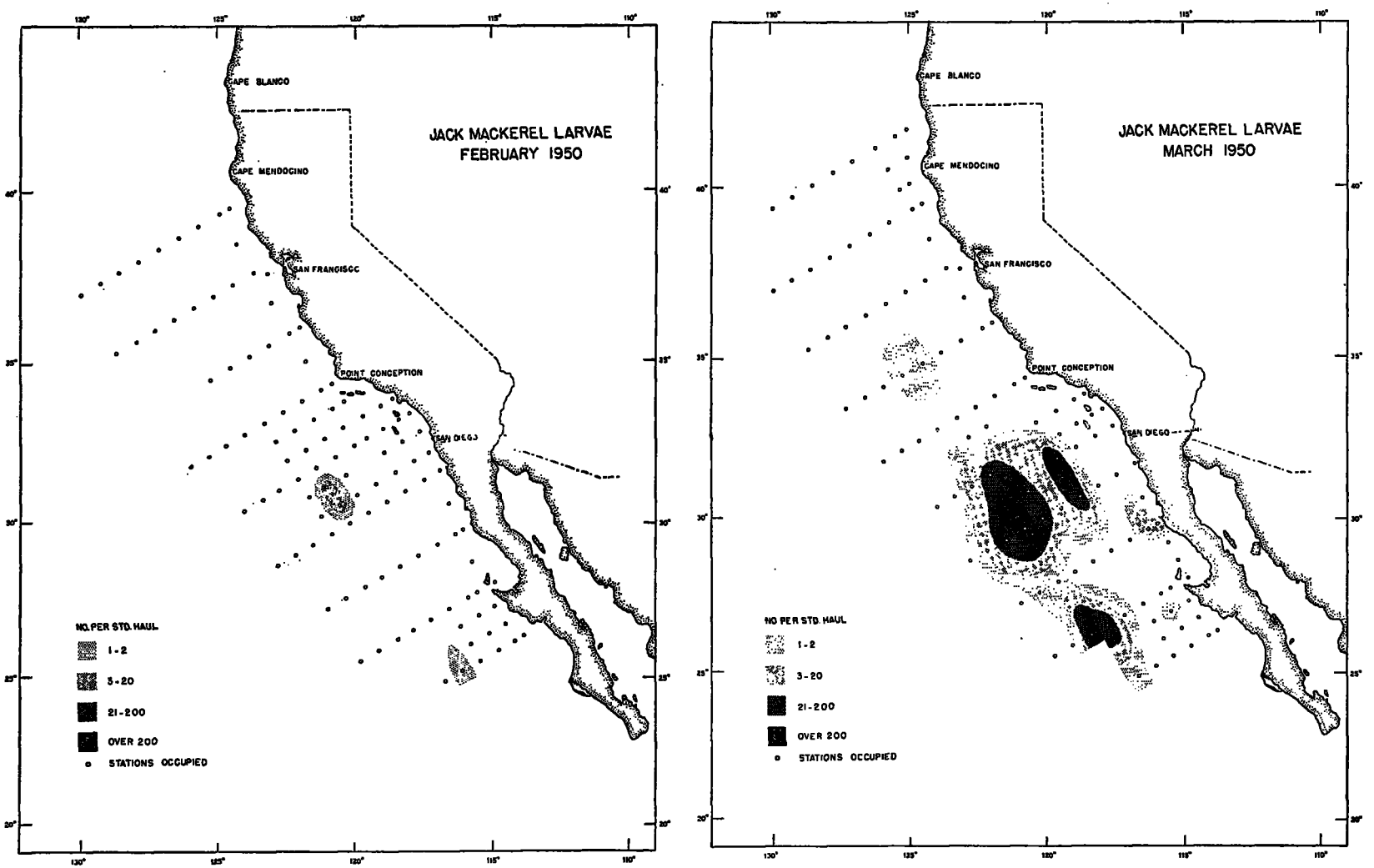

FIGURE 22.—Distribution and abundance of jack-mackerel larvae during February and March 1950.

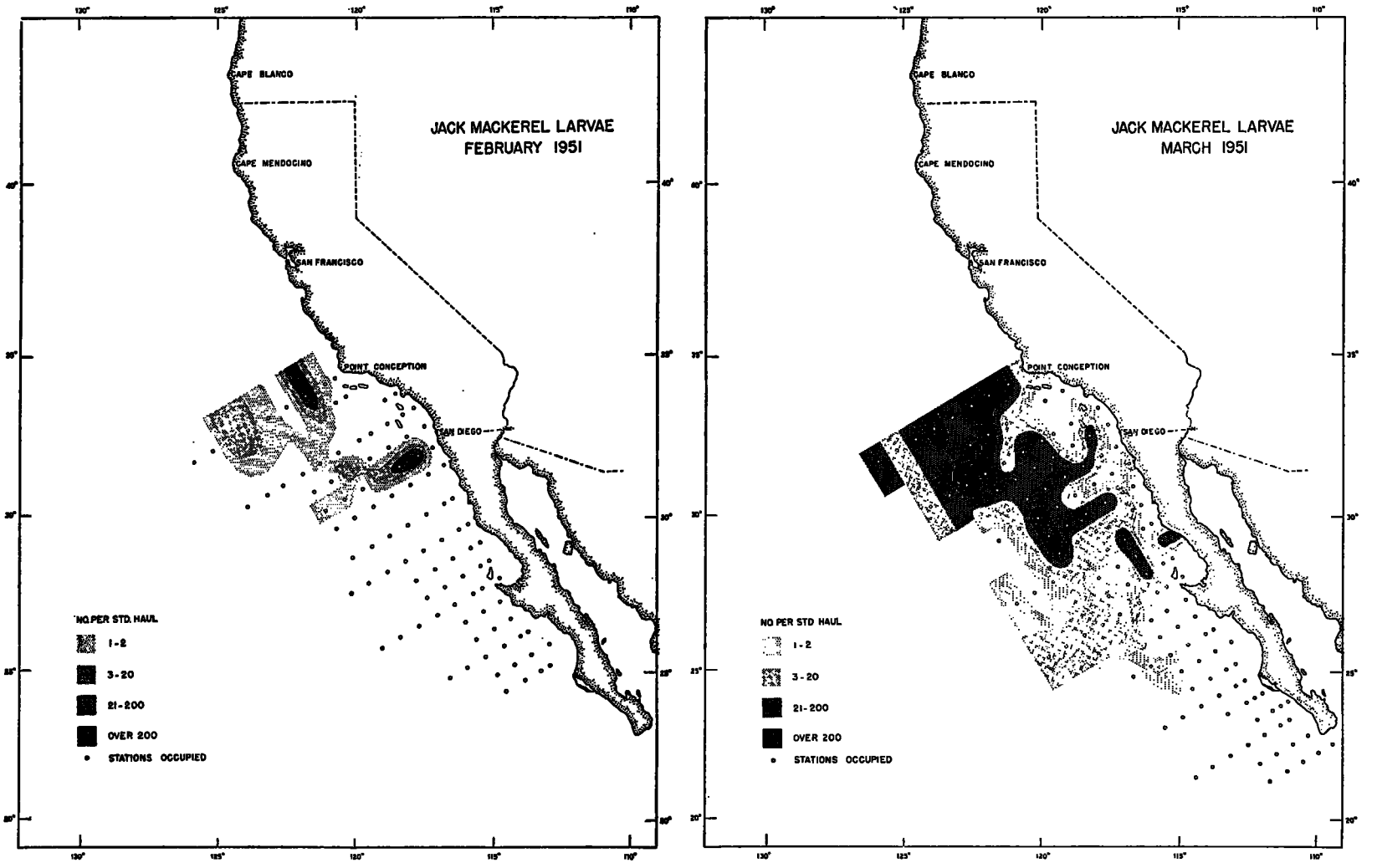

FIGURE 23.—Distribution and abundance of jack-mackerel larvae during February and March 1951.

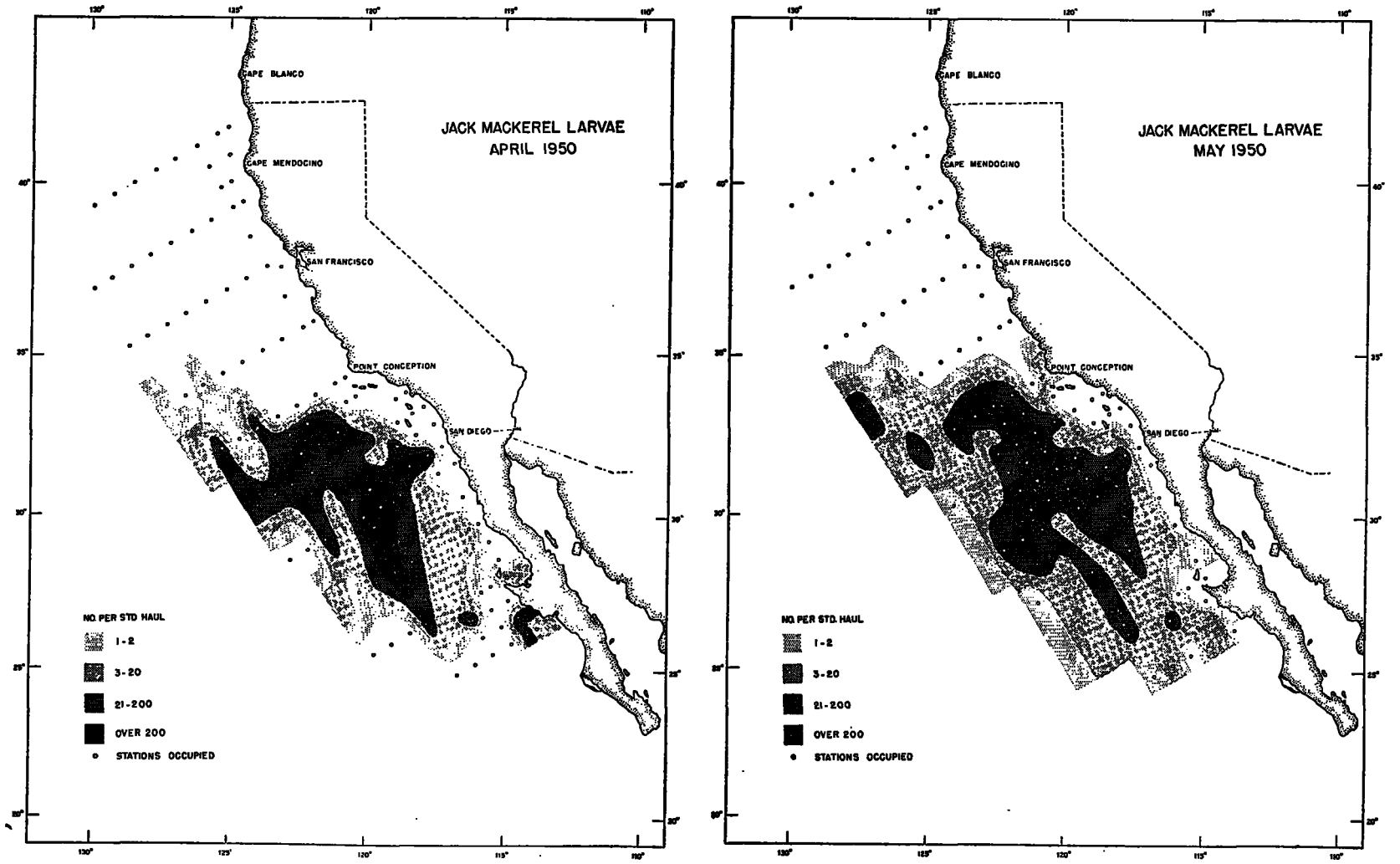

FIGURE 24.—Distribution and abundance of jack-mackerel larvae during April and May 1950.

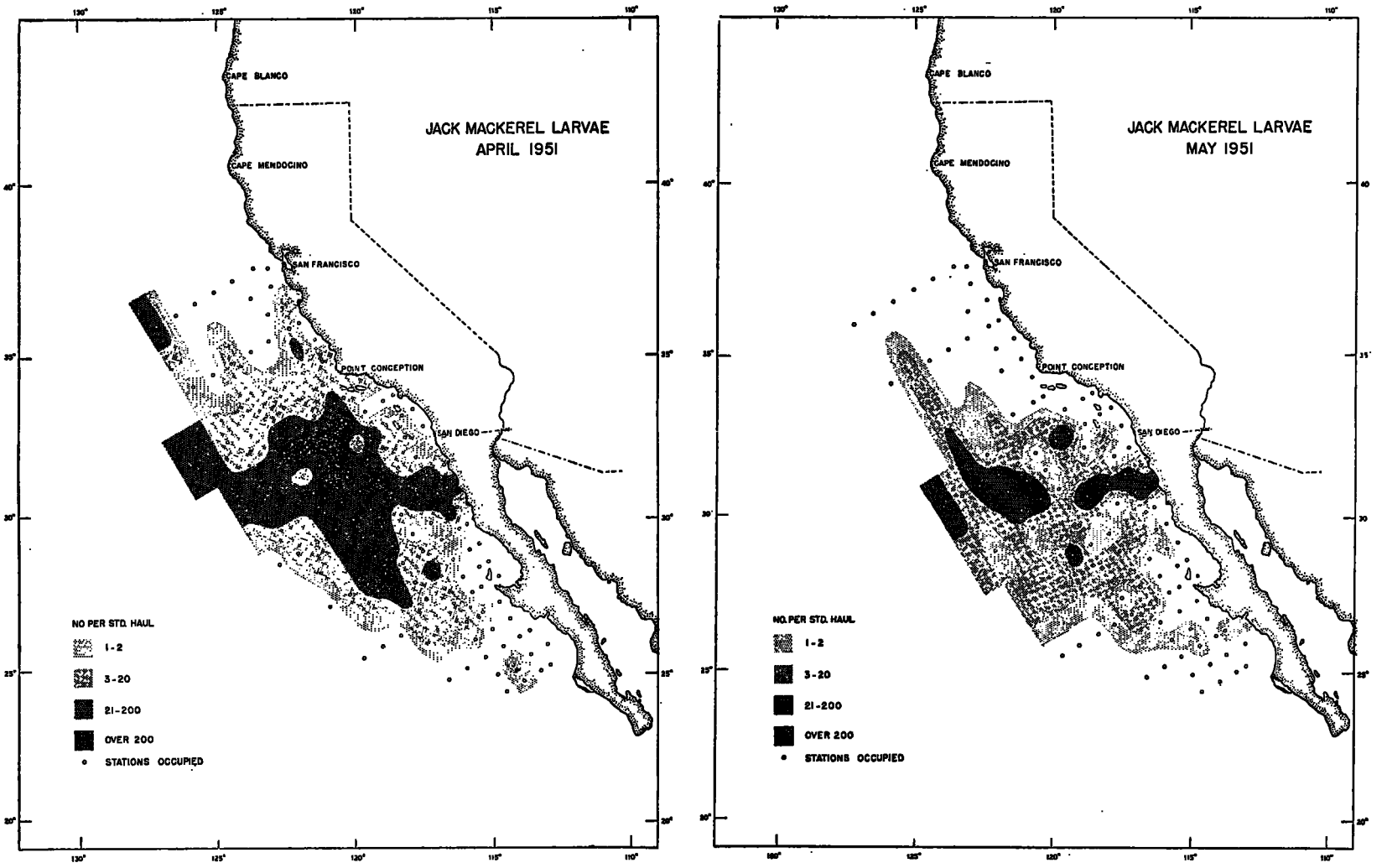

FIGURE 25.—Distribution and abundance of jack-mackerel larvae during April and May 1951.

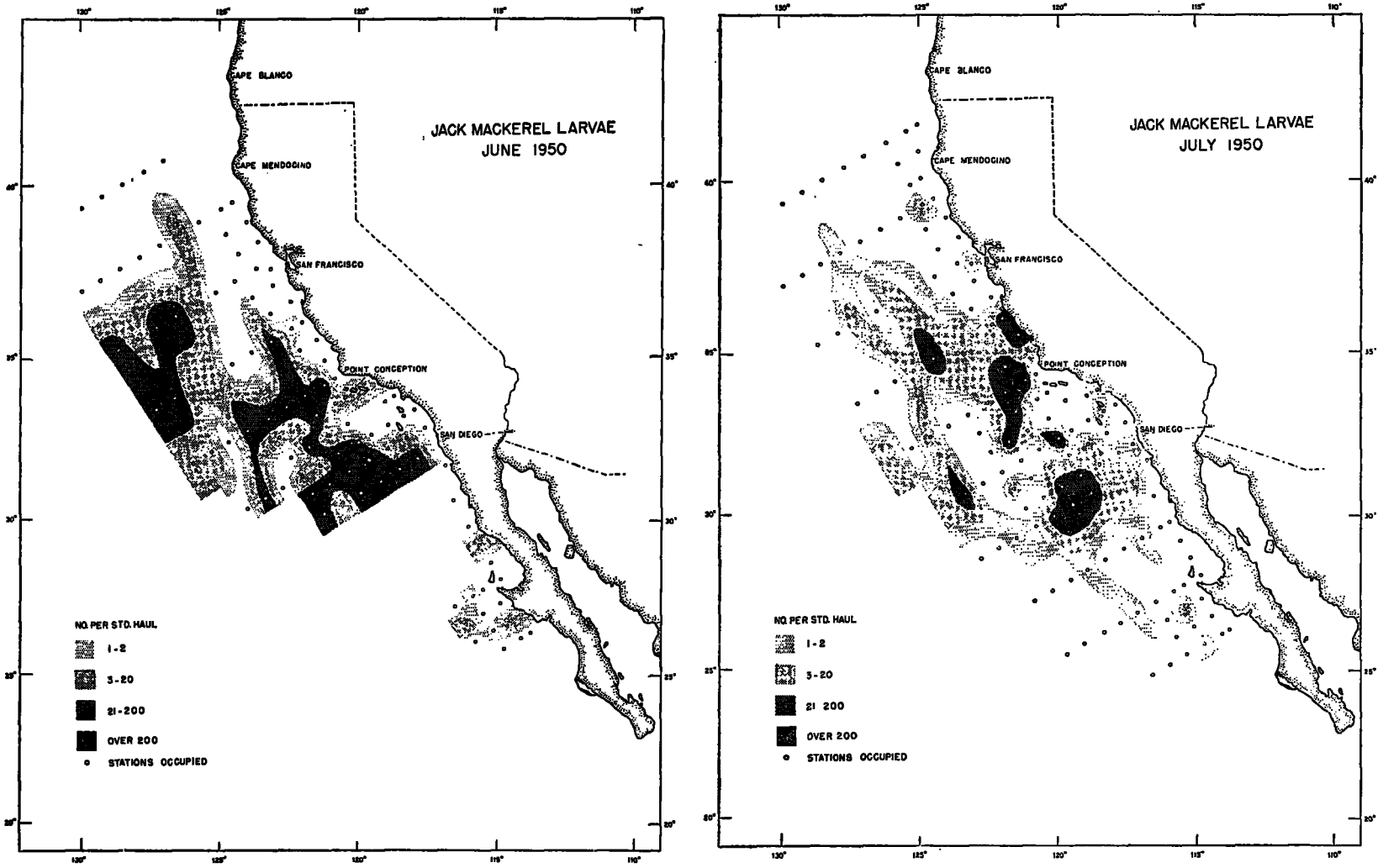

FIGURE 26.—Distribution and abundance of jack-mackerel larvae during June and July 1950.

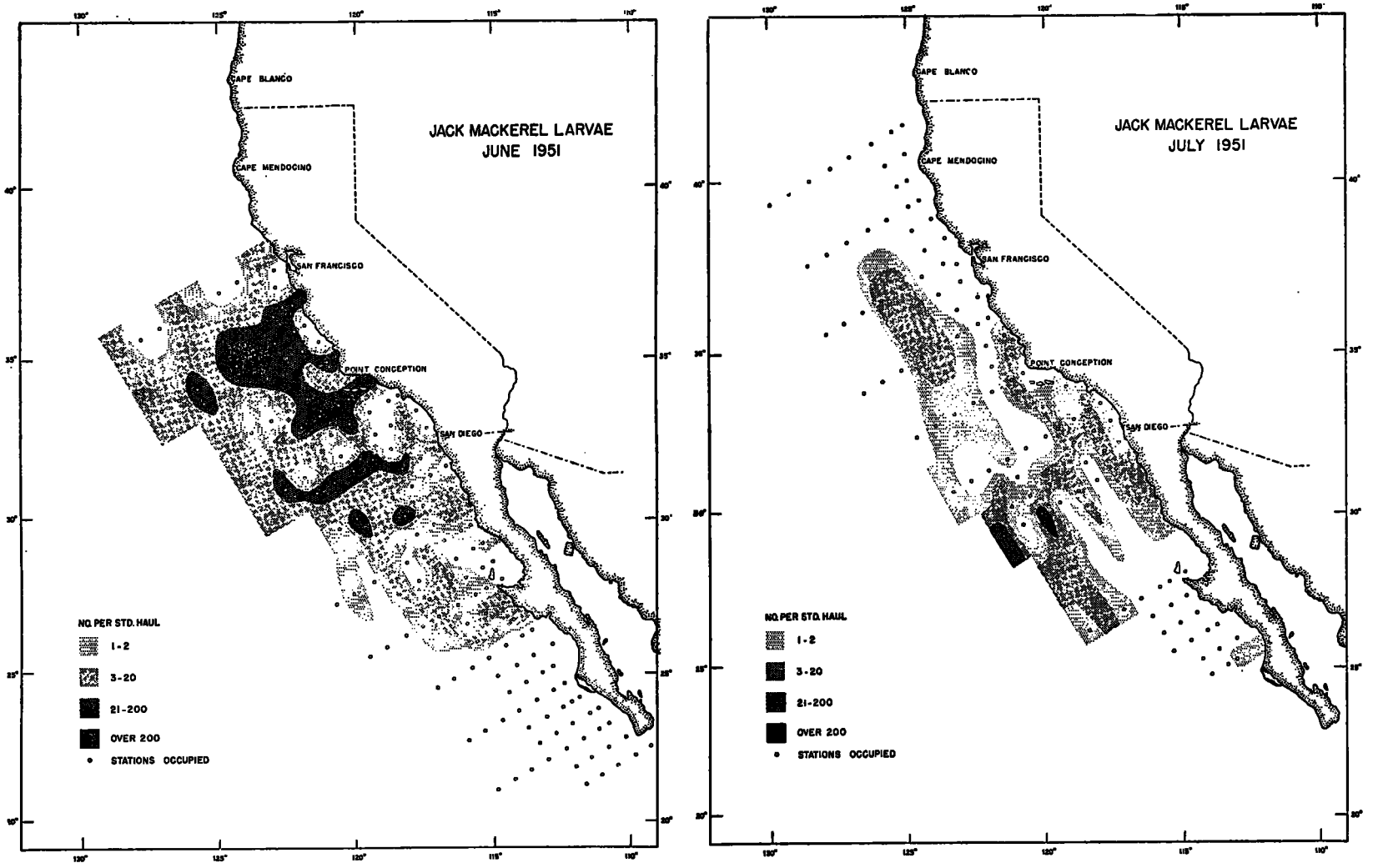

FIGURE 27.—Distribution and abundance of jack-mackerel larvae during June and July 1951.

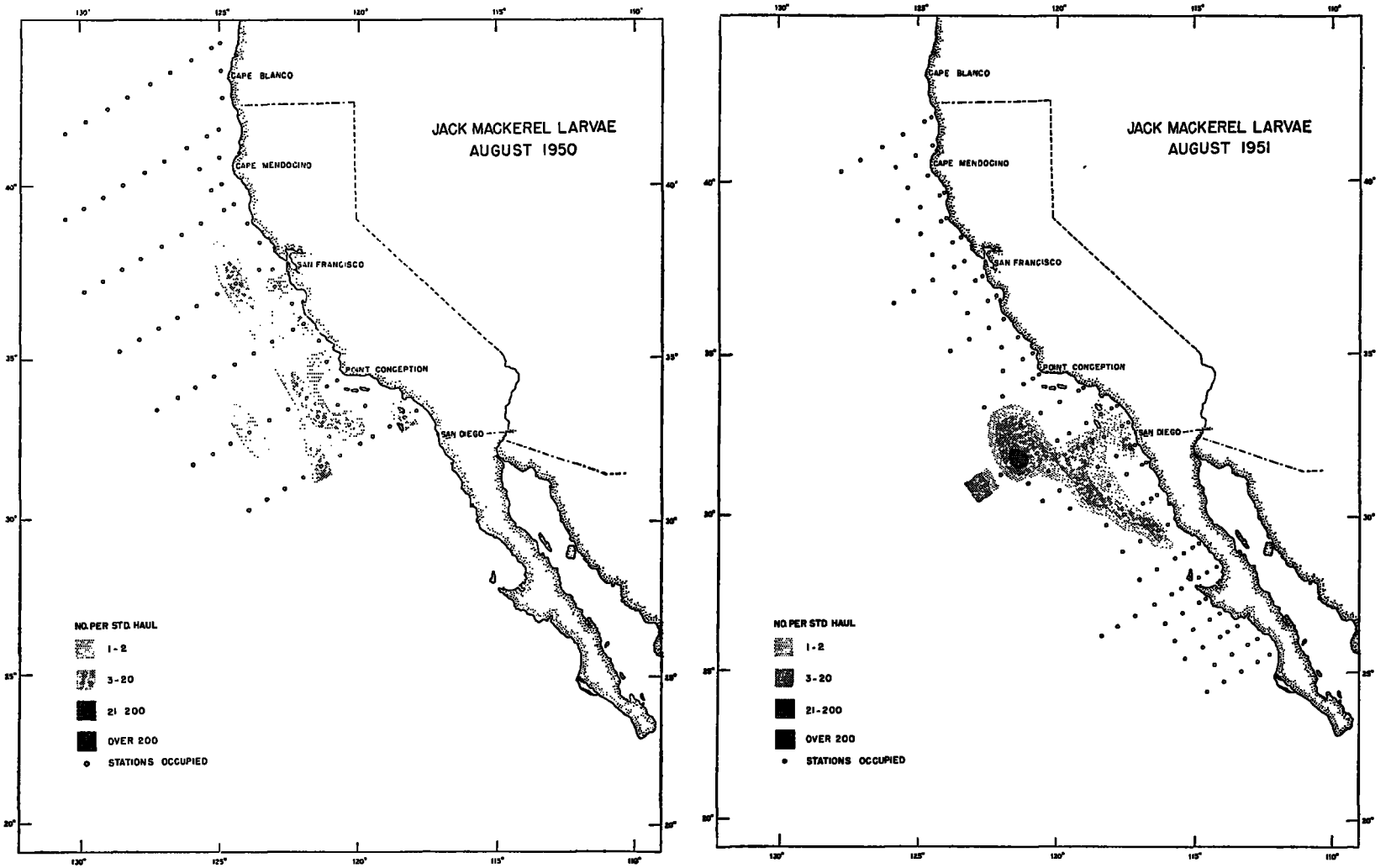

FIGURE 28.—Distribution and abundance of jack-mackerel larvae during August 1950 and August 1951.

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APPENDIX

METHODS OF COLLECTING EGGS AND LARVAE

Eggs and larvae used in the description of the embryonic and larval stages of the jack mackerel were collected on cruises of the California Cooperative Oceanic Fisheries Investigations, which have covered an extensive oceanographic area off California, Baja California, and at times Oregon, usually at monthly intervals, since March 1949. The cruises employ 2 to 4 vessels covering different sections of the area being surveyed. They have been run cooperatively by the Scripps Institution of Oceanography and the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, with the Bureau of Marine Fisheries of the California Department of Fish and Game participating on some of the cruises. Discussion of the distribution and abundance of jack-mackerel larvae has been limited to the 1950 and 1951 cruises, inasmuch as the data for 1949 are not as complete as for later years, and the 1952 material has not been completely worked up as yet.

Nets used.—The plankton nets used throughout the survey period have been 1 meter in diameter at the mouth, and approximately 5 meters long. The anterior section of the nets, approximately a meter in length, is cylindrical, while the longer, posterior section is conical. A cod-end bag, approximately 14 cm. in diameter and 30 cm. long, is attached to the end of the net by a bronze coupling device. The body of the nets has been constructed of No. 30xxx grit gauze (a sturdy grade of Swiss silk bolting cloth); the posterior 40 cm. of the cone and the cod-end bag of No. 56xxx grit gauze. The grit-gauze numbers refer to the number of threads per lineal Swiss inch, which has a slightly different length than the English inch.

Method of sampling.—The plankton nets were hauled obliquely while the vessels were moving at a speed of about 1.5 to 2 knots. During 1949 and 1950, the hauls sampled approximately the upper 70 meters of depth; since then the depth of the stratum sampled has been approximately 140 meters, except at shallow stations. In making a haul, the net is lowered at approximately 35 meters a minute, and retrieved at a rate of either 3.5, 7, or 14 meters a minute. These figures are an estimate of the actual vertical distance being covered, and not of the length of the towing wire payed out or retrieved.

Measurement of the volume of water strained by the nets.—Throughout our operations, each plankton net was provided with a current meter, held rigidly in the center of the mouth opening by three bronze rods. The current meters are routinely calibrated before and after each cruise on which they are used. The details of calibration, as well as the method of computing the volume of water entering a net during a haul, are given by Ahlstrom (1948 and 1953).

Standardization of plankton hauls.—Although our plankton hauls have differed in the depth of the stratum sampled and in the speed of hauling, we can determine for each haul the average amount of water strained per unit of depth sampled. For comparability, all hauls have been referred to a standard haul of 10 cubic meters of water strained per unit of depth sampled.

A basic requirement of this procedure is that the vertical distribution of the organism be encompassed. Hauls that are not deep enough to sample the complete depth distribution will underestimate the abundance of the organism. We have no reason to suppose that even the shallower stratum routinely sampled during 1949 and 1950 did not encompass the depth distribution of jack-mackerel larvae. Although our data on the depth distribution of jack-mackerel larvae are fragmentary, they indicate a shallow distribution, mostly above 50 meters. Also, the fact that somewhat larger standard numbers of jack-mackerel larvae were taken during the 1950 season than during the 1951 season, despite the difference in vertical depth covered by the hauls, tends to support this belief.

CENSUS ESTIMATES

It has not been possible for us to derive estimates of actual abundance of jack-mackerel larvae at different stages of larval development. The techniques for making such estimates are discussed in Ahlstrom (1954). One of the requirements is a determination of the size composition of all jack-mackerel larvae taken in net hauls. Size measurements have not been made routinely on jack-mackerel larvae collected during 1950 or 1951. The rate of growth of the larvae has not been determined as yet, and this information is also needed in deriving population estimates.

The estimate used is a census estimate of the number of jack-mackerel larvae in the survey area

at the time of each cruise. It is obtained by integrating the standard-haul totals for larvae over area. Since it is made on total jack-mackerel larvae, equal weighting is given to larvae of all sizes, whether newly hatched or approaching the juvenile stage. Since the cruises were spaced at regular monthly intervals during both years, the totals should be comparable. The estimates of abundance given in tables 6 through 9 are monthly census estimates.

MEASUREMENTS AND MERISTIC COUNTS

This study is based on plankton material preserved in buffered 10-percent formalin (4-percent formaldehyde). Living material has not been available, but this is not considered a serious lack, since our need, and that of most investigators, will be to identify preserved material. Larvae on which detailed size measurements and meristic counts were made had been previously stained with alizarin and cleared in glycerin. The material was selected at random from collections of jack-mackerel larvae made during 4 years of systematic surveys, 1949 through 1952, and it was representative of the distribution of jack-mackerel larvae both in time and space. Unstained material was used for studying larval pigmentation.

Most measurements were made with the aid of an ocular micrometer under a low-power binocular dissecting microscope. No magnification greater than 36 times was used. On larger specimens it was necessary to use calipers for most of the measurements.

The clearing and staining method used was modified from the technique described by Hollister (1934). A good generalized discussion of this technique is given in a short article by Evans (1948).

We feel that this type of prepared larval material should play an important role in accurate descriptive work. Cleared and stained material is especially useful for making accurate meristic counts; when the fins are developing it is indispensable. It is also the only simple means of following the sequence of ossification, and of determining accurately the vertebral number.

The procedures followed in making measurements and in enumerating meristic elements will be briefly described.

Standard length.—In yolk-sac larvae before differentiation of the mouth, we considered the measurement from the forward tip of the head to the end of the notochord to be equivalent to the standard length. In larval stages before the caudal fin is formed, we used the measurement from the tip of the snout to the end of the notochord; when the caudal fin is fully formed, at about 11 mm. in length, we measured from the tip of the snout to the base of the caudal.

Head length.—The measurement was made from the tip of the snout to the posterior edge of the operculum. In yolk-sac larvae, and even in some small larvae, the length of the head is difficult to measure exactly. Inasmuch as the head length very closely approximates the length from the snout to the pectoral base, this latter measurement was taken to be equivalent to the head length in small larvae.

Eye diameter.—Measured on the horizontal.

Snout to anus.—The length from the tip of the snout to the anal opening. In the earlier stages the tip of anal papilla was considered equivalent to the anal opening.

Depth at pectoral.—Body depth was measured at the base of the pectoral fin. This is usually the point of greatest depth. The measurement was not made on specimens that still retained yolk material, hence is lacking for yolk-sac larvae.

Fin rays and spines.—In making meristic counts of fin rays and spines, only those elements that stained with alizarin were counted. Usually, rays and spines stain a deep red with alizarin; however, all rays that took any color, even a slight pinkish tinge, were counted. It is often difficult to distinguish spines from rays when these structures are first forming; consequently, for a period during fin differentiation, some spines were counted as rays. This applied to the soft dorsal, anal, and pelvic fins. In the soft dorsal, for example, the single spine that precedes the rays could not be distinguished as such in larvae of about 7 to 8 mm., and for this size group it was counted as a ray.

Vertebrae.—The neural and haemal spines take stain on small specimens before the centra. A vertebra is considered as forming if any of its elements stain red with alizarin.

Tabulation of larval measurements and meristic counts (table 2).—A summary tabulation of larval measurements and meristic counts is presented in table 2. For larvae between 2 and 5 mm. in length, the measurements are summarized for each 0.5-mm. size interval; for larvae between 5 and 15

mm. in length, the measurements are grouped by 1-mm. intervals; while for specimens beyond 15 mm. (juveniles), the grouping is irregular depending upon available material.

For each interval, the number of individuals measured is indicated. Approximately 15 individuals were used for each category, when available. The size measurements and meristic counts given under any interval are the mean values for the specimens measured.

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FEEDING MECHANISM OF THE SEA LAMPREY AND ITS EFFECT ON HOST FISHES

BY ROBERT E. LENNON

FISHERY BULLETIN 98

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The feeding mechanism and predatory habits of the sea lamprey, *Petromyzon marinus*, have extensive and complex effects on host fishes which are not always lethal but are invariably serious. Comparative observations on the parasite-host relations were obtained from lampreys and their prey in Lake Huron and in aquariums at the Fish and Wildlife Service Laboratory at Hammond Bay, Mich.

The feeding mechanism consists of the buccal-gland system, the armed tongue, the tooth-studded oral disk, and the suctorial mouth. The secretion of the buccal glands, which bathes the wound of a victim fish, possesses a property for inducing lysis in the torn tissues, in addition to its anticoagulant and hemolytic powers.

The effects of lamprey attacks on fishes, both in aquariums and in the lake, were ascertained from examination of a total of 2,879 wounds on 20 species of fishes. No type of host tissue was wholly impervious to injury by the parasite. Hematological tests on eastern brook trout, brown trout, rainbow trout, and white suckers demonstrated that the volume and constituents of blood are drastically altered in mortal attacks by sea lampreys. The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* occurred at times as contaminants of wounds on fishes that had survived lamprey attacks, and some mortalities were attributed to them.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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FEEDING MECHANISM OF THE SEA LAMPREY AND ITS EFFECT ON HOST FISHES

BY ROBERT E. LENNON, *Fishery Biologist*

Economic and biologic consequences of the invasion of the upper Great Lakes by the sea lamprey have been extensively reported (e. g. Applegate 1947). Basic features of the life history and possibilities for control of this predatory parasite have been described in detail by Gage (1929), Hubbs and Pope (1937), Shetter (1949), and others.

The sea lamprey is a primitive and anadromous fish of the north Atlantic Ocean and its tributary waters. It spends 4 or 5 years of larval life in the parent stream before it metamorphoses and descends to the sea as a parasitic feeder on fish. Its growth and development in the ocean are rapid, and the animal may attain a length of 30 inches before it ascends a stream to spawn and die. The species is also native to Lake Ontario, but Niagara Falls prohibited access to the upper lakes until the Welland Canal was completed in 1829. Nearly a century elapsed before sea lampreys were observed in Lake Erie, and their establishment there was not verified until 1932 (Creaser 1932). By 1937 the parasites had been reported from Lakes Huron and Michigan, and adult specimens were collected in Lake Superior in 1946 (Applegate 1950).

Recent statistics of the commercial fisheries on the Great Lakes indicate the efficiency and deadliness of sea-lamprey attacks on fishes (Hile, Eschmeyer, and Lunger, 1951). The production of lake trout (*Salvelinus namaycush*) from United States waters of Lake Huron and from Lake Michigan declined from 8,600,000 pounds to less than 26,000 pounds in a period of 10 years. The production of lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota maculosa*), suckers, and several other varieties had also been drastically reduced.

As late as 1950, little was known of the exact effects of lampreys on host fishes. It was necessary to collect a large quantity of data on the feeding mechanism employed by parasitic-phase sea lampreys, on the locations of their attachments on the bodies of host fishes, on the nature of the wounds and the effects on the tissue and blood of the victims, and on the properties of the lamprey's buccal-gland secretion. Additional material was needed on the incidence of secondary infections in wounds inflicted on fishes by sea lampreys. This work was part of the sea-lamprey investigations carried on to devise a practical lamprey-control program.

Several special adaptations are to be found in sea lampreys that make possible the parasitic feeding habit—an extremely rare behavior among vertebrates. Outstanding among these structural features are the buccal glands and their secretion, the rasping tongue, and the oral sucking disk. Singular morphological and physiological aspects of these organs and the results of their action on host fishes make up the major considerations of this study.

The Fish and Wildlife Service's laboratory at Hammond Bay on Lake Huron provided the aquarium facilities. Fishing operations in Lake Huron by the laboratory staff made it possible to collect data on attacks by the sea lamprey in nature during the period from July 1950 to September 1952. The studies reported here were begun as a project of the Trust Fund for Fishery Research of the Sport Fishing Institute (formerly the Associated Fishing Tackle Manufacturers). They were expanded and in large part completed while I was employed for the purpose by the Fish and Wildlife Service.

The assistance of the staffs of agencies involved in this investigation is deeply appreciated. Special thanks are due Karl F. Lagler, Chairman, Department of Fisheries, University of Michigan; James W. Moffett and Ralph Hile, Great Lakes Fishery Investigations; Vernon C. Applegate, Phillip S. Parker, and other members of the staff at the Hammond Bay Fishery Laboratory; and W. James Leach, Department of Anatomy, Ohio State University.

FOOD OF ADULT SEA LAMPREYS

The evidence is overwhelming that the principal food of adult sea lampreys is blood sucked from prey fishes. Body juices enter the parasitic diet to a lesser extent. A considerable amount of reduced flesh is also ingested by the parasites since their buccal-gland secretion possesses a property for liquefying certain fish tissues; the study of wounds made on a large number of fish by actively feeding lampreys supports this conclusion. Whether the products of cytolysis are utilized is unknown, but reason dictates that they probably are.

Many investigators have reported on the food of adult lampreys. Günther (1853) listed worms and insects as well as fish, and Abbott (1875) stated in reference to *P. americanus* Le Sueur that they wander over breeding grounds of other fishes and devour every egg they can find.

Gage (1893 and 1929) reported that in all lake lampreys (*P. marinus*) obtained out of breeding season, the digestive part of the alimentary canal contained blood or was empty. He found no partly digested worms, insects, small fish, or parts of fish flesh, although diligent search was made; consequently he believed that this species is wholly parasitic during its adult life and lives on blood sucked from other fishes. Dawson (1905) concluded that *P. marinus unicolor* may feed not only on blood but on more solid tissues as indicated in the extensive injuries produced on hosts.

Creaser (1933) listed blood and muscle fiber as the food of sea lampreys, whereas Hubbs and Pope (1937) and Storer (1943) described the food as blood. In a brief account of their life history, Vladykov (1949) wrote that parasitic lampreys feed on blood which is obtained by attaching themselves to fishes and rasping holes through their body covering. Applegate (1950) stated that the parasitic sea lamprey in the Great Lakes feeds on the blood and body juices of fishes.

The feeding mechanism of the sea lamprey is adapted for obtaining liquid food. Blood and body juices are sucked from host fishes and swallowed; fish flesh which is liquefied at the site of the injury is also ingested and may be utilized by the parasite.

FEEDING MECHANISM

The Sucking Disk

The sucking or oral disk of a lamprey serves as the entry to the mouth, or buccal funnel. It is on the anterior, ventral side of the head (fig. 1) and is armed with sharp, horny teeth which are of taxonomic significance in their number and arrangement. The size of the disk of the mature sea lamprey approximates the length of the branchial region (Vladykov 1949).

The mouth of a free-swimming sea lamprey is carried almost closed. The lateral margins of the disk are folded in a ventral and median direction, creating a slit-like opening from the posterior to anterior margins of the oral disk. Dawson (1905) stated in reference to inland species that when swimming the adult lamprey brings the sides of the buccal funnel together to form a vertical, wedge-shaped cut-water which is more streamlined than the open funnel. When a lamprey attaches itself to an object, however, the sucking disk is extended laterally as well as anteriorly and posteriorly (fig. 1). It is in this open position that the lamprey applies itself to host fishes, as well as to stones and, in the case of the male, to its mate during spawning (Reynolds 1931).

As a sea lamprey grows, the diameter of the sucking disk increases and hence the size of the wound inflicted on a host fish becomes greater. From the regression of diameter of sucking disk on length of lamprey it is possible (1) to estimate length of a lamprey responsible for a disk mark on a fish and (2) to verify earlier estimates by Applegate (1950) of the length of the parasitic-feeding period of the sea lamprey in the Great Lakes.

During 1951 and 1952, sucking-disk diameters were measured on 487 sea lampreys ranging from 4.8 to 22.1 inches long. Included in the total were small, newly transformed sea lampreys, 4.8 to 6.9 inches in length, obtained during their downstream migration in Carp Lake River. Some measurements of larger adults were obtained from specimens reared in aquariums at the Hammond Bay Fishery Laboratory. Most of the large lampreys were taken in weirs in Ocqueoc and Trout Rivers and Carp Creek during their spawn-

ing migrations. A few adults were captured in trap nets in Hammond Bay and Duncan Bay, Lake Huron. It was impossible to gather as many data as desired, and for one size group it was necessary to interpolate to reach an estimate of the mean diameter of the disk.

The mouths of the lampreys were pressed firmly against a piece of plate glass. The disk diameters were measured through the glass, from the anteriormost part of the marginal membrane to the posteriormost point of the margin, that is, across the center of the mouth from front to rear. This measurement was consistently the maximal diameter. The relations between total lengths of lampreys and diameters of their oral disks are shown in table 1 and figure 2. In the preparation

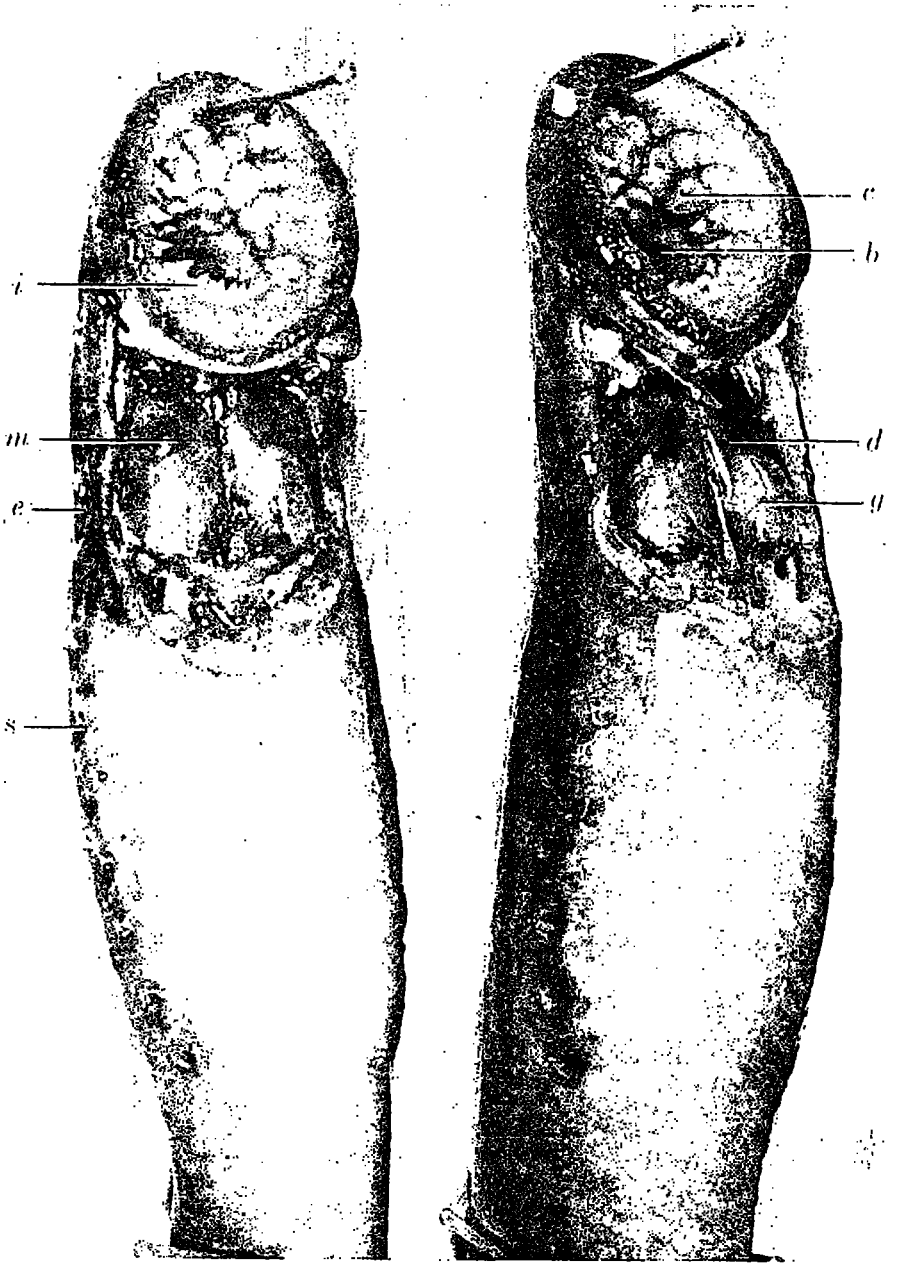

FIGURE 1.—Ventral view of sucking disks and buccal glands of two sexually mature sea lampreys. *i*=infraoral lamina; *c*=circumoral cusps; *b*=buccal funnel; *m*=musculus basilaris; *d*=duct of buccal gland; *g*=buccal gland; *e*=eye; *s*=gill sac.

of the table and the figure, the data for the sexes were combined. The males did tend to have slightly larger disks than females of corresponding length, but the difference was not great enough to warrant separate tabulations. There was a trend toward relatively smaller disks with an increase in length of lampreys as shown when the disk diameters are expressed as percentages of body length (table 1). All percentages greater than 9.0 included lampreys from 4.0 to 10.9 inches long; all percentages in range of 8.6 to 9.0 included lampreys from 9.0 to 14.9 inches long; and the percentages less than 8.5 included the larger lampreys 15.0 to 22.9 inches long.

TABLE 1.—*Relation of diameters of sucking disks to lengths of lampreys in 487 specimens from northern Lakes Huron and Michigan or their tributaries*

Length range (inches)	Number of lampreys	Mean length		Mean diameter of sucking disks	Ratio, disk diameter to body length
		Inches	Millimeters	*Millimeters*	*Percent*
4.0–4.9	6	4.9	124	11.5	9.3
5.0–5.9	78	5.5	140	12.9	9.2
6.0–6.9	49	6.2	157	14.4	9.2
7.0–7.9	0	[1] 7.2	[1] 182	[1] 17.5	[1] 9.6
8.0–8.9	3	8.2	208	20.7	10.0
9.0–9.9	2	9.4	237	21.5	9.0
10.0–10.9	4	10.3	260	24.0	9.2
11.0–11.9	12	11.5	293	26.3	9.0
12.0–12.9	27	12.5	318	28.3	8.9
13.0–13.9	37	13.4	340	30.5	9.0
14.0–14.9	49	14.5	367	31.6	8.6
15.0–15.9	69	15.5	393	33.1	8.4
16.0–16.9	50	16.4	416	34.6	8.3
17.0–17.9	36	17.5	444	36.6	8.2
18.0–18.9	25	18.4	467	37.9	8.1
19.0–19.9	24	19.3	480	38.8	8.1
20.0–20.9	12	20.3	514	40.2	7.8
21.0–21.9	3	21.4	543	43.3	8.0
22.0–22.9	1	22.1	561	45.0	8.0

[1] Values obtained by linear interpolation.

The Tongue

The development and form of the tongue are similar in adults of the various species of both parasitic and nonparasitic lampreys (Leach 1940, *I. fossor;* Vladykov 1949, *P. marinus*, *Entosphenus lamottenii*, and *Lampetra aepytera;* Johnels 1948, *P. marinus*). The tongue appears during metamorphosis and, in the parasitic forms at least, it develops into an effective organ accessory to feeding. Reynolds (1931, p. 15) described the tongue of *E. tridentatus* as a unique structure—

> made up of a number of complex elements that by combining their functions, make that organ an efficient vacuum pump, or when occasion requires, direct its anterior cutting edge against the body wall of the lamprey's host.

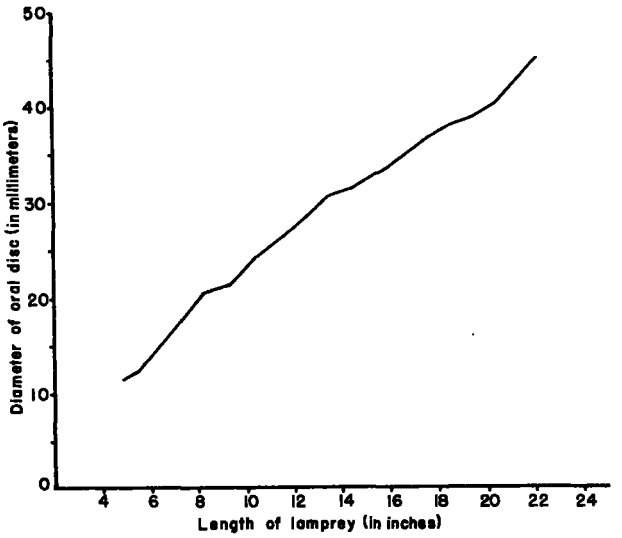

FIGURE 2.—Relation between total lengths of sea lampreys and diameters of their oral disks.

General structure

The tongue of the sea lamprey is a prominent organ in the buccal funnel. The anterior end of the tongue, the apicalis, is furnished with two sets of corneous laminae, each set bearing tooth-like cusps. The laminae constitute the cutting armament. The anterior one is termed the transverse lamina, and the posterior two are termed the longitudinal laminae; all these laminae bear strongly denticulate ridges (Hubbs and Trautman 1937). The transverse lamina, which is bilobed and bent strongly inward along a median longitudinal line, forms the main cutting edge.

The lamprey tongue is supported by the long lingual or glossal cartilage which is median and lies between the large, paired basilaris muscles (fig. 1). According to Reynolds (1931), the lingual cartilage in *E. tridentatus* is practically fixed in position and takes up the thrust of the working member of the tongue, the apicalis. In this Pacific species, the lingual cartilage can be moved slightly forward by the paired muscles, the basilariglossus, which originate on the basilaris muscles and insert on the glossal cartilage. The chief function of the lingual cartilage is to furnish a firm base to support the tissue-cutting mechanism which is erected on an apical cartilage and is united to it by a tendon in a hingelike bond. The system allows the dorsal tip of the

tongue to be rocked backward over a considerable arc into the funnel of the mouth. These observations on *E. tridentatus* by Reynolds appear to apply equally well to *P. marinus*.

A sea lamprey attaches itself to a fish by a strong suction pressure which serves also to bring the skin of the victim into contact with the lamprey's tongue-teeth. The rocking motion of the armed tongue causes a feeding hole to be rasped through the skin and tissues of the host.

Throughout the parasitic life of a sea lamprey, the teeth of the tongue and sucking disk are continually replaced by new ones. Hubbs and Trautman (1937) wrote that each new tooth is formed on the core of its predecessor and is the image of the former tooth which is sloughed off as a hollow corneous structure. The new teeth are invariably hard and sharp, but I concur with Vladykov (1949) who noted that the cusps of fully mature, parasitic lampreys are weaker than cusps of half-grown adults. It seems reasonable to hold that the feeding efficiency of older lampreys is impaired by truncated teeth, a failing that is not wholly remedied by regeneration.

Tongue-teeth in newly transformed sea lampreys

A study of the seasonal development of the tongue-teeth, or lingual laminae, was made on newly transformed sea lampreys. Small, parasitic individuals of this species usually emerge from their larval beds in cool seasons of the year and then migrate to their adult habitat. In Michigan, the migration is characterized by a low peak of activity in November and a greater one during late March and early April. All increases in emergence appear to be closely associated with rising water levels (Applegate 1950).

During the winter months, newly transformed sea lampreys held in aquariums did not feed. On November 22, 1950, 41 recently transformed lampreys, captured during the peak of the fall downstream migration in Carp Lake River, Emmett County, Mich., were stocked in the laboratory aquariums, and small eastern brook trout (*Salvelinus fontinalis*) and white suckers (*Catostomus commersoni*) were added as prey. Water temperatures in the aquariums ranged from 33° to 35° F. until spring. In April 1951, coincident with spring thaws and the peak downstream migration of the lamprey species, the captive individuals suddenly began to feed on the trout and the suckers. On May 3, 1951, 60 spring migrants were placed in the laboratory tanks, and they too began to prey immediately on the fishes provided for them. The temperature of the water in the tanks averaged 44° F. at this time.

Winter water temperatures alone would not seem to explain the tardiness of the fall migrants in starting to feed, since larger, older specimens continued to feed during the same time in adjacent aquariums. The condition of dentitional structures was studied for explanations. Downstream migrants captured in January 1952 possessed tooth characters typical of parasitic individuals except for the tongue-teeth. In the three specimens examined, the transverse and longitudinal lingual laminae were soft and pale yellow, evidencing that they were as yet incompletely cornified and probably incapable of efficient rasping action.

To verify further the influence of the development of the tongue-teeth of both fall and spring emigrants on feeding efficiency, certain collections preserved in 10-percent formalin were examined. Whereas it is known that this preservative tends to harden tissues stored in it, the corneous nature of fully formed teeth was easily distinguished from immature teeth of no feeding value. The observations were made macroscopically; the fingers, probes, and a sharp scalpel were used to test the hardness of the structures. Complete, functional laminae were orange brown, and their cusps were sharply pointed and hard. Incomplete teeth were pale yellow or white and had cusps comparatively blunt and soft. Other specimens possessed teeth of intermediate color and hardness; these were recorded as partially complete (table 2).

TABLE 2.—*Tooth development on tongues of newly transformed sea lampreys captured in Carp Lake River, Emmett County, Mich.*

Item	Fall migrants	Spring migrants
Number of lampreys	96	50.
Date captured	Nov. 15 and 17, 1949.	Apr. 4, 1951.
Length:		
Average, inches	5.7	5.8.
Range, do	4.9–6.5	4.8–6.9.
Weight:		
Average, grams	4.0	5.1.
Range, do	2.0–7.0	3.0–10.0.
Tongue-teeth:		
Complete, percent	9.4	72.0.
Partially complete, do	16.7	18.0.
Incomplete, do	73.9	10.0.

Although the criteria for evaluating the development of the lingual laminae were not sharply quantitative, a great difference in laminal development was found between the fall and spring downstream-migrant sea lampreys. At least 74 percent of the fall migrants were judged to be incapable of feeding on fish owing to incomplete development of the transverse and longitudinal teeth on the tongue. Of the spring migrants only 10 percent showed incomplete tongue-teeth development.

Additional support for the view that most fall migrants are incapable of feeding before the next spring is found in my data concerning the incidence and progressive increase in size of sea-lamprey wounds on host fishes in Lake Huron. For example, on February 28, 1951, a lake-incurred lamprey wound, 18 millimeters in diameter and penetrating the body-cavity wall, was observed on a white sucker, 16.5 inches long, captured in our trap nets in Duncan Bay, Lake Huron. This was the earliest date on which evidence of attack by a newly transformed sea lamprey was ever found. The wound was judged to be that of *P. marinus* because of the scarcity of parasitic *I. castaneus* and *I. unicuspis* in the area.

Factors besides development of lingual laminae may be concerned in the delayed start in parasitic feeding by fall-migrant sea lampreys. This study of the tongue-teeth indicates only that metamorphosis is incomplete in the majority of individuals migrating to the lake in the fall and that the animals are incapable of feeding until spring.

The Buccal Glands

A most interesting feeding mechanism possessed by the sea lamprey is the buccal-gland system whose secretion exhibits anticoagulant, hemolytic, and cytolytic properties when applied to blood and tissue of prey fishes. The mechanism consists of the glands, the central lumina of which serve as reservoirs for the secretion, and the connecting ducts which lead to openings in the mouth cavity.

The buccal glands are a pair of conspicuous, roughly bean-shaped bodies partly imbedded in the ventral surface of the two basilaris muscles of the head (fig. 1). One gland is associated with each of these muscles, and the pair are so situated that a transverse section of the head at eye level passes through them. These secretory organs in the European lamprey, *Petromyzon fluviatilis*, are called salivary glands by foreign workers (Johnels 1948). I concur with Gage (1928) and others in designating them as buccal glands, for this term does not imply homology with the salivary glands of higher vertebrates—a relationship that has not yet been demonstrated.

Buccal glands first become evident, in lampreys in general, during transformation of free-living larvae into the parasitic phase, as shown by Kaensche (1890) for *P. fluviatilis* and Gage (1928) for *P. marinus*. They result from the invagination of solid cords of cells from the oral ectoderm before the tongue musculature begins to differentiate.

In serial sections of the nonparasitic *Ichthyomyzon fossor*,[1] and the parasitic *P. marinus* that I examined, the buccal glands are well formed at early metamorphosis. They contain but little secretion and are lined with simple, columnar, epithelial cells. These cells have their nuclei basally located and, apically, tiny globules of what appears to be secreted material.

Each buccal gland is drained by a duct which leaves its medial, convex side about the middle of its length and turns sharply in an anterodorsal direction in the basilar muscles. The pair of ducts follow the median piston cartilage which lies between the basilar muscles, until the mouth region is reached. There they turn laterally to their respective openings into the mouth cavity, one on each end of the infraoral lamina. In the newly metamorphosing specimen of *I. fossor* the ducts appeared solid at their anterior extremities, although hollow posteriorly; those in *P. marinus* were open.

In serial sections of several actively parasitic lampreys (*P. marinus* and *I. fossor*) that I studied, the development of the buccal system was complete (fig. 3). The reservoirs were turgid with secretion. In each gland, underlying the inner layer of simple columnar epithelium, was a stratum of dense, areolar-type connective tissue. Prominent constrictor muscles, striated and voluntary, partially enveloped the gland externally to this fibrous zone. These muscles doubtless serve to force the secretion into the mouth by way of the duct system. Sharp and irregular contractions of

[1] I am indebted to Dr. W. James Leach of Ohio State University for making available his preparations of this species.

the muscles of exposed glands were observed in adult specimens of *P. marinus* that were anesthetized with urethane. Outlying the muscle layer was a strong capsule of connective tissue which isolated the organ from the *musculus basilaris* which largely surrounded it.

At the point where the duct leaves a buccal gland a sharp transition occurs from glandular epithelium to duct epithelium. The latter is stratified and columnar, and the cells possess large basal nuclei. The lumen is not lobate like that of the gland. The duct is surrounded by a sheath of connective tissue which is prominently extended in the dorsal and ventral directions. Longitudinal muscle fibers course through the sheath to aid in the propulsion of the glandular secretion to the mouth.

The Buccal-Gland Secretion

Physical characteristics

The secretion pooled in the reservoir of a buccal gland was easily and quickly obtained. Portions of the ventral integument and superficial skeletal muscles were removed (fig. 1), leaving the pair of prominent buccal glands exposed. A small-gage hypodermic needle mounted on a syringe was then inserted into the glands in turn, and the contents were withdrawn. Each gland collapsed quickly as its contents were exhausted. Opening of organs collapsed by this routine demonstrated that practically all the fluid was removed. The yield per gland was measured to the nearest 0.01 milliliter on the graduated barrel of the syringe.

I called the secretion from buccal glands of the sea lamprey lamphredin. The color of fresh samples of this fluid ranged from light amber to straw. The material was slightly sticky and somewhat less labile than water. Macroscopically it appeared clear, but at a magnification of 430 diameters much suspended material could be seen which was finely divided and bore no resemblance to cells or crystals of any sort. In addition, numerous translucent, light-refracting globules that resembled fat or oil droplets were present. Their size varied from about 2 to 8 microns. The largest globules were also the largest of inclusions; collectively they were the only objects observed that had consistent form in the samples.

Upon desiccation, the globular constituents of fresh, or frozen and thawed, samples of lamphredin became more pronounced and darker in color when observed under magnification. Before dehydration became complete, numerous transparent, rodlike crystalliform objects formed throughout the sample. These structures were slender, their margins were well defined, and their ends tapered to sharp points. Many were variously branched (fig. 4). The formation of these rods progressed rapidly as the liquid dried. One or more of the globules were observed at each branching or along the shaft of each rod, but most of the globules remained free. Both kinds o.

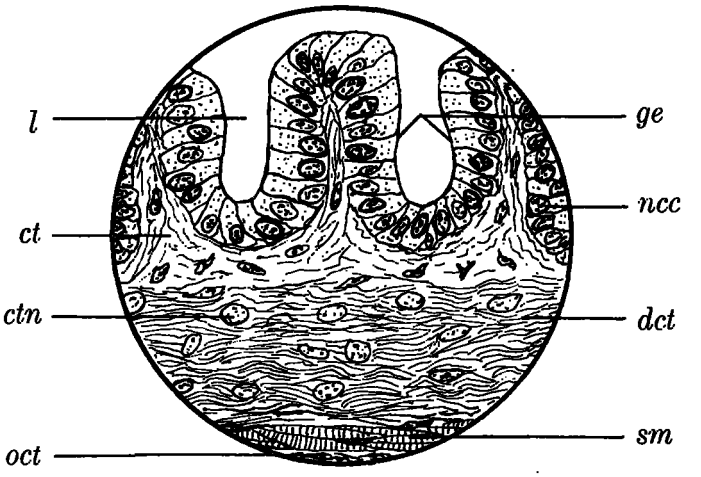

FIGURE 3.—Sketch of a portion of buccal-gland wall taken from a parasitic sea lamprey 7.5 inches long and 10 grams in weight: *l*=lumen of gland; *ge*=gland epithelium; *ct*=connective tissue; *ncc*=nucleus of columnar cell; *ctn*=connective tissue nucleus; *dct*=dense connective tissue; *oct*=outer layer of connective tissue; *sm*=striated muscle layer (x800).

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structures appeared dark when desiccation was complete.

In all, I aspirated the buccal glands of 301 sexually mature, spawning-migrant sea lampreys for experiments. These specimens were captured in weirs operated by the Fish and Wildlife Service in Trout and Ocqueoc Rivers and Carp Creek, tributaries to Lake Huron in Presque Isle County, Mich., during the 1951 and 1952 spawning seasons. It is at this time only that sea lampreys of mature size and sufficient numbers can be collected to provide any sizable quantity of secretion, although many glands are past their prime. Applegate (1950) reported on the degeneration of the viscera and other tissues of the sea lamprey as it attains sexual maturity and ceases active feeding. The buccal systems of some of the 301 lampreys showed similar structural and functional deterioration. In general, the more obviously sexually mature lampreys had one or both buccal organs devoid of fluid content. In the 602 glands examined, 25.1 percent yielded little or no secretion; the remaining 74.9 percent were in good condition (table 3). In 10.8 percent of the lampreys both glands possessed nothing, and in 13.6 percent a single gland of the pair was void. Eight fall-caught feeding lampreys of comparable size had completely functional organs; the yield of secretion from their buccal glands was not appreciably greater than that obtained from sexually mature migrants with glands in good condition.

TABLE 3.—*Yields of secretion from buccal glands of 301 spawning-migrant sea lampreys captured in Trout and Ocqueoc Rivers and Carp Creek, Presque Isle County, Mich., April–June 1951 and 1952*

Length range (inches)	Number of lampreys	Number of glands that were—		Mean yield per pair of glands	
		Good	Degenerate	All glands	Good glands only
				Milliliters	*Milliliters*
10.0–10.9	1	2	0	0.10	0.10
11.0–11.9	7	10	4	.09	.12
12.0–12.9	26	33	19	.07	.10
13.0–13.9	47	78	16	.09	.10
14.0–14.9	51	92	10	.11	.12
15.0–15.9	52	73	31	.10	.13
16.0–16.9	40	59	21	.12	.15
17.0–17.9	27	39	15	.13	.17
18.0–18.9	24	36	12	.14	.18
19.0–19.9	21	25	17	.13	.22
20.0–20.9	4	4	4	.11	.23
21.0–21.9	1	0	2	.10	----------

Functional degeneration of the buccal glands was accompanied by definite morphological manifestations. Some of these organs were of nearly full length but were flaccid; others were greatly reduced in all dimensions. In either of these conditions, little or no secretion was present. The reservoirs of a small number of glands in obvious deterioration contained a black fluid which, under magnification, showed no discernible differences from the normal product, except in color. Under a microscope, the most atrophied glands showed a reduction in height of epithelial cells from columnar shape to cuboidal.

The average yield of lamphredin per sea lamprey was determined. The lengths of the 301

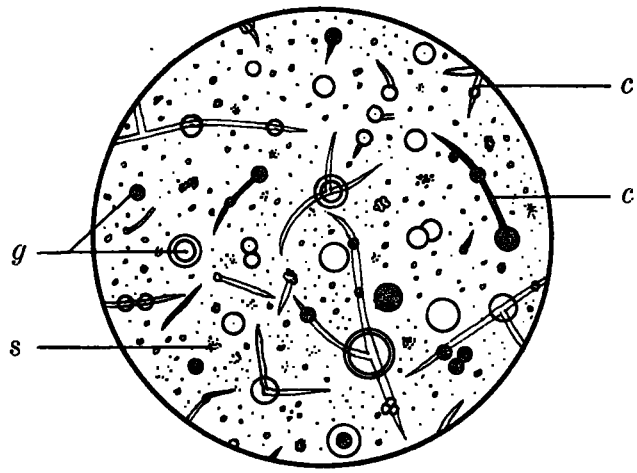

FIGURE 4.—Sketch of desiccated sample of lamphredin (buccal-gland secretion) from mature sea lampreys; *c*=crystalline rods; *g*=globules; *s*=secretion granules (x430).

lampreys from which lamphredin was aspirated (table 3) ranged from 10.6 to 21.4 inches. No sex difference could be detected, and the yields for the males (61 percent of the sample) and females (39 percent) have been combined. The data show that there is a regression of yield of secretion on the length of lampreys; the glands of large lampreys usually contain more secretion than the glands of smaller individuals. The average yield of buccal-gland secretion per lamprey (including those specimens with degenerate glands) was 0.106 milliliter. The mean yield of the 226 lampreys with glands in good condition was 0.142 milliliter. On this basis, 7 lampreys, 15.5 inches in length, would be required to obtain 1 milliliter of lamphredin.

Anticoagulant properties

Experiments by Gage and Gage (1927) indicated that buccal-gland secretion of certain lampreys inhibits clot formation in blood and has hemolytic properties. I tested the action of lamphredin on fresh blood specimens from the hearts of anesthetized sea lampreys, rainbow trout (*Salmo gairdneri*), eastern brook trout, longnose suckers (*Catostomus catostomus*), and white suckers. Most of the lamphredin was obtained from spawning-migrant sea lampreys in good condition. The secretion of six full-grown, sexually immature sea lampreys, taken from Lake Huron in the fall of 1950, was used as a control on the quality of material taken. The lamphredin drawn from the glands of the active feeders and tested on the blood taken from the hearts of wild brook trout and white suckers gave results identical with those obtained with the secretion from spawning migrants.

Lamphredin prevented coagulation of fish blood within specified time limits in all trials when the concentration of buccal-gland secretion equalled or exceeded 25 percent of the total volume of the mixture. Tests were declared positive and observations were terminated when no coagulation took place within 20 to 30 minutes, whereas untreated samples of blood used as controls usually coagulated within 3 minutes. With lesser proportions of secretion, the clotting of the blood was retarded, not prevented. The extent of delay in the coagulation was directly proportional to the quantity of lamphredin in the mixture.

Results were similar when the glandular secretion was diluted with Ringer's physiological saline solution for fish and mixtures made up containing 25 percent or more of lamphredin and 50 percent fish blood; that is, the blood did not clot. Again when the amount of secretion was less than 25 percent, the coagulation of the blood was only delayed.

Effect of storage on anticoagulant properties

Tests were made not only with fresh lamphredin but with lamphredin that had been stored under various conditions. Comparison of the results of experiments based on the secretion in fresh-frozen, dried, and refrigerated conditions showed that the anticoagulant and hemolytic properties of lamphredin are altered by storage. No biochemical analyses were made to determine the causes of the changes.

Freezing.—Several tests proved that frozen lamphredin could be kept for at least a month with no apparent loss of anticoagulant powers, but longer storage reduced the effectiveness. Three samples of lamphredin collected in July 1951 were placed in 1-milliliter amounts in centrifuge tubes, sealed, and frozen. One year later, July 1952, they were thawed and tested on the blood of white suckers and rainbow trout. The lamphredin prevented the coagulation of the fish blood only when mixed in equal proportions. Lamphredin used at less than equal proportions merely delayed the clotting. The strength of the anticoagulant had been reduced as compared with fresh material.

Alternate freezing and thawing seemed to hasten the deterioration of lamphredin. A sample of the material collected on August 4, 1950, was kept frozen in a sealed tube until September 5, 1950, when it was thawed completely. Fifteen minutes after the last ice had disappeared, it was refrozen in the same container and held until October 6, 1950, when it was melted again and tested with blood specimens from the heart of a white sucker. In each of two experiments the slide that contained undiluted blood clotted in 5 minutes; equal parts of lamphredin and sucker blood coagulated solidly in 10 minutes; fish blood and distilled water in a 1:1 ratio clotted in 15 minutes.

Refrigeration.—A milliliter of lamphredin aspirated from live lampreys in June 1951 was placed in a centrifuge tube, sealed, and stored at 40° F. Overnight, a precipitate appeared on the bottom

of the tube to an extent of 25 percent of the original volume. The supernatant fluid was clear and light amber. Through the following days, the volume of the precipitate and debris in the bottom did not increase, but the color of the top fluid darkened strikingly. At the end of a week, the supernatant fluid and the settled substance were dark brown, and the deterioration was marked by an order of putrefaction.

Examination of a sample taken from the tube after agitation to mix the settled and liquid portions revealed no marked changes except in color. Another sample was mixed with an equal amount of fresh blood from the heart of a white sucker. The blood in the mixture clotted in normal time (3 minutes). No evidences of anticoagulant action or hemolysis could be observed. When the ratio of the storage-altered lamphredin to blood was increased to 2:1, the results were the same.

Drying.—To determine the effect of drying on the anticlotting properties of lamphredin, three samples of the material were collected from spawning-migrant sea lampreys on August 4, 1950. A quantity of 0.5 milliliter was placed in each of three centrifuge tubes, which were then held and rotated in the warmth (100° F.) of a space heater. The material was still liquid 2 hours after control tubes holding 0.5 milliliter of distilled water were dry. In 4 hours the lamphredin was dry and had a clear, greenish-yellow appearance. The loss in volume was estimated at 50 percent. On August 8, 1950, a 0.3-milliliter specimen of lamphredin was collected, placed in a centrifge tube, and held by hand in the heat (not in excess of 120° F.) of an alcohol burner. The material in the tube dried after 2½ hours. Its appearance was similar to the other dried samples, and again the volume had been reduced an estimated 50 percent. Each of the four tubes of dried lamphredin was sealed on the date of its desiccation and was stored immediately at approximately 40° F.

The dried lamphredin was tested 5 months later, in January 1951. Small amounts of distilled water were added successively to the tubes in the attempts to reliquefy the material. Not until a 2:1 ratio of water to lamphredin was used did the mixture become liquid; that is, the total volume of the redissolved lamphredin was 50 percent greater than that of the original solution. With smaller proportions of water, part of the lamphredin remained solid.

When blood from white suckers and the solution of redissolved lamphredin were mixed on clean glass slides in equal proportions, the coagulation of the blood was delayed only 2 to 3 minutes longer than the clotting time of the control slides containing an equal volume of undiluted blood. In 10 minutes, the hemolyzing action of the lamphredin had affected only 50 percent of the red cells in the blood. When the lamphredin solution and blood were mixed in a 2:1 ratio, coagulation of the blood once more took place after a short delay. Microscopic examination of the slides after a 10-minute interval showed only an estimated 50 to 60 percent of the erythrocytes destroyed.

These results, which indicate a reduction in the potency of lamphredin reclaimed from the dried state, are not conclusive. There is a possibility that the method of desiccating the lamphredin by gentle heating may have damaged it.

The foregoing experiments have shown that the anticoagulant and hemolyzing properties of lamprey buccal-gland secretion are easily lost under storage. The facilities at the Hammond Bay Fishery Laboratory did not permit the biochemical analysis of the secretion that would be needed to explain the nature and reactions of the lamphredin or its various fractions.

Lytic properties of lamphredin

The study of numerous wounds created by sea lampreys on fishes in laboratory aquariums and in nature indicated that cytolysis or autolysis were involved, as well as mechanical injury. The damage to muscle tissues often appeared greater than that which could have been caused by the rasping tongue and/or suction pressure exerted over the wound. Microscopic examination of fresh and stained sections of tissue from typical wounds on white suckers and rainbow trout were disappointing. Evidences of possible lysis due to lamphredin were by their nature largely destroyed during the processing of the mounts. The marks of cellular erosion that appeared on the slides could have been the result of the mechanical action of the tongue of the lamprey and/or suction pressures exerted on the wound. The injection of lamphredin into live fish yielded more definite results.

Injections of lamphredin in fish

Brook trout.—On May 27, 1952, two 8-inch eastern brook trout from the hatchery-reared supply in the laboratory holding tank were anesthetized in urethane, and the first fish was injected with 0.20 milliliter of lamphredin. The injection was made on the right side of the fish into the dorsal musculature at a point well above the lateral line and midway between the dorsal fin and the head. A small hypodermic needle was inserted through the skin and then directed anteriorly for 1 inch so that the secretion could be released at a location away from the insertion hole in the skin, and yet not too deeply into the muscle. The latter precaution was taken so that any reaction of lamphredin in the fish might be reflected on or near the skin and thereby observed. In spite of precautions, at least half of the injected lamphredin oozed from the hole as soon as the needle was withdrawn.

The second trout was injected in the same manner and in the same body area with 0.20 milliliter of distilled water as a control.

Both fish were put into a 50-gallon aquarium supplied with running lake water, where they rapidly recovered from the anesthesia. The fish had been fin-clipped for identification. Lamphredin produced a positive reaction in brook trout No. 1. The dark-green skin became discolored and edematous; it changed to jet black, then to gray, and back to black. After 2 days the fish refused food placed in the aquarium. It appeared sluggish. Eleven days after the inoculation, the size of the swelling was reduced, the mouse-gray discoloration became black, and the fish again accepted food. After about 3 weeks, recovery was sufficiently advanced to permit the assumption that it would eventually have been complete. The small injection puncture in the skin persisted unhealed until the fish was discarded. Owing to the temporary failure of the water system which necessitated the removal of the fish from the aquarium, the degree of recovery from the injection of lamphredin remains unknown. The control fish showed no abnormal reaction to the injection of distilled water. The puncture remained pale for a day and then became obscure and disappeared. This trout was normal in every respect, and fed normally.

Longnose sucker.—The next fish to be inoculated with lamphredin was a male longnose sucker, 15.0 inches long and weighing 580 grams. On June 3, 1952, a 0.20-milliliter sample of lamphredin, collected from sea lampreys on the same date, was introduced into the musculature of the fish on the left side, at a point midway between the dorsal fin and the posterior limit of the head, and about 1 inch above the lateral line. A hypodermic needle was directed anteriorly for 1.5 inches at a depth not more than 0.3 inch below the skin. The buccal-gland secretion was slowly released as the needle was carefully withdrawn. Again part of the lamphredin—at least 0.05 milliliter—escaped from the injection hole as soon as the needle was removed.

Within 3 hours after the inoculation, there was a whitish discoloration of the skin at the site of injection. The discoloration became more and more pronounced in the next 2 days, although its area increased only a little. During this time, all else about the fish appeared normal.

On the third day, the discoloration began to spread, and a rapidly increasing swelling of the area was noted. An area 2 inches in diameter was affected, and the maximum height of the protuberance was estimated at 0.5 inch above the normal skin level. The skin over this swelling had turned a pale yellow.

The distention involved such an area and pressures that the fish became contorted; its body was flexed as if it were making a shallow, right-hand turn. The specimen did not move at all during the day, and its rate of respiration was more rapid than that of other longnose suckers in the aquariums. On the fifth day, the sucker died, presumably as a result of the injection. It was removed from the aquarium, examined in detail, and photographed (figs. 5 and 6).

The normally dark fish was very pale just before death and remained the same after death. The gills, too, were blanched. The swelling now appeared reddish, owing to the contamination of the mucous on the surface with a small amount of blood residue that issued from the injection hole. Beneath the stained mucous, the skin tone was jet black except for a whitish-yellow area in the center of the swelling. The distention measured 3.0 inches long, 2.5 inches wide in dorsoventral direction, and 0.8 inch high at the maximum; it was not peaked, but appeared high and rounded. The injured region was soft and rubbery, indicating that the distention was edematous.

Any slight pressure on the area caused a bloody issue from the injection hole.

When a small incision was made in the swelling with a scalpel, a large quantity of murky, purplish liquid poured out, as if under internal pressure. The exact volume of the issue could not be determined, but 5 milliliters were collected in a syringe and 2 to 3 milliliters were lost. There is no way to estimate how much of this material had previously escaped by oozing through the injection hole.

The liquid in the vesicle exceeded the total volume of blood found in normal longnose suckers of this size. It was more labile than normal whole blood and contained no clots or lumplike aggregations. The odor was sweetish, but unpleasant, and resembled that of flesh in the initial stage of decomposition.

Two smears of the exudate were examined under high- and low-power magnification. The purplish color of the liquid was due probably to the hemolysis of erythrocytes, but no red blood cells were present. Leucocytes were abundant and appeared normal, though generally of small size. Cellular debris was prominent, which perhaps included unidentifiable remains of destroyed red-blood cells and muscle and connective-tissue cells. Numerous, sharply pointed rods were piled like jackstraws which exhibited the characters noted in drying samples of lamphredin (fig. 4). There was no evidence of clotting. The liquid remained free flowing for 20 minutes, at which time it was discarded.

No flesh or connective tissue remained attached to the skin in the affected area. The skin was blackish and had suffered a loss of elasticity. When the skin covering the entire affected area was trimmed away, a deep, blood-red crater was revealed, from which the fluid had escaped (fig. 6). The lining of the cavity consisted of soft, reddish, mushy material which averaged 5 millimeters in depth. A smear of this substance, though showing no definite cell structures, was interpreted as a mass of muscle-tissue cells in an advanced stage of cytolysis. Immediately beneath the mushy layer, the flesh was white, firm, and apparently normal.

FIGURE 5.—Vesicle produced by a subcutaneous injection of lamphredin into a longnose sucker 15.0 inches in length (fish No. 3 in table 4). See also figure 6.

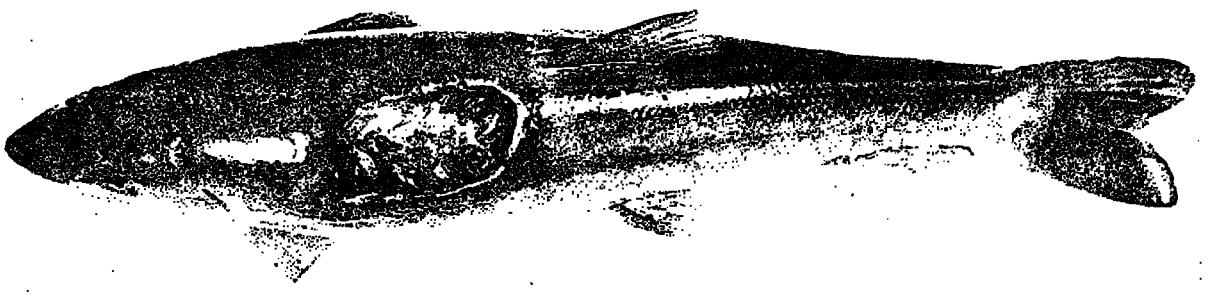

FIGURE 6.—Tissue lysis produced by the action of lamphredin in a longnose sucker 15.0 inches in length (fish No. 3 in table 4). See also figure 5.

The crater had many stringlike fragments of connective tissue extending into it, all revealing apparently severe erosion which we may presume to have been caused by the lamphredin. Several strands were traced into the surrounding, unaffected flesh to prove their identity. No traces of the vascular-system structures could be found within the excavation.

The depth of the hole was measured downward from the normal level of the skin, and the greatest reading of 0.8 inch extended over a wide area. The total dimensions of the vesicularized area were recorded as follows: Length, 3.0 inches (long axis of fish); width, 2.25 inches (dorsoventral); and total depth, 1.6 inches (surface of swelling to bottom of cavity).

The results of this experiment indicate that the lamphredin acted as a lytic agent on the flesh of the longnose sucker. Of the four affected tissues, the integument was the most resistant and the muscle and vascular tissue the least resistant. The reaction of the fish was positive, and its death was directly attributable to the effects produced by the injection of 0.20 milliliter of lamphredin. The viscera of the fish appeared normal, but blood was notably lacking in the atrium and ventricle of the heart. The color of the ventricle was light rather than the normal red.

Trouts and suckers.—The results of the preceding and other experiments with lamphredin injections performed in June and July 1952 are summarized in table 4. The fish used in the tests, except for the brook trout and rainbow trout, were delivered alive from our trap nets in Hammond Bay. The eastern brook trout were supplied by the State Fish Hatchery at Oden, Mich., and the rainbow trout by the Federal Fish Hatchery at Northville, Mich. The specimens were held in large aquariums supplied with running lake water, and there were never more than 2 fish in a 50-gallon aquarium.

Reaction of a fish to lamphredin injection was considered positive when dissection of the affected area disclosed evidence of cytolysis and hemolysis. These conditions were usually accompanied by swelling and discoloration of the skin over the site of the reaction. The severity of a positive reaction was arbitrarily rated as 1+ for the least degree of effect that could be considered positive, and 4+ for the maximum reaction. Ratings of 3+ and 4+ were ascribed to those reactions whose results approached or reached fatal proportions. Values of 1+ and 2+ indicate that recovery from the injection effects was not only possible but likely.

Most injections of lamphredin into the muscle of 4 species of fish produced extensive damages. It is not known whether these effects on fish tissue are due to the direct enzymatic action of a cytolytic constituent or to autolysis induced by a histotoxic element in the lamphredin. Positive lytic reactions were recorded in all but 3 of the 17 tests performed. Although a wider range of volumes might have been used in injections, we chose to deal with quantities that approximate the normal content of buccal glands in living lampreys (aver-

TABLE 4.—*Reactions produced in fishes by injections of lamphredin, June and July 1952*

[M = male; F = female. See text for explanation of the several degrees of positive reaction]

Fish No.—	Species	Length	Weight	Sex	Lamphredin injected	Location of inoculation	Reaction	Degree
		Inches	*Grams*		*Milliters*			
1	Eastern brook trout	8.0			0.20	Dorsal muscle	Positive	3+
2	Rainbow trout	16.0	794	F	.25	do	do	4+
3	Longnose sucker	15.0	580	M	.20	do	do	4+
4	do	15.2			.20	do	do	4+
5	do	14.1			.10	do	do	2+
6	do	14.9			.20	do	do	4+
7	do [1]	14.3		M	[2].20	do	do	4+
8	White sucker	13.1	366	M	.20	do	do	2+
9	do [1]	15.3	660	F	[3].20	do	Negative	
10	do	14.0	486	M	[3].20	do	Positive	2+
11	do	13.3	330	M	[4].20	do	do	1+
12	do [5]	15.5	740	F	[4].20	Right side	Negative	
					.25	Left side	Positive	4+
13	do	13.9	448	F	[4].25	Dorsal muscle	do	1+
14	do	13.0	312	M	.25	do	do	4+
15	do	14.1	476	M	[4].10	Pericardial cavity	Questionable	
16	do	14.0			.10	Dorsal muscle	Positive	4+

[1] Fishes bore healed scars resulting from attacks by sea lamphreys in the lake.
[2] Lamphredin was frozen and stored for 5 days.
[3] Lamphredin was frozen and stored for 2 days.
[4] Lamphredin was frozen and stored for 1 year.
[5] Fish injected twice as indicated.

age yield, 0.15 milliliter, and ranging upward to 0.25 milliliter per pair of glands in larger individuals). Two things at least are not known about the volumes used by feeding lampreys: (1) The total amount employed in a feeding attack; (2) the rate of production of the fluid.

Inoculations ranging from as little as 0.10 up to 0.25 milliliter produced 9 severe reactions—1 rated as 3+ and eight as 4+ (figs. 7 and 8). Of this number, 2 resulted in the deaths of subjects: Longnose sucker, 15.0 inches, 5 days after injection of 0.20 milliliter of fresh lamphredin; longnose sucker, 14.9 inches, 9 days after receiving 0.20 milliliter of fresh lamphredin. The observations on the other 6 fish that showed responses were terminated for various reasons before death due to the lamphredin could occur. Death was not a necessary criterion in determining the lytic powers of the lamphredin, however; the extent of necrotic tissue provided an adequate, though only roughly quantitative, measurement.

Only 2 fish giving a 2+ reaction had been injected with fresh lamphredin, and in 1 of these the amount was small (specimen No. 5, 0.10 milliliter).

It appears that buccal-gland secretion that has been frozen and stored for some time suffers a loss in its cytolytic or histotoxic power, as well as in the

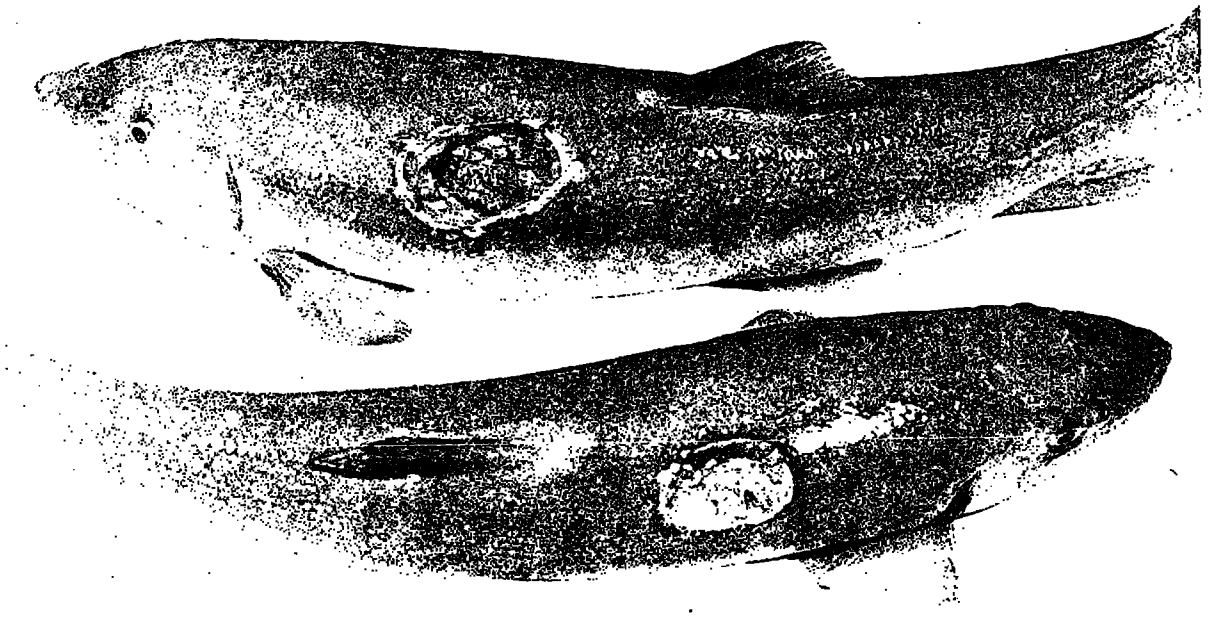

FIGURE 7.—Lytic reactions produced in longnose suckers by subcutaneous injections of lamphredin. Top fish was 14.9 inches long (fish No. 6 in table 4); lower fish was 14.3 inches long (fish No. 7 in table 4). The skin and fluid contents of the vesicles were removed immediately before photographing.

FIGURE 8.—Lytic reaction produced in dorsal muscles of a rainbow trout by an injection of lamphredin (fish No. 2 in table 4). The skin and fluid content of the vesicle were removed immediately before photographing.

hemolytic and anticoagulant properties previously described. Material collected from spawning-migrant lampreys in June 1951 and kept frozen for 1 year was thawed and injected into the dorsal muscles of three white suckers and into the pericardial cavity of a fourth. Two of the muscle tests were called positive but rated only 1+; the other was considered negative. The results of the heart test were recorded as questionable. The quantities of lamphredin used in these experiments were comparable to those that produced strong, positive reactions in hosts when fresh material was used.

A 0.20-milliliter sample of lamphredin that had been frozen and stored for 5 days caused a 4+ reaction when injected into the dorsal muscles of a longnose sucker 14.3 inches in length. Two 0.20-milliliter samples of secretion that had been frozen and stored only 2 days were introduced into two white suckers, one 15.3 inches and the other 14.0 inches long. The effect in the first fish was entirely negative, but lysis in the second one was called positive and rated 2+.

The observed variation in reactions of hosts to injections of lamphredin may be attributed to individual differences in the fishes, to the species involved, to the location of the point of inoculation, to the quality of the secretion, either fresh or frozen, to the size of the injection, and to the amount of secretion that escaped from the subject as the hypodermic needle was withdrawn. In every test, an undetermined quantity of lamphredin oozed from the hole in the skin of the fish immediately after the inoculation. In some cases the loss of lamphredin from the test fish was estimated at one-quarter to one-half of the total volume injected. If the whole amount of fluid introduced into the subject had remained there, the effects unquestionably would have been greater.

We now have the evidence that lamphredin from sea lampreys exerts a lytic action on the skeletal muscle, blood vessels, connective tissue, and integument of living fish. Add to this injury the action of the rasping tongue, abrasion of circumoral cusps, and suction pressure, and the explanation of feeding penetrations is basically in hand.

Attachment and Feeding

Attachments on fish

Gage (1929) alone has reported on feeding experiments with "lake lampreys" (*P. marinus*) and fish. His work was carried out in aquariums at Cornell University and in a bathtub in his home during 1914 and 1915. Many of Gage's findings have been confirmed and extended at the Hammond Bay Fishery Laboratory where there was unparalleled opportunity to observe sea lampreys feeding on prey fishes. Twenty 50-gallon, glass-sided aquariums, supplied with running water from Lake Huron, were in operation from April 1950 to July 1952. During this time, several hundred sea lampreys ranging from 4.8 to 18.3 inches in length passed a part or all of their parasitic lives in the aquariums. A report is in preparation concerning the growth, food consumption, and maturity of some of the captive lampreys.

Eleven common species of fishes were used in the laboratory aquariums as prey for the sea lampreys: Brown trout (*Salmo trutta*), rainbow trout, eastern brook trout, lake whitefish, white sucker, longnose sucker, brown bullhead (*Ameiurus nebulosus*), northern pike (*Esox lucius*), burbot, yellow perch (*Perca flavescens*), and rock bass (*Ambloplites rupestris*). Most of these fishes have some angling or commercial importance in the Great Lakes. Two or three species usually were represented in each aquarium.

Of great value to the sea lampreys in their predatory, parasitic existence in the sea or in lakes are their acute vision and strong and rapid swimming. The lampreys have an additional and important advantage in the fact that the prey species of fishes are not ordinarily frightened by them. Even under aquarium conditions, prospective victims typically ignore the lampreys and take no actions to avoid them.

In a laboratory aquarium, the attack on a prey fish is often direct, swift, and accurate. The lamprey sights the fish, and as it closes for the attack the disk is opened and the head is elevated; this elevation brings the suctorial apparatus into a position that facilitates attachment. As soon as contact is made with the fish, the lamprey maintains its hold by suction. The reaction of the fish is usually violent, but its struggles to dislodge the attacker are almost always in vain.

Sometimes there is an amazing lack of coordination in an attempted attack on a fish. The approach is negotiated as just described, but the lamprey may overshoot or undershoot the fish and attach itself to the bottom, to the glass wall, or to

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the standpipe drain. The lamprey perceives its error within a few seconds, but at times as many as three or four attempts are made before contact with the fish is achieved. These clumsy attacks were not characteristic of particular lampreys; frequently a lamprey that attacked with accuracy on one occasion was inaccurate on a later one.

A moving fish or one that is struggling to dislodge a lamprey frequently draws other attacking lampreys to itself. Many times a fish in a laboratory tank was host to several lampreys simultaneously (fig. 9), while other fish of the same species in the tank remained untouched. If neglected fish became agitated by the frantic struggles of other fish bearing lampreys, they apparently became more subject to attack themselves.

The location of the fish in an aquarium did not affect its chances of being attacked. Fishes such as brook trout, brown trout, rainbow trout, yellow perch, rock bass, and northern pike, which usually maintain midwater positions in aquariums, were no more immune than species that typically remain on the bottom. The parasites have been observed to ignore suckers resting nearby on the bottom and to rise and attack unerringly the specimens hovering at a higher level.

The great tenacity with which a lamprey maintains its attachment on a fish was demonstrated repeatedly. Each aquarium was covered with fine-mesh, wood-framed copper screens of sufficient weight to prevent the specimens from escaping. A host engaged in a violent struggle to throw off its attacker frequently scraped the lamprey along the screen, causing an appreciable abrasion of the skin. Not once, however, was a lamprey dislodged when hurt in this manner.

Norman (1947) wrote that sea lampreys are able to attach themselves so firmly to victims that it is rare indeed for the fish to shake off its persecutor before succumbing from loss of blood. He also suggested that the great strength of the

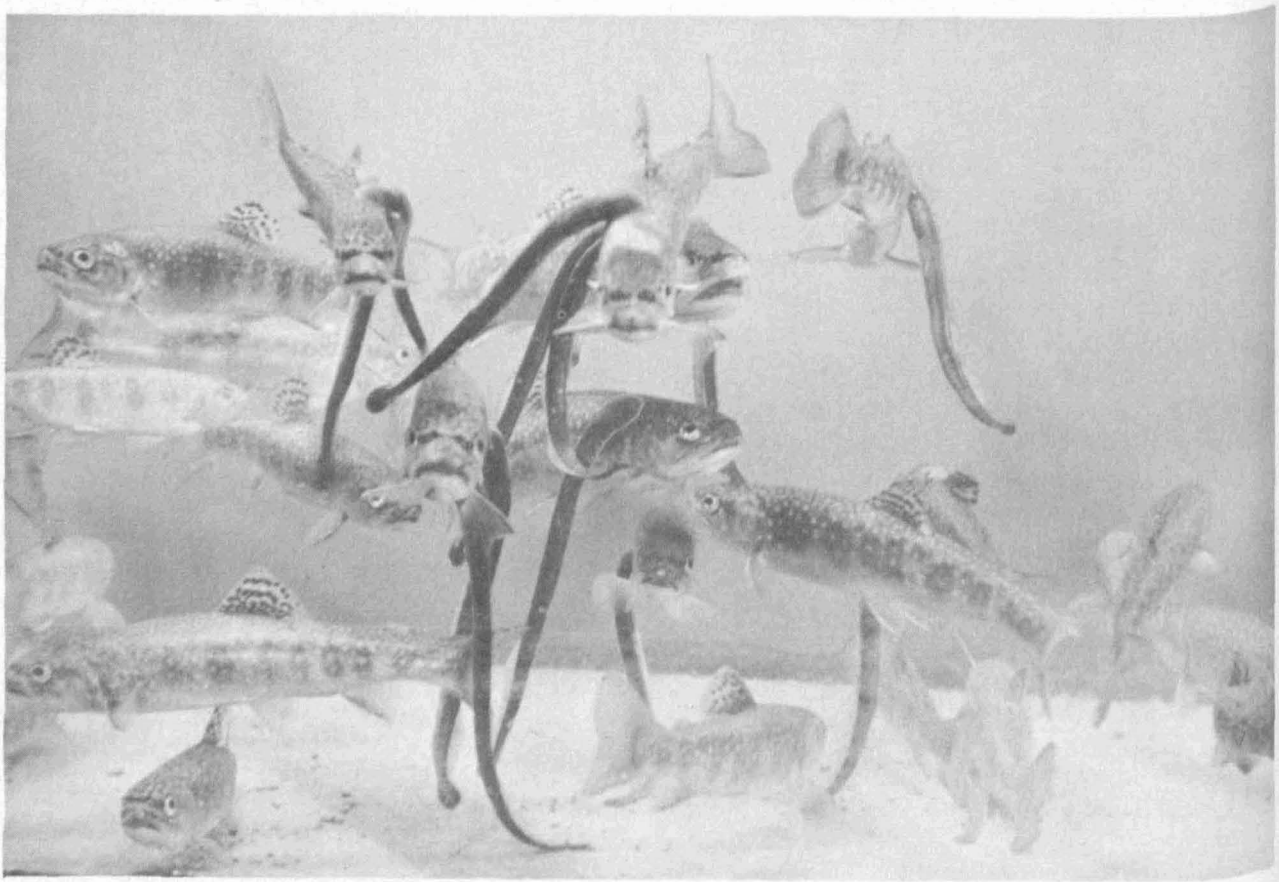

FIGURE 9.—Brook trout under attack by small, recently transformed sea lampreys in a laboratory aquarium, April 1951. Note multiple attachments on some fish.

sucking disk could be tested by allowing a lamprey to attach itself to one's hand or arm, whereupon it would be almost impossible to detach the organism without lifting it from the water. The power of the suction is also demonstrated by the large edema or hyperemia that appears at the site of attachment before the skin is broken. At times, suction is indicated by a noticeable indentation of the skin on the opposite side of the fish. Many observations were made on rainbow trout, brown trout, and white suckers in which suction pressure was reflected across the body through 1.5 to 2.0 inches of dorsal musculature.

In general, fish possess no means for ridding themselves of attached lampreys. The initial, excited reaction of a fish to attachment was typical of all the species observed. The more active kinds, such as the trouts and perch, gradually slowed in their struggles, but tended to remain in motion for the duration of the attack, with brief periods of struggle intervening between increasingly longer periods of passivity. The white suckers and longnose suckers usually returned to resting positions on the bottom after their initial battles for relief. At times during the attachment they were stimulated to new but brief periods of frenzy.

The wounding process

When the efforts of the fish to dislodge its attacker have subsided, the lamprey proceeds to create a wound. Many new wounds clearly reflect the application, pattern, and utility of buccal dentition. The suction exerted by the predator brings the disk teeth into close application with the surface of the host. There the cusps penetrate the scales or skin sufficiently to anchor the lamprey. To a lesser extent, these teeth may dislodge scales over the intended site of the feeding hole. Some of the loosened scales are ingested and pass out of the anus of the parasite, but most of them are cleverly forced aside, presumably by tongue action, and emerge beneath the marginal membrane of the funnel and fall away to the bottom. The process is particularly remarkable when observed on prey fishes that possess scales of considerable size. The coating of mucous on the victim obviously permits the passage of such scales between the marginal membrane of the lamprey and the surface of the fish with no interruption of the suction pressure.

Within the tooth-studded disk, the large, supraoral cusps, the eight circumorals, and the infraoral lamina encircle the zone of action of the lamprey's tongue. There they appear to hold the slippery and elastic surface of the fish sufficiently rigid so that the tongue can quickly make a penetration. The lingual retractor muscles are brought into play, and the tip of the tongue is hooked strongly in a dorsal and posterior direction which causes the flesh of the fish to be ripped by the transverse and longitudinal teeth of the tongue as they describe an arc upwards and backwards. About six or seven respiratory movements take place between drives of the tongue. The rasping action appears to continue at this rate until a flow of the fish's blood is obtained. Thereafter, the application of the tongue is normally less frequent. During the wounding process the secretion of the buccal glands is brought in contact with the torn flesh of the fish.

Gage (1929, p. 163) gave a colorful and accurate description of the wounding process as he observed attacks by sea lampreys on suckers and bullheads:

> After several minutes the fish seemed exhausted and thoroughly discouraged and remained rather quiet. On watching the lamprey it seemed to be working hard to get something from the fish. The movements of its head and body reminded one of the actions of a suckling pig or kitten. After some especially hard suck the fish would jump and struggle as if hurt.

Lamprey attacks on other lampreys

Sea-lamprey attachments on their own kind are not uncommon, but they rarely result in wounds. Numerous such attachments were observed in the laboratory. In individuals close to sexual maturity, such activities were interpreted as prespawning manifestations of the reproductive urge. Before maturity, the attack of one upon another of its kind is made in an attempt to feed.

Remarkable responses are elicited from the victim lamprey to prevent the creation of a feeding wound. The only successful penetration observed was on a spawning migrant captured in Ocqueoc River. In an aquarium, a host lamprey invariably dislodges the offender by tying itself into a knot in the immediate vicinity of the point of attachment. Thereby, pressure is applied directly on the attacking individual in such a way as to cause it to slide away from the original site. The knot-tying is repeated again and again until the attacker is forced to release its hold.

Attachments on humans

There have been numbers of authentic reports of sea lampreys attaching themselves to persons in the Great Lakes area. Creaser (1950) mentioned reports of such attachments on human swimmers in Lake Ontario and in Burt and Crooked Lakes in northern Michigan. Vladykov (1949) also recorded attachments on swimmers in Lake Ontario. Neither author mentioned any injuries sustained by the human hosts, and since such associations are rapidly terminated by the victims there is little likelihood that the lamprey would have the opportunity to create an injury.

Observations in the laboratory seem to indicate that sea lampreys are repelled by the warmth of human skin; all induced attachments on the hands, except one, were terminated by the lampreys within a matter of seconds. The "host" in the one exception was Oliver R. Elliott, a member of the laboratory staff. During the servicing of aquariums one day in August 1950, his hands became cold from the low water temperature, and a lamprey affixed itself to the back of one. Elliott was urged to allow it to remain thereon as long as it would. The parasite initiated a rasping action and the consequent discomfort caused Elliott to remove the animal. The attack lasted 5 minutes, and in this time the lamprey had lacerated the skin slightly. The site of the attack was markedly reddened, and apparently a flow of blood would have been started soon had the attachment continued.

EFFECTS ON HOST FISHES

The effects of sea-lamprey attacks on fishes were investigated to determine the following: The characteristics of wounds; whether wounds heal; where attachments are made on fish; whether wounds are more harmful in some loci than in others; and whether lampreys have host-species preferences. Later points deal with tissue destruction, the hematology of prey fish before and after lamprey attacks, and secondary pathology of vulnerable species.

Characteristics of Wounds

The study of sea-lamprey wounds was based on detailed observations made April 1950–July 1952 of 1,189 wounds on 18 species of fish in Lake Huron and 1,690 wounds on 11 species attacked in laboratory aquariums. The following data

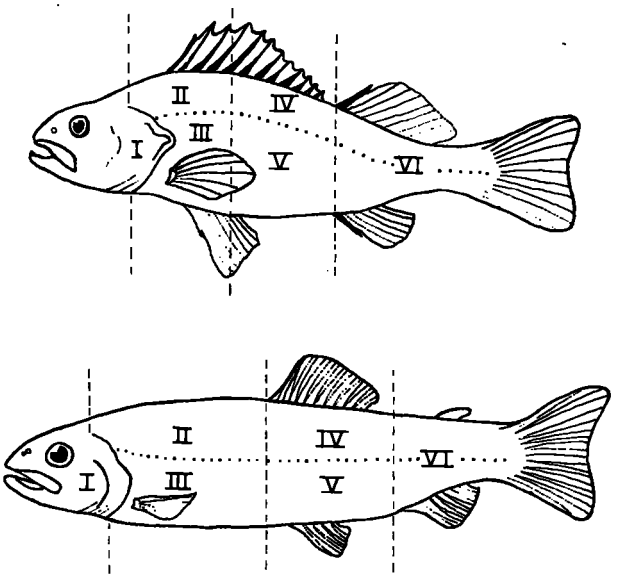

FIGURE 10.—Diagram of a typical spiny-rayed fish (above) and a soft-rayed fish (below) showing body regions used in plotting the location of sea-lamprey attacks.

were recorded for the wounds on lake and laboratory fish: Completeness; recentness; location on body of prey; duration of the attack; and dimensions of the wound. Each of these characters will be discussed in turn later in this section.

The form devised for recording the wound data included sketches of a fish, on which each lamprey injury was plotted. Certain regions were delineated on the bodies of both spiny-rayed and soft-rayed fishes, and each region included parts of the right and left sides of a fish (fig. 10). Region I included the head; regions II and IV included the dorsal section of the trunk; regions III and V included the ventral section of the trunk; and region VI included the caudal peduncle. A further designation was made of the number and types of wounds that occurred over either eye in region I, of those found in the immediate vicinity of the pectoral fins in region III, of those that occurred close to the pelvic fins in region V, and of those that penetrated the body wall into the coelomic cavity in regions III and V.

The white sucker was the most consistently available species for examination in the areas fished by our experimental nets in Lake Huron (fig. 11). Unblemished fish captured in trap nets were used in the laboratory feeding experiments; the many specimens bearing lake-incurred sea-

lamprey injuries were studied for the wound characters. Of the total number of lamprey scars examined from both lake and laboratory sources, 68.8 percent were on white suckers and 31.2 percent were on the other 19 species.[2] Regrettably lacking in our data are records of wounds on lake trout, the principal victim of the sea lamprey. At the time these observations were made, the lake trout had disappeared as a commercial species in northern Lake Huron.

Completeness

Each wound was classed as complete or as incomplete. A wound was classed as complete if the skin of the prey fish was pierced and feeding took place. A wound was classed as incomplete if no feeding had occurred; incomplete wounds varied from wounds that showed only temporary marks on the surface of fish to those in which the scales had been torn but the skin had not been punctured. Of the 1,189 lake-incurred wounds, 93.4 percent were complete and 6.6 percent were incomplete (table 5). Of the 1,690 aquarium-incurred wounds, 89.8 percent were complete and 10.2 percent were incomplete. For our principal species, the white sucker, the percentages of complete and incomplete wounds were about the same as the percentages for all species. Of 979 lake-incurred wounds on white suckers, 93.4 percent were complete and 6.6 percent were incomplete; of 1,001 aquarium-incurred wounds, 88.0 percent were complete and 12.0 percent were incomplete. The percentages for the incidence of incomplete wounds on fish in the aquariums are probably more indicative of the true incidence in nature,

[2] Part of the study of scarring is reported in a paper on the relation of length of fish to incidence of sea-lamprey scars on white suckers in northwestern Lake Huron by A. E. Hall, Jr., and Oliver R. Elliott, to appear in *Copeia*.

FIGURE 11.—Examination of fish captured in experimental trap nets set under the ice in Duncan Bay, Lake Huron, 1953. Note the sea-lamprey mark on the white sucker below its dorsal fin and between the hands of the investigator.

TABLE 5.—*Numbers and percentages of complete and incomplete sea-lamprey wounds, and of new and healed wounds on prey fishes captured in Lake Huron*

Species	Total number of wounds	Complete wounds		Incomplete wounds		New wounds		Healed wounds	
		Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage
Rainbow trout	22	21	95.5	1	4.5	14	63.6	8	36.4
Round whitefish (*Prosopium cylindraceum quadrilaterale*)	4	4	100.0			1	25.0	3	75.0
Lake whitefish	10	8	80.0	2	20.0	5	50.0	5	50.0
Lake herring (*Coregonus artedii*)	10	10	100.0			8	80.0	2	20.0
Smelt (*Osmerus mordax*)	1	1	100.0			1	100.0		
White sucker	979	913	93.4	66	6.6	780	79.7	199	20.3
Longnose sucker	59	55	93.2	4	6.8	22	37.3	37	62.7
Carp (*Cyprinus carpio*)	4	3	75.0	1	25.0	4	100.0		
Lake chub (*Couesius plumbeus*)	1	1	100.0			1	100.0		
Channel catfish (*Ictalurus lacustris*)	6	6	100.0			6	100.0		
Brown bullhead	2	2	100.0			2	100.0		
Black bullhead (*Ameiurus melas*)	2	2	100.0			2	100.0		
Northern pike	6	6	100.0			6	100.0		
Burbot	1	1	100.0			1	100.0		
Walleye (*Stizostedion v. vitreum*)	6	5	83.3	1	16.7	6	100.0		
Yellow perch	72	69	95.8	3	4.2	62	86.1	10	13.9
Smallmouth bass (*Micropterus d. dolomieui*)	2	2	100.0			2	100.0		
Rock bass	2	2	100.0			2	100.0		
All species	1,189	1,111	93.4	78	6.6	925	77.8	264	22.2

since some of the incomplete wounds incurred in the lake may have healed without leaving an observable scar.

Recentness

All representative samples of prey fish captured in northern Lake Huron exhibit lamprey wounds of various ages, possibly including some only hours old and others one or more years old. The 1,189 lake-incurred wounds on 929 host fish were examined for evidences of recovery from the sea-lamprey attacks. These wounds were classified as new and open, or old and healed (table 5). The ratio of recent injuries to older ones may be used in estimating the recovery potential in attacked fishes.

For the present purposes, new wounds are those of recent origin on the fish, varying from hours to several weeks in age. They are characterized by a lack of any evidence of healing, and often by signs of recent hemorrhage and histolysis. Old ones exhibit scar tissue varying in extent to complete closure, and any wound that showed healing tissue was classed as old. The system employed does not indicate the severity of the lesion, because major damages to structure or function of deeper tissues or organs may be obscured by superficial regeneration. Many feeding sites were entirely healed, and holes formerly very deep showed as mere surface indentations. Such areas were sometimes covered with new, irregularly arranged scales.

The rate and extent of healing in sea-lamprey wounds depends on the severity of the original damage. Some incomplete wounds heal quickly. Others are complete but the damage is slight, and these too may be repaired soon. Many prey fishes are debilitated to a point just short of death, and healing in their wounds is probably delayed until the victims regain vitality. Yet even these may heal.

Wounds were observed to begin formation of repair tissue sooner in summer than in winter. The higher metabolic rate of fishes in relatively warm water may explain this seasonal difference. On the other hand, the higher rate of metabolism in warm water undoubtedly works a disadvantage at times in prey specimens under attack by lampreys. The efficiency of the attack is presumably greater and the tolerance of the victim to injury is lower under such conditions. Furthermore, growth of any secondary invader of the site, such as bacteria or molds, may be favored by higher temperatures.

Of the 1,189 sea-lamprey wounds observed on 18 species of fish from Lake Huron, 77.8 percent were new wounds and 22.2 percent were healing or healed (table 5). Nearly all of the wounds were on white suckers and, of these, 79.7 percent were new marks and 20.3 percent were healed or in the process of healing.

The listing of the 199 old wounds on white suckers (table 6) by body region shows the highest percentages of recovery from lamprey damage in body regions IV (27.7 percent), II (27.6 percent), and V (21.7 percent). Lower values were found for regions VI (16.0 percent), III (12.1 per-

cent), and I (5.9 percent). Although the total number of 979 wounds on white suckers included 66 incomplete attacks which might be expected to heal more readily than complete ones, the ratio of old wounds to incomplete ones was 3 to 1.

Among the reasons for the greater percentage of new than of old wounds on white suckers may be listed the strong probability that most suckers attacked by sea lampreys die as a direct or indirect result of the attacks. Secondary infections by fungus are known to kill some of the fish that are not fatally injured by the lampreys. In addition, the incidence of healed wounds is modified to an unknown extent by subsequent mortal attacks by lampreys on the recovered fish.

TABLE 6.—*Distribution of 780 new and 199 healing or healed sea-lamprey wounds observed among the 979 wounds on white suckers from Lake Huron*

[See fig. 11 for definitions of body regions]

Body region	Total number of wounds	New wounds		Healed wounds	
		Number	Percentage	Number	Percentage
I	17	16	94.1	1	5.9
II	163	118	72.4	45	27.6
III	313	275	87.9	38	12.1
IV	184	133	72.3	51	27.7
V	277	217	78.3	60	21.7
VI	25	21	84.0	4	16.0
All regions	979	780	79.7	199	20.3

Material concerning new and old lamprey injuries on trout species in nature is sparse, but Royce (1950, p. 75) observed wounds made by landlocked sea lampreys on male lake trout, 22.4 to 33.3 inches in length, in Seneca Lake. He reported that—

> When the incidence of recent and old attacks is compared it is found that the lake trout averaged 2.8 total lamprey marks per fish and (in another group of fish) 1.0 unhealed sores. If we assume again that a sore remains unhealed only 1 month, then it appears that these lake trout possessed more unhealed sores in proportion to healed scars than would be expected from a random distribution of incidence of attack throughout the year. A random distribution of two attacks each year should cause about one-sixth of the marks to be unhealed rather than more than one-third. Possibly the concentration of spawning lake trout attracts lampreys and the spawning urge makes a fish take less notice of attacks.

In April and May 1951, 11 scarred rainbow trout, 18.3 to 25.0 inches long and 4 to 6 years of age, were trapped by lamprey weirs during their upstream, spawning migrations in tributaries of northern Lake Huron. Their sea-lamprey injuries numbered 1.9 scars per fish; of these, 1.2 were new and unhealed and 0.7 were healed. Most of the injuries were so severe that it was presumed that few of the trout would live to reach their spawning grounds. These limited data on large rainbow trout in Lake Huron indicate that, in contrast to Royce (1950), the paucity of healed wounds in comparison with unhealed ones is attributable to the high mortality, direct or indirect, from sea-lamprey wounds.

Distribution of wounds

The patterns of the distribution of sea-lamprey wounds on the bodies of host fishes were observed on 1,111 complete marks on 18 species of fish in Lake Huron and on 1,518 complete attacks on 11 species in the laboratory (table 7). The differences in the two sets of data were considerable. More than 60 percent of the lake-incurred wounds were in regions III and V, whereas 45 percent of the laboratory-incurred wounds were in regions II and IV. Only 2.1 percent of the lake wounds occurred on the heads of the fishes, but in the laboratory 18.5 percent of the attacks were in this region.

TABLE 7.—*Locations of complete sea-lamprey wounds according to body region on lake and laboratory fishes*

[See fig. 11 for definition of regions. Data for all species have been combined; see table 8 for information on individual species]

Body regions	Lake-incurred wounds		Laboratory-incurred wounds	
	Number	Percentage of total	Number	Percentage of total
I Entire region	23	2.1	281	18.5
Eye	5	.5	98	6.5
II	166	14.9	362	23.8
III Entire region	377	33.9	313	20.6
Pectoral fins	75	6.8	52	3.4
Body cavity [1]	172	15.5	72	4.7
IV	198	17.8	321	21.2
V Entire region	318	28.6	175	11.5
Pelvic fins	98	8.8	41	2.7
Body cavity [1]	68	6.1	33	2.2
VI	29	2.7	66	4.4
All regions	1,111	100.0	1,518	100.0

[1] Wounds that penetrated the body.

It is believed that the differences between laboratory and lake fish with respect to distribution of sea-lamprey wounds on the body can be attributed to the fact that all wounds were available for study in the laboratory, whereas the scarred fish from the lake included only fish that had survived sea-lamprey attacks. Observations on the mortality rate from attacks on different body locations in laboratory fish strongly supported this view.

The data on lake-incurred scars may have been biased by the fact that some of the marks were created while the fish were confined alive in trap nets. On many occasions when the nets were being lifted, lampreys detached themselves from prey and dropped through the meshes into the water. Although the nets were usually tended every third day, there is no way of determining the number or percentage of victims that suffered lamprey attacks while confined, but it is estimated that they did not exceed one-quarter of the total number of scarred fishes in the catch. Therefore, it was presumed that the pattern of lake-incurred injuries was not modified greatly by sea-lamprey attacks in the nets.

Laboratory data on the location of attacks are open to criticism in that conditions, at best, were artificial. Whether the habits of the sea lampreys in aquariums were typical is not known, but their growth, though considerably slower, paralleled that of lampreys in the wild. This similarity was considered indicative that the feeding habits of the animals was not particularly affected by confinement. The lampreys did feed in captivity; the prey fishes provided them were typical; and the water conditions in the tanks were satisfactory. The aquarium did limit movements, but no influence due to these space conditions could be detected in the pattern of lamprey attacks. In the lake, a lamprey may approach a fish without limitations imposed by lack of space.

The average size of hosts used in the experiments may have had some influence on site selection. The tank fishes, other than the longnose suckers, averaged slightly smaller (table 8) than the lake fish (table 9) but among the species that contributed most of the wound records, the differences were small.

TABLE 8.—*Mean lengths and weights of fishes used in the sea-lamprey feeding experiment and examined for wound locations from August 1950 to February 1952*

Species	Number of specimens	Mean length	Mean weight
		Inches	*Grams*
Brown trout	26	10.7	200
Rainbow trout	385	9.6	129
Eastern brook trout	70	8.7	111
Lake whitefish	1	12.1	238
White sucker	858	12.4	350
Longnose sucker	36	15.4	702
Brown bullhead	1	8.2	66
Northern pike	2	14.4	290
Burbot	2	19.6	860
Yellow perch	15	8.9	140
Rock bass	1	7.2	120

TABLE 9.—*Mean lengths and weights of fishes captured in northern Lake Huron and examined for wound locations from August 1950 to February 1952*

Species	Number of specimens	Mean length	Mean weight
		Inches	*Grams*
Rainbow trout	11	21.4	1,631
Round whitefish	3	14.1	392
Lake whitefish	8	17.7	886
Lake herring	9	10.6	145
Smelt	1	7.0	
White sucker	759	12.9	406
Longnose sucker	46	15.2	683
Carp	2	15.1	1,186
Lake chub	1	5.3	20
Channel catfish	1	24.3	2,752
Brown bullhead	1	8.2	66
Black bullhead	4	12.0	357
Northern pike	7	20.7	1,193
Burbot	2	19.6	860
Yellow perch	65	9.3	158
Walleye	3	17.4	851
Smallmouth bass	2	11.6	400
Rock bass	3	9.2	279

On white suckers.—The distribution of sea-lamprey attacks [3] by body regions on host fishes from Lake Huron and the laboratory tanks is best seen in the white sucker. For this species, we have the locations of 913 complete wounds from natural water (table 10) and of 881 from the feeding experiment. The suckers bearing these injuries were nearly of the same size, since the individuals used in aquariums were from the same catches that provided the data on scarring in the lake (tables 8 and 9).

The areas of the six body regions used to designate the locations of the lake and laboratory wounds were by no means equal. The actual dimensions of each region were measured on a white sucker, 15.3 inches long and 537 grams in weight (fig. 12). A comparison of the percentage distribution of the total body surface among the different regions with the percentage distribution of the total numbers of wounds reveals certain marked discrepancies (table 11).

[3] The points of attack discussed in this section should not be interpreted as descriptive of the points of original attachment. Lampreys commonly shifted considerable distances from the point of original attachment before starting the wounding process.

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
Brown trout:				
I	3	2.3		
II	40	31.2		
III. Entire region	31	24.2		
Pectoral fins	9	7.0		
Body cavity	5	3.9		
IV	32	25.0		
V. Entire region	12	9.4		
Pelvic fins	2	1.5		
Body cavity	1	.8		
VI	10	7.8		
All regions	128	100.0		
Rainbow trout:				
I. Entire region	8	2.7		
Eye	6	2.0		
II	90	29.8	1	4.8
III. Entire region	72	23.9	1	52.4
Pectoral fins	11	3.6	3	14.3
Body cavity	11	3.6	1	4.8
IV	64	21.2	3	14.3
V. Entire region	39	12.9	5	23.8
Pelvic fins	8	2.7	1	4.8
Body cavity	3	1.0	1	4.8
VI	29	9.3	11	3.7
All regions	302	100.0	21	100.0
Brook trout:				
I. Entire region	2	2.0		
Eye	2	2.0		
II	47	47.0		
III. Entire region	21	21.0		
Pectoral fins	4	4.0		
Body cavity	3	3.0		
IV	21	21.0		
V. Entire region	7	7.0		
Pelvic fins	1	1.0		
Body cavity	1	1.0		
VI	2	2.0		
All regions	100	100.0		
Round whitefish:				
III			1	25.0
V. Entire region			3	75.0
Pelvic fins			1	25.0
All regions			4	100.0
Lake whitefish				
II	1	50.0		
III			3	37.5
V. Entire region	1	50.0	5	62.5
Pelvic fins			3	37.5
All regions	2	100.0	8	100.0
Lake herring:				
II			1	10.0
III			2	20.0
IV			2	20.0
V. Entire region			5	50.0
Pelvic fins			4	40.0
Body cavity			1	10.0
All regions			10	100.0
Smelt:				
V			1	100.0

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*—Continued

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
White suckers:				
I. Entire region	244	27.7	17	1.9
Eye	80	9.1	5	0.6
II	160	18.2	152	16.7
III. Entire region	173	19.6	300	32.9
Pectoral fins	25	2.8	61	6.7
Body cavity	49	5.6	140	15.3
IV	180	20.4	170	18.6
V. Entire region	106	12.0	253	27.7
Pelvic fins	25	2.8	67	7.3
Body cavity	25	2.8	52	5.7
VI	18	2.0	21	2.3
All regions	881	100.0	913	100.0
Longnose suckers:				
I. Entire region	22	23.2	1	1.8
Eye	10	10.5		
II	24	25.3	2	2.7
III. Entire region	14	14.7	10	18.2
Pectoral fins	3	3.2	1	1.9
Body cavity	3	3.2	1	1.9
IV	22	23.2	17	30.9
V. Entire region	6	6.3	23	41.8
Pelvic fins	4	4.2	6	10.9
Body region	1	1.1	2	3.6
VI	7	7.4	2	3.6
All regions	95	100.0	55	100.0
Carp:				
III. Entire region			2	66.7
Pectoral fins			1	33.3
Body cavity			1	33.3
IV			1	33.3
All regions			3	100.0
Lake chub:				
II			1	100.0
Channel catfish:				
I			1	16.7
III. Entire region			3	50.0
Pectoral fins			1	16.7
Body cavity			2	33.3
V			2	33.3
All regions			6	100.0
Brown bullhead:				
V. Entire region	1	100.0		
Body cavity	1	100.0		
Black bullhead:				
III. Entire region			2	50.0
Pectoral fins			2	50.0
Body cavity			2	50.0
IV			1	25.0
V			1	25.0
All regions			4	100.0
Northern pike:				
II			1	16.7
III. Entire region			3	50.0
Pectoral fins			1	16.7
IV	1	33.3	1	16.7
V	1	33.3	1	16.7
VI	1	33.3		
All regions	3	100.0	6	100.0

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*—Continued

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
Burbot:				
I	2	66.7		
II			1	100.0
IV	1	33.3		
All regions	3	100.0	1	100.0
Yellow perch:				
I			3	4.4
II			8	11.6
III. Entire region	2	100.0	34	49.3
Pectoral fins	1	50.0	3	4.4
Body cavity			22	31.9
IV			2	2.9
V. Entire region			18	26.0
Pelvic fins			16	23.2
Body cavity			12	17.4
VI			4	5.8
All regions	2	100.0	69	100.0
Walleye:				
I			1	20.0
III. Entire region			3	60.0
Pectoral fins			1	20.0
Body cavity			2	40.0
V. Entire region			1	20.0
Pelvic fins			1	20.0
All regions			5	100.0
Smallmouth bass:				
III. Entire region			1	50.0
Body cavity			1	50.0
VI			1	50.0
All regions			2	100.0
Rock bass:				
III			1	50.0
V. Entire region	1	100.0	1	50.0
Body cavity	1	100.0		
All regions	1	100.0	2	100.0
Total number of wounds	1,518		1,111	

TABLE 11.—*Comparison of distribution of 913 lake-incurred and 881 laboratory-incurred complete sea-lamprey wounds on white suckers with percentage of total body surface contained in each region*

[See fig. 11 for definition of regions]

Body region	Percentage [1] of total area	Lake-incurred wounds		Laboratory-incurred wounds	
		Number	Percentage of total	Number	Percentage of total
I	15.8	17	1.9	244	27.7
II	15.5	152	16.7	160	18.2
III	18.8	300	32.8	173	19.7
IV	14.3	170	18.6	180	20.4
V	18.2	253	27.7	106	12.0
VI	17.4	21	2.3	18	2.0
All regions	100.0	913	100.0	881	100.0

[1] Exclusive of all fin surfaces.

In the laboratory fish, the only group in which all wounds inflicted were available for examination, the discrepancies were particularly large for

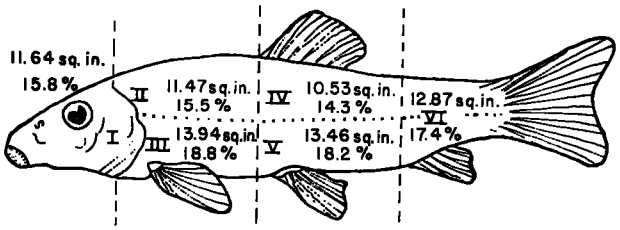

FIGURE 12.—Diagram of a white sucker showing actual sizes and percentage distribution of total body surface among the six regions used in recording the locations of lamprey wounds. Measurements taken from a female fish, 15.3 inches in length, 537 grams in weight, captured in Hammond Bay, Lake Huron, July 25, 1952. The total area of the fish, exclusive of fins, was 73.90 square inches.

the peduncular region (region VI, 17.4 percent of the total area but only 2.0 percent of the wounds) and the head (region I, 17.8 percent of the area and 27.7 percent of the wounds). In the central part of the body, the percentage of wounds was greater than the percentage of area in regions II, III, and IV, but was less in region V. If this observed distribution reflects the true behavior of the lamprey (that is, if we may assume that the artificial conditions in the laboratory did not lead to a distribution pattern different from that which would have occurred in nature) the parasite can be said to exhibit a strong preference for the head as a point of attack and a similarly strong avoidance of the peduncle. Possible preferences among other regions seem less clear-cut, although there is some indication of preference for region IV and avoidance of region V.

The distribution of wounds on white suckers captured in the lake differed sharply both from the area percentages (on a regional basis) and from the observed distribution on laboratory fish. The disagreements among the three sets of percentages were not particularly large for region II (range from 15.5 to 18.2) but elsewhere amounted to at least 6.1 percent (the range for region IV). On the whole, therefore, both patterns of wound distribution differed from the area percentages and from each other.

The most striking difference between the lake and laboratory data was in the percentage of wounds on the head (27.7 percent in region I for the lake fish but only 1.9 percent for the laboratory fish). The percentages for the lake fish were much higher in regions III and V (values of 32.9 and 27.7, as compared with 19.6 and 12.0 for laboratory

fish). The differences between the two groups of fish were relatively small for other regions; it is to be noted especially that they agreed in showing extremely few scars in region VI.

It is believed that the differences in wound distributions on laboratory and lake fish are attributable to the fact that wounds are more likely to bring about early death if inflicted on one body location than if inflicted on another. As was explained earlier, all wounds on laboratory fish were available for examination whereas the suckers examined from the lake were survivors of past attacks—some made a considerable time earlier and others recent.

Among the cranial wounds (region I) there were about 17 times as many in the eyes of the aquarium hosts than in the eyes of lake fish. Considering the size of the eyes of white suckers, it is noteworthy that these organs should attract as many as 9.1 percent of the total number of attacks studied in the laboratory. The small percentage (0.6) of eye wounds in the lake samples makes it appear that the fishes attacked in such a vital area do not usually survive the lamprey attachments.

A comparison of the percentages of wounds that penetrated into the coelomic cavity (in regions III and V) showed that 8.4 percent of all attacks in the laboratory and 21.0 percent of all attacks on the lake fish pierced the body wall. Severe damages to visceral organs and disruptions of vital physiological processes frequently resulted from wounds that punctured the body wall, but it was also observed that such wounds were less likely to prove immediately fatal than others located elsewhere on the fish (regions I, II, and IV). Many white suckers attacked by sea lampreys in the lake survived their eventually mortal, body-cavity wounds long enough to become captured in our trap nets.

The contention of Gage (1929) that sea lampreys usually attach themselves on fishes in the vicinities of the paired fins does not appear valid. Injuries that occurred beneath the normal, retracted positions of these fins or closely approached or included fin insertions were recorded. Only 5.7 percent of the complete wounds on white suckers in aquariums were proximal to the pectoral and pelvic fins. Among the suckers attacked in Lake Huron, 14.0 percent of the complete wounds were located in the neighborhood of the paired fins.

On trout.—The pattern of sea-lamprey attacks on salmonids was plotted for the most part from data obtained in aquariums at the laboratory. Numbers of complete wounds recorded were 128 on brown trout, 302 on rainbow trout, and 100 on eastern brook trout (table 10). Twenty-one additional wounds were observed on rainbow trout from Lake Huron. The trout used in the sea-lamprey feeding experiment were mostly provided by Wolverine Rearing Station and Oden Hatchery of the Michigan Department of Conservation. Additional specimens were furnished by the Fish and Wildlife Service Hatchery at Northville, Mich.

One or more species of trout were employed as hosts in aquariums from December 1950 to July 1952. The majority of the attack records were compiled from April through August 1951. During this period, the parasitic lampreys in the same tanks averaged 5.5 inches long on May 3, 1951, and 11.0 inches on September 1, 1951. It is believed that the relatively small size of the lampreys that created most of the marks on trout in no way altered the pattern of attacks.

The data collected in the laboratory on the rainbow trout may be more representative than those listed for brown trout and brook trout. The larger total number of complete wounds on the rainbow trout and their better distribution throughout the lamprey-feeding experiment lend advantage to the data. However, the patterns of wound distribution on the brown trout and brook trout support the findings on the rainbow species.

The six body regions used to plot the locations of wounds on the rainbow trout were not equal in extent. The actual dimensions of each region were measured on a rainbow trout, 8.2 inches long and 90 grams in weight (fig. 13). The percentage distribution of the total body surface among the different regions closely resembled that determined for the white sucker (fig. 12). Further, as was noted with the white sucker, a comparison of the percentage distribution of the total body surface with the percentage distribution of the total numbers of wounds reveals some marked discrepancies.

A large discrepancy exists in region I, the head, which contained 16.0 percent of the total surface area but only 2.7 percent of the wounds. The percentage distribution of head wounds on the three species of trout ranged from 2.0 to 2.7 percent in contrast with the 27.7-percent incidence

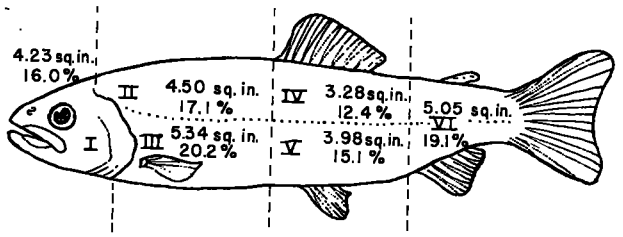

FIGURE 13.—Diagram of a rainbow trout showing actual sizes and percentage distribution of total body surface among the six regions used in recording the locations of lamprey wounds. Measurements taken from a male fish, 8.2 inches in length, 90 grams in weight, captured in the Ocqueoc River, Presque Isle County, Mich., August 18, 1952. The total area of the fish, exclusive of fin surfaces, was 26.38 square inches.

on the heads of white suckers attacked in aquariums and a 23.3-percent incidence in region I on laboratory longnose suckers. No explanations can be given for this difference. In the central part of the body on rainbow trout, the percentage of wounds exceeded the percentage of area in regions II, III, and IV, but was less in region V. The difference between area and incidence in region VI on the trout (19.0 percent of the area and 9.3 percent of the wounds) was not as large as that found in the same region on white suckers (17.4 percent of the area and 2.0 percent of the wounds). The percentage incidence of attacks on the peduncular region of brown trout approached that of the rainbow trout, whereas only 2.0 percent of the wounds in brook trout were in region VI. Except for the lampreys' avoidance of attaching on region I on trout, the pattern of their attacks on these species was similar to that on white suckers in aquariums.

The percentage distribution of 21 sea-lamprey wounds on rainbow trout from Lake Huron roughly followed the pattern for lake-incurred attacks on white suckers. More than 75 percent of the 21 wounds occurred in the lower middle third of the body (regions III and V) and the upper middle third contained only 14 percent of the scars.

On yellow perch.—A total of 69 complete wounds were studied on yellow perch captured in Lake Huron (table 10). The distribution of these attacks fell into the pattern already discussed for white suckers, longnose sucker, and rainbow trout which bore lake-incurred sea-lamprey marks. The preponderance (75 percent) of feeding attachments on perch occurred on the lower middle third of the body, and wounds on other regions were seen with less frequency, presumably because they were more quickly fatal.

Two complete wounds were obtained from yellow perch used as prey in lamprey-feeding experiments. Both attacks occurred in region III, and one of them was adjacent to a pectoral fin. The other penetrated the coelom. The perch that were held in aquariums were largely ignored by the sea lampreys when other species such as white sucker or rainbow trout were available. Only when the perch was alone did the lampreys seem inclined to attack.

It has been suggested that the yellow perch is relatively more immune to lamprey attack than soft-rayed fishes because it is more heavily scaled. This view is untenable, however, because prowling lampreys do not attach themselves to the perch and test the covering; the lampreys usually take no notice of them except when they are the sole prey available. No explanation can be offered for this selection. The midwater position maintained by the yellow perch in aquariums was shared by brook, brown, and rainbow trout, which were very susceptible to sea-lamprey attacks.

The commercial fishery for yellow perch in northern Lake Huron collapsed in the winter of 1950–51. Until that time, the perch was largely disregarded by sea lampreys in the lake, but early in the winter, the incidence of lamprey wounds on yellow perch suddenly increased to as much as 75 percent of the entire catch in some lifts of the laboratory trap nets. By the following spring, the species in the northwestern part of the lake apparently ceased to exist in commercial proportions. Since other species had become extremely scarce during immediately preceding years (Moffett 1950; Hile, Eschmeyer, and Lunger, 1951), it appeared to workers at the laboratory that the sea lampreys had turned to the yellow perch as a last resort.

On other species.—Records on sea-lamprey wounds were obtained in small numbers from 15 additional species of fish captured in Lake Huron (table 10). The material provides further evidence that the majority of scars on prey fish in Lake Huron are in regions III and V. Attacks were recorded in the laboratory on eight of these hosts, but their numbers were so small that discussion is not warranted.

Duration of attack

Observations on sea lampreys in aquariums showed that, in general, the parasites are quick to perceive an insufficient food return from wounds. They are then likely to move to other sites on their hosts (this behavior was also observed by Gage, 1929). If the host is dead or dying, they usually detach themselves and immediately seek fresh victims, a habit mentioned by Bigelow and Welsh (1925).

In this experimental work, it was possible to record the duration of a number of parasitic attacks on the various body regions of host fishes. Records were kept on the sizes and kinds of fish, the dates when they were placed in aquariums. the dates and time when attacks were initiated by the lampreys, the locations of the attachments on the bodies of the victims, the number of hours of feeding at each wound, the date and time of death of the hosts, and the sizes of the lampreys.

The time that the lampreys spent attached to individual fish appeared to depend to a large extent on size of the lamprey, size of the host, site of attack, and proximity of blood vessels to the site. Obviously important but largely conditioned by the factors just listed is the length of time the victim survives. A lamprey seldom remains long attached to a dying or dead fish. Still another seemingly significant but unmeasurable factor was the vigor with which the individual lamprey fed.

Among the attacks by sea lampreys on host fishes observed in aquariums, the lengths of lampreys responsible for 435 attacks of certain durations were known (table 12). The relation between the size of a lamprey and the mean duration of its attack on a host (fig. 14) shows that the longest attacks (220.2 hours) were made by newly transformed feeders that averaged 5.5 inches long, whereas the shortest attacks (38.7 hours) were made by lampreys that averaged 12.9 inches. Attacks by lampreys of still larger size could be described as even more brief if we could accurately measure the time that efficient feeding continued. With the approach of sexual maturity and attendant degeneration of the feeding mechanism, more total hours though less hours of feeding were spent per attack. Hence the mean durations for lampreys that averaged 15.2 and 16.5 inches long (43.0 and 42.3 hours respectively)

TABLE 12.—*Duration of 435 attacks by sea lampreys of known length on 11 species of prey fish in laboratory aquariums*

Number of lampreys	Length of lampreys		Average duration of attack
	Range	Mean	
	Inches	*Inches*	*Hours*
58	4.0– 5.9	5.5	220.2
80	6.0– 7.9	6.6	90.2
27	8.0– 9.9	8.8	57.4
42	10.0–11.9	11.3	50.7
64	12.0–13.9	12.9	38.7
121	14.0–15.9	15.2	43.0
43	16.0–17.9	16.5	42.3
435		11.3	76.2

showed slight increases over the minimum (38.7 hours).

The records of attack durations on various body locations for 614 complete sea-lamprey wounds on white suckers in aquariums (table 13) showed that attachments averaged longest on region II (35 hours), followed in decreasing order by body regions IV, VI, III, I, and V. On the basis of both duration and number of attacks, regions II, IV, and I and III in that order provided the most used feeding sites.

Region I was included among the best feeding sites on this species owing to the high incidence of attacks, and in spite of the more rapid lethality of the wounds in this region. Attachments over

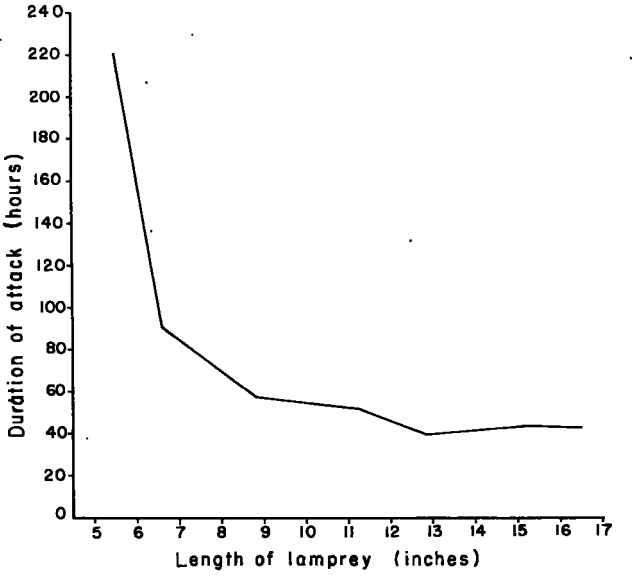

FIGURE 14.—Relation of length of lamprey to duration of attack. Data obtained from study of 435 wounds on 11 species of fish attacked by lampreys of known length in aquariums.

the eyes, which comprised 32.1 percent of the 168 wounds recorded on the head, had an average duration of 19.1 hours compared with the grand average of 22.4 per attack in region I as a whole.

The total amount of feeding time logged in aquariums for 512 complete sea-lamprey wounds on the three trout species was 22,281 hours (table 14). The data for brown, rainbow, and brook trout were combined since no large differences were noted between them. The majority of the attacks occurred in regions II, III, and IV, which regions combined supported 392, or 76.9 percent of the total wounds and 79.8 percent of the total hours; the average duration of attack was 45.3 hours.

Region I, the head, contained 14 wounds, or 2.7 percent of the total number. The average duration of attachment here was 15.1 hours. The six attachments on the eyes had an average duration of only 9.0 hours. In most of these attacks, the eyeball injuries were fatal before the detachment of the attacker. Head wounds generally led to death more rapidly than attacks on other parts of the body.

The duration of lamprey attacks on trout was longest on region II. The 168 feeding attacks made in this locale averaged 49.5 hours. As was true for the white suckers, more injuries penetrated the body cavity in region III than in region V, but in the later region these attachments consumed more time individually.

The determination of the incidence and average durations of sea-lamprey attacks according to body regions on host fish demonstrates that feeding attachments may be more satisfactory to the parasites on certain sites than on others. The regions favored by lampreys, as indicated by the numbers and durations of attachments, on white suckers were I, II, III, and IV, whereas on the three species of trout the attackers created the most wounds and spent the longest times in regions II, III, and IV.

The data on hours per lamprey attack on white suckers and brown, rainbow, and brook trout are not directly comparable. The durations of attachment were longer on trout because the majority of wounds on these species were made by relatively small sea lampreys. When the sea lampreys reached greater size, the normal length of attack was shorter and suckers were the main prey available. The hours per attack on white suckers can therefore be considered more typical than those on trout since they represent lampreys of greater size range.

Observations made in the laboratory on the parasites themselves offer some explanation for the seeming preference for certain body regions. For example, lampreys that attacked fish briefly on regions V and VI usually made only small wounds and then shifted anteriorly and/or dorsally to new regions where more efficient feeding took place.

TABLE 13.—*Locations and attack durations for complete sea-lamprey wounds on white suckers from laboratory aquariums*

[Data represent 614 attacks by lampreys 5.5 to 17.0 inches long]

Body region	Wounds		Hours per attack	
	Number	Percentage of total	Number	Perentage of total
I. Entire region	168	27.4	22.4	23.0
Eye	54	8.8	19.1	6.3
II	128	20.9	35.4	27.8
III. Entire region	118	19.2	24.9	18.0
Pectoral fins	26	4.2	26.3	4.2
Body cavity [1]	41	6.7	22.5	5.7
IV	120	19.5	28.8	21.2
V. Entire region	69	11.2	19.3	8.2
Pelvic fins	21	3.4	20.8	2.7
Body cavity [1]	12	2.0	10.2	.8
VI	11	1.8	26.7	1.8
All regions	614	100.0	26.5	100.0

[1] Wounds that penetrated the body wall.

TABLE 14.—*Locations and attack durations for the combined complete sea-lamprey wounds on brown, rainbow, and brook trout in aquariums*

[Data represent 512 attacks by lampreys 5.5 to 17.0 inches long]

Region	Wounds		Hours per attack	
	Number	Percentage of total	Number	Percentage of total
I. Entire region	14	2.7	15.1	1.0
Eye	6	1.2	9.0	.2
II	168	32.8	49.5	37.3
III. Entire region	99	19.4	43.1	19.1
Pectoral fins	21	4.1	33.5	3.2
Body cavity [1]	28	5.5	27.0	3.4
IV	125	24.4	41.6	23.3
V. Entire region	65	12.7	41.5	12.1
Pelvic fins	14	2.7	17.9	1.1
Body cavity [1]	10	2.0	40.1	1.8
VI	41	8.0	39.0	7.2
All regions	512	100.0	43.5	100.0

[1] Wounds that penetrated the body wall.

Dimensions of wounds on fishes

Three dimensions of 2,629 sea-lamprey wounds on 20 species of fishes from Lake Huron and laboratory sources were measured and recorded: Diameter of the oral-disk mark; diameter of the hole

rasped in the fish tissues; and depth of the hole.

Accurate measurements of wounds were sometimes difficult. The exact dimensions of many of the marks of both complete and incomplete wounds were obscured by healing or by closely adjacent or overlapping attacks by other lampreys. The parasites often moved somewhat on the attachment sites, thereby distorting or obliterating the original boundaries. Some attachments were of too short duration for the marks to be sharply defined.

Oral-disk marks.—The imprint of the oral disk on a fish forms the largest measurable dimension of a sea-lamprey wound. On some fish this imprint is clearly defined, but on the majority of hosts the oral-disk mark is distorted slightly (1 to 2 millimeters) by edema at the wound site or by the effects of the oral-suction pressure on the fish skin or flesh. The marks made by newly transformed lampreys and those that are close to sexual maturity are often greatly distorted owing to changes of position at the wound sites. Scrape-like marks up to 100 millimeters long are sometimes produced, and the dimensions of the original wounds are obliterated.

The diameters of the oral-disk marks were measured on 832 complete and incomplete wounds incurred by 18 species of fish in Lake Huron (table 15) and on 1,630 wounds examined on 11 species of hosts in aquariums (table 16). The measurements were obtained between July 1950 and July 1952, and when they were plotted by calendar months the existence of a 16-month wound cycle was demonstrated. This cycle of wounds is created by a single year class of lampreys and supports the conclusion by Applegate (1950) that sea lampreys spend 12 to 16 months in their parasitic phase of life. Captive lampreys in aquariums were slaughtered after 15 months of parasitic living; nearly all were sexually mature.

The smallest wounds in both groups of hosts were observed during the first month (April) of parasitic feeding by newly transformed lampreys. By the seventh month of the parasitic phase (October), the diameters of the oral-disk marks on lake and laboratory fishes had doubled. Thereafter the mean diameters of marks on Lake Huron hosts increased more rapidly than those on prey fish in aquariums. The maximum mean diameters occurred in both sets of data during the eleventh month (February), at which time the disk marks averaged 40.2 millimeters (270-percent overall increase) on lake fish, and 36.8 millimeters (230-percent overall increase) on hosts in aquariums. Thereafter, from the twelfth to sixteenth month (March to July), the mean sizes of the disk marks on lake and laboratory fishes decreased sharply for several reasons: the largest lampreys were generally the first to cease feeding and become sexually mature, therefore a larger proportion of the wounds each month were made by smaller lampreys; most of the parasites reduce their feeding activities and undergo considerable shrinkage in length (from 1 to 3 inches in aquariums) and

TABLE 15.—*Minimum, average, and maximum dimensions of new, complete sea-lamprey wounds as they occurred during 16-month wound cycle of fish in Lake Huron*

Month	Diameter of oral-disk mark				Diameter of wound hole				Depth of wound hole			
	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum
		Millimeters	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*
April [1]	1	15	15.0	15	1	5	5.0	5	1	3	3.0	3
May	5	15	18.8	21	5	6	6.2	7	4	1	1.5	2
June	9	14	18.7	23	7	3	4.1	7	5	1	1.8	3
July	10	16	19.2	24	8	4	5.8	11	8	1	1.4	2
August												
September	27	20	29.3	42	25	2	9.3	22	47	1	3.3	10
October	89	22	30.7	39	74	4	9.8	25	48	1	4.2	9
November	175	24	35.6	50	180	3	11.3	28	136	1	4.1	15
December	71	25	38.1	50	94	3	16.5	43	77	1	4.9	10
January	102	26	38.8	50	111	2	14.9	40	100	1	4.5	12
February	66	30	40.2	53	76	3	15.4	40	78	1	4.3	12
March	102	25	39.6	55	116	2	13.2	35	90	1	5.0	13
April	118	22	36.9	50	105	3	12.6	25	122	1	3.3	13
May	38	30	35.9	48	42	3	15.0	25	41	1	2.7	7
June	12	27	32.1	42	15	4	9.9	26	8	1	2.5	2
July [2]	7	27	30.0	39	9	2	6.2	16	3	1	2.0	3
Total number	832				868				768			

[1] Start of parasitic feeding. [2] End of parasitic feeding.

TABLE 16.—*Minimum, average, and maximum dimensions of new, complete sea-lamprey wounds as they occurred during 15-month wound cycle on 11 species of fish in laboratory aquariums*

Month	Diameter of oral-disk mark				Diameter of wound hole				Depth of wound hole			
	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum
		Millimeters	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*
April [1]	47	10	15.9	18	56	2	4.2	12	55	1	2.0	4
May	113	12	16.7	21	125	1	4.0	8	119	1	2.1	4
June	253	10	18.7	23	257	1	6.5	20	251	1	2.4	6
July	235	13	20.0	27	211	1	4.2	15	202	1	2.4	6
August	282	10	26.1	36	274	1	6.0	17	233	1	3.0	10
September	174	13	27.5	37	154	3	6.3	26	125	1	3.1	10
October	243	18	30.8	39	234	2	6.7	18	186	1	3.7	12
November	48	22	34.4	41	46	2	7.8	25	32	1	4.4	12
December	47	22	34.5	42	48	2	8.3	30	39	1	3.8	14
January	28	28	34.6	42	28	2	7.5	13	25	2	5.1	8
February	46	30	36.8	45	39	2	10.4	23	36	1	3.9	12
March	35	29	34.5	40	35	2	11.4	30	27	1	3.6	8
April	42	26	33.9	38	38	3	8.7	23	34	1	3.0	8
May	34	30	34.8	39	34	3	7.4	18	30	2	4.0	9
June [2]	3	28	32.7	35	4	5	9.8	10	3	3	4.3	6
Total number	1,630				1,583				1,397			

[1] Start of parasitic feeding. [2] End of parasitic feeding.

weight as their gonads ripen; the smaller lampreys of the year class may continue to feed actively until the fifteenth or sixteenth month before becoming sexually mature, but their increase in size, if any, is small.

The terminal average of oral-disk marks on lake fishes was 30 millimeters, a reduction by 40 percent from the maximum mean size recorded in the eleventh month. The final average disk mark obtained on laboratory hosts in the fifteenth month was 32.7 millimeters, a reduction of 20 percent from the maximum mean size listed for this group. During the period from April to July the wounds made by the outgoing year class (thirteenth to sixteenth month) of sea lampreys were readily separable by their dimensions from those of the incoming year class (first to third month).

The curves showing the development in sizes of oral-disk marks on fishes during certain calendar periods (fig. 15) may be useful in estimating the growth of sea lampreys in the lake and in aquariums. This view is supported by data obtained on individually identifiable lampreys held in aquariums; their lengths were periodically determined, and the measured diameters of their oral disks were found to be equal to the diameters of their individual disk marks on host fish. These feeders doubled their lengths by the seventh month and reached maximum average length in the eleventh month of parasitic habit. Thereafter most of the specimens shrank in length and weight as they tended to cease feeding and become sexually mature. It is therefore likely that a similar direct relation exists between the growth of lampreys in the lake and the size development of their oral-disk marks on host fishes.

In order to compare the growth of lampreys in the lake and in the laboratory, the mean diameters of fresh oral-disk marks on wounds from both sources were converted to mean lengths of lampreys by referring to table 4 which lists length groups of lampreys with the mean diameters of their oral disks. These lengths-by-conversion are included in table 17 along with some actual lengths of sea lampreys captured in the Great Lakes by Applegate (1950) during certain calendar periods in 1948. In considering these data, it is necessary to keep in mind the fact that a decline in the average size of spawning-migrant lampreys in Lake Huron is in progress (Applegate et al. 1952); spawning lampreys in Carp Lake River, a tributary to Lake Huron, averaged 17.4 inches long in 1947 and 15.8 inches long in 1951. Nevertheless, it appears that the growth trends of lampreys in the Great Lakes, in Lake Huron, and in laboratory aquariums are comparable.

The lampreys listed by Applegate (1950) were longer at the start of their parasitic phase than the ones which made the lake- and laboratory-incurred wounds studied in 1950 through 1952, but the differences in monthly increments of mean growth in the three sets of data in table 17 were small (0.2 to 1.8 inches). By the seventh month of parasitic life, the three groups of lampreys had at least doubled their lengths. Applegate's last

measurement for the Great Lakes lampreys was 17.3 inches in the ninth month; at the same stage, the lengths-by-conversion of lampreys in Lake Huron and in the laboratory were 18. 5 and 16.3 inches. The parasites seem to grow until the eleventh month, at which time the lampreys in the lake (20.3 inches) averaged 2.5 inches longer than those held in the aquariums (17.8 inches).

TABLE 17.—*Mean lengths of sea lampreys from the Great Lakes measured by Applegate (1950) during calendar months of 1948, and average lengths-by-conversion of sea lampreys in Lake Huron and aquariums during corresponding calendar months of 1950 through 1952*

Month	Mean lengths of sea lampreys		
	In Great Lakes [1]	In Lake Huron [2]	In aquariums [2]
	Inches	*Inches*	*Inches*
April	7.5	6.4	6.7
May	8.1	7.6	7.0
June	8.2	7.6	7.6
July	10.0	7.8	8.0
August	12.6	.....	11.4
September	13.6	12.8	12.1
October	16.0	13.6	13.7
November	16.7	17.0	16.1
December	17.3	18.5	16.3
January	.....	19.3	16.4
February	.....	20.3	17.8
March	.....	19.8	16.3
April	.....	17.7	16.0
May	.....	17.1	16.6
June	.....	14.8	15.3
July	.....	13.2	.....

[1] Applegate (1950, p. 175).
[2] Mean lengths obtained by conversion from average oral-disk diameters (table 4).

Thereafter, the mean lengths of lampreys in the three groups of data decreased and the final average lengths were smaller than those for the ninth month.

Wound-hole dimensions.—The wound hole which lies within the oral-disk mark on a fish represents the actual penetration point into the tissues of the host. The diameter and depth of the wound hole were measured on lake and laboratory fishes (tables 15 and 16). These measurements do not necessarily have a clear-cut relation to the sizes of the lampreys that made the wounds, since the area and depth of a wound hole depend also on the duration of the attack, the amount of rasping by the tongue, the extent of tissue lysis caused by the action of the buccal-gland secretion, the location of the attack on the fish, and the extent of movement by the lamprey from the original site.

The smallest wound holes on fish from the lake and aquariums were made by recently transformed lampreys during the first month (April) of feeding; the mean diameter of holes was 5.0 millimeters on lake fish and 4.2 millimeters on aquarium hosts. The greatest mean diameter occurred on fish from the lake in the ninth month (December) (16.5 millimeters) and on fish in aquariums in the eleventh month (February) (11.4 millimeters).

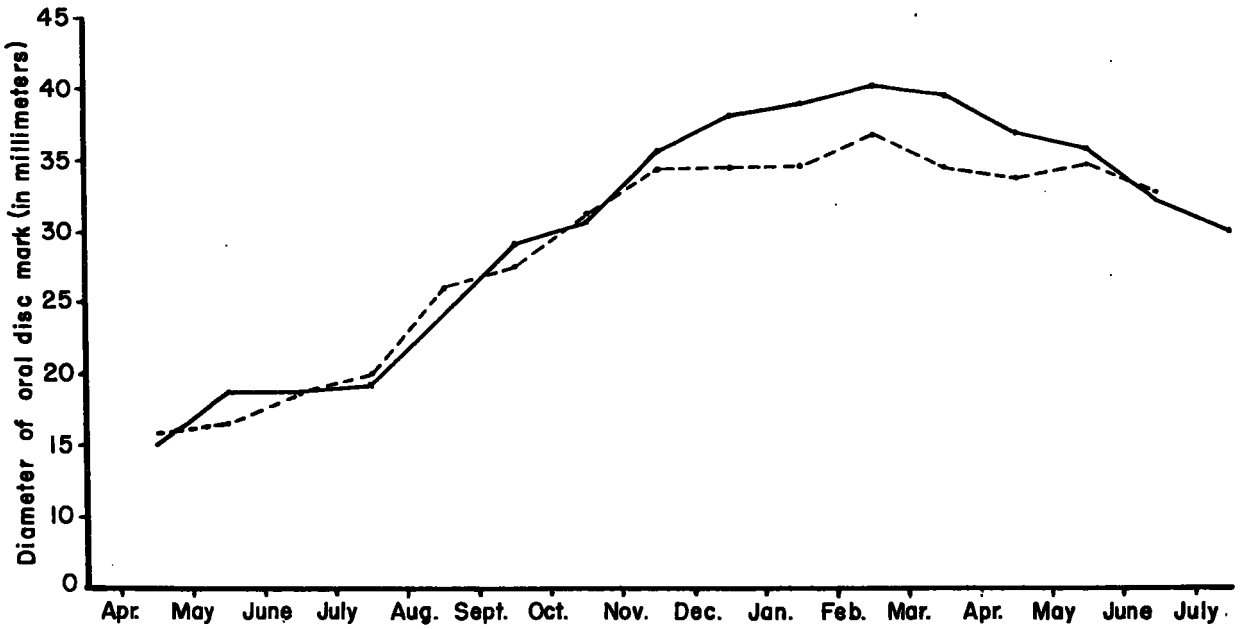

FIGURE 15.—Curves showing seasonal changes, 1950–52, in the mean diameter of oral-disk marks on fishes that bore sea-lamprey wounds. Solid line represents 832 measurements of marks on 18 species of host fish attacked in Lake Huron, broken line represents 1,630 oral-disk marks on 11 species of fish in aquariums.

The mean diameters of holes in both groups of hosts then decreased as the lampreys in the lake and aquariums approached sexual maturity and death.

The mean depths of wound holes listed in tables 15 and 16 for lake and laboratory fishes include only those wounds in which accurate measurements of depths could be made. Many wounds were observed which penetrated the body wall and extended into the viscera of hosts. No depths could be recorded for such penetrations, but they undoubtedly exceeded the depths measured in other wounds. The mean depths expressed for the holes in fishes from lake and laboratory are therefore smaller than they should be. The holes on lake-incurred wounds ranged from 1 to 15 millimeters in depth, with a maximum mean of 5.0 millimeters recorded in the twelfth month (March) of the lampreys' parasitic phase. The range of wound depths on fish in aquariums was 1 to 14 millimeters, with a maximum average depth of 5.1 millimeters recorded in the tenth month (January).

Significance of wound dimensions.—The dimensions of sea-lamprey wounds are not reliable criteria for evaluating the deadliness of attacks on host fishes. In general, wounds of small dimensions made by newly transformed feeders have the same mortal consequences for their hosts as the more extensive wounds made by large lampreys.

One of the largest fatal sea-lamprey wounds examined was on a white sucker, 12.0 inches long and 340 grams in weight, captured in Lake Huron. The injury was new and located on the right side of the fish, slightly below the lateral line in region III. The diameter of the distinct oral-disk mark was 50 millimeters, which indicated that the length of the attacker exceeded 23 inches. The wound hole had a diameter of 42 millimeters and extended deep into the body cavity. Portions of many myomeres were missing and the viscera were exposed. The margins of the hole on skin and muscle were smoothly chiseled as the result of lysis and suction as well as erosion by the tongue.

Among the smallest wounds seen was one created in a laboratory aquarium by a 5.3-inch sea lamprey on a white sucker, 6.6 inches in length and 40 grams in weight. The parasite remained attached to the host for 24 hours in region II. The diameter of the oral-disk mark was 13 millimeters and the wound hole was 2 millimeters in diameter and 1 millimeter deep.

Pathology of Sea-Lamprey Injury

Destruction of tissue and organs

Sea-lamprey wounds, either complete or incomplete, always entail injuries to the host fishes. The extent of damage to the tissues or organs depends on the size of the attacking lamprey, the duration and intensity of its attack, the size of the host fish, and the site of the attachment. The effects of damage were indicated by Surface (1898) who stated that the injured fish do not always die, but in every case they are seriously weakened and reduced in flesh, in blood, and in their ability to reproduce.

Integument.—The skin of the prey fish, with its protective coverings of mucus and usually of scales, is always affected in attacks by sea lampreys. Incomplete attachments involve interruptions in the mucous coat and scales, and the skin may be scored, even though unbroken. Where feeding by the lampreys takes place, the skin is eroded away. The extent of the skin disruption varies from a spot 1 millimeter in diameter to patches as long as 75 millimeters in cases where the parasite progressively moved from the original site.

The injury to, or the destruction of, the integument at the point of attachment renders the host fishes susceptible to various types of infection or disturbs the osmotic balance between exposed tissues and the lake water. The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* were observed as secondary invaders of wounds. Their effects are described later in this paper (p. 288).

A waterlogged condition was noted frequently in white suckers and at times in trout species in the laboratory aquariums. The suckers bearing open wounds from which the lampreys had recently departed gained as much as 100 grams in weight in the hours or few days before death. The increase in weight was attributed to an influx of water into the tissues through the site of attack. Pincher (1948) reported that damage to the waterproof covering of scales and slime of a fish is followed by serious trouble. A fresh-water fish becomes waterlogged and dies when water streams into the body faster than it can be excreted.

The greatest increase in weight due to waterlogging was recorded in a female white sucker, 13.8 inches in length, which weighed 527 grams when first placed in a laboratory aquarium on August 31, 1951. The fish suffered three lamprey attacks almost immediately. The diameters of the holes in the flesh were 6 (region IV), 5 (region III), and 6 (region I) millimeters. The lampreys remained on the wounds 47, 48, and 31 hours, respectively. Immediately after the death of the fish on September 4, 1951, after less than 5 full days in the tank, its weight was 630 grams, a gain of 103 grams or nearly 20 percent of the original body weight.

A typical case of waterlogging in trout was noted in a female brook trout, 10.8 inches long, which weighed 192 grams when placed in the aquarium. The fish was attacked on region II, starting January 11, 1951, for 28.5 hours. A hole 6 millimeters in diameter and 6 millimeters deep was cut into the dorsal muscles by a sea lamprey 16.1 inches long. The dying trout weighed 208 grams a few hours after the lamprey left the wound. The fish died slightly less than 48 hours after the detachment. The weight was 223 grams immediately after death, a gain of 31 grams or about 16 percent.

Muscular tissue.—The skeletal muscles were often penetrated and damaged to a considerable extent by the rasping tongue and the lysis-producing secretions of the lampreys (fig. 16). Wounds located near the pectoral fins at times involved injuries to the fin musculature, resulting in impairment of action in the appendage thus afflicted. The greatest amount of tissue, other than blood, ingested by the lampreys was skeletal muscle.

Connective tissue and cartilage.—The connective tissues lying beneath the skin and between the segments of the body muscles suffered damages in the wounding process. Cartilages in the head and in the paired fins were also destroyed on occasion. Complete wounds were observed on the "lips" of white suckers in which the tough tissue and cartilage had been efficiently cut, disrupted, or dissolved.

Vascular system.—The capillaries in areas under lamprey attack were destroyed within the confines of the wound. Veins and small arteries in certain organs, such as the eyes and liver, were often severed during feeding attachments involving these parts. Some wounds continued to hemorrhage for various intervals of time, usually short, after the lampreys left the fishes.

Blood and lymph.—Blood and lymph are pumped from the wounds on fishes and ingested by the sea lampreys as food. Studies of the blood remaining in host fishes after attacks revealed, in some instances, that the erythrocytes had been altered, perhaps by lamphredin which entered the ruptured blood vessels. The red cells were distorted into odd shapes, suggestive of the first stages of hemolysis, and the blood contained much unidentified debris. The white cells, generally abundant during and after attacks, seemed resistant to adverse effects. A detailed account of studies on the blood of host fishes is given on page 284.

Gills.—A lamprey wound was occasionally located partly under the operculum; in others the operculum had been penetrated. In some such cases, the gill filaments were torn extensively on one or more gill arches. The irritation in so vital an area usually evoked a rapid and copious secretion of mucus in the gill chamber, with the result that the fish then suffered a pneumonialike condition, which possibly contributed to death.

Lateral-line system.—Pincher (1948) mentioned that the lateral-line system functions mainly in the perception of sound waves of low frequency. The canals, sense organs, and nerves included in the system are at times interrupted and destroyed in wounds. The degree to which the hearing and balance of the fish is disturbed by such an attack is difficult to evaluate.

Nerve tissue.—No sea-lamprey wounds were observed that penetrated into the brain of a host fish. Injuries were recorded, however, that in-

FIGURE 16.—Damage created on a rainbow trout by a sea-lamprey attack of short duration. The trout died after 5 hours, but the lamprey remained an additional 6 hours on the wound. The actual hole was 26 millimeters in diameter and 6 millimeters deep. Several neural processes of the vertebrae were exposed and damaged.

volved parts of main trunks or major rami or one or more of all cranial nerves except the auditory. Deep penetrations located on the eyes, over the nasal apertures, on the ventral side of the head, in the gill area, or extending into the viscera certainly affected many branches of both cranial and spinal nerves. Severe attacks sometimes appeared to cause a degree of paralysis in the host fishes. Some of these attacks were quickly lethal, possibly owing in part to nerve damage.

Bone tissue.—Bones of a host fish were ineffective as barriers to penetrations by sea lampreys. Among the wounds examined on fish from Lake Huron and in laboratory aquariums, were some that involved injury to, including complete severance of, one or more of the following bones of the head: Premaxillary, maxillary, mandible, nasal, lacrimal, circumorbital, frontal, parietal, supraoccipital, opercular, supracleithrum, cleithrum, gular, and the branchiostegals. On the body proper, bones damaged by lampreys included neural processes of vertebrae (fig. 16), ribs, and bony rays of the pectoral, pelvic, dorsal, anal, and caudal fins.

An example of severe bone destruction was seen on a female white sucker 17.7 inches in length and 992 grams in weight. The fish, captured in Duncan Bay in Lake Huron on March 11, 1952, was close to death due to a pair of new and complete wounds which probably were inflicted in the trap net. The most damage was over the left eye where the well-defined disk mark measuring 46 millimeters across indicated that the attachment was made by a lamprey approximately 22 inches long. The wound hole, which included the eye, was 19 millimeters across the center, or at least 8 millimeters greater than the normal socket diameter on a fish of this size. The eyeball was missing, the circumorbital bone was largely destroyed, and parts of the lacrimal and frontal bones near the eye were naked and their margins eroded. The socket was full of newly coagulated blood.

The second wound on this fish was on the base of the caudal fin on the left side. An oral-disk mark 39 millimeters in diameter indicated a sea lamprey about 19 inches long. The wound hole was 5 millimeters across the center and 3 millimeters deep. Two fin rays were severed or broken. This attachment appeared to have been of shorter duration than the one over the eye.

Eyes.—Attachments over the eyes of the fishes by sea lampreys invariably resulted in the destruction of vision in those organs, and usually in the death of the hosts. Damage varied from mere excoriation of the conjunctiva and cornea to the complete removal of the eyeball. Wounds of intermediate severity penetrated the eyeballs, tapping both aqueous and vitreous humors, in addition to the richly supplied blood vessels that overlie the ventral part of the retina. The lens was usually missing after a puncture of the eyeball. The optic nerve, blood vessels, and eye muscles attached to the ball were often severed or otherwise damaged.

Fish do not always succumb immediately or directly from wounds over the eyes. Many grievous eye injuries from recent lamprey attacks were observed, but only one healed eye wound occurred among the total of 264 healing or healed injuries examined on fishes from Lake Huron. It is likely that the weakened condition and impaired vision of the host fish make it easy prey for other enemies or to disease even if it does survive the attack.

Nasal apertures.—Deep and effective sea-lamprey wounds were observed which included nostrils of fishes. The blind passages and the olfactory sense cells were often destroyed, and the hemorrhage attending such attachments was usually profuse. Very few healed wounds on this area of the head were seen.

Intestine.—The intestines were at times damaged in attacks that penetrated the body wall of host fishes. The digestive tube was punctured, or severed completely, which allowed the intestinal contents to escape into the body cavity or to the exterior through the wound hole. Many of the live hosts bearing such injuries were bloated to some degree and the materials in their body cavities were foul, sometimes with attendant peritonitis.

Several white suckers and yellow perch taken in Lake Huron exhibited body-wall perforations in advanced stages of healing. The gonads or intestine in some fish had adhered to the body wall. Suction pressure exerted by the lamprey apparently drew parts of the organs close to the excavation, and during the healing the intestinal or gonad tissues became firmly bound to the body wall by the scar tissue.

The only case of a healed fistula was found in a yellow perch which displayed unusual recovery from a severe lamprey wound. The 10.2-inch fish, a spawned-out female in good condition, was captured in Hammond Bay on July 3, 1951. Its injury was located just posterior to the left ventral fin and was almost fully healed about its margins. The oral-disk mark was 30 millimeters in diameter, and the hole which penetrated the body wall was 7 millimeters in diameter. The intestine had been severed at a point 158 millimeters of gut length posterior to the pylorus, and the ruptured end had been pulled through the wound hole. During the process of healing, the margin of the wound hole and the wall of the protruding intestine became firmly joined. Any portion of the intestine exterior to this point sloughed off. The lumen of the tube at the point of adhesion with the body wall was open and was apparently a functional anal opening. There was no trace in the coelom of the posterior part of the ruptured organ. The vent was nearly blocked off by adhesions. The stomach and short pieces of intestine contained no food at all but the good condition of the fish attested its ability to handle food.

Leach (1951, p. 215) reported a similar case of "accidental and unintentional colostomy" performed by a sea lamprey on a pike in Cayuga Lake, N. Y. The wound served as the new outlet of the perforated intestine, and the original anus appeared to be nonfunctional.

The pyloric caeca.—The pyloric appendages in trout species and yellow perch were extensively lacerated in some body-cavity penetrations. Doubtless the production of trypsin by the caeca was reduced by such wounds. Whether leakage of this enzyme about the injury had a harmful effect is not known.

Liver.—The vital functions of the liver were reduced in the several fish in which a lobe of the organ was damaged by sea-lamprey attacks. The more serious effects of injuries to the liver are perhaps the attendant hemorrhage and reduction in the victim's hemopoietic, excretory, and digestive efficiency.

Pancreas.—The pancreas, an organ important to a fish in the manufacture of digestive enzymes and the hormone insulin, was badly lacerated in a few perch and rainbow trout whose body walls were pierced by sea lampreys.

Spleen.—Several lamprey attacks resulted in direct erosion of the spleen of rainbow trout and yellow perch. Aside from the hemorrhage, there was a possible reduction of the host's hemopoietic and blood-storage capacities.

Airbladder.—One yellow perch taken in a trap net in Lake Huron had suffered a deep lamprey wound which punctured the airbladder. The direct effects of the deflation of this organ are difficult to assess. The primary function of the bladder in the physoclistous perch is presumably hydrostatic, although Pincher (1948) reported that an accessory respiratory function has been both claimed and denied for it in this species.

Gonads.—Ova of coregonid fishes have been observed in the intestines of parasitic sea lampreys. The eggs were probably ingested when the body walls and gonads of the fishes were perforated by the attackers. In the study of lake- and laboratory-incurred lamprey wounds, damages to ovaries and testes were observed in rainbow trout, yellow perch, and white suckers.

Anus.—Some severe, open wounds were observed in the anal area of host fishes, but no healed ones involving this site were found on hosts captured in Lake Huron. The destruction of the anus could be fatal to the victim.

Significance of injuries to tissue and organs.—The rasping tongue, the lamphredin, and the suction pressure employed by the sea lamprey to create feeding attachments on fish cause injuries to many tissues and organs with consequent impairment of functions in the hosts. Fish that do not succumb directly to the effects of their lamprey wounds are more subject to the lethal or detrimental influences of fungi, other parasites, predators, and the possible malfunction of their own vital processes. The extent and nature of injuries received in the attacks often render surviving hosts unfit for commercial marketing.

Effect of Lamprey Injury on Blood of Prey

Of the tissues affected by sea-lamprey wounds on host fishes, the blood was usually the most drastically altered. The severe hemorrhage attending the attacks of this largely sanguivorous parasite brings death to most of the victims. The importance of fish blood in the diet of sea lampreys indicated the necessity for some hematological observations on prey fishes.

The blood of normal fishes

The blood of a bony fish, like that of other vertebrates, is a circulating tissue. The major constituents are the plasma, a fluid combination of water, proteins, and inorganic salts; erythrocytes; and leucocytes. The erythrocytes of fishes are flattened, oval, nucleated cells whose cytoplasm contains hemoglobin. The leucocytes include agranulocytes and granulocytes, both of which show varying degrees of ameboid motion.

Blood plasma is contributed by the liver, and the blood cells develop in the reticular connective tissues of the blood-forming organs. In fishes, the spleen is the fundamental blood-cell contributor, while in some species the development of the leucocytes, especially the granulocytes, is held to take place in the mesonephros (Cole 1941).

Fishes, in common with all vertebrates, possess hemoglobin in the blood for the transport of oxygen. The capacity of fish blood for carrying oxygen depends on the individual specimen, on the species, and on some environmental conditions. For example, the load capacity is reduced by increases in water temperature or in the concentration of dissolved carbon dioxide.

Bony fishes have a small supply of blood. In spite of the efficiency of their circulatory system, the low volume of blood places them at a disadvantage when attacked by parasitic lampreys. Prosser et al. (1950) noted that teleosts have the least amount of blood of any of the vertebrate groups. The quantity was listed as 1.5 to 3 percent of the body weight as compared with 7 to 10 percent in mammals. The volume of lymph in fishes is not known.

The respiratory exchange between fishes and their environment takes place in the gills. Considering their respiratory area, the gills of teleosts have been regarded as surpassing lungs in efficiency (Prosser et al. 1950).

White suckers.—The sea-lamprey feeding experiments at the Hammond Bay Fishery Laboratory afforded an opportunity to study the blood levels in lamprey-wounded prey fishes. The determination of blood values in normal specimens of the same species provided the comparative material for evaluation of the effects of lamprey attacks.

The white sucker was the species best suited for the accumulation of hematological data in quantity, because of its local availability, its favorable average size, and its physiological characteristics. Furthermore, the sucker is a typical host fish for sea lampreys in Lake Huron and the properties of its respiratory pigments are comparable to those of the Salmonidae. Black (1940) pointed out that fish blood with a high sensitivity to carbon dioxide and low affinity for oxygen was associated with cold-water habit. In Prosser et al. (1950), the sucker was grouped with the brook, brown, and rainbow trouts with respect to its sensitivity to temperature and to carbon-dioxide tension. The effects of temperature and carbon dioxide on the availability of oxygen for these species is certainly a factor in their distribution. They characteristically seek cold, highly oxygenated waters, although the suckers have a wider distribution in warmer waters than do trout. In view of the similarity of the blood in suckers and salmonids the data given here on the former may be held descriptive, in a general way at least, of conditions in trouts and coregonids.

Twenty-three white suckers captured in good condition in Lake Huron were anesthetized and sampled for their total blood volumes by the caudal-severance technique.[4] The amount of blood in them averaged 1.5 percent of the total body weight (table 18). On the basis of a conclusion by Gage (1928) it appears that the blood volume of an average-sized white sucker would hardly satiate an active and hungry lamprey and still leave enough to sustain life in the host fish. He determined that a full-grown lake lamprey (12 to 13 inches long) required about 25 milliliters of fish blood to fill its intestine.

To obtain information on white-cell counts, blood samples were obtained from 119 white suckers by a cardiac-puncture method described by McCay (1929) and Field, Elvehjem, and Juday (1943). The white counts computed on a hemocytometer averaged 3,869 cells per milliliter of whole blood and ranged from 380 to 12,000 cells per milliliter (table 21).

The number of erythrocytes per milliliter of blood in white suckers was computed from the 119 specimens from which the white-cell counts were made. The mean count for these fish was 1,159,256 red cells per milliliter (table 20). Most of the 119 counts were made during the months of February, March, and April, 1951, when low

[4] Severance of the tail in nonanesthetized fish produced a state of shock that inhibited bleeding.

TABLE 18.—*Mean blood volumes in 23 white suckers from Lake Huron*

Weight range of fish (grams)	Number of fish	Mean length	Mean weight	Mean blood volume	Ratio, weight of blood [1] to total weight
		Inches	*Grams*	*Milliliters*	*Percent*
200–299	9	11.9	270.3	4.1	1.6
300–399	7	13.6	328.5	4.9	1.6
500–599	2	14.6	521.0	6.4	1.3
600–699	1	14.8	607.0	8.7	1.5
800–899	1	17.1	866.0	12.5	1.5
900–999	3	17.9	941.3	11.8	1.3

[1] Specific gravity of the blood estimated at 1.05 (average for human blood is 1.055).

water temperatures (34° to 41° F.) prevailed in the lake and in the laboratory holding facilities.

Katz (1950) reported an apparent correlation between the increase and decrease in the average blood counts in silver salmon, *Oncorhyncus kisutch*, with an increase and decrease in water temperatures. He demonstrated that the erythrocyte counts in silver salmon were higher in summer than in the spring and autumn, and suggested the possibility that the increase of water temperature in summer may have lowered the oxygen content of the water enough to cause a slight, compensatory increase in erythrocytes. On the other hand, the work of Hart (1943) suggested that the concentration of carbon dioxide may be a major factor in the blood count of white suckers. Prosser et al. (1950) further observed that in the presence of very small amounts of dissolved carbon dioxide, the oxygen-carrying capacity of sucker blood is reduced, causing the fish to seek waters with lower carbon-dioxide concentrations or with a greater supply of dissolved oxygen.

The suckers upon which the blood counts were made were held in the laboratory tanks and aquariums. Periodic chemical analyses of water and continuous temperature records demonstrated oxygen concentrations approaching saturations at all times. The low temperatures which prevailed during the period when the counts were made, however, may have tended to depress the red-cell counts. Nevertheless, the holding facilities registered carbon-dioxide concentrations which, while very low, were invariably 1 to 2 p. p. m. higher than in Lake Huron. It is reasonable to suppose that lake fish introduced into the tanks would effect a compensatory increase in their erythrocytes to offset the influence of the carbon dioxide. In fact, increases up to 15 percent in erythrocytes were observed in white suckers after 4 days in captivity in the tanks. After 8 days, the erythrocyte counts on this species declined but still continued to average slightly higher than counts made on blood samples from fish freshly caught in Lake Huron.

It appears reasonable to conclude that the red-cell determinations as made in the blood of white suckers are representative of normal levels. Influences which tend to affect the numbers of erythrocytes were in force simultaneously and were to a degree compensating.

The hemoglobin content in the red cells of 119 white suckers was determined by an acid-hematin method, in which a hemoglobinometer was used as described in Todd and Sanford (1948). The mean value was 8.24 grams of hemoglobin per 100 milliliters of normal fish blood, or about half the amount contained in the blood of humans.

Observations on the clotting time of the blood of 119 white suckers confirmed the views of Gage and Gage (1927) and Smith, Lewis, and Kaplan (1952) that fish blood normally coagulates rapidly outside the blood vessels of the animal. The blood clotted in less than 1 minute in capillary tubes; or, when several drops of blood were placed on greased glass slides, solid clots were formed in about 3 minutes at room temperatures of 68° to 70° F.

Trout.—Only a few values on the normal blood of trout were obtained (table 19), because the fish were usually too small to make possible satisfactory sampling by cardiac puncture.

Three brown trout had mean counts of 1,379,167 red cells and 8,120 white cells per milliliter, and averaged 8.0 grams of hemoglobin per 100 milliliters of blood. Wunder (1936) listed average counts of 1,140,000 red cells and 25,000 white cells per milliliter for this species.

Two rainbow trout had mean values of 1,107,500 red cells and 7,980 white cells per milliliter, and an average of 7.5 grams of hemoglobin per 100 milliliters of blood. These figures were lower than those found by Marsh and Gorham (1906) who reported that 11 domestic rainbow trout sampled by them had an average of 1,487,000 red cells per milliliter whereas hemoglobin content in 19 individuals averaged about 9.0 grams per 100 milliliters of whole blood.

No determinations were made on brook trout, but Marsh and Gorham (1906) listed an average red-cell count of about a million and a hemoglobin

content of slightly less than 8.0 grams per 100 milliliters of normal blood (based on 35 individuals). Field, Elvehjem, and Juday (1943) found means of 1,013,000 erythrocytes and 3,910 leucocytes and 8.5 grams of hemoglobin. Little difference was noted by these workers in the red-cell levels of domestic and of wild trout.

TABLE 19.—*Blood levels in healthy wild brown trout and in hatchery-reared rainbow trout*

Length (inches)	Weight (grams)	Blood cell counts (per milliliter)		Hemoglobin (grams per 100 milliliters)
		Red	White	
Brown trout				
10.9	220	1,437,500	3,180	9.0
12.8	311	1,340,000	14,800	8.0
15.2	536	1,360,000	6,380	7.0
		1,379,167	8,120	8.0
Rainbow trout				
9.5	114	1,002,500	7,960	7.5
10.4	152	1,212,500	8,000	
		1,107,500	7,980	7.5

The blood of wounded fishes

White suckers.—The hematological data treated in this section are only from fishes that were dying as a direct result of attacks by sea lampreys in aquariums. The blood of each wounded fish was sampled near death by cardiac puncture. Certain obvious symptoms made it possible, with experience, to identify dying victims. Among these symptoms were the slowed and shallow respiratory movements, the pale pink or whitish color of the gill lamellae, the loss of equilibrium and departure from customary level or position in the tanks, the lack of response to visual and tactile stimuli, and the paled color of the body.

Many of these fishes that suffered lingering deaths demonstrated a gradual progression of body rigor from the caudal region towards the head. The tetany was due possibly to accumulated metabolic wastes, and the affected regions of the fish became stiff and immobile and at times contorted. Death invariably occurred before the anterior third of the body became thus affected. Interestingly, the muscles relaxed their tension soon after the fishes died. So far as I could determine, this reaction is without parallel in humans or other mammals subjected to fatal hemorrhage.

The mean red-cell count in 119 mortally wounded white suckers [5] (table 20) was 189,705 per milliliter of blood. This figure represents a net loss of 83.6 percent from the mean of 1,159,256 red cells per milliliter in uninjured fish of the same species. Curves showing the distribution of red-cell counts in the wounded and in the healthy white suckers are presented in figure 17. The gross loss of erythrocytes is the quantity of these cells which pass from the fish's blood stream during an attack by a lamprey; therefore the net-loss value as given represents a smaller portion than that actually consumed by the parasite. Hemopoiesis makes an unknown contribution but obviously cannot keep up with the rate of loss.

TABLE 20.—*Number of erythrocytes per milliliter in blood specimens drawn from hearts of 119 healthy white suckers and 119 white suckers fatally wounded by sea lampreys*

Number of erythrocytes	Number of fish	
	Healthy	Wounded
0–99,999		37
100,000–199,999		36
200,000–299,999		20
300,000–399,999		17
400,000–499,999		6
500,000–599,999		3
600,000–699,999		
700,000–799,999	3	
800,000–899,999	7	
900,000–999,999	8	
1,000,000–1,099,999	17	
1,100,000–1,199,999	33	
1,200,000–1,299,999	30	
1,300,000–1,399,999	13	
1,400,000–1,499,999	6	
1,500,000–1,599,999	2	
Total	119	119

Average count for healthy white suckers, 1,159,256.
Average count for fatally wounded white suckers, 189,705.

The lowest hemoglobin level that could be read on the hemoglobinometer was 3.75 grams per 100 milliliters of whole blood. The acid-hematin content of the blood tested in mortally wounded suckers was invariably too low to register on the scale of the instrument. Consequently, the hemoglobin values were listed as "less than 3.75" grams per 100 milliliters, which represents a reduction of at least 54 percent in the oxygen-carrying capacity of the blood. The actual reduction of hemoglobin in the blood of the suckers is estimated to range as low as 20 percent of normal.

The numbers of white cells were counted in the blood samples from 115 suckers of this series. The average per milliliter of blood was 8,514 cells or 2.2 times the normal mean of 3,869 leucocytes (table 21); but in many dying individ-

[5] The identity of number (119) in the groups examined to obtain normal and pathological blood data was accidental; only 6 fish were common to the groups. Data on these 6 suckers are discussed in the next section.

uals the white-cell counts were below normal. Curves showing the distribution of counts in the 115 dying white suckers and in the 119 healthy fish are presented in figure 18. The gross increase of white cells in the blood as a defensive mechanism apparently exceeds the loss of cells due to hemorrhage. It was concluded that, in general, the suckers were able to manufacture leucocytes faster than the cells were removed by the lampreys.

The blood samples from the hearts of wounded suckers clotted more rapidly than normal blood. A solid clot usually formed on a glass slide in 1 minute at room temperature. Frequently it was impossible to obtain cell counts on dying fish owing to the extremely rapid coagulation of the blood specimens. Even blood samples that were very pale and of low viscosity retained the ability to clot within a few minutes.

The ability of the blood in a wounded prey fish to coagulate rapidly is a protective response designed to arrest further hemorrhage. This defense mechanism is probably provoked by reactions in the liver which produce fibrinogen and/or by thrombokinase picked up in the blood stream at the site of tissue damage. Apparently the positive actions of these materials overcame any opposite influence of lamphredin which may have diffused away from the wound site; alternatively, this anticoagulant does not leave the lamprey's point of penetration in any appreciable quantity.

No measurements were made on the volumes of residual blood in dying suckers. Many dissections were performed on specimens that were dying or dead as the result of sea-lamprey attacks and the volume of blood was always much reduced. Rapidly fatal attacks on suckers usually resulted in the greatest reduction of the fluid in the vascular

TABLE 21.—*Number of white cells per milliliter in blood specimens drawn from hearts of 119 healthy white suckers and 115 white suckers fatally wounded by sea lampreys*

Number of white cells	Number of fish	
	Healthy	Wounded
0–1,999	45	8
2,000–3,999	35	16
4,000–5,999	12	22
6,000–7,999	11	15
8,000–9,999	8	11
10,000–11,999	5	14
12,000–13,999	3	9
14,000–15,999		7
16,000–17,999		6
18,000–19,999		1
20,000–21,999		2
22,000–23,999		1
24,000–25,999		3
Total	119	115

Average count for healthy white suckers, 3,869.
Average count for mortally wounded white suckers, 8,514.

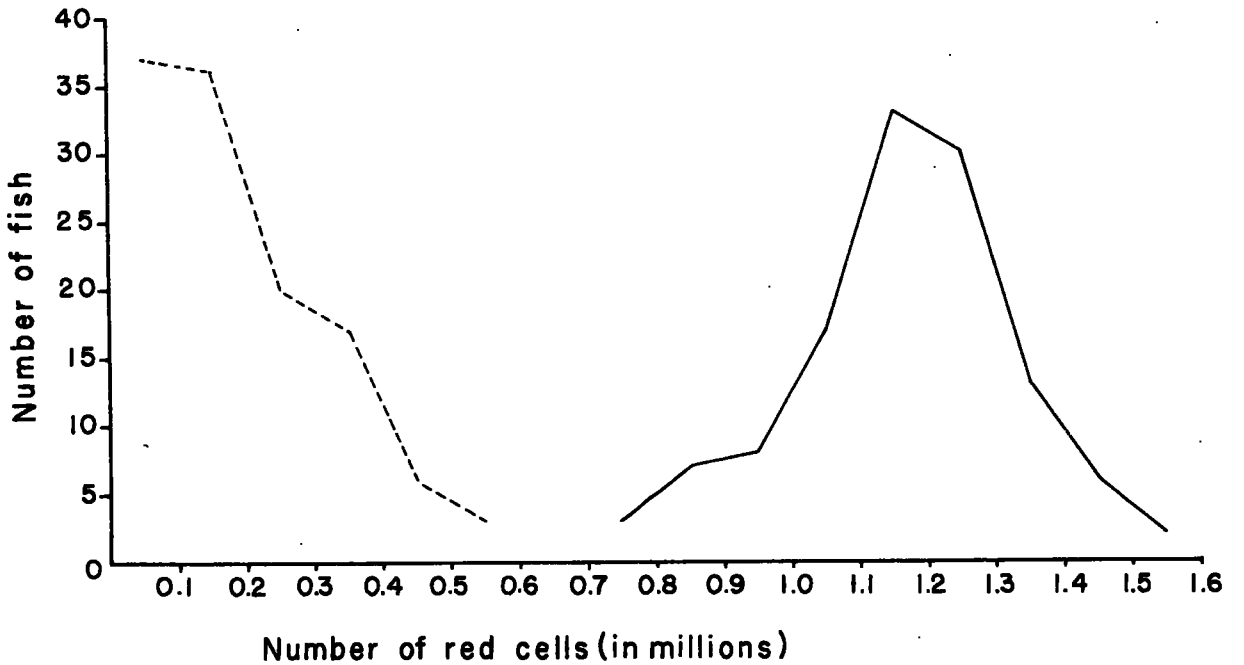

FIGURE 17.—Distribution of red-cell counts in 119 white suckers that were dying as a result of sea-lamprey wounds (broken line) and in 119 healthy white suckers (solid line).

system. It was sometimes impossible to obtain blood in sufficient quantity from these fish to perform hematological tests. Those fish that suffered lingering deaths from attachments of longer duration more often contained larger volumes of very dilute blood, closely resembling water in color and viscosity.

Changes in individual white suckers.—It was possible to obtain both preattack and postattack samples of blood from 6 white suckers (table 22). The data on the red cells, white cells, and hemoglobin in the blood of these fish do not differ greatly from the values for the same characters in blood samples taken from the 119 normal and 119 mortally wounded white suckers previously discussed. There were average reductions of 81.3 percent in red-cell counts and 52 percent in hemoglobin contents between the preattack and postattack blood samples from the 6 white suckers as compared with mean decreases of 83.6 percent in red-cell counts and 54 percent in homoglobin contents between the blood samples drawn from 119 normal and 119 mortally wounded white suckers. It was only after repeated attempts failed to secure preattack and postattack blood samples on many individual fish, that average values for the blood of normal white suckers were established for comparison with levels measured in mortally wounded fish.

The cardiac puncture employed to collect blood specimens apparently was not injurious, and no effects could be detected in the fish used as controls and hosts that would alter significantly the values of subsequent samples. White suckers were bled as many as three times at intervals of 1 to 4 days, with no mortalities.. Field, Elvehjem, and Juday (1943) bled brook trout and carp as many as eight

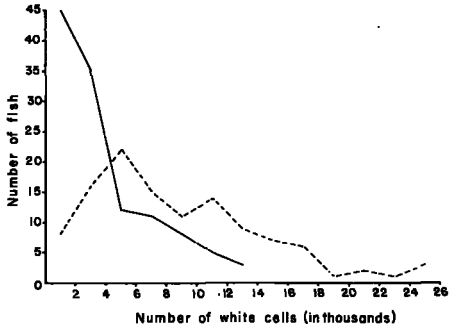

FIGURE 18.—Distribution of white-cell counts in 115 white suckers that were dying as a result of sea-lamprey wounds (broken line) and in 119 healthy white suckers (solid line).

times with the same technique and experienced a total mortality of only 5 percent for repeated treatments.

Trout.—The blood values were recorded for 1 brown trout, 12 rainbow trout, and 3 brook trout which were dying as a result of sea-lamprey wounds incurred in the aquariums (table 23).

The brown trout had 76,457 red cells, which indicates a net loss of 94.5 percent from the mean of 1,379,167 cells listed (table 19) for healthy fish of the same species. The number of white cells was 58.1 percent less than the mean value for normal fish. The hemoglobin content had declined from a normal mean of 8.0 to less than 3.75 grams per 100 milliliters of blood, a loss of at least 53.1 percent.

Twelve dying rainbow trout had an average count of 165,167 erythrocytes, which is 85.1 percent less than the mean count of 1,107,500 in 2 healthy fish. White cells decreased 49.2 percent as indicated by a comparison of 4,052 cells in the wounded trout with the average of 7,980 leucocytes

TABLE 22.—*Preattack and postattack hematological data obtained from white suckers that were mortally wounded by sea lampreys in aquariums at the Hammond Bay Fishery Laboratory*

Length (inches)	Weight (grams)	Sex	Hours under attack	Red cell counts (per milliliter)		Percentage decrease of red cells	White cell counts (per milliliter)		Percentage change of white cells	Hemoglobin [1]		Percentage reduction of hemoglobin [3]
				Preattack	Postattack		Preattack	Postattack		Preattack	Postattack [2]	
12.6	330	M	54	1,100,000	192,500	82	2,640	7,900	199	8.0	<3.75	>53
13.0	380	M	11	1,287,500	207,500	84	7,640	5,200	−32	8.0	<3.75	>53
13.1	418	F	69	1,225,000	105,000	91	8,340	1,740	−79	8.0	<3.75	>53
13.3 [4]	357	F	11	822,500	365,000	56	7,100	1,960	−72	6.0	<3.75	>38
13.9	450	F	30	1,157,500	130,000	89	7,440	10,320	38	8.5	<3.75	>60
14.3	518	F	96	1,500,000	210,000	86				9.0	<3.75	>58

[1] In grams per 100 milliliters.
[2] <3.75 indicates values less than lowest reading possible on the hemoglobinometer used.
[3] >indicates that the reduction of hemoglobin actually exceeds percentages listed.
[4] The attack on this fish was already in progress and thus the preattack levels listed are less than normal; the number of hours given refers to time after the preattack blood determinations.

in healthy rainbow trout. The hemoglobin in the blood was reduced by at least 90 percent.

The 3 blood samples obtained from mortally wounded brook trout had an average of 86,667 red cells, which represents a net loss of 91.4 percent from the mean count of 1,013,000 cells recorded by Field, Elvehjem, and Juday (1943). The average number of 2,030 white cells in the dying trout was 48.1 percent less than the mean of 3,910 leucocytes found by the same authors in healthy brook trout. The reduction of hemoglobin content in the host fish again exceeded 50 percent.

TABLE 23.—*Blood levels in wild brown trout, hatchery-reared rainbow trout, and wild brook trout fatally wounded by sea lampreys in aquariums at the Hammond Bay Fishery Laboratory*

Length (inches)	Weight (grams)	Blood cell counts (per milliliter)		Hemoglobin (grams per 100 milliliters) [1]
		Red	White	
Brown trout				
12.6	297	76,457	3,400	<3.75
Rainbow trout				
15.0	622	200,000	9,320	<3.75
10.0	158	400,000	4,220	<3.75
10.0	132	30,000	300	<3.75
10.6	174	52,000	1,440	<3.75
10.6	132	60,000	440	<3.75
12.0	260	397,500	6,020	<3.75
11.0	178	170,000	9,920	<3.75
9.2	114	50,000	2,120	<3.75
9.0	114	110,000	2,400	<3.75
9.4	124	67,500	10,000	<3.75
8.9	114	185,000	1,320	<3.75
9.8	122	260,000	1,120	<3.75
Average		165,167	4,052	<3.75
Brook trout				
7.8	71	60,000	2,280	<3.75
6.5	42	170,000		<3.75
5.9	27	30,000	1,780	<3.75
Average		86,667	2,030	<3.75

[1] <3.75 indicates values less than lowest reading possible on the hemoglobinometer used.

Phillips (1947) demonstrated that under the stimulation of asphyxia, eastern brook trout increase the number of erythrocytes in their blood by 17.2 percent in 1 hour. This figure indicates a considerable hemopoietic potential which is possibly overcome or exhausted when a specimen suffers hemorrhage and is killed by a feeding sea lamprey. The gross loss of blood in the fish is presumably greater than a comparison of the normal and postattack counts of erythrocytes would show.

Significance of hematological tests.—Comparison of blood data obtained from examinations of healthy fish and those close to death from the effects of sea-lamprey attacks revealed profound differences. The numbers of erythrocytes, the hemoglobin content, and the total volumes of blood in prey fishes were often reduced to small fractions of their normal values. The deaths of many host fishes no doubt occur as direct results of the hemorrhages.

The lethal factors in extensive hemorrhage cannot be identified exactly for fish. The reduction of the oxygen-carrying capacity of the blood causes some degree of anoxia and accumulation of metabolic wastes in the tissues. The distribution of essential endocrine secretions via the blood may be greatly reduced. The decrease in blood volume is probably attended by a fall in arterial pressure, which according to Carlson and Johnson (1948) constitutes an immediate danger to life in humans during sudden and severe hemorrhage.

A condition akin to shock was observed in many fishes dying from lamprey-feeding attacks. The specimens were pale, largely immobile; respiratory movements were slow and weak. They were mostly powerless to perceive or respond to tactile, sonic, or visual stimuli. The hemorrhage also produced disruptions in other physiological mechanisms of the host fishes such as in the osmotic balance between the blood and tissues and probably in the function of the kidneys.

Although the white suckers, rainbow trout, brown trout, and brook trout included in the hematological study represent only a fraction of the fish killed by lamprey attacks in laboratory aquariums they were typical of the group, and hence the data are believed to be truly descriptive of the effects of lamprey predation. The mean values listed for the fishes at the point of death are considered the minimum levels. The critical blood levels, below which the fish are doomed, are undoubtedly higher. It is believed that the trout species and white suckers are in mortal danger when their counts of erythrocytes fall below 300,000 cells per milliliter during lamprey-induced hemorrhages.

The wounded white suckers and trout for which the mortal blood losses were determined are typical of the prey species for sea lampreys in the Great Lakes. The suckers were of average size for northern Lake Huron. They were shown to

be susceptible to extensive and lethal hemorrhages caused by the attacks of sea lampreys of all parasitic-phase sizes.

The trout species used in the aquariums averaged smaller (table 8) than the suckers, and their blood supplies were frequently exhausted beyond critical levels in a short time. Many of the victims in the aquariums suffered multiple attachments which usually brought about quicker death. Attacks by more than one lamprey on a host fish in the lake are also common (fig. 19). Single wounds, however, may be equally deadly.

Secondary Infection of Sea-Lamprey Wounds

The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* were the only common secondary invaders observed on sea-lamprey wounds on fishes. Both infectious species, representatives of the aquatic Phycomycetes, were found on wounded fishes in the aquariums and from Lake Huron.

Saprolegnia parasitica, well known as "fish mold", belongs to the order Saprolegniales. Sparrow (1943) listed the members of this order primarily as saprophytes of plant and animal debris in fresh water or damp soil; some species are parasitic on microscopic and macroscopic animals (fish, amphibia) and roots of higher plants. Allison (1950) reported that a heavy infection of *S. parasitica* may cause the death of the fish. When fish are injured, perhaps by external parasites, careless anglers, or spawning activity, the wounds provide openings for attack by bacteria and fungus. One zoöspore of the fungus is sufficient to initiate an extensive growth.

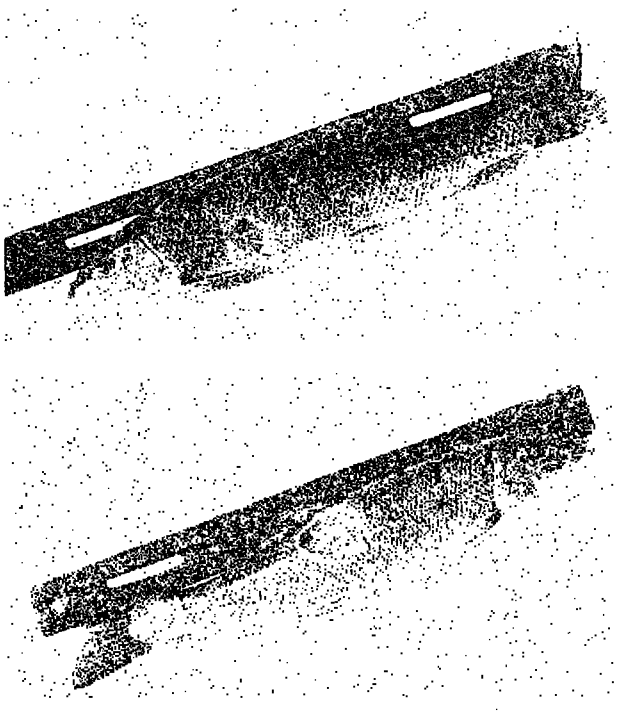

FIGURE 19.—Two complete sea-lamprey wounds on a single white sucker captured in Lake Huron, March 13, 1951. The specimen in both photographs was a male, 11.4 inches in length and 254 grams in weight. The fish was close to death as a result of the attacks. Top picture, wound on region III (note the exposed ribs); bottom picture, wound on region IV.

It was necessary on several occasions to arrest outbreaks of "fish mold" on the sea lampreys and host fishes in the laboratory aquariums. Solutions of malachite green-oxalate in 1:15,000 dilutions were used. The treatment proved selective for *Saprolegnia*, but any *Leptomitus* present on specimens in the tanks was unaffected.

Leptomitus lacteus, of the order Leptomitales, occurred more often than *Saprolegnia* on lamprey wounds on fish from Lake Huron and in the aquariums. The large, tough mats of gray-brown, foul, and odorous growth were found directly over the sites of lamprey attacks on the hosts.

Our first identification of *Leptomitus* was based on an infection observed on a white sucker, 11.1 inches long and weighing 233 grams, captured in Duncan Bay, Lake Huron, on January 16, 1951. This fish bore an open sea-lamprey wound on its right side in region III, near the insertion of the pectoral fin. During the lamprey's attack, the pectoral fin was pinned to the side of the fish by the sucking disk and was partially eroded away. The subsequent fungus infection over the wound area involved the fin; the growth adhered in part to the inserted portion and in part to the naked, eroded fin rays. Fin tissues beyond the limits of the original lamprey wound also appeared to be affected adversely by the secondary invader. The large growth of fungus was removed from the fish and sent to Dr. Frederick K. Sparrow, who identified it (personal communication) as—

> almost wholly *Leptomitus lacteus*. Occasional filaments of *Saprolegnia* mixed in, but 99.44 percent is the *L. lacteus*. It is rather unusual in my experience to find *Leptomitus* so dominant on this type of material. It is entirely possible that the *Saprolegnia* initiated the action after the wounding, but that conditions favored the growth of the other fungus. From what we know of the physiology of *Leptomitus*, I would suspect that this fish had lain in quiet water under conditions of very little dissolved oxygen.

Additional fungus specimens from host fishes were also identified by Sparrow as almost entirely *L. lacteus*.

In 1943 Sparrow wrote that *Leptomitus* is saphrophytic on debris and occurs often in heavily polluted fresh waters but rarely in purer waters. It typically forms large, turflike masses on organic detritus. The fishes in Lake Huron that bore infections of this fungus were captured mostly alive in the Straits of Mackinac, Duncan Bay, and Hammond Bay. None of these waters can be considered polluted to any appreciable extent, nor is organic debris present in quantity except in Duncan Bay. In a later, verbal communication, Dr. Sparrow expressed surprise at the sources of our fungus samples, i. e., living fishes from the laboratory aquariums and Lake Huron.

It is not known whether *Leptomitus lacteus* is parasitic alone or whether it must be preceded by or exist in combination with *Saprolegnia* over wound areas on fish. The numerous observations on infections by this fungus indicate that the invader is detrimental to fishes. The sizes of many fungus growths on lamprey wounds suggests parasitism. These growths, in a form resembling a dark-gray, raglike streamer, were often 10 to 20 inches long, and trailed from their points of attachment over the wounds. The tissue beneath the fungus colonies was often soft and creamy, or charged with blood.

In laboratory aquariums, many fish that contracted infections of *L. lacteus* following nonfatal attacks by sea lampreys, died after 2 or 3 weeks of gradual decline in vitality. For example, a male rainbow trout, 9.0 inches in length and 114 grams in weight, was attacked by two lampreys on November 27, 1951, for a total of 24 hours. Both incomplete attachments, made in region II, resulted in slight hyperemias, but no feeding took place. Within 3 days, *L. lacteus* was observed to grow rapidly and extensively over the lamprey marks. The fish died on December 10, 1951, 13 days after the lamprey attack. The death was chiefly attributed to the secondary infection. The skin was unbroken, but beneath it at the wound sites the flesh was semiliquid to a 5-millimeter depth.

Brown trout, rainbow trout, brook trout, white suckers, longnose suckers, yellow perch, and sea lampreys were subject to infections by both *Leptomitus lacteus* and *Saprolegnia parasitica* in laboratory aquariums. The incidence for both species of fungi was large during all seasons of the year, but *Leptomitus* (probably in combination with a small amount of *Saprolegnia*) was encountered more frequently than *Saprolegnia* alone.

The occurrences of the fungi in such proportions was surprising since the water used in aquariums was pumped from Hammond Bay. The bay area is devoid of aquatic vegetation except for periphyton on the rocks, and lacks any appreciable amount of organic debris. It has a sand, gravel, and boulder bottom. The usually clear, colorless, cold water in the aquariums was unpolluted, and periodic chemical analyses indicated high concentrations of dissolved oxygen and only small amounts of dissolved carbon dioxide. Since the water supply was of excellent quality in all respects, the zoöspores of the fungi must be considered omnipresent in the water or on the fishes.

In Lake Huron, *L. lacteus* and *S. parasitica* were observed at all seasons of the year on white suckers, longnose suckers, carp, yellow perch, and walleyes captured by trap nets fished in Duncan, Hammond, and Spens bays and in the Straits of Mackinac. *Leptomitus* was the more common of the two species.

In 715 complete and incomplete, unhealed, sea-lamprey wounds on white suckers from Lake Huron, growths of *L. lacteus* occurred on 6.2 percent and *S. parasitica* on 0.4 percent. The percentages of fungal incidence on the white suckers in nature actually are greater than given above since unknown numbers of growths on wounds were rubbed off the fish during the net-lifting operations. In addition, most of the fish were examined during the colder months of the year when the incidence of fungus infections may be less than during the warmer seasons.

OTHER PARASITES ON FISH

Ten forms of invertebrate parasites were observed in fishes from Lake Huron and hatchery sources which were studied for their sea-lamprey wounds or used as prey fish in aquariums. These parasites were as follows (for some parasites indicated by "sp." it is not known whether one or more species were present).

Scientific name	Common name
External parasites:	
Protozoa: *Ichthyophthirius multifilis.*	Itch.
Trematoda:	
Gyrodactylus sp.	Anchorworm.
Neascus sp.	Blackspot.
Hirudinea	Leech.
Copepoda:	
Argulus sp.	Fish louse.
Salmincola sp.	Gill louse.
Internal parasites:	
Cestoda: *Ligula intestinalis.*	Tapeworm.
Nematoda:	
Philometra sp.	Red roundworm.
Cystidicola sp.	Bladderworm.
Acanthocephala: *Echinorrhyncus* sp.	Spiny-headed worm.

Fishes harboring these animals usually exhibit no ill effects unless the host-parasite relations are modified by certain conditions, such as a lamprey attack on the fish. Such an attack might weaken a fish to the point where it is affected by an invertebrate parasite that normally would cause no appreciable damage. In no instance could it be determined that an invertebrate parasite followed a sea-lamprey attack on a host fish as a secondary invader.

SUMMARY

The studies reported herein are concerned with the structural characteristics of the sea lamprey that adapt it to a parasitic existence, the mechanism of its attacks on fish, and the consequences of the injuries inflicted.

The feeding mechanism of the adult sea lamprey includes the buccal-gland system, the rasping tongue, the toothed oral disk, and the suctorial mouth. All are peculiarly adapted for the procurement and ingestion of liquid materials from prey fishes. Although blood and body fluids are the primary food materials sought by the parasites, evidence was obtained that some liquefied flesh may be ingested.

The buccal glands of a parasitic-phase sea lamprey are a pair of prominent bean-shaped structures in the head. During feeding they drain into the mouth cavity through a pair of ducts. The glands and their accessories appear in an early stage of metamorphosis and function throughout the parasitic phase.

The capacity of the central reservoirs of the buccal glands varies according to the size of the animal. A pair of prime glands in an average sea lamprey, 15.5 inches long and 121 grams in weight, was found to contain a total of 0.14 milliliter of secretion. As the individual achieves sexual maturity, this exocrine system follows along the irreversible degeneration of other organs and tissues in the body. Nevertheless, liquid of good quality (that is, physiologically effective) was easily aspirated from the glands of many lampreys which were captured during their upstream spawning migration.

Lamphredin (a term applied to the fluid product of the buccal glands) bathes the wound on a prey fish under attack. It prevents the coagulation of the fish's blood, exerts a hemolytic influence on the erythrocytes, and induces a lytic action in the torn flesh. The presence of a cytolytic or histotoxic property in the secretion was strikingly demonstrated in experiments with living fishes into which small amounts of lamphredin were injected subcutaneously. Reactions were observed in brook trout, brown trout, rainbow trout, longnose suckers, and white suckers which brought death in certain of the test specimens. Attempts were made to preserve lamphredin by refrigeration, freezing, and desiccation, but postpreservation tests indicated that the material suffered a reduction of potency as an anticoagulant, hemolytic, and lytic agent. The least rapid deterioration took place in frozen samples.

The tongue of an adult lamprey, with its hinged tip bearing cutting armament of transverse and longitudinal laminae, serves as a powerful rasp to effect a penetration of the skin, scales, and flesh of a fish. No host tissues were found to be entirely impervious to the excoriation. The tongue appears during the process of metamorphosis from ammocoete to parasite and is one of the last of the feeding mechanisms to become fully developed. In newly transformed lakeward-bound sea lampreys, captured in Carp Lake River in November 1951, 73.9 percent exhibited lingual laminae in a state of incomplete development, a condition that rendered them incapable of feeding. Members of the same year class, lakeward bound in the following April, included only 10 percent with incomplete development of the tongue-teeth.

The oral disk of a parasitic lamprey, entrance to the mouth cavity, constitutes a part of the powerful suctorial apparatus. Its circular, tooth-studded, inner surface provides traction and a

measure of erosive action when applied closely to the skin of a prey fish. The imprint of the oral disk on a host usually furnishes the largest dimension of the typical "lamprey mark." From a knowledge of the regression of the diameter of the sucking disk on the length of a lamprey, it is possible to estimate closely the size of a parasite responsible for any given wound on a prey fish. The accuracy of an individual estimate is influenced by reason of a slight sexual dimorphism in the size of the oral disk. Males generally possess somewhat larger disks than females of the same length.

Eleven species of fish were employed as hosts in laboratory studies of sea-lamprey feeding. The fish showed no fear of and took no actions to avoid the lampreys. The approach of a lamprey on a host is usually direct and rapid. Once the attachment is secured, the frantic struggles of the victim to dislodge its persecutor are seldom successful.

Among the factors that determine effects of a lamprey's attack on a host fish are the species. size, and condition of the victim; the site of the feeding attachment; the size of the wound; the duration of the attack; the severity of blood loss; and the incidence of secondary invaders in the injury.

The sites of 2,629 complete sea-lamprey wounds (wounds in which feeding took place) were plotted for 20 species of fish attacked in the laboratory or in Lake Huron to determine the pattern of scar distributions on the surfaces of the hosts. The surface most used on the aquarium hosts was the upper half of the middle third of a fish's body. In contrast, wounds incurred in the lake were most common on the lower half of the middle third of the fish. Head and eye injuries were observed more frequently in the aquariums than in the lake samples; on the other hand, penetrations of the body cavity were relatively more frequent in natural hosts. The differences in wound distribution on laboratory and lake fish were attributed to the greater mortality from dorsal and head attacks over those on ventral surfaces of the prey. The data on wounds on fish from Lake Huron represented mostly the undetermined but possibly small percentage of fish that had survived their injuries long enough to be caught in our nets. In the laboratory, all lamprey attachments were available for examination. It is accordingly probable that the experimental data have less bias and present the truer picture of the distribution of wound in natural populations.

Three dimensions were measured on 2,629 "complete" wounds, (1) diameter of oral-disk mark, (2) diameter of the hole, and (3) the depth of the hole. Lampreys 5 to 23 inches long produced wounds that ranged from 12 to 50 millimeters in maximum diameter. Even the smallest of injuries frequently led to grievous injury or death. The smallest wounds, found in April, were caused by the attacks of recently transformed feeders. By the following October, the mean size of the wounds doubled. The maximum proportions, reached by the following February, represented a total increase of 262 percent over the size of the April wounds.

Lamprey attachments on fishes do not always result in feeding penetrations. Of 2,879 attacks studied, 9.2 percent involved occasional loss of scales but no skin ruptures or damages to underlying tissues. Nevertheless, hosts which bore such incomplete wounds were susceptible to invasions of fungi at the attachment sites.

In a sample of 1,189 complete wounds on 18 species of fish from Lake Huron, only 22.2 percent were classified as healing or healed. This low incidence of healed or healing wounds indicates strongly that a host subjected to an attack is usually doomed.

Fish under attack died in as little as 4 hours, whereas other attachments continued up to 9 days, or longer, before the fish died. The actual time a parasite remained on a fish depended usually on the length of time the fish lived. The durability of the fish in turn was affected greatly by its size and species, the size of the predator and the vigor with which it pressed the attack, and the site of the feeding penetration.

Accounts are given of the gross pathology of attacks on the following regions of the fish's body: the integument, skeletal muscles, cartilage and connective tissues, vascular system, blood, lateral-line system, nerve tissue, bones, eyes, nasal passages, gills, intestine, anus, pyloric caeca, liver, spleen, pancreas, and gonads.

The severe hemorrhage that attends the sanguivorous attacks of lampreys on fishes is the direct cause of death of most of the victims. At best, teleosts possess only a small quantity of blood which places them at a disadvantage when they are beset by parasitic lampreys. Hemato-

logical studies on dying brown trout, rainbow trout, brook trout, and white suckers showed that the volume, red-cell count, and hemoglobin content of their blood are drastically reduced in mortal attacks. The mean blood values for 119 normal white suckers were 1,159,256 erythrocytes and 3,869 leucocytes per milliliter, and 8.24 grams of hemoglobin per 100 milliliters of whole blood. In contrast, the average determinations made on postattack blood samples from 119 mortally wounded suckers were 189,705 red cells and 8,514 white cells per milliliter, and less than 3.75 grams of hemoglobin per 100 milliliters of blood. The erythrocyte and hemoglobin levels indicated net reductions of 83.6 percent and at least 54.0 percent, respectively, whereas leucocytes were increased 2.2 times in the injured fish. The differences between preattack and postattack values are not necessarily indicators of extent of blood consumption, for the net changes recorded do not take into consideration the hemopoietic potentials of the hosts. The prey suckers had a mean length of 13.0 inches; their deaths occurred in an average of 59.1 hours; and their attackers averaged 12.1 inches long.

The lethal factors in extensive hemorrhage could not be specifically defined in the host fishes. The large losses of erythrocytes, hemoglobin, and blood volume itself, as observed in dying specimens, were undoubtedly attended by serious physiological derangements, some of which in turn produced such conditions as shock, anoxia, loss of equilibrium, lack of responses to external stimuli, and lack of osmotic balance between exposed tissues and the surrounding water. The trout species and white suckers were considered to be in mortal danger when their erythrocyte counts fell below 300,000 cells per milliliter of blood.

Many fishes that fall prey to sea lampreys already harbor one or more invertebrate endoparasites or ectoparasites. Although 10 such organisms were found on hosts, no example was observed of penetration by any invertebrate into a wound as a secondary invader. However, the fungi *Leptomitus lacteus* and *Saprolegnia parasitica* did produce secondary infections in wounds. A sample of 715 complete and incomplete, unhealed, lamprey injuries on white suckers from Lake Huron showed 6.2 percent infected with *Leptomitus* and 0.4 percent with *Saprolegnia*. It is possible that the large growths of *Leptomitus* were contaminated to some extent by *Saprolegnia*. In the laboratory aquariums, fishes that survived their lamprey attachments often succumbed from subsequent infection by fungi.

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EGGS AND LARVAE OF THE PACIFIC HAKE *MERLUCCIUS PRODUCTUS*

By ELBERT H. AHLSTROM AND ROBERT C. COUNTS

FISHERY BULLETIN 99

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The larvae obtained in greatest abundance on the biological-oceanographical survey cruises of the California Cooperative Oceanic Fisheries Investigations are those of the Pacific hake, *Merluccius productus*. The hake egg is pelagic, spherical, transparent, with a tough, unsculptured shell membrane; it measures 1.07 to 1.18 mm. in diameter; the single oil globule is 0.27 to 0.34 mm. in diameter; the yolk is unsegmented. The hake hatches at about 2.4 mm.

During the early larval period (3 to 10 mm.), the most conspicuous pigment areas are (1) a large spot on the back of the head, and (2) an area of heavy pigmentation about midway between the anus and the end of the notochord. There is a marked increase in pigmentation in the later larval period, at first on the head and along the dorsum, but spreading to the midline and below.

During the larval period, the head grows at a constant rate in relation to the standard length (0.3 mm. for each 1 mm. increase in length); the distance from snout to anus increases 0.42 mm. for each 1 mm. increase in standard length. The initial ossification of most vertebrae occurs in larvae between 7.5 and 10 mm. long. The full complement of gill rakers is obtained by about 25 mm. in length.

The sequence of fin formation in the hake is as follows: larval pectorals (without rays), caudal, ventrals, first dorsal, second dorsal and anal (simultaneously), pectorals (with rays). The development of the caudal fin and supporting structures is discussed in some detail; a somewhat different interpretation of development of the tail in Gadoids is given than the explanation of Barrington (1937). Development of the second dorsal and the anal fin begins from two centers, showing the close relation of hake development to that of typical cods.

Hake larvae were taken as far seaward as 350 miles (off southern California), as far north as San Francisco, and as far south as Cape San Lucas. They were taken in greatest abundance off southern California and adjacent Baja California. Hake larvae were obtained mostly during a 3-month period February through April. The estimates of abundance for 1951 and for 1952 are almost identical.

Data available on vertical distribution of hake larvae indicate that the center of depth distribution is between 50 and 100 meters, within or just below the thermocline. The large concentrations of hake larvae occurred in a 4.5-degree temperature range (10.6° to 15.0° C.).

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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Drawings by GEORGE MATTSON

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EGGS AND LARVAE OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

By ELBERT H. AHLSTROM and ROBERT C. COUNTS, *Fishery Research Biologists*

The larva most abundant in the extensive monthly plankton collections of the California Cooperative Oceanic Fisheries Investigations is that of the hake, *Merluccius productus* (Ayres) 1855. The collections are made primarily to study the distribution and abundance of sardine eggs and the rate of survival of sardine larvae; information on other species of present or potential commercial importance is a byproduct. This paper is the second in a series describing the eggs and larvae of the more important species.[1]

The California Cooperative Oceanic Fisheries Investigations are sponsored by the California Marine Research Committee, and are being carried on by the Scripps Institution of Oceanography of the University of California, the California Department of Fish and Game, the California Academy of Sciences, the Hopkins Marine Station of Stanford University, and the South Pacific Fishery Investigations of the United States Fish and Wildlife Service.

Hake larvae are taken over almost all of the area being surveyed, from northern California to Cape San Lucas in Baja California, and offshore for more than 350 miles. Although neither the north-south nor the offshore extent of spawning of this species has been delimited, it is unlikely that spawning outside the survey area is of much importance. Since hake have a rather short spawning season, most larvae are taken during the 3-month period February through April.

In his revision of the species of *Merluccius*, Norman (1937) recognized seven species: *M. merluccius* (Linnaeus) from the coasts of Europe, northwest Africa, and the Mediterranean; *M. bilinearis* (Mitchill) from the Atlantic coast of the United States; *M. hubbsi* (Marini) from the east coast of South America; *M. gayi* (Guichenot) from the coasts of Chile and Peru; *M. capensis* Castelnau from off South Africa; *M. australis* (Hutton) from off New Zealand; and *M. productus* (Ayres) from the Pacific coast of North America. *M. angustimanus* Garman, described from off Panama, was placed by Norman as a possible synonym of *M. gayi;* it may be a valid species, however. Unfortunately, we did not have access to the revision of American hakes (whitings) by Isaac Ginsburg (Fishery Bulletin 96) until too late to incorporate his findings in this paper. See page 329.

Merluccius productus can be distinguished from other species of the genus by the following combination of morphological characters:

1. A more slender body form than that of any other species, with the possible exception of *M. hubbsi;* depth is 7 to 7⅔ in standard length as compared with 5 to 6¼ for all other species except *M. hubbsi* (5¾ to 8(?)).

2. A high gill-raker count (4 or 5 + 14 to 17); only *M. gayi* has a comparably high count.

3. Several more rays in the second dorsal and anal fins than any species except *M. australis* (D. 39 to 42; A. 40 to 43).

A literal translation of the name *Merluccius productus* would be "drawn-out sea pike" or "slender sea pike."

Of the above species, *Merluccius merluccius*, *M. gayi*, *M. bilinearis*, and *M. capensis* are of considerable commercial importance. These species are sold in the fresh-fish trade, or are used for meal and oil. Various references mention the fact that the flesh of these species is well-flavored when fresh, but spoils rapidly. Apparently this is characteristic of the genus. Pacific-coast fishermen have found the flesh of *M. productus* to be similar; however, no regular commercial fishery has been established for this species. At one time it was used for animal food by mink farmers, but was deficient in some nutrients. Recently, the hake has been utilized to some extent as a fish-hatchery food. It seldom appears in the Pacific-coast fresh-fish markets.

Reports on the great availability of hake by commercial fishermen, and the large annual spawn, as determined by the California Cooperative

[1] Descriptions of the methods and materials used for collecting and standardizing the net tows, clearing and staining specimens, and measuring body proportions of larvae are given in Fishery Bulletin 97 (Ahlstrom and Ball, 1954).

Oceanic Fisheries Investigations, give evidence that there is a large untapped fishery resource in the hake. The demand for protein foodstuffs may, in the near future, force the exploitation of this hitherto unused and potentially large resource. This would entail some research into the capture, proper handling, preparation, and marketing of the species. Perhaps much of this information could be gathered from a study of the processing and marketing procedures developed for the several species of hake that now support commercial fisheries.[2]

Employees of the Scripps Institution of Oceanography and the California Department of Fish and Game cooperated in the collection of data at sea. The whole staff of the South Pacific Fishery Investigations of the Fish and Wildlife Service contributed to this study. The authors thank especially John C. Marr, Rolf Bolin, and James Böhlke for critically reading the manuscript, James R. Thrailkill for preparing the graphs and distribution charts.

EGGS AND LARVAE OF OTHER SPECIES OF *MERLUCCIUS*

The egg and larval stages have been described for several species of *Merluccius*. A number of descriptions have been published of the eggs and larvae of *M. merluccius*, among which the following four accounts are particularly noteworthy:

1. Raffaele (1888) published descriptions of the egg and yolk-sac larvae, obtained by artificially fertilizing eggs stripped from hake caught in the Bay of Naples.

2. J. Schmidt (1907) described and figured the development of hake larvae from 4.25 mm. to 31 mm. in length (13 specimens) from material obtained off Ireland, Bay of Biscay, Scotland, and the Skaggerak.

3. Ehrenbaum (1905–9) supplemented Schmidt's descriptions with material from the Jutland Auszen-ground.

4. D'Ancona (1933), in Fauna e Flora del Golfo di Napoli, gives a résumé of previous work and a group of 8 figures of larvae 4 to 32 mm. in length, obtained from the Mediterranean.

The eggs and larvae of *Merluccius bilinearis*, the hake occurring off the east coast of the United States, were described by Kuntz and Radcliffe (1917), but some of the descriptions and figures in their paper are inaccurate. For example, a late-stage egg (fig. 53) is shown with more than 70 myomeres, and a yolk-sac larva (fig. 54) has only 45 myomeres. Furthermore, figures 64 and 65, included in the series of *Poronotus triacanthus*, are based on specimens of *Merluccius bilinearis* (Pearson, 1941, called attention to this discrepancy, but suggested that these figures might be young of *Urophycis*.). These latter figures were copied without change by Bigelow and Welsh (1925) in Fishes of the Gulf of Maine, but are omitted from the revision of this work by Bigelow and Schroeder (1953).

The early development of *Merluccius capensis* (egg and yolk-sac larval stages) was described by Matthews and Jager (1951). A figure of a later larval stage is given in a short paper by Hart and Marshall (1951).

Neither the eggs nor the larvae of *Merluccius productus* have been described previously.

EGGS OF *MERLUCCIUS PRODUCTUS*

Embryonic development of hake eggs has been studied in both living and preserved material. The following descriptions are based on preserved material, since such samples are examined much more frequently than living specimens. Two important differences between living and preserved material should be noted: (1) Living hake eggs have a glassy transparency and the yolk material is almost colorless, while preserved eggs appear opaque and the yolk material is more highly colored; and (2) living embryos contain evanescent pigments, especially yellow pigments, that are destroyed in preservation (Melanophores are not so affected, however).

General description.—The hake egg is pelagic. It is spherical, has a tough, transparent, unsculptured shell membrane, and contains a single, rather large oil globule. The yolk material is clear, homogenous, and of a dark straw color; however, it may appear granular after being enclosed by the germ ring. The egg often appears cloudy or opaque in the stages preceding blastopore closure. This probably is due to mechanical rupture of the delicate vitelline membrane surrounding the yolk, which allows the yolk material to escape into the perivitelline space. The following size measurements are based on 200 eggs taken at ran-

[2] A San Francisco plant operator recently has been granted a permit for experimental reduction of hake to meal and oil.

dom from preserved samples: The average diameter of the hake egg is 1.12 mm. (range, 1.07 to 1.18 mm.); the average diameter of the oil globule is 0.30 mm. (range 0.27 to 0.34 mm.); the diameter of the yolk is approximately 1.00 mm.; and the width of the perivitelline space is approximately 0.06 mm. A comparison of the size of the egg and of the contained oil globule in *Merluccius productus*, *M. bilinearis* (data from Kuntz and Radcliffe, 1917), *M. merluccius* (data from Raffaele, 1888) and *M. capensis* (data from Matthews and Jager, 1951) follows:

Species	Diameter (in millimeters) of—	
	Egg	Oil globule
M. productus	1.07–1.18	0.27–0.34
M. bilinearis	0.88–.95	.19–.25
M. merluccius	.94–1.03	.27
M. capensis	1.03	.16

The time required for embryonic development of hake eggs has not been determined. It may be similar to that of the sardine. This conclusion is based on finding two or three stages of egg development in many samples. From studies on the sardine (*cf.* Ahlstrom 1943), such stages have been shown to represent as many days' spawning. Kuntz and Radcliffe (1917) attributed an incubation period of only 48 hours to the silver hake (*M. bilinearis*), Raffaele (1888) reported an incubation period of 60 to 70 hours for *M. merluccius*, while Matthews and Jager (1951) gave 60 hours as the time required for the embryonic development of *M. capensis*. None of these investigators supplied temperature data.

In discussing the development of the hake eggs, we shall divide the embryonic period into three stages:

Early—from fertilization to closure of the blastopore (fig. 1, *a* and *b*).

Middle—from closure of the blastopore to the time that the separating tail begins to curve laterally away from the embryonic axis (fig. 1, *c* and *d*).

Late—from the time that the tail is curved away from the embryonic axis to the time of hatching (fig. 1, *e* and *f*).

Early-stage eggs.—In early-stage hake eggs (fig. 1, *a* and *b*), the yolk is clear and unsegmented, and the oil globule is situated at the vegetative pole. The developing egg floats with the oil globule uppermost, as do most pelagic eggs. At the time of blastopore closure, the oil globule is situated immediately adjacent to the blastopore, close to the tail of the embryo. It keeps this position throughout the remainder of the embryonic period and during the yolk-sac larval stage. In this early stage, the embryo develops at a fairly rapid rate. When the embryonic shield has enveloped approximately three-fourths of the yolk, the embryo has a discernible eye. Just before blastopore closure, 10 to 13 myomeres are visible behind the head of the developing embryo. No pigment is found in this early stage.

Middle-stage eggs.—The best character for identifying middle-stage hake eggs (fig. 1, *c* and *d*) is the pigmentation that develops immediately after blastopore closure. Pigment appears in three areas, (1) on the oil globule, (2) on the head and dorsum of the embryo, and (3) on the yolk mass. The pigment on the oil globule is restricted to the hemisphere nearest the embryo. Pigment on the embryo is found first on the dorsum behind the head, where it outlines the myomeres adjacent to the head. It soon spreads over the head and most of the dorsum, although it is not equally dense in all parts, and the distal portion remains immaculate. The anterior portion of the yolk mass has a few scattered pigment spots, usually on either side of the head. At the termination of this stage, the tail has become partially separated from the yolk, and has started curving laterally away from the embryonic axis. The embryo has received its full complement of 50+ myomeres.

Late-stage eggs.—During this stage (fig. 1, *e* and *f*) the melanophores become restricted into several conspicuous patches of pigment, leaving portions of the embryo, previously with melanophores, immaculate. When viewed from above, the pigment on the embryo occurs in four areas: (1) on the head and four or five adjacent myomeres, (2) on the body just anterior to the anus, (3) on the body just behind the anus, and (4) about midway between the anus and the end of the notochord. We call the latter area the medio-postanal pigment area. The only conspicuous ventral pigment on the embryo is a counterpart to the dorsal patch in the medio-postanal region. Before hatching, some melanophores can be discerned in the peritoneum. The buds of the pectoral fins may be seen in late-stage eggs. The best single feature for identifying late-stage hake eggs is undoubtedly the characteristic pigmentation.

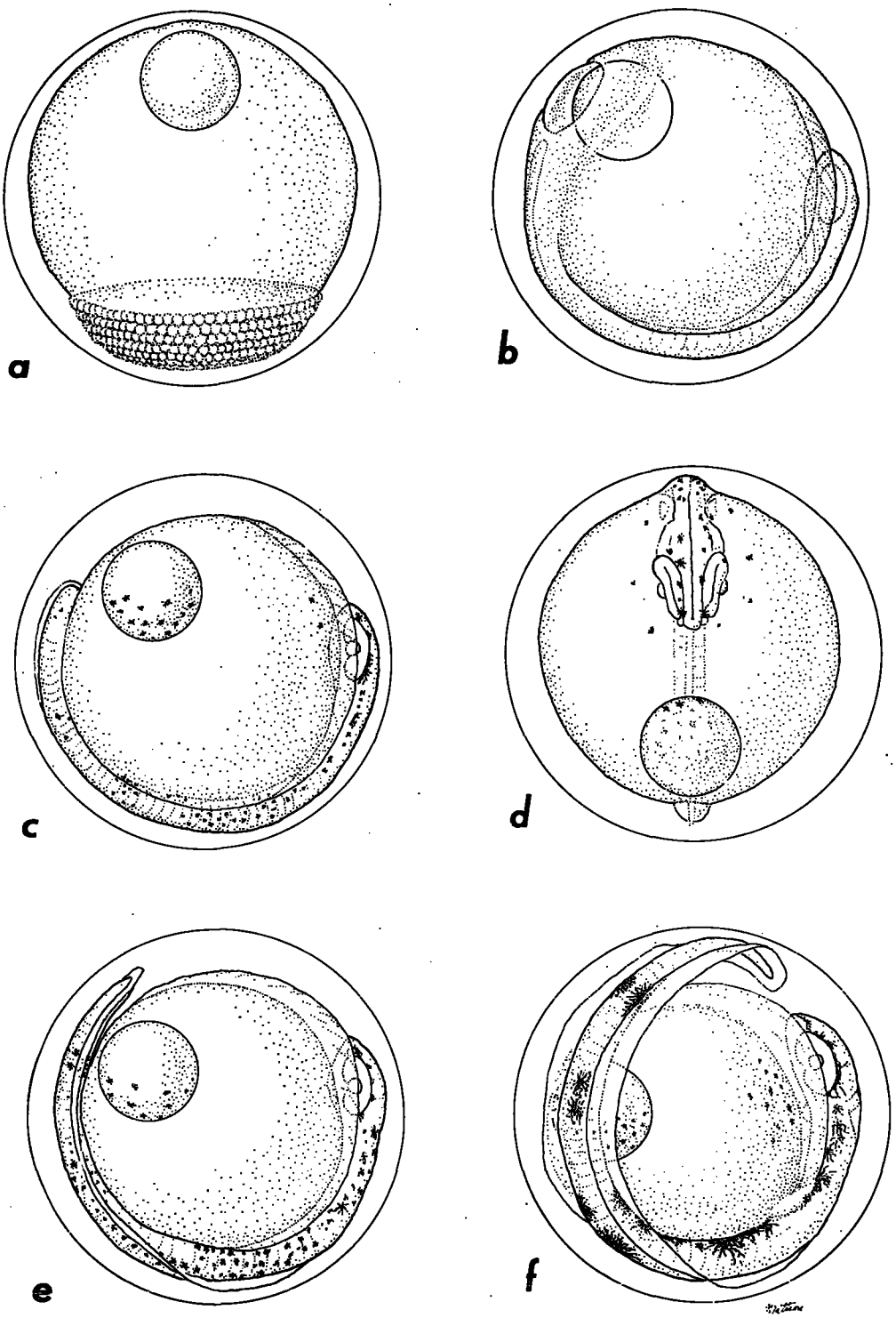

FIGURE 1.—Development of the egg of the hake, *Merluccius productus*: *a*. Early stage, at time of development of blastodermal cap; *b*. early stage, immediately preceding blastopore closure; *c*. middle stage, lateral view; *d*. middle stage, polar view; *e*. late stage, tail just beginning to twist out of plane of embryonic axis; *f*. late stage, just before hatching.

Other features that aid in identifying hake eggs at this stage of development are—

1. Number of myomeres—more than 50 can be counted.
2. Length of intestine—extends for about four-tenths of the total length.
3. Position of oil globule—situated near the anus.

In the waters inhabited by the Pacific hake, there are two other common species with rather similar eggs: the jack mackerel (*Trachurus symmetricus*), and the Pacific mackerel (*Pneumatophorus diego*). To avoid confusion in identification, table 1 has been prepared.

TABLE 1.—*Characters which aid in distinguishing the eggs and newly hatched larvae of hake, jack mackerel, and Pacific mackerel*

	Hake	Jack mackerel	Pacific mackerel [1]
EGG			
Size	1.07 to 1.18 mm.	0.96 to 1.02 mm.	1.05 to 1.08 mm.
Oil globule	Single—0.30 mm.	Single—0.25 mm.	Single—0.26 mm.
Yolk	Clear.	Segmented.	Clear.
Perivitelline space	Moderate (0.06 mm. wide).	Moderate (0.09 mm. wide).	Narrower than either hake or jack mackerel.
Pigmentation:			
Yolk	On yolk near head.	None.	Scattered on yolk.
Embryo	Dorsal pigmentation continuous in middle-stage eggs, separated into patches in late-stage eggs.	Dorsal pigment extends most of length of embryo; ventral pigment occurs behind anus; pigment seldom occurs forward of the eyes.	Double dorsal row of pigment spots extends forward between the eyes; no ventral pigment.
Number of myomeres	51–54.	24.	31.
YOLK-SAC LARVAE			
Pigmentation	Collects in patches.	Dorsal and ventral retained.	Dorsal pigment migrates ventrally.
Oil globule	In rear of yolk sac.	Under head in forward portion of yolk sac.	In rear of yolk sac.

[1] Data taken, in part, from Fry 1936.

LARVAE OF *MERLUCCIUS PRODUCTUS*

State of development at hatching.—The hake hatches in a relatively undeveloped condition. It begins its postembryonic existence before the mouth forms and before the eyes become pigmented. The young of most other fish with pelagic eggs, including the sardine, anchovy, Pacific mackerel, jack mackerel, and tunas, are in a similarly undeveloped state at hatching.

A group of approximately 200 hake larvae, representative of the size range obtained in the plankton hauls, was selected for detailed study. The larvae were chosen at random from samples that adequately covered their geographical and seasonal distribution. The specimens were cleared and stained by a procedure modified from that described in Hollister (1934).[3] Meristic counts can be determined accurately from specimens prepared in this manner, and the sequence of ossification of vertebrae and other bony parts can be followed. However, stained specimens are not satisfactory for observing the sequence of pigment changes, and for this purpose other larvae, taken at random, were used.

The period of larval development is considered to extend from hatching to the completion of fin formation, but the end of the larval stage is not sharply defined in the hake. The size at hatching, determined from preserved material, is approximately 2.4 mm. All fins except the pectorals have their full complement of rays by the time the fish is 20 mm. long. The pectorals seldom have more than 2 or 3 rays differentiated at this size, with 7 formed by 25 mm., and probably the full complement when the larvae are about 30 to 35 mm. in length.

We shall trace the changes that occur during larval development in the following characters: (1) Changes in pigmentation, (2) changes in body form, (3) sequence of ossification, and (4) sequence of fin formation.

CHANGES IN PIGMENTATION

There is considerable variation in the amount of pigment found on hake larvae of comparable size, especially noticeable in larvae under 10 mm. in length. In discussing pigment augmentation, we shall describe the usual pattern, not the aberrant. Larvae with the most intense, as well as those with the sparsest, pigmentation were collected more often in the southern part of the survey area than elsewhere.

The newly hatched larva (fig. 2*a*) has a pigment pattern similar to that of a late-stage egg. Before yolk-sac absorption is completed, however, the pigment has migrated or coalesced to

[3] Improvements on Hollister's technique were suggested by Evans (1948) and Clothier (1950).

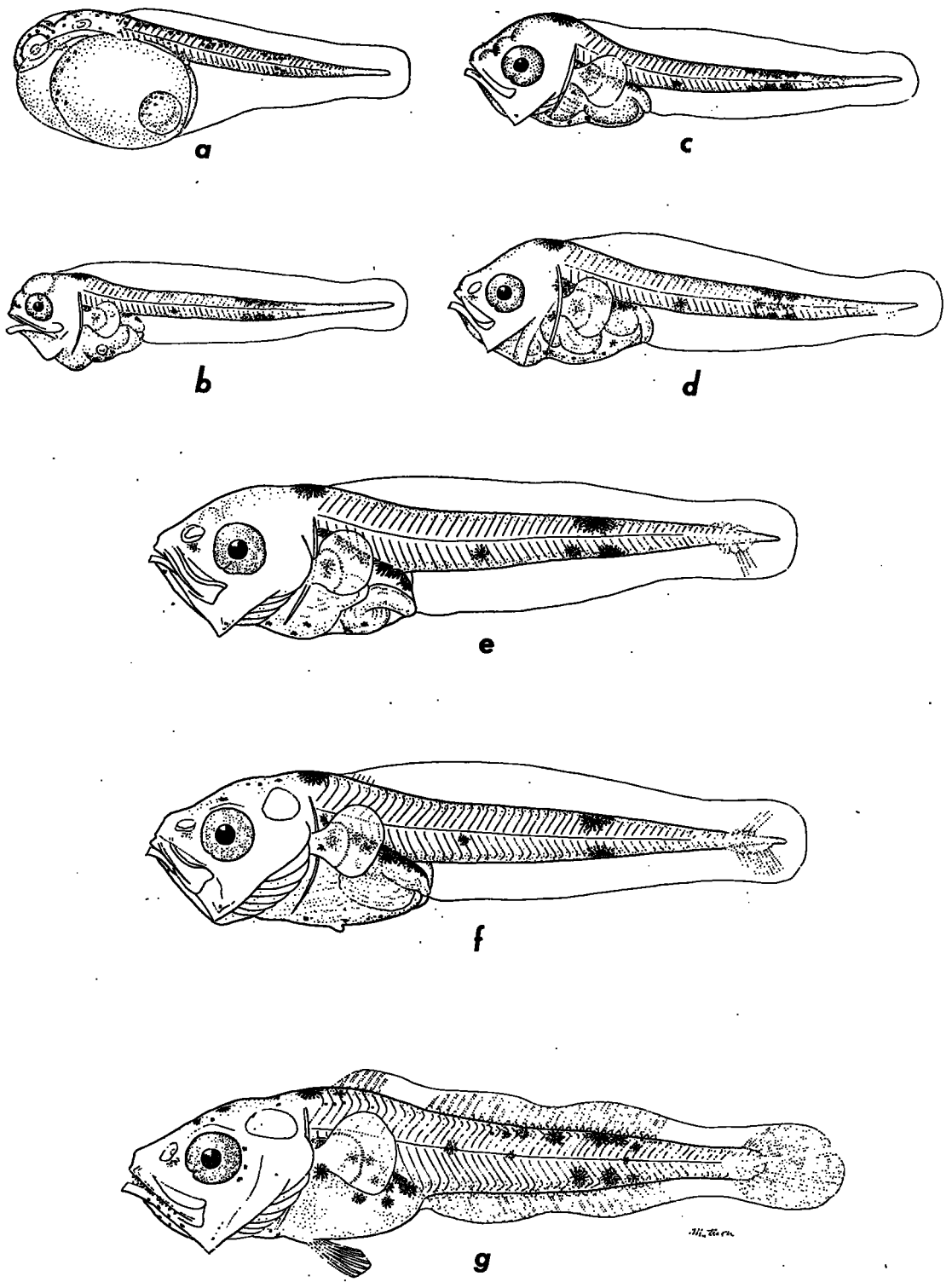

FIGURE 2.—Development of the larva of the hake, *Merluccius productus: a.* Yolk-sac larva, 2.4 mm. long, immediately after hatching; *b.* larva 3.0 mm. long; *c.* larva 4.3 mm. long; *d.* larva 4.7 mm. long; *e.* larva 6.3 mm. long; *f.* larva 7.7 mm. long; *g.* larva 10.1 mm. long.

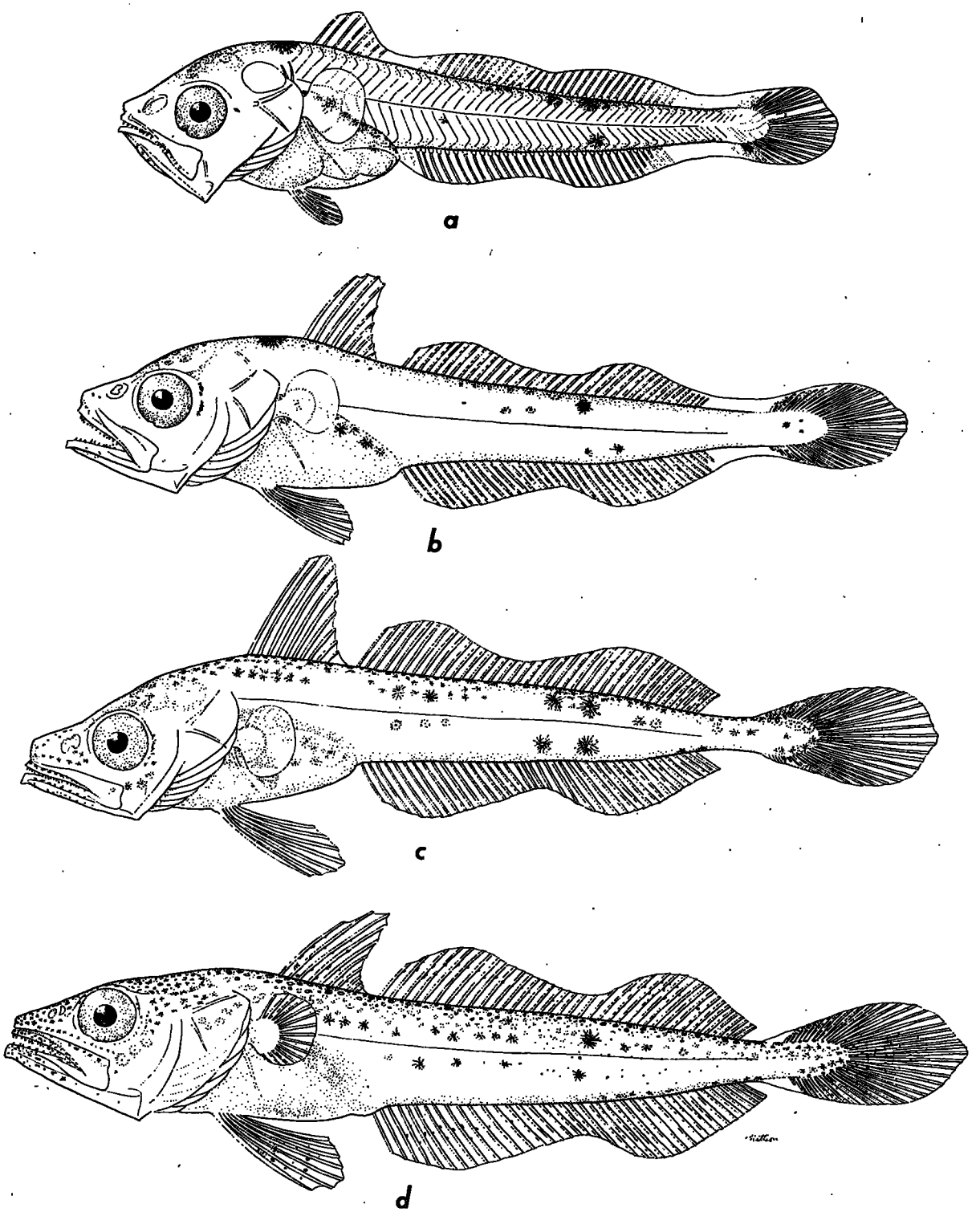

FIGURE 3.—Development of the larva of the hake, *Merluccius productus: a.* Larva 11.0 mm. long; *b.* larva 15.75 mm. long; *c.* larva 20.0 mm. long; *d.* early juvenile. 36.0 mm. long.

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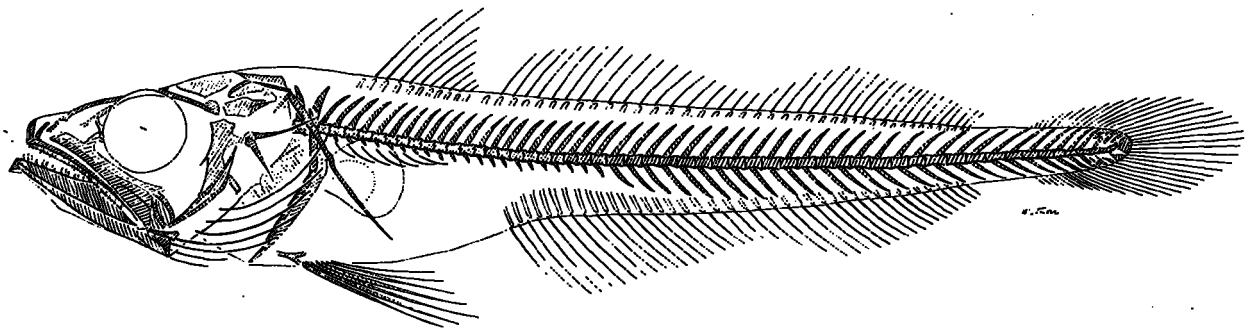

FIGURE 4.—Larva of hake, *Merluccius productus*, 25.0 mm. long, showing details of skeletal structure.

form the three conspicuous pigment areas characteristic of hake larvae: (1) a large spot on the back of the head, referred to hereafter as the occipital spot, (2) the conspicuous medio-postanal pigment area about midway between the anus and the end of the notochord (or base of caudal), and (3) a heavy concentration of pigment along the dorsal peritoneal wall. In addition, there is a frontal patch between the eyes, scattered spots on the ventral surface of the belly and a lateral spot immediately behind the anus. This pigmentation is characteristic of larvae between 3 and 10 mm. in length. The larva of *M. productus* does not have a caudal spot like that found on specimens of *M. bilinearis* and *M. merluccius*. Occasionally larvae are found with a row of lateral pigment spots between the anus and the medio-postanal pigment area.

Pigment is added gradually during the larval period. Until about 10 mm. in length, most of the increase in pigmentation is in the head region. Between 10 and 20 mm. there is a rapid augmentation of the pigment on both the body and head. Pigmentation of the fins occurs during the late larval period.

Head pigmentation.—In young larvae the only conspicuous pigmentation on the head is the large occipital spot. This is usually a single, stellate melanophore. But a few scattered small melanophores are found on the top of the head of some larvae at the end of the yolk-sac stage. By 10 mm. in length, a cap of discrete pigment spots is usually present on the crown. On larvae of approximately 13.5 mm. in length, pigment appears along the premaxillary and mandible, and a conspicuous vertical bar forms behind the eye. On larvae 20 mm. in length, pigment spots are generally distributed along the top and sides of the head except in the opercular area behind the eye. Meanwhile, the occipital spot has become less conspicuous, although it still may be distinguished.

Body pigmentation.—There is little change in body pigmentation between 3 and 10 mm. in length, but on larvae more than 10 mm. long the pigment increases rather rapidly along the dorsum, and later along the sides of the body as well. When the dorsal pigment starts augmenting, it appears to spread in both directions from the medio-postanal pigment area, but only posteriorly from the region of the occipital spot. The last areas along the dorsum to become pigmented are at the origin and termination of the second dorsal fin. A continuous band of dorsal pigment from the tip of the snout to the base of the tail is found on larvae as small as 16.5 mm. in length. Larvae larger than this show a marked increase in number of melanophores and ventral spreading of pigment to the lateral line. Meanwhile, peritoneal pigment spreads laterally.

As the larvae become more heavily pigmented, the several important pigment areas of the younger stages tend to become less conspicuous. The medio-postanal group concentrates into several lateral melanophores, usually one or two above and as many below the lateral line on either side of the body. This pigment group still may be conspicuous on some larvae 20 mm. long (fig. 3*c*), but on other larvae is distinguished with difficulty at a smaller size than this (fig. 3*b*). The group has lost its identity by the time the juvenile stage is reached (fig. 3*d*). The lateral pigment spot immediately behind the anus, seldom conspicious at any size, is indistinguishable from other scattered ventral pigment spots in older larvae (fig. 3*c*).

Ventral pigmentation is never as conspicuous in hake larvae as dorsal pigmentation. The mel-

anophores on the ventral surface of the abdomen remain few in number and gradually disappear. Only during the late larval period is there a noticeable increase in pigmentation below the lateral line, and even then it is sparse along the ventral margin of the body.

Fin pigmentation.—The fins never become heavily pigmented in larval hake. There are usually either scattered pigment spots or a single conspicious stellate spot on the fleshy base of the larval pectoral fins. In some larvae under 20 mm. in length, a few small pigment spots have been observed bordering the central rays of the caudal fin. By 36 mm. in length, the caudal fin is much more heavily pigmented, especially along the median rays. The first dorsal has pigment spots outlining its rays, especially anteriorly. The second dorsal has some inconspicuous lines of pigment along its rays, and there is even less pigment on the anal fin. The ventral fins usually lack pigment, but occasionally a heavily pigmented larva will have pigment on the ventral fin even at formation.

CHANGES IN BODY FORM

The hake larva is moderately elongate, with the greatest body depth at or near the pectoral fin, and with the body narrowing abruptly behind the anus. The digestive tract underlies only the forward part of the body, the distance from snout to anus being approximately 42 percent of the standard length. The intestine has a single loop, readily observable in small larvae before it is obscured by overlying musculature.

Measurements made on the group of larvae studied included the following: Standard length, head length, diameter of eye, greatest body depth, and distance from snout to anus. The data are summarized in columns 3 to 7 of table 2. The measurements and counts in this table are average values based on 10 or fewer specimens (number of specimens listed in column 2).

TABLE 2.—*Measurements and meristic counts of hake larvae*

Size	Number of specimens examined	Average measurements (in millimeters)					Meristic counts							
		Standard length	Head	Eye	Depth	Snout to anus	Vertebrae	Branchiostegal rays	Caudal fin	Ventral fins	First dorsal	Second dorsal	Anal fin	Pectoral fins [1]
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
3.0–3.4 mm	7	3.2	0.73	0.30	0.95	1.4								LP
3.5–3.9 mm	5	3.7	.86	.36	1.02	1.6								LP
4.0–4.4 mm	10	4.3	1.00	.40	1.07	1.8	1.0							LP
4.5–4.9 mm	10	4.6	1.09	.46	1.18	2.0	1.8	0.7						LP
5.0–5.4 mm	10	5.0	1.14	.49	1.38	2.2	2.1	2.2						LP
5.5–5.9 mm	10	5.7	1.36	.56	1.50	2.6	3.4	4.3	0.3					LP
6.0–6.4 mm	10	6.3	1.46	.60	1.51	2.6	3.9	4.4	.7					LP
6.5–6.9 mm	5	6.7	1.74	.68	1.66	3.0	4.8	5.4	2.4					LP
7.0–7.4 mm	10	7.1	1.89	.70	1.81	3.2	6.9	6.4	8.3	0.6				LP
7.5–7.9 mm	5	7.8	2.00	.74	1.80	3.4	8.0	6.0	6.8	2.2				LP
8.0–8.4 mm	10	8.2	2.19	.78	1.81	3.6	15.1	6.5	13.2	2.5	1.4			LP
8.5–8.9 mm	10	8.6	2.22	.85	2.09	3.8	29.6	6.6	15.7	3.6	2.7	3.6	6.0	LP
9.0–9.4 mm	10	9.1	2.53	.88	2.18	4.0	45.4	7.0	19.6	5.5	4.6	7.5	10.8	LP
9.5–9.9 mm	3	9.7	2.57	.90	2.23	4.0	49.3	7.0	18.3	5.3	6.0	21.7	27.7	LP
10.0–10.4 mm	10	10.1	2.75	.98	2.35	4.5	52.9	7.0	23.9	6.7	6.4	26.7	28.1	LP
10.5–10.9 mm	7	10.6	2.99	.97	2.49	4.9	53.0	7.0	25.1	6.9	6.7	30.1	30.7	LP
11.0–11.9 mm	6	11.3	3.03	1.07	2.47	5.0	53.5	7.0	28.5	7.0	7.3	32.5	34.0	LP
12.0–12.9 mm	5	12.5	3.36	1.14	2.62	5.4	53.8	7.0	30.0	7.0	7.8	33.2	36.0	LP
13.0–13.9 mm	6	13.4	3.82	1.27	2.85	5.9	52.8	7.0	34.0	7.0	8.5	37.0	37.3	LP
14.0–14.9 mm	4	14.5	3.95	1.30	2.92	6.3	53.0	7.0	33.5	7.0	9.0	37.2	38.0	LP
15.0–15.9 mm	5	15.5	4.40	1.36	3.12	6.6	53.0	7.0	36.8	7.0	10.0	38.8	40.0	LP
16.0–16.9 mm	2	16.7	4.80	1.45	3.10	7.0	53.5	7.0	39.0	7.0	11.0	40.0	41.5	0.5
17.0–17.9 mm	4	17.5	4.85	1.40	3.32	7.4	53.0	7.0	39.8	7.0	10.5	40.0	41.0	.5
18.0–18.9 mm	6	18.3	5.28	1.63	3.42	7.7	53.0	7.0	40.5	7.0	10.5	39.7	41.0	.2
19.0–19.9 mm	2	19.6	5.60	1.55	3.80	8.2	54.0	7.0	42.5	7.0	11.0	40.5	42.5	.0
20.0–20.9 mm	4	20.3	5.95	1.65	3.80	8.4	53.8	7.0	42.0	7.0	10.5	40.2	41.2	.8
21.0–21.9 mm	5	21.2	6.04	1.66	4.18	8.9	53.8	7.0	41.6	7.0	10.4	40.0	41.6	2.2
22.0–22.9 mm	1	22.0	6.40	1.80	4.10	9.3	54.0	7.0	42.0	7.0	11.0	41.0	42.0	.0
23.0–23.9 mm	2	23.6	6.70	1.95	4.30	10.0	53.0	7.0	43.0	7.0	10.5	40.0	40.5	.0
24.0–24.9 mm	1	24.8	7.00	1.90	4.20	10.1	53.0	7.0	43.0	7.0	11.0	40.0	41.0	7.0
25.0–25.9 mm	1	25.5	7.30	2.20	4.50	11.0	55.0	7.0	44.0	7.0	11.0	42.0	40.0	7.0
40.0–40.9 mm	1	40.5	10.40	3.00	6.50	16.1	53.0	7.0	45.0	7.0	11.0	42.0	43.0	14.0
46.0–46.9 mm	1	46.2	13.00	3.20	8.00	16.8	53.0	7.0	44.0	7.0	11.0	42.0	43.0	15.0

[1] LP = larval pectoral.

Head.—The head grows at a constant rate in relation to the standard length during the larval period, increasing 0.30 mm. in length for each millimeter increase in standard length. This is shown in a regression of head length on standard length for larvae between 3 and 25 mm. in length

(fig. 5). The statistics describing the line fitted to the scatter of points by the method of least squares are given in table 3. It will be noted that actual measurements of head length are plotted against standard length in this graph. A quite different type of plot is obtained if head length, expressed as a percentage of the standard length, is plotted against the standard length (fig. 6). The latter is the usual method of dealing with body proportions in taxonomic studies. The head length is approximately 23 percent of the standard length in newly hatched larvae, increasing to 27 percent at 10 mm., and to approximately 28.5 percent at 20 mm. (table 4). This is not evidence of an accelerating rate of growth of the head as compared to standard length, although it might be misinterpreted as such. Rather it arises from the fact that the head length at hatching constitutes a smaller part of the standard length (23 percent) than the relation that obtains thereafter, i. e., a uniform rate of increase of head length to standard length of 30 percent.

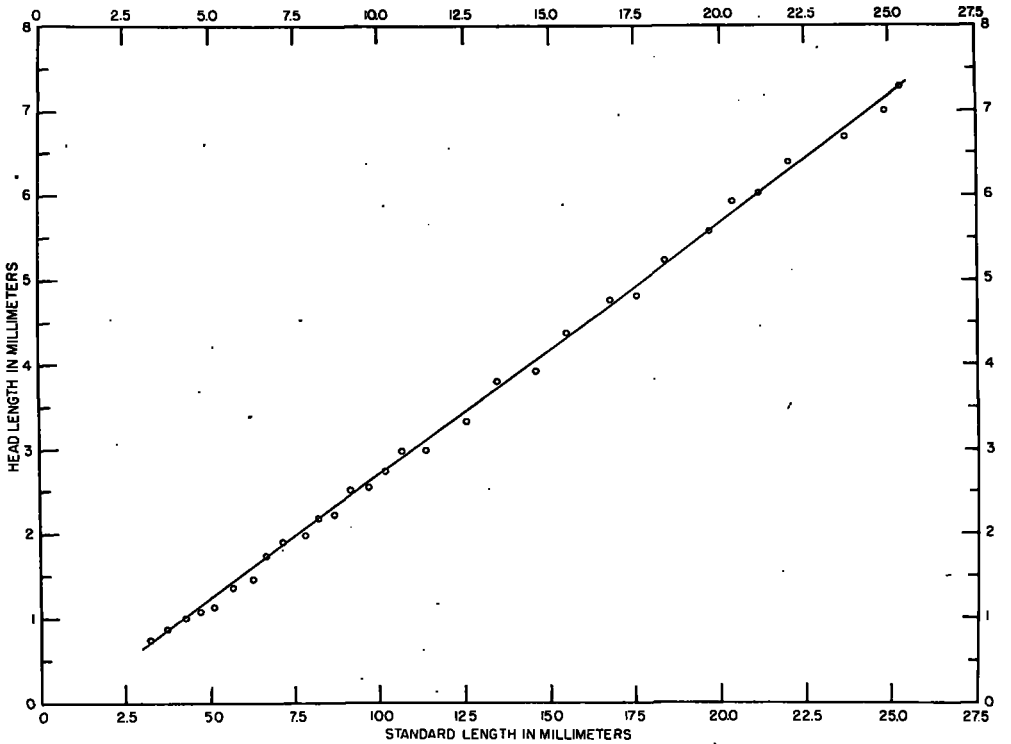

FIGURE 5.—Regression of head length on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 4). Regression line fitted to the data by the method of least squares. Statistics describing the line given in table 3.

TABLE 3.—*Statistics describing regressions of body proportions on standard length for hake larvae*

Independent variable x	Dependent variable y	Size of larvae	$\bar{x}$	$\bar{y}$	N	b	a	$sy{\cdot}x$
		Mm.						
Standard length	Head length	3.2–25.5	12.50	3.45	31	0.299	−0.289	0.079
Do	Body depth	3.2–10.6	6.92	1.69	16	.207	.257	.063
Do	do	10.6–25.5	17.96	3.45	16	.142	.901	.119
Do	Eye diameter	3.2–12.5	7.47	0.71	18	.092	.030	.022
Do	do	12.5–25.5	18.98	1.50	14	.069	.255	.077
Do	Distance, snout to anus	3.2–25.5	12.50	5.37	31	.419	.129	.193

$\bar{x}$=mean of values of x.
$\bar{y}$=mean of values of y.
N=number of size groups.
b=rate of increase of y.
a=y intercept of regression line.
$sy{\cdot}x$=standard deviation from regression (standard error of estimate).

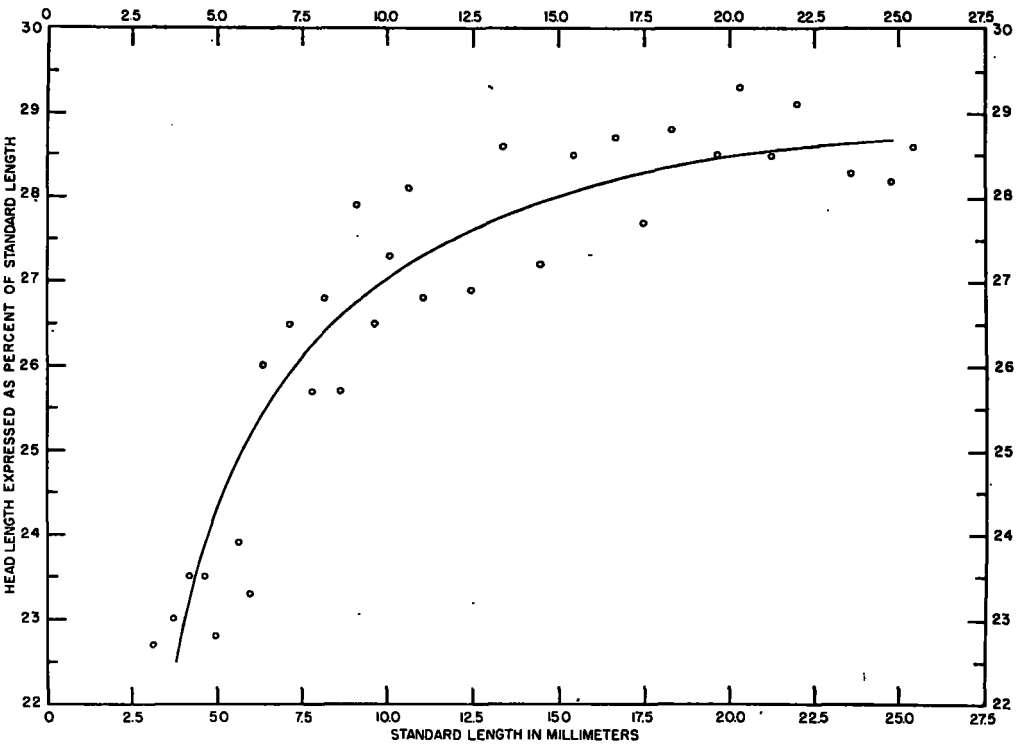

FIGURE 6.—Regression of head length, expressed as a percentage of standard length, on standard length. The curve is fitted from the statistics given in table 3.

TABLE 4.—*Body proportions of hake larvae*

Size	Standard length	Body proportions expressed as percentage of standard length			
		Head length	Eye diameter	Depth at pectorals	Distance from snout to anus
3.0–3.4 mm	3.2	22.7	9.3	29.6	42.7
3.5–3.9 mm	3.7	23.0	9.6	27.3	42.8
4.0–4.4 mm	4.3	23.5	9.4	25.1	42.7
4.5–4.9 mm	4.6	23.5	9.9	25.4	43.3
5.0–5.4 mm	5.0	22.8	9.7	27.4	43.3
5.5–5.9 mm	5.7	23.9	9.8	26.4	45.0
6.0–6.4 mm	6.3	23.3	9.6	24.1	42.3
6.5–6.9 mm	6.7	26.0	10.2	24.8	44.6
7.0–7.4 mm	7.1	26.5	9.8	25.4	45.2
7.5–7.9 mm	7.8	25.7	9.5	23.1	43.4
8.0–8.4 mm	8.2	26.8	9.5	22.1	43.4
8.5–8.9 mm	8.6	25.7	9.8	24.2	44.0
9.0–9.4 mm	9.1	27.9	9.7	24.0	43.8
9.5–9.9 mm	9.7	26.5	9.3	23.0	40.9
10.0–10.4 mm	10.1	27.3	9.7	23.3	44.9
10.5–10.9 mm	10.6	28.1	9.1	23.4	46.4
11.0–11.9 mm	11.3	26.8	9.5	21.9	44.5
12.0–12.9 mm	12.5	26.9	9.1	21.0	43.2
13.0–13.9 mm	13.4	28.6	9.5	21.3	44.0
14.0–14.9 mm	14.5	27.2	9.0	20.1	43.2
15.0–15.9 mm	15.5	28.5	8.9	20.2	42.7
16.0–16.9 mm	16.7	28.7	8.7	18.6	41.9
17.0–17.9 mm	17.5	27.7	8.0	19.0	42.4
18.0–18.9 mm	18.3	28.8	8.9	18.7	42.0
19.0–19.9 mm	19.6	28.5	7.9	19.3	41.5
20.0–20.9 mm	20.3	29.3	8.1	18.7	41.4
21.0–21.9 mm	21.2	28.5	7.8	19.7	41.9
22.0–22.9 mm	22.0	29.1	8.2	18.6	42.3
23.0–23.9 mm	23.6	28.3	8.2	18.2	42.5
24.0–24.9 mm	24.8	28.2	7.7	16.9	40.7
25.0–25.9 mm	25.5	28.6	8.6	17.6	43.1
40.0–40.9 mm	40.5	25.7	7.4	16.0	39.8
46.0–46.9 mm	46.2	28.1	6.9	17.3	36.4

Distance from snout to anus.—The anus is situated about four-tenths of the way back along the body, and it retains this relative position throughout the larval and juvenile stages. The distance from snout to anus increases 0.42 mm. for each 1 mm. increase in standard length (fig. 7 and table 3). Since the relation is constant, this is a useful taxonomic character. The distance from snout to anus in jack-mackerel larvae, for example, is nearly six-tenths of the standard length; hence jack-mackerel larvae could be separated from hake larvae on the basis of this character alone.[4]

Body depth (at pectoral).—The larva increases in depth more rapidly during the early part of its development than during the later part. The rate of increase in body depth for larvae between 3.2 and 10.6 mm. in length is 0.21 mm. for each 1 mm. increase in standard length, and for larvae between 10.6 and 25.5 mm. in length, the increase in body depth averages only 0.14 mm. for each millimeter increase in standard length

[4] Of course, there are other and more trenchant characters for separating these two species, such as the difference in number of vertebrae (24, as compared with more than 50), in pigmentation, in sequence of fin formation, and in numbers of fin rays.

(fig. 8 and table 3). As a result, the hake larva becomes progressively more slender with increase in size over 10.6 mm.

Eye.—The eye of the hake larva is round, with a ventral cleft developed in varying degree at the point of the choroid fissure. The eye does not grow at a uniform rate throughout the larval period. In larvae between 3.2 and 12.5 mm. in length, the diameter of the eye increases approximately 0.09 mm. for each millimeter increase in standard length, while in larvae between 12.5 and 25.5 mm. in length, the increase is only about 0.07 mm. for each millimeter increase in standard length. The distance from the snout to the anterior margin of the eye is about equal to the diameter of the eye.

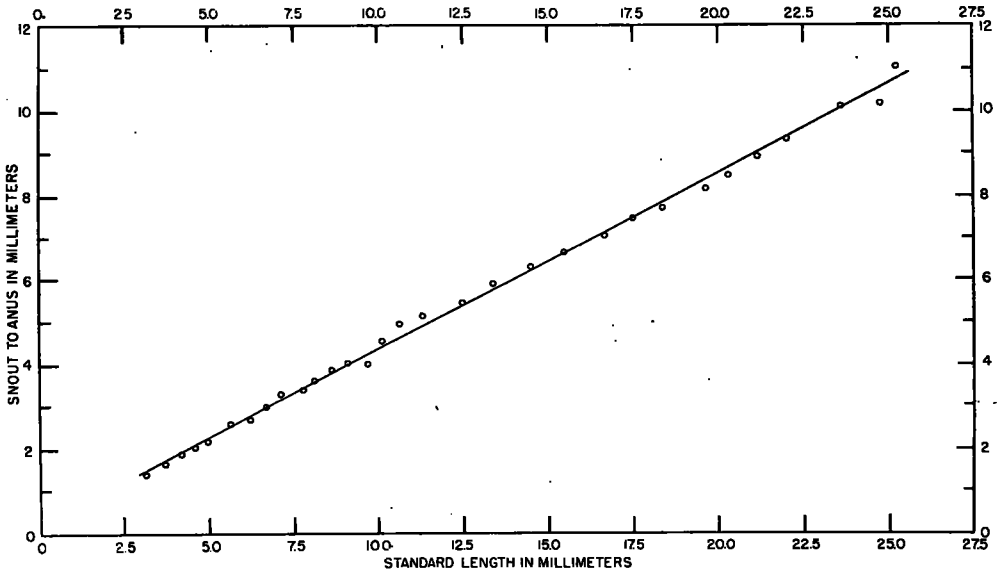

FIGURE 7.—Regression of the distance from snout to anus on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 7). Statistics describing the regression line, fitted by the method of least squares, are given in table 3.

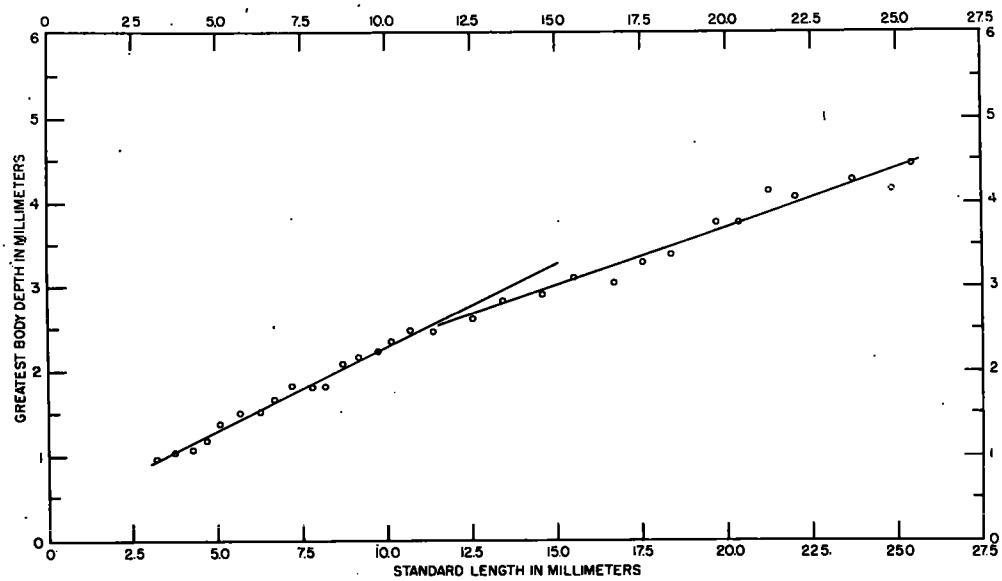

FIGURE 8.—Regression of greatest body depth on standard length. Each circle is the average of a group of measurements, often 10 (refer to table 2, columns 2, 3, and 6). Two regression lines have been fitted to the data by the method of least squares: one for larvae 3.2 to 10.6 mm. in length, the other for individuals 10.6 to 25.5 mm. in length. Statistics describing the two lines are given in table 3.

SEQUENCE OF OSSIFICATION

Vertebral development.—When any part of a vertebra (spine or centrum) takes alizarin stain, the vertebra is considered as forming, and is entered in our counts (table 2, column 8). In general, vertebral development is from anterior to posterior. However, there are some interesting deviations from this sequence which will be discussed below.

The first vertebral elements to show ossification are neural spines, the anterior one or two being formed on some specimens as small as 4 mm. in length. Development of vertebrae proceeds slowly until the larva achieves a length of 7.5 mm., whereupon it is greatly accelerated (fig. 10, and table 2, column 8). The centra do not show ossification in smaller specimens but once initiated, ossification of centra proceeds rapidly. As a result, the centra outstrip the neural spines in development, as is shown in the following table, based on four typical specimens.

Size of larva	Number of neural spines showing ossification	Number of centra showing ossification
7.0 mm	5	0
7.5 mm	7	0
8.5 mm	7	20
9.0 mm	9	35

Some specimens 8.5 mm. in length have all of the vertebrae developed, and all specimens 10 mm. long have the full complement.

The range in number of vertebrae for hake larvae on which accurate counts could be made was from 51 to 55, distributed as follows:

	Number of specimens
51 vertebrae	2
52 vertebrae	14
53 vertebrae	40
54 vertebrae	25
55 vertebrae	3

Although the sequence of ossification is, in general, from anterior to posterior, there are several exceptions. The neural and haemal spines of the third to sixth vertebrae preceding the urostyle begin to ossify before other vertebrae in this part of the body. These are the most posterior of the vertebrae with normally developed neural and haemal spines. However, the centra of these vertebrae are late in forming, being preceded by the centra of the penultimate and antepenultimate vertebrae.

The distinction between caudal and abdominal vertebrae (i. e., vertebrae with or without haemal spines) is evident when larvae have attained a length of approximately 9.5 mm. The range in number of abdominal vertebrae is from 23 to 26, with the majority of specimens having either 24 or 25. Soon after this distinction can be made, all abdominal vertebrae except the first six show an outward and downward growth of the parapophyses to form a bony roof over the abdominal cavity. This is a distinctive characteristic of the genus.

Branchiostegal rays.—Specimens of 4.5 mm. in length may show ossification of the upper branchiostegal ray. The sequence of ossification is from upper to lower. The full complement of 7 rays is found on some specimens as small as 7 mm., and on all specimens 9 mm. or more in length (column 9 of table 2).

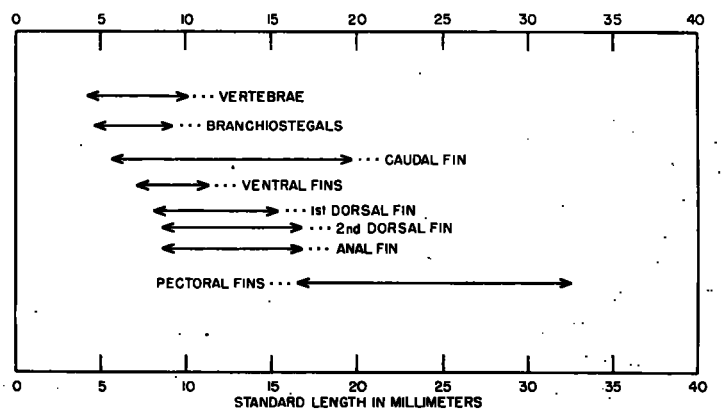

FIGURE 9.—Diagrammatic summary of the sequence of ossification of basic meristic structures in hake larvae.

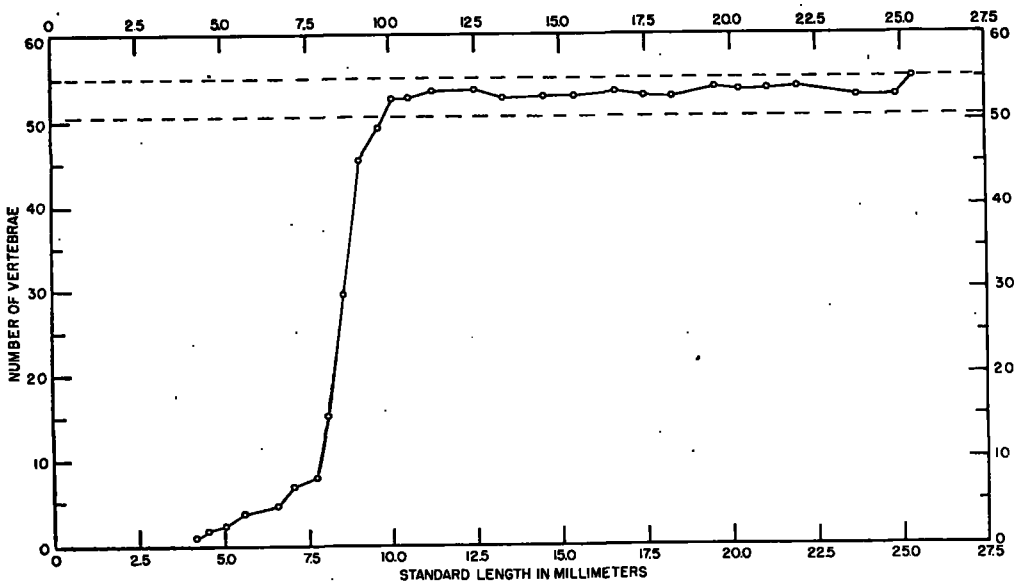

FIGURE 10.—Diagram of average number of vertebrae ossified in hake larvae between 3.2 and 25.5 mm. in length. Each circle is the average of 10 or fewer measurements (refer to table 2, columns 2, 3, and 8). When fully developed, the number of vertebrae ranges between 51 and 55.

Teeth.—Teeth are present on the premaxillary and mandible of larvae approximately 5 mm. in length. In small larvae, the mandible has a greater number of teeth than the premaxillary. By 11 mm. in length, the number of teeth on premaxillary and mandible is approximately equal, and on specimens larger than this, the premaxillary has the greater number. This may be seen from the following tabulation:

Size of larva	Count of teeth on one side	
	Premaxillary	Mandibl
6.8 mm.	4	5
7.0 mm.	4	7
11.0 mm.	9	9–10
17.5 mm.	22	15
20.5 mm.	45	40
40.0 mm.	78+	65+

The teeth are unevenly spaced, not uniform in size, and tend to occur in irregular groups. All of the teeth are either acutely conical or recurved. The anterior teeth are recurved and the posterior teeth are more nearly straight. The premaxillary and mandibular dentitions become biserial when the larva reaches approximately 30 mm. The teeth of the inner row on either jaw are longest and depressible posteriorly, as are those of the adults. A double row of vomerine teeth are found on larger larvae; we have not determined the exact size at which these form.

Gill rakers.—*Merluccius productus* has a higher gill-raker count than any other species of hake except *M. gayi*. Adult specimens of *M. productus* have 4 or 5+14 to 17 gill rakers. The first of the developing gill rakers are evident on larvae just under 10 mm. in length. For example, on a specimen 9.8 mm. in length, 6 gill rakers were present on the lower limb of the first arch; they were only short primordia, and none were developed on the upper limb. The counts on 8 specimens of graded size were as follows:

Size of larva	Gill-raker count	
	Upper limb	Lower limb
9.8 mm.	0	6.
12.0 mm.	0	8.
14.0 mm.	0	11.
18.0 mm.	2	12.
23.5 mm.	2	14.
25.0 mm.	4	14.
41.0 mm.	4	15 or 16.
46.0 mm.	4	15.

The full complement of gill rakers is obtained by about 25 mm. in length.

Opercular and preopercular spines.—There are no spines evident on the head or preoperculum during the larval period. On the operculum are two needle-like ridges, which could be mistaken for spines (fig. 3).

Scales.—On hake larvae, the developing scales are highly deciduous, and the sequence of scale

formation has not been carefully studied. No scales were observed on larvae of 28 mm., but small scales were found on larvae 35 mm. in length. The 40.5-mm. and 46-mm. specimens were heavily scaled.

SEQUENCE OF FIN FORMATION

The sequence of fin formation in the hake is as follows:

1. Larval pectorals (without rays).
2. Caudal.
3. Ventrals (pelvics).
4. First dorsal.
5 and 6. Second dorsal and anal (simultaneously).
7. Pectorals (with rays).

These fins are discussed in order of their formation.

Larval pectoral fins.—The pectorals begin forming during the late embryonic period, and are fully developed on larvae about 3 mm. in length. They consist of a fleshy base and a wide undifferentiated membrane without rays. Rays do not appear until late in the larval period, and until then the pectorals are designated as larval fins.

Caudal fin.—The caudal fin of the hake has been classed as a "pseudocaudal" type by Barrington (1937) and other workers. The development of the caudal in the hake differs in a number of ways from typical homocercal caudal development as found in most fishes (for example, the jack mackerel, discussed in the first paper of this series). However, we cannot agree in all details with Barrington's interpretation of caudal development in the cod and related groups, as is pointed out in the following discussion.

The first evidences of caudal-fin formation are ventral and dorsal thickenings near the posterior tip of the notochord, found on some hake larvae as small as 4 mm. in length. Even in specimens only slightly larger than 4 mm. the rudiments of most hypural and epural elements can be distinguished. Rays do not appear (i. e., take stain) until the larvae are 5.8 mm. or more in length. The first rays form ventrally. Usually, when any rays can be distinguished, several have already ossified. Ray differentiation is initiated simultaneously on the penultimate and posterior hypurals. The 3 rays associated with the penultimate hypural differentiate anteriorly; the 6 rays on the posterior hypural differentiate posteriorly. Usually, when about 7 ventral rays are differentiated (3 on posterior hypural, 3 on penultimate hypural, and 1 anterior to the penultimate hypural), rays begin forming in the dorsal portion of the fin. The first dorsal ray to form will be the ray immediately adjacent to the urostyle. Differentiation of dorsal rays then proceeds anteriorly.

Soon after dorsal rays begin forming, the posterior portion of the notochord flexes upward and the posterior hypural assumes a terminal position. At first, the notochord extends almost 0.5 mm. beyond the posterior hypural plate, but it gradually shortens so that in specimens of 17.5 mm. in length it barely projects beyond the hypural.

The 9 rays associated with the posterior and penultimate hypurals have no dorsal counterparts; as interpreted by us, these rays represent the "homocercal" element in the development of a gadid caudal fin. This point was missed by Barrington. Ventral rays other than these 9 will be equal in number or 1 less than the total number of dorsal rays. This is true both during formation and after the caudal fin is fully formed. The following table based on selected specimens illustrates this:

Size of larva	Number of caudal rays originating—			
	Dorsally	Ventrally		Total
		Associated with 2 principal hypurals	Not associated with 2 principal hypurals	
6.3 mm	0	4	0	4
7.8 mm	3	8	3	14
9.0 mm	6	9	6	21
11.0 mm	9	9	9	27
13.0 mm	13	9	13	35
14.4 mm	15	9	14	38
18.0 mm	16	9	15	40
21.4 mm	17	9	17	43
170.0 mm. (approx.)	17	9	17	43

The average number of caudal rays found on larvae between 5.5 and 46 mm. in length is given in column 10 of table 2. The full complement of 42 to 45 caudal rays is present in specimens of approximately 20 mm. in length. Young hake as large as 46 mm. in length still have the posterior edge of the caudal rounded and not somewhat truncate as in adults.

The fully developed caudal fin is associated with the last 9 or 10 vertebrae (fig. 11). All except the last 3 of these appear to be normal vertebrae with long, sharply inclined neural and haemal spines. We have noted earlier that these spines ossify earlier than surrounding vertebral struc-

tures. The antepenultimate and the penultimate vertebrae have normal centra, but modified spines. The haemal spines of these vertebrae have been modified into hypurals by fusion with ventral radials;[5] the neural spine of the antepenultimate vertebra has been similarly modified into an epural, but the neural spine of the penultimate vertebra has been reduced to a short remnant. In addition, there are five rod-shaped radials (three dorsal, two ventral) associated with these two vertebrae: two of the dorsal radials lie above the penultimate vertebra, the other dorsal radial lies forward of the anterior epural; the ventral radials are located on either side of the anterior hypural. The terminal vertebra, or urostyle, is roughly conical in shape but bent upward. It fuses with the single, broadly triangular posterior hypural. Since the urostyle forms from a single center of ossification and fuses with a single undivided hypural, there is no indication that more than one vertebra is involved in its origin.

An examination was made of the caudal portion of a number of young hake between 150 and 200 mm. in length. The principal rays number 23 or 24 (21 or 22 branched rays, plus the adjacent unbranched ray on either side); of these, 7 or 8 are dorsal in origin, 16 are ventral in origin. The posterior 4 rays of dorsal origin are attached to the dorsal radials and the epural, one to each element. Twelve of the 16 principal rays of ventral origin are associated with hypural elements: 6 with the posterior hypural, 3 with the penultimate hypural, and 1 each with the other 3 ventral elements. Some of the more anterior caudal rays, both dorsal and ventral, appear to be articulated with unmodified neural and haemal spines; the remaining rays lie between the spines and have no basal skeletal supporting elements whatsoever.

Ventral (pelvic) fins.—At approximately 6 mm. in length, ventral buds can be discerned. Rays may be distinguished in some specimens as small as 7 mm., and the full complement has formed in all specimens 11 mm. long. Our specimens invariably had 7 ventral rays (column 11 of table 2). When the larva is 6.8 mm. in length, the ventral fin is 0.25 mm. long. At about 17.5 mm. the ventral fin is 2.5 mm. long and extends just to the anus. The posterior tip of the ventral fin reaches no farther than the anus until the larva is at least 23.8 mm. in length. A specimen 46 mm. long had ventral fins that were 5.5 mm. in length and extended 2 mm. beyond the anus. The following table shows this development:

Size of larva	Length of ventral fin
	Mm.
6.8 mm	0.3.
8.5 mm	0.5.
9.4 mm	0.8.
14.0 mm	2.1.
17.5 mm	2.5 (extends to anus).
17.6 mm	2.6 (extends to anus).
23.8 mm	3.2 (extends to anus).
46.0 mm	5.5 (extends 2 mm. beyond anus).

First dorsal fin.—The anterior rays of the first dorsal develop first; differentiation then proceeds posteriorly. About half of the specimens in the 8 to 8.5 mm. size group possess 1 or more rays in this fin, and all specimens more than 15.5 mm. have the full complement of 10 or 11 rays (column 12 of table 2). The third ray is longest; the second and fourth are nearly as long; the first ray is approximately three-fourths as long as the third. Behind the third ray the elements become progressively shorter, with the eleventh ray about one-tenth the length of the third.

Second dorsal and anal fins.—Since these fins are formed simultaneously, they will be considered together. Anal rays are found on some specimens as small as 8.5 mm., and on all specimens more than 9.2 mm. in length. The rays usually appear suddenly; the lowest number counted on larvae having differentiated anal rays is 15. The rays form from two centers, which would correspond to the divided anal fins in other gadoids. By 9.7 mm. in length, the average number of rays per specimen is 28; by 16 mm., the full complement of 41 to 43 rays is developed (column 14 of table 2).

Rays in the second dorsal are always found on specimens showing ossification of anal rays, but as few as 4 rays may be observed on some specimens. Soon, the numbers of second dorsal and anal rays correspond rather closely, although there are usually a few less second dorsal rays than anal rays. Rays in the second dorsal also

[5] We are using the same nomenclature as that given in Whitehouse (1910, p. 138) and Barrington (1937, p. 448). According to Barrington, "A hypural may be defined as a ventral element supporting one or more lepidotrichia and making contact with the notochordal axis, being subsequently attached to a vertebra; it is presumed to be composed of a haemal spine fused with a ventral radial. An epural is a dorsal element with analogous relationships, and is presumed to be composed of a neural spine fused with a dorsal radial. A radial is a dorsal or ventral element supporting one or more lepidotrichia, but not making contact with the notochordal or vertebral axis." It should be noted that this terminology differs from that used by Hollister (1936).

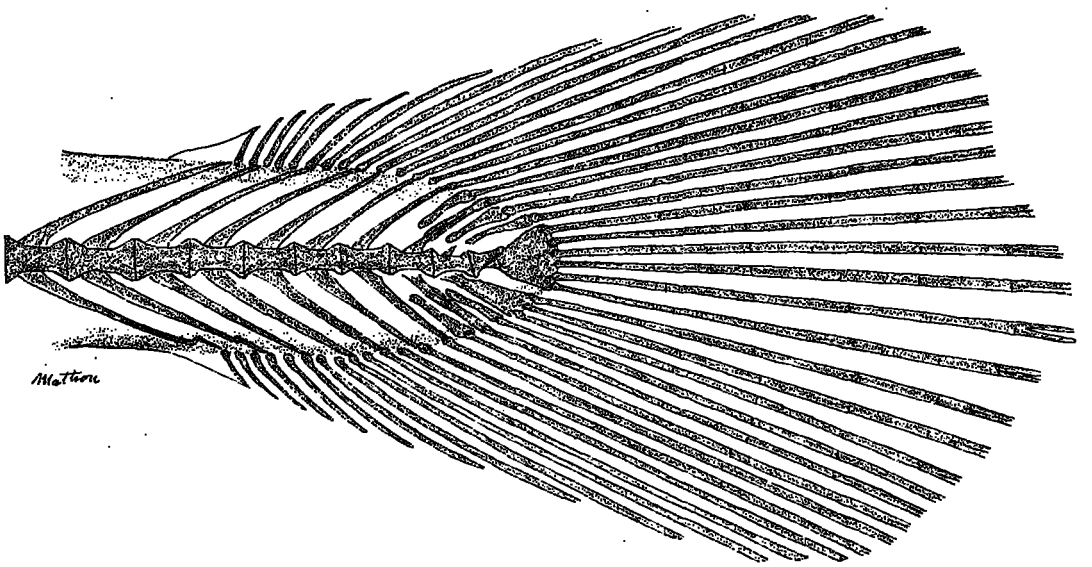

FIGURE 11.—Caudal fin and supporting skeletal structures of a 45-mm. juvenile hake.

form from two centers, which would correspond to the second and third dorsal fins in typical cods. The full complement of 40 to 42 rays in the second dorsal is found on specimens of approximately 16 mm. in length (column 13 of table 2).

The posterior rays of both the anal and the second dorsal are the last to form. The terminal ray of each is short and unbranched, differing in this respect from the majority of fishes, which have bifurcate terminal rays on dorsal and anal fins.

Pectoral fins.—The larval pectoral, which develops shortly before hatching as a fleshy-based, fan-shaped structure without rays, persists unchanged until about 17 mm. In some specimens as long as 25 mm., no rays were observed, but most specimens more than 24 mm. long have 7 or more pectoral rays. The upper rays of the pectoral form first, and differentiation then proceeds ventrally. The number of pectoral rays on 7 specimens between 23.8 and 36.5 mm. were as follows:

Size of larva	Number of pectoral rays	Size of larva	Number of pectoral rays
23.8 mm	7	29.5 mm	13
25.5 mm	7	35.5 mm	15
27.8 mm	10	36.5 mm	15
28.5 mm	12		

The full complement of 14 to 17 rays is attained between 30 and 35 mm. in length. Unfortunately, we did not have hake larvae in this size range, so that we could more exactly delimit the size at which pectoral ray formation is completed.

DISTRIBUTION AND ABUNDANCE OF LARVAE, 1951 AND 1952

The hake larvae taken in plankton collections made on survey cruises of the California Cooperative Oceanic Fisheries Investigations have been identified and enumerated routinely. The basic data on occurrence and abundance of hake larvae in 1951 and 1952 are given by Ahlstrom (1953 and 1954).

During 1951 and 1952, cruises were spaced at monthly intervals, except in December 1952. During these years the least extensive coverage was from Point Conception, Calif., to Point San Juanico, Baja California; the most extensive was from the California-Oregon border to the southern tip of Baja California; the usual coverage was from San Francisco to Point San Juanico. The coverage during 1952 was somewhat less extensive than the coverage during 1951, but was more intensive, especially within 100 to 150 miles of the coast.

Census estimates of abundance.—Estimates of abundance of hake larvae in 1951 and 1952 are given in table 5. The values represent census estimates of the number of hake larvae in different parts of the survey area at the time of each monthly cruise. Such an estimate is obtained by integrating the standard-haul totals for larvae over area, but not over time. Size of larvae is not taken into account; hence, a 3-mm. larva is given as much weight as a 30-mm. larva. Although rate of growth of hake larvae has not been determined, complete larval development must re-

TABLE 5.—*Census estimate of number of hake larvae in survey area during each cruise of 1951 and 1952*

[In billions]

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1951													
Lines 60–67	84			170	6	0	0	0	0	0	0	0	260
70–77	77			501	5	9	2	0	0	0	0	0	594
80–87	1	839	4,387	4,452	94	7	0	0	0	0	1	8	9,789
90–97	5	982	1,968	1,288	34	18	0	0	0	4	0	0	4,299
100–107	1	1,422	14,888	2,384	47	3	0	0	0	0	0	0	18,745
110–117	0	197	461	338	24	34	0	1	4	1	4	12	1,076
120–127	27	318	73	169	103	25	11	0	0	0	0	0	726
130–137	36	739	612	193	37	8	1	0	0	0	0	0	1,626
Line 140 and below			120			10			0				130
Total	231	4,497	22,509	9,495	350	114	14	1	4	5	5	20	37,245
1952													
Lines 60–67				34	0	0	0	0	0	0	0		34
70–77				49	4	0	0	0	0	0	0		53
80–87	2	12	2,234	121	26	9	0	0	0	0	0		2,404
90–97	7	5,531	13,803	7,922	97	14	1	0	0	0	0		27,375
100–107	0	51	2,087	901	6	0	0	0	0	0	0		3,045
110–117	0	1,797	605	88	3	0	0	2	0	3	0		2,588
120–127	4	280	256	39	2	3	0	0	0	0	0		584
130–137	310	317	291	211	8	3	0	0	0	0	0		1,140
Line 140 and below		93											93
Total	323	8,081	19,366	9,365	146	29	1	2	0	3	0		37,316

quire more than a month; consequently we resampled some identical groups of larvae on successive cruises. With these limitations, it is obvious that a census estimate is a rather primitive measure of abundance. Nevertheless, census estimates that cover similar areas at regular intervals of time (in our case, monthly) are comparable for succeeding years, even though the estimates are relative, rather than absolute, measures of abundance.

The estimates for 1951 and for 1952 are remarkably similar—37,250 billions as compared with 37,300 billions.

Area of occurrence.—The abundance of hake larvae in different parts of the survey area may be summarized as follows:

Area	Station lines	Census estimate			
		1951		1952	
		Number	Percent	Number	Percent
		Billions		*Billions*	
North of Point Conception	60–77	854	2.3	87	0.2
Southern California and adjacent Baja California	80–107	32,833	88.1	32,824	88.0
Central Baja California	110–137	3,428	9.2	4,312	11.6
Southern Baja California	140 and below	130	.4	93	.2
Total		37,245	100.0	37,316	100.0

Hake larvae were taken as far north as San Francisco, as far south as Cape San Lucas, and as far seaward as 350 miles (off southern California).

Hake larvae were taken in greatest abundance off southern California and adjacent Baja California, between Point Conception and San Quintin, station lines 80–107. Approximately 88 percent of the hake larvae collected in both 1951 and 1952 were taken in this area.

Two centers of hake abundance were encountered in 1951 (fig. 12), one just south of Point Conception (lines 80–87), the other centering off northern Baja California (lines 100–107). During 1952 (fig. 13), the center of abundance was off San Diego (lines 90–97), falling off sharply both to the north and to the south of this area.

Only a minor percentage of the hake larvae were taken to the north of Point Conception: 2.3 percent during 1951, and 0.2 percent during 1952. However, coverage of this area was inadequate, since it was not visited during February and March of either year, and coverage did not extend north of San Francisco during the hake spawning season.[6]

Season of occurrence.—The monthly abundance of hake is summarized in table 6. Hake larvae were taken in abundance only during a 3-month period, February through April. Approximately 98 percent of the hake larvae were taken during these months in both 1951 and 1952. The peak month during both seasons was March; more than

[6] The area between Point Conception and Cape Mendocino (lines 40–77) was surveyed at monthly intervals, February through September 1950, and nearly 19 percent of the hake larvae collected in 1950 were obtained in this area. However, all collections from north of Point Conception, except one occurrence off Cape Mendocino, were obtained on lines 60–77. Hence, in 1950, hake spawning north of San Francisco was negligibly small in amount.

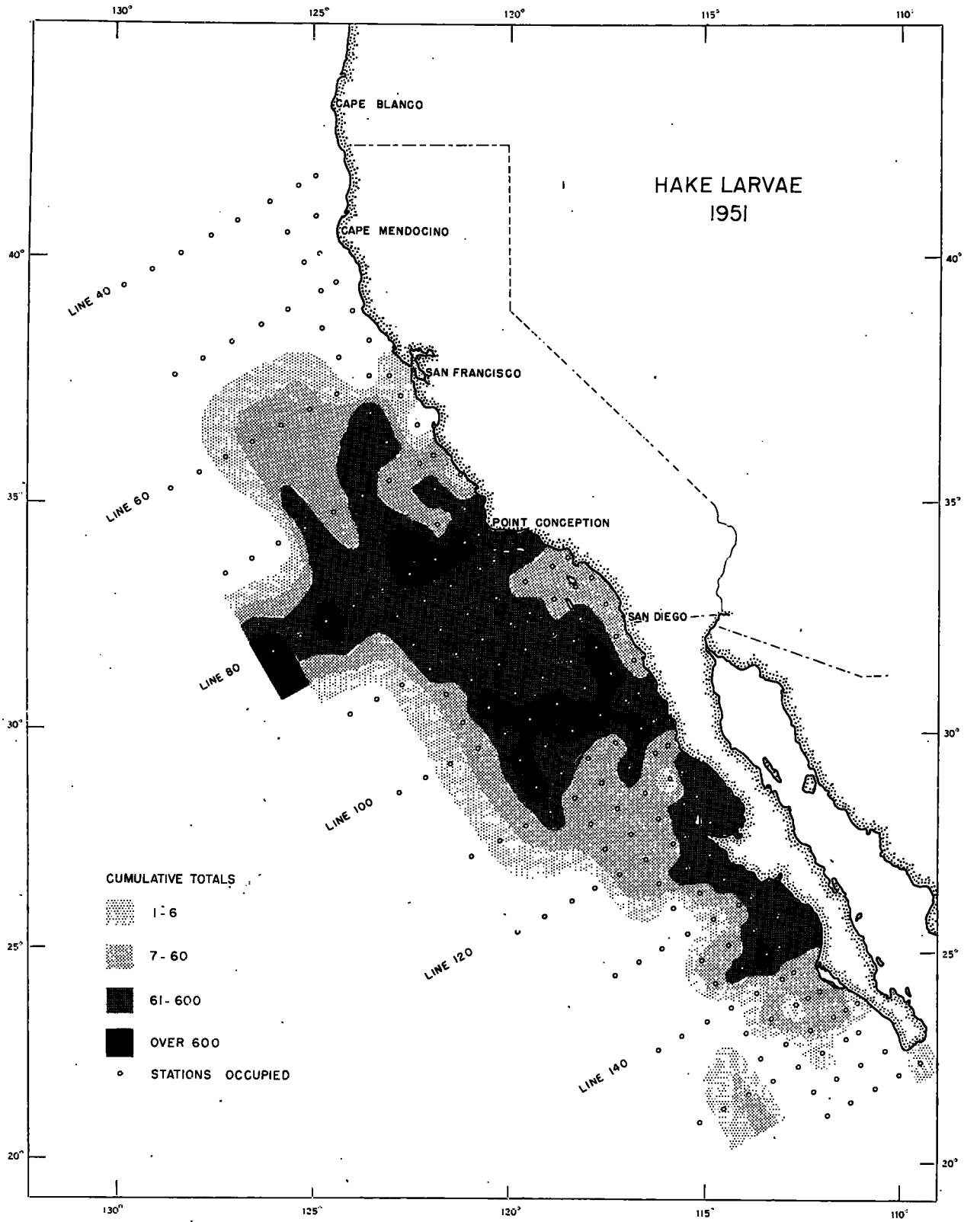

FIGURE 12.—Distribution and abundance of hake larvae in 1951. Cumulative totals represent the summation for the year of the standard-haul totals of hake larvae taken at each station on each cruise.

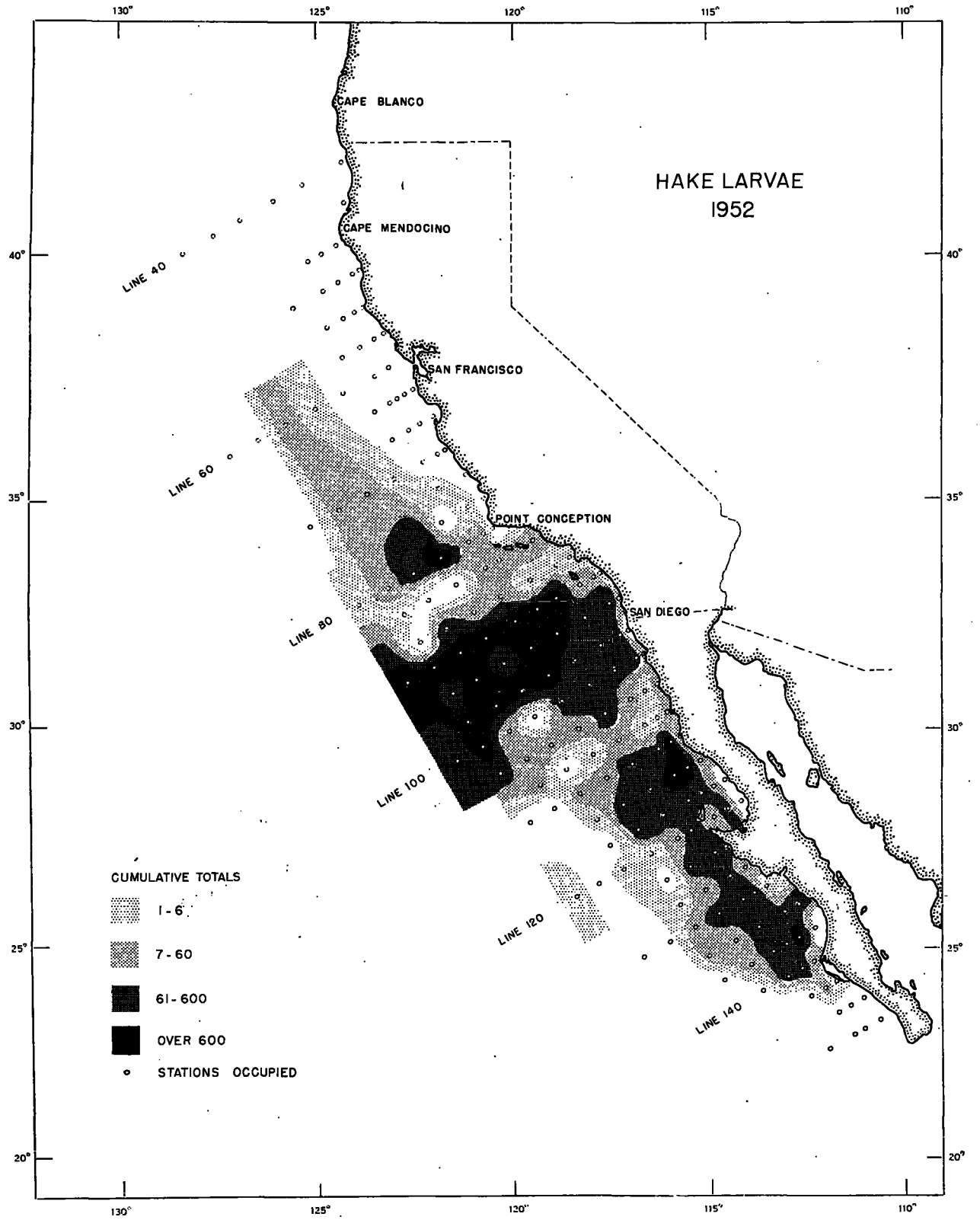

FIGURE 13.—Distribution and abundance of hake larvae in 1952. Cumulative totals represent the summation for the year of the standard-haul totals of hake larvae taken at each station on each cruise.

half of the yearly total was obtained during this month. Only negligible amounts were taken during the latter half of each year.

TABLE 6.—*Census estimates of abundance of hake larvae by months, 1951 and 1952*

Month	1951		1952	
	Number	Percent	Number	Percent
	Billions		*Billions*	
January	231	0.62	323	0.87
February	4,497	12.07	8,081	21.66
March	22,509	60.43	19,366	51.89
April	9,495	25.49	9,365	25.10
May	350	.94	146	.39
June	114	.31	29	.08
July	14	.04	1	0
August	1	0	2	.01
September	4	.01	0	0
October	5	.01	3	.01
November	5	.01	0	0
December	20	.05		
Total	37,245	99.98	37,316	100.01

The distribution and abundance of hake larvae on the monthly survey cruises made during the first 6 months of 1951 and 1952 are shown in figures 14 through 25. On most cruises, neither the north-south extent nor the offshore extent of hake larvae was delimited.

Vertical distribution.—In late March 1954, on a special cruise of the research vessel *Crest*, an area of abundant hake spawning was located about 200 miles off San Diego. To obtain information on the vertical distribution of hake eggs and larvae, two series of hauls were taken at station 94.80: one during daylight, the other during darkness. Each series consisted of 10 horizontal hauls made at successively deeper levels. The hauls were made with a net that could be opened and closed at any desired level. A comparable fishing time of 10 minutes (between opening and closing of the net) was allowed for each haul. The results are summarized in table 7.

Hake eggs were taken between 27 and 102 meters deep, hake larvae between the surface and 102 meters deep. The largest concentrations of larvae were taken between 50 and 100 meters deep. More than 98 percent of the hake larvae collected in the night series occurred at this level, with most of the larvae clustered at one depth (64 meters). The stratification was less marked in the day series: the five hauls above 50 meters averaged 46 larvae per haul, while the two hauls between 50 and 100 meters averaged 219 larvae, about 4.7 times as many. No hake larvae were taken in the two lower hauls of each series.

TABLE 7.—*Horizontal closing-net hauls made at station 94.80 on March 24–25, 1954, to study vertical distribution of hake eggs and larvae*

Midtime of haul [1]	Average depth of haul	Water temperature	Abundance of hake eggs [2]	Number of hake larvae
Day series:	*Meters*	° *C.*		
0910	6	14.1	0	65
0940	7	14.1	0	85
1005	18	14.1	0	24
1025	28	14.0	0	13
1105	41	14.0	C	45
1140	53	13.8	A	156
1230	68	13.2	A	282
1305	102	11.1	R	22
1350	135	9.7	0	0
1425	201	8.6	0	0
Night series:				
2030	0	14.3	0	15
2100	7	14.3	0	6
2125	17	14.3	0	4
2145	27	14.3	R	1
2310	42	14.3	A	2
2330	52	14.3	A	92
0000	64	14.1	A	1,619
0025	101	10.8	R	8
0135	127	9.9	0	0
0215	200	8.7	0	0

[1] Pacific standard time.

[2] Hake eggs were not counted. Symbols used to indicate abundance: R=few; C=common; A=abundant.

In addition to the above series, some hake larvae have been collected incidentally in hauls made for studying the vertical distribution of sardine eggs and larvae. These were taken off southern California, in 1941 and subsequently, all within a radius of 120 miles of San Diego. The hake larvae taken in these collections are listed in table 8.

TABLE 8.—*Occurrence of hake larvae in closing-net hauls made to investigate the vertical distribution of fish eggs and larvae*

[All hauls made off southern California]

Middepth of haul	Number of larvae									
	Series 1832 Apr. 10, 1941 1100–1530	Series 2032 May 2, 1941 0800–1400	Series 2043 May 2, 1941 2000–2400	Series 2046 Apr. 30, 1941 1700–2100	Series 2452N [1] June 17, 1941 2200–0330	Series 2452D [1] June 18, 1941 0900–1400	Series 2463D June 20, 1941 0800–1430	Series 9138N [1] June 12, 1952 2130–0430	Series 9138D [1] June 13, 1952 0900–1500	Total
3 meters	0	0	0	0	0	0	0	0	0	
10 meters	------	0	0	0	0	0	0	0	0	
20 meters	0	0	0	0	0	0	0	0	0	0
27 meters	0	0	3	0	0	1	0	0	0	4
40 meters	3	0	5	2	2	3	0	0	3	18
57 meters	10	14	9	20	0	4	0	2	2	61
75 meters	9	7	4	13	1	0	0	12	0	46
100 meters	------	------	1	------	0	0	0	0	0	1
140 meters	------	------	------	------	------	0	1	------	0	1
Total	22	21	22	35	3	8	1	14	5	131

[1] Series repeated in same locality, N=at night, D=during daylight.

Hake were obtained in seven series in small numbers (1 to 35 larvae per series). The depth distribution of these samples is similar to that obtained at station 94.80: most larvae were obtained between 50 and 100 meters; however, no larvae were taken above 27 meters deep.

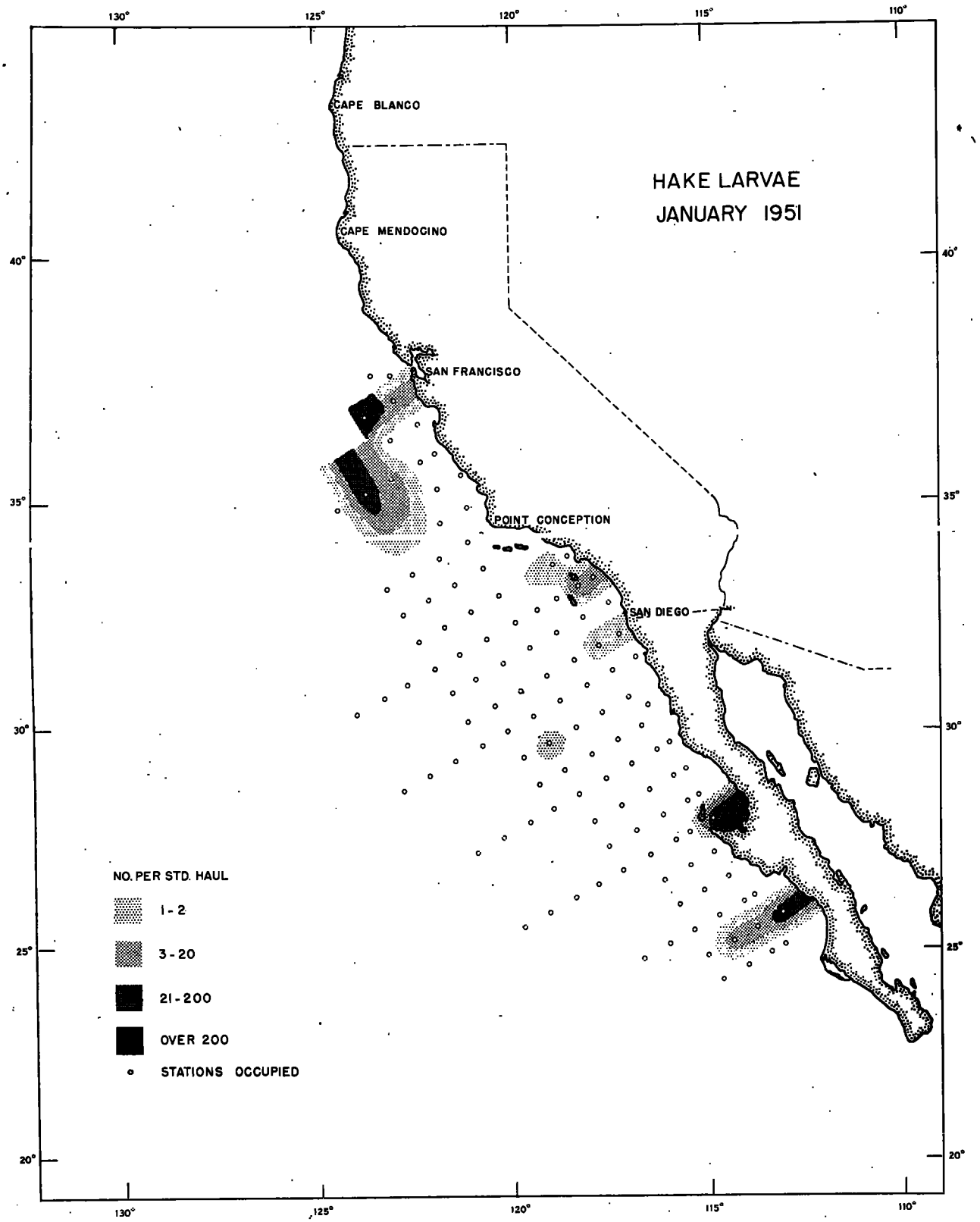

FIGURE 14.—Distribution and abundance of hake larvae during January 1951.

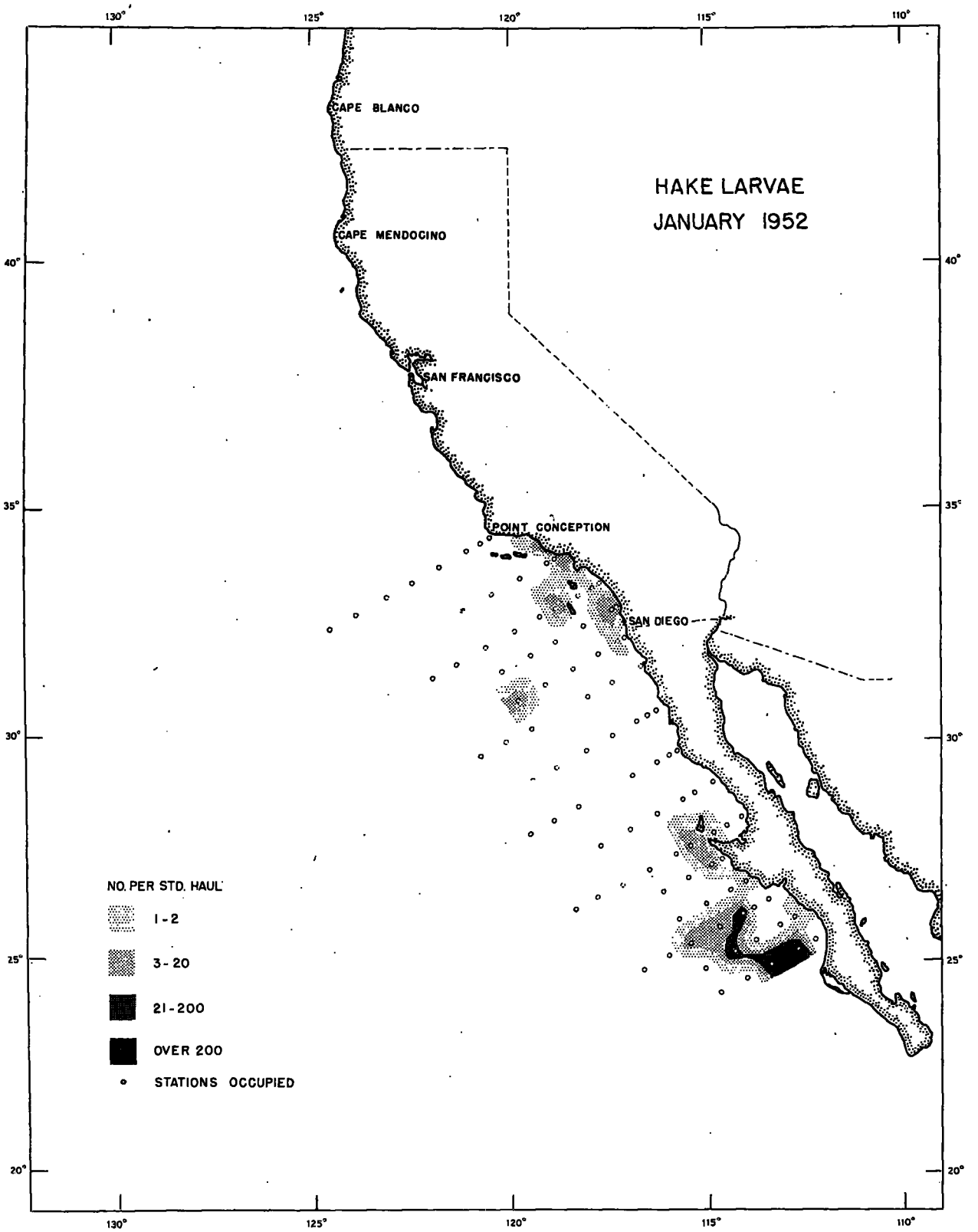

FIGURE 15.—Distribution and abundance of hake larvae during January 1952.

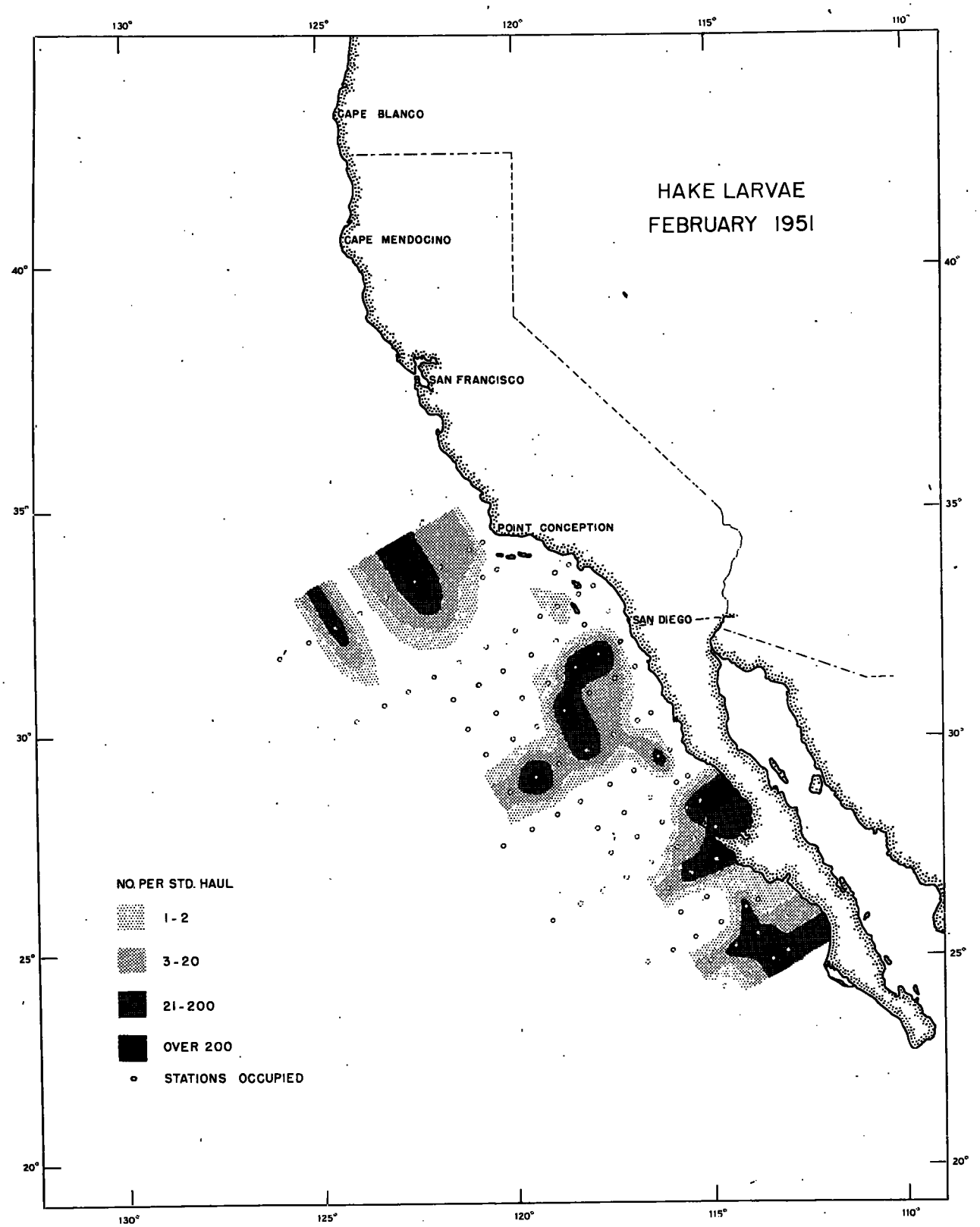

FIGURE 16.—Distribution and abundance of hake larvae during February 1951.

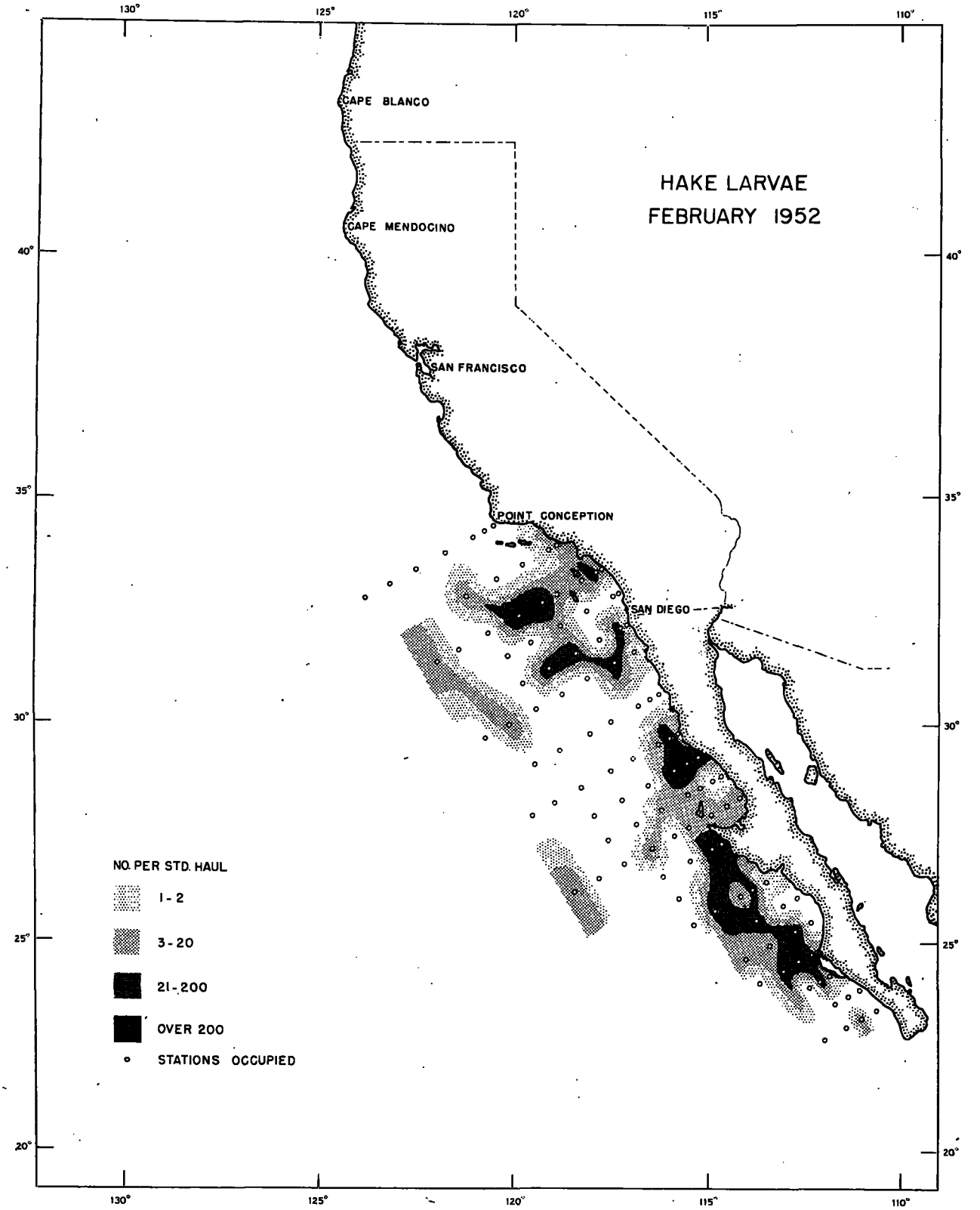

FIGURE 17.—Distribution and abundance of hake larvae during February 1952.

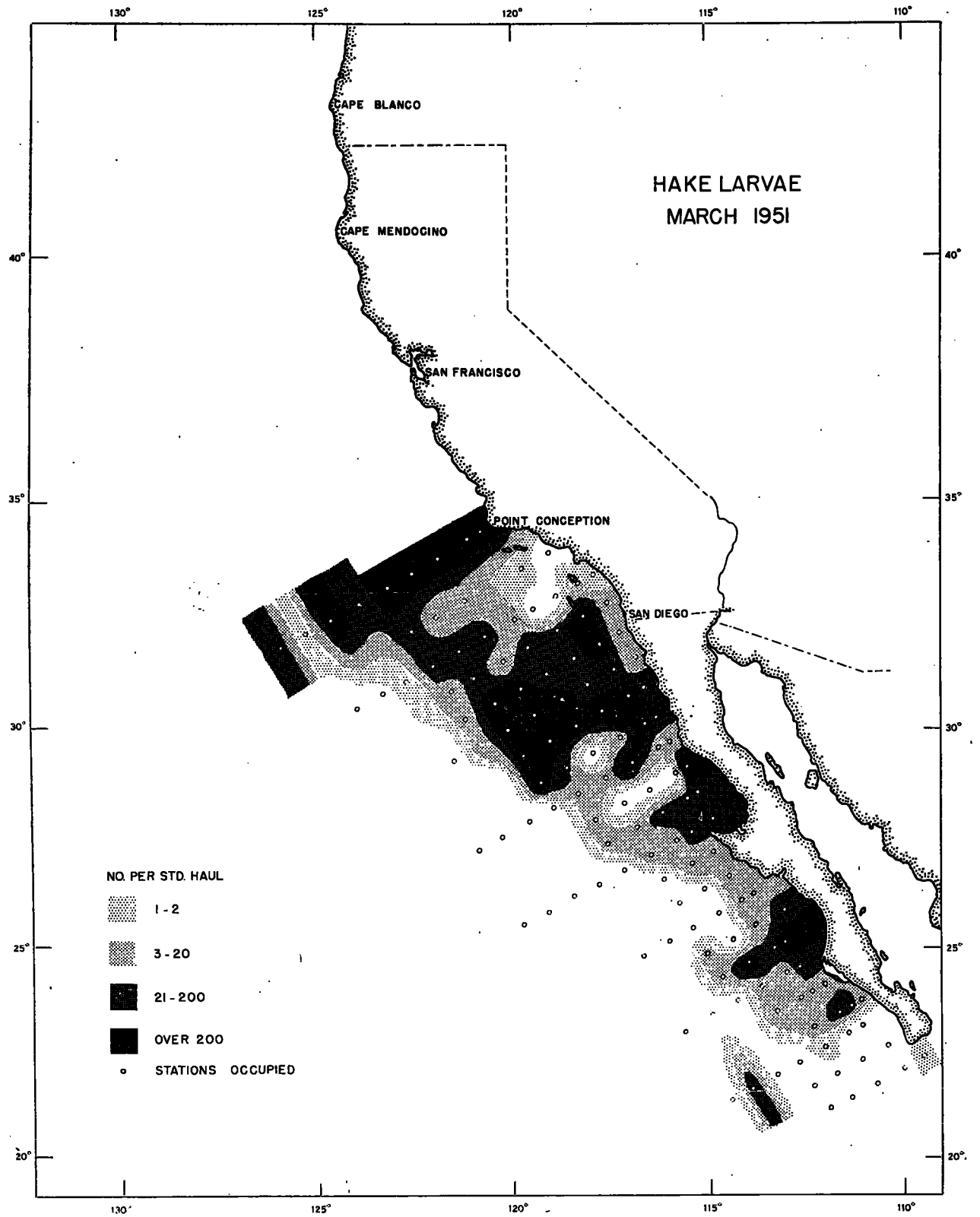

FIGURE 18.—Distribution and abundance of hake larvae during March 1951.

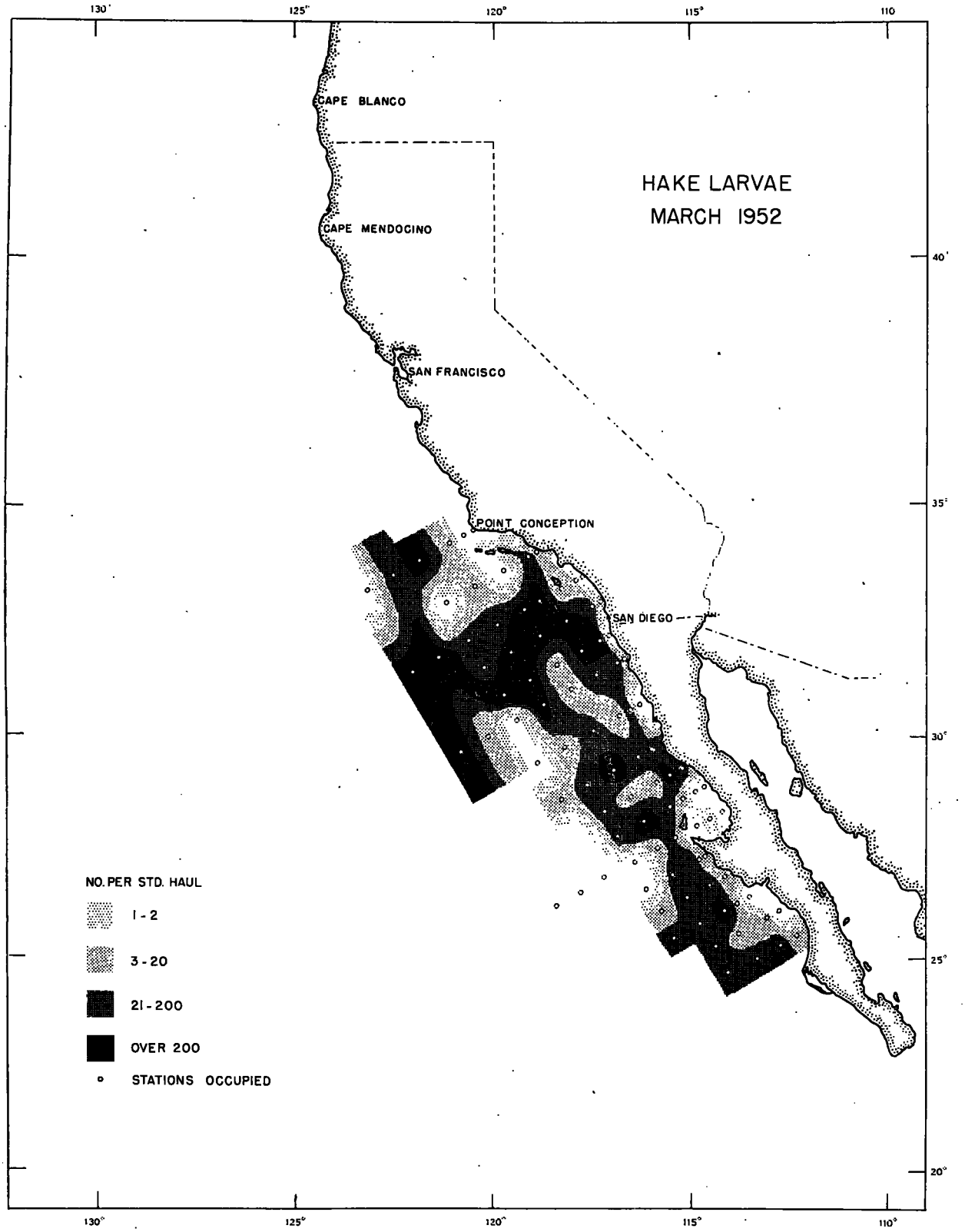

FIGURE 19.—Distribution and abundance of hake larvae during March 1952.

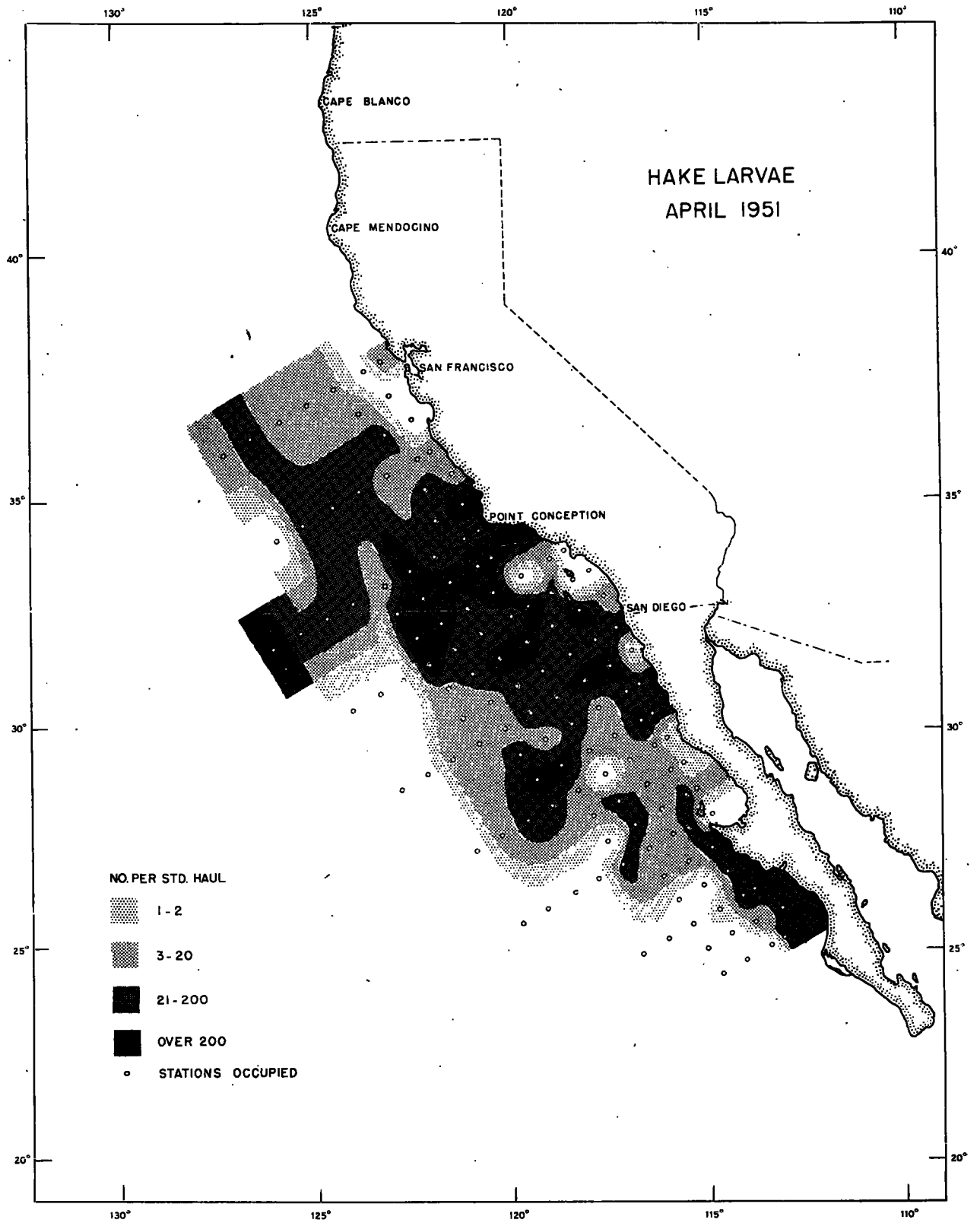

FIGURE 20.—Distribution and abundance of hake larvae during April 1951.

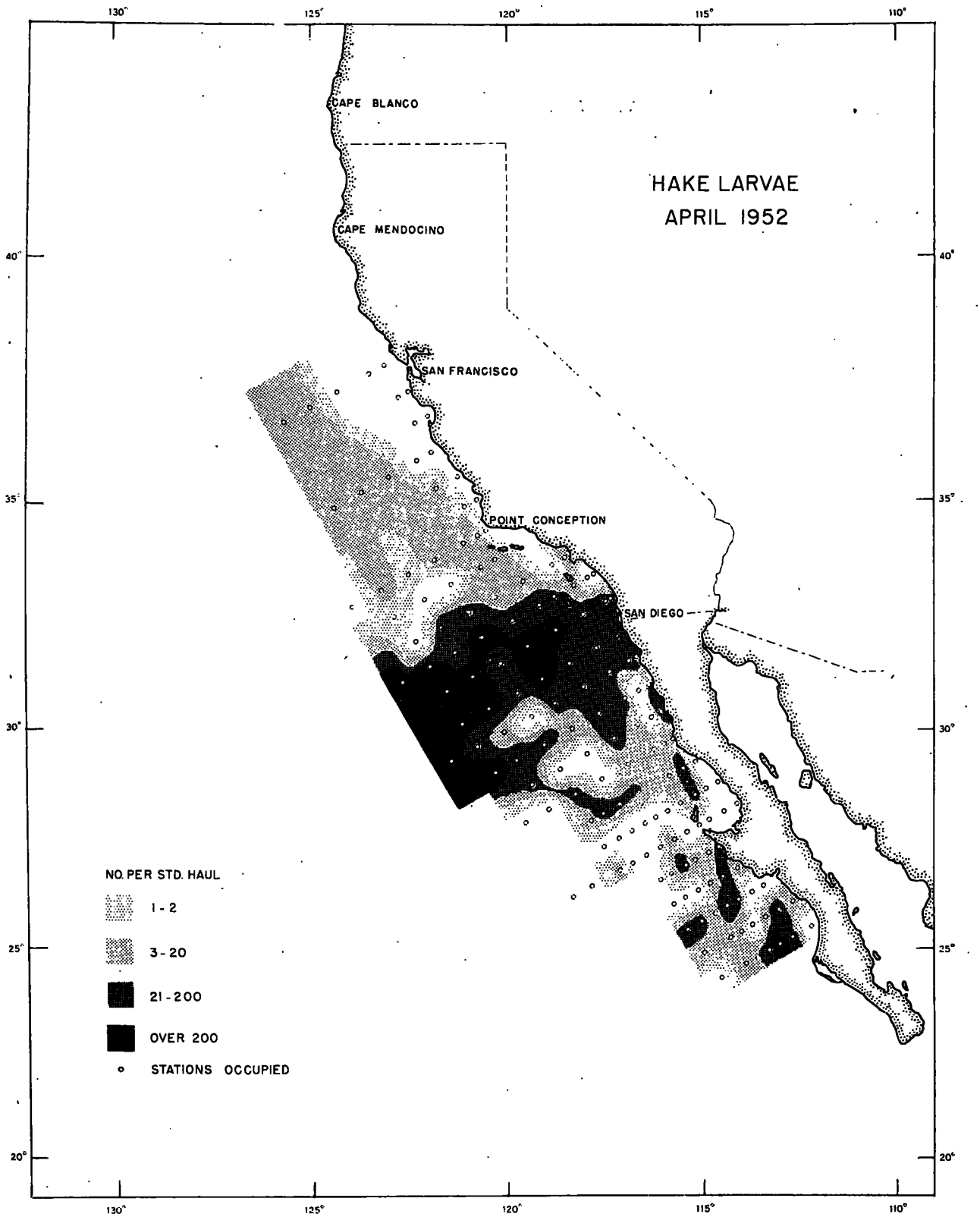

FIGURE 21.—Distribution and abundance of hake larvae during April 1952.

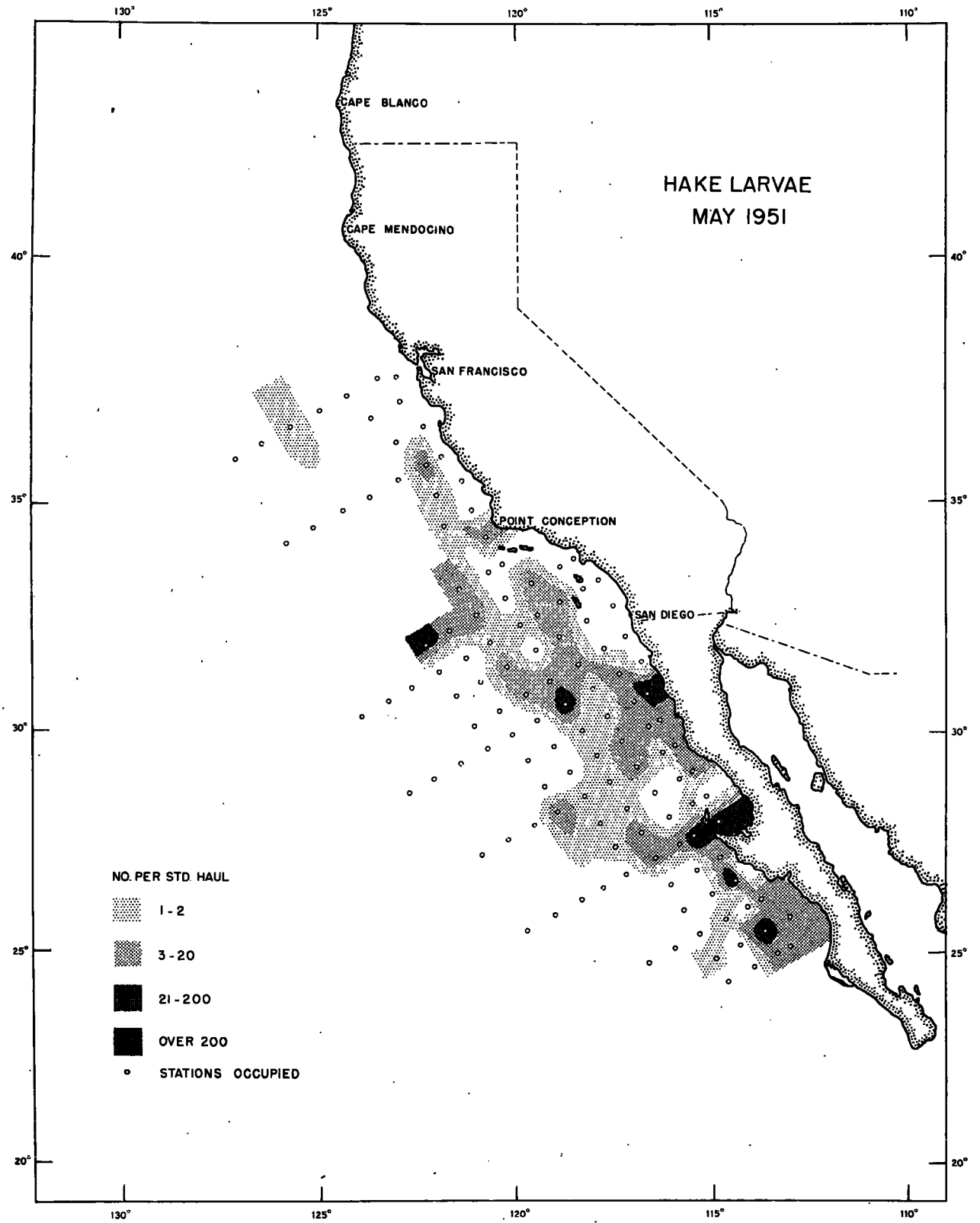

FIGURE 22.—Distribution and abundance of hake larvae during May 1951.

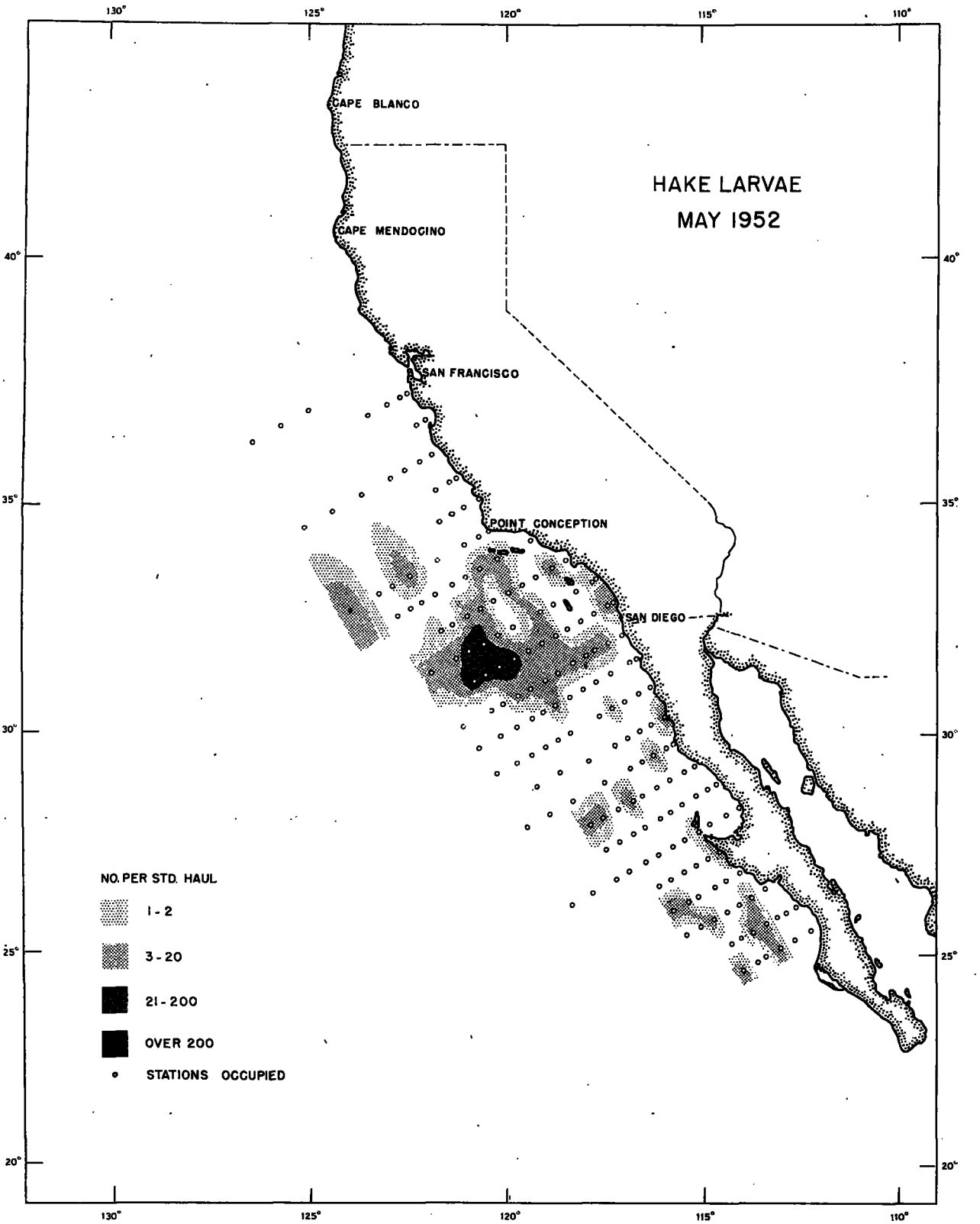

FIGURE 23.—Distribution and abundance of hake larvae during May 1952.

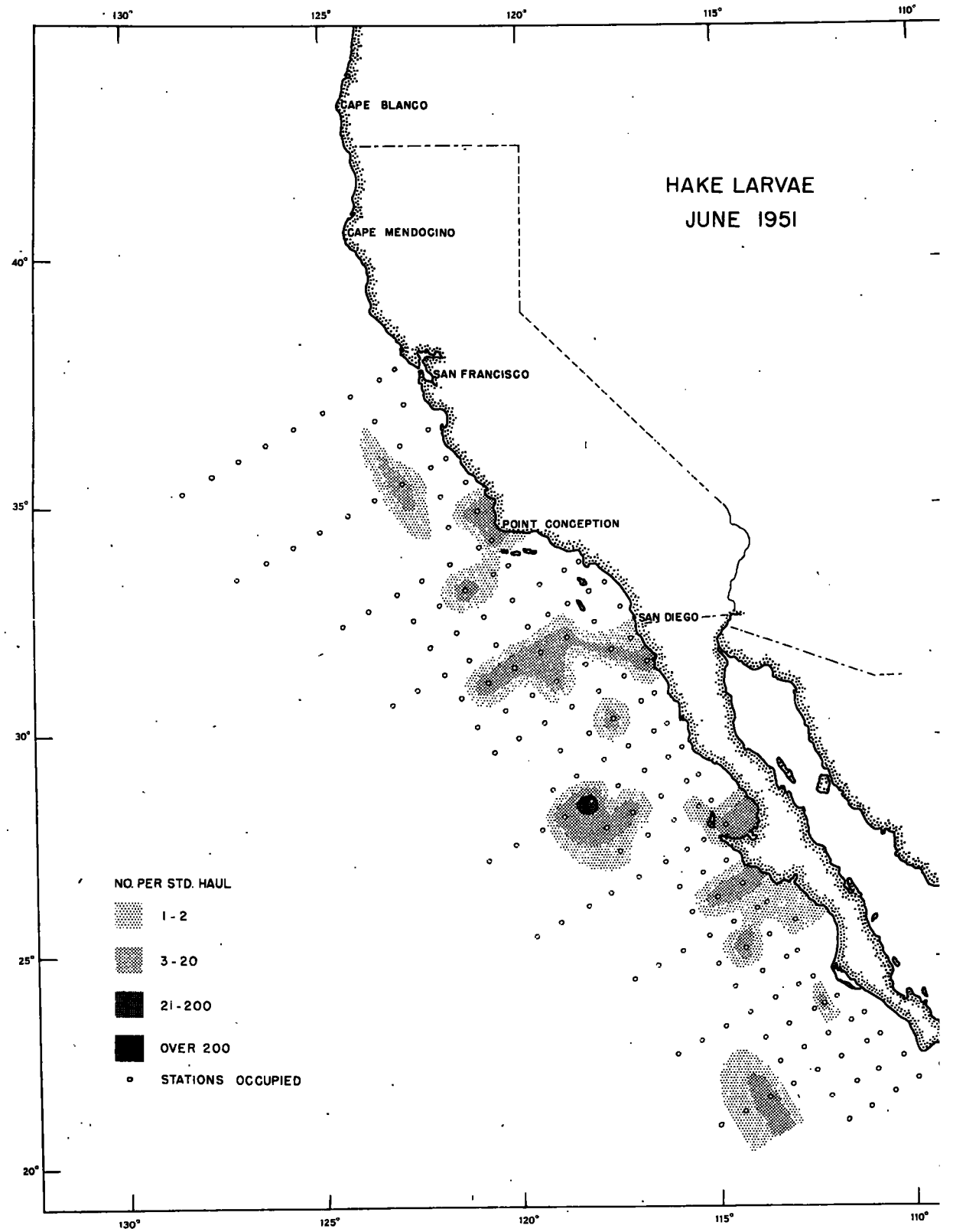

FIGURE 24.—Distribution and abundance of hake larvae during June 1951.

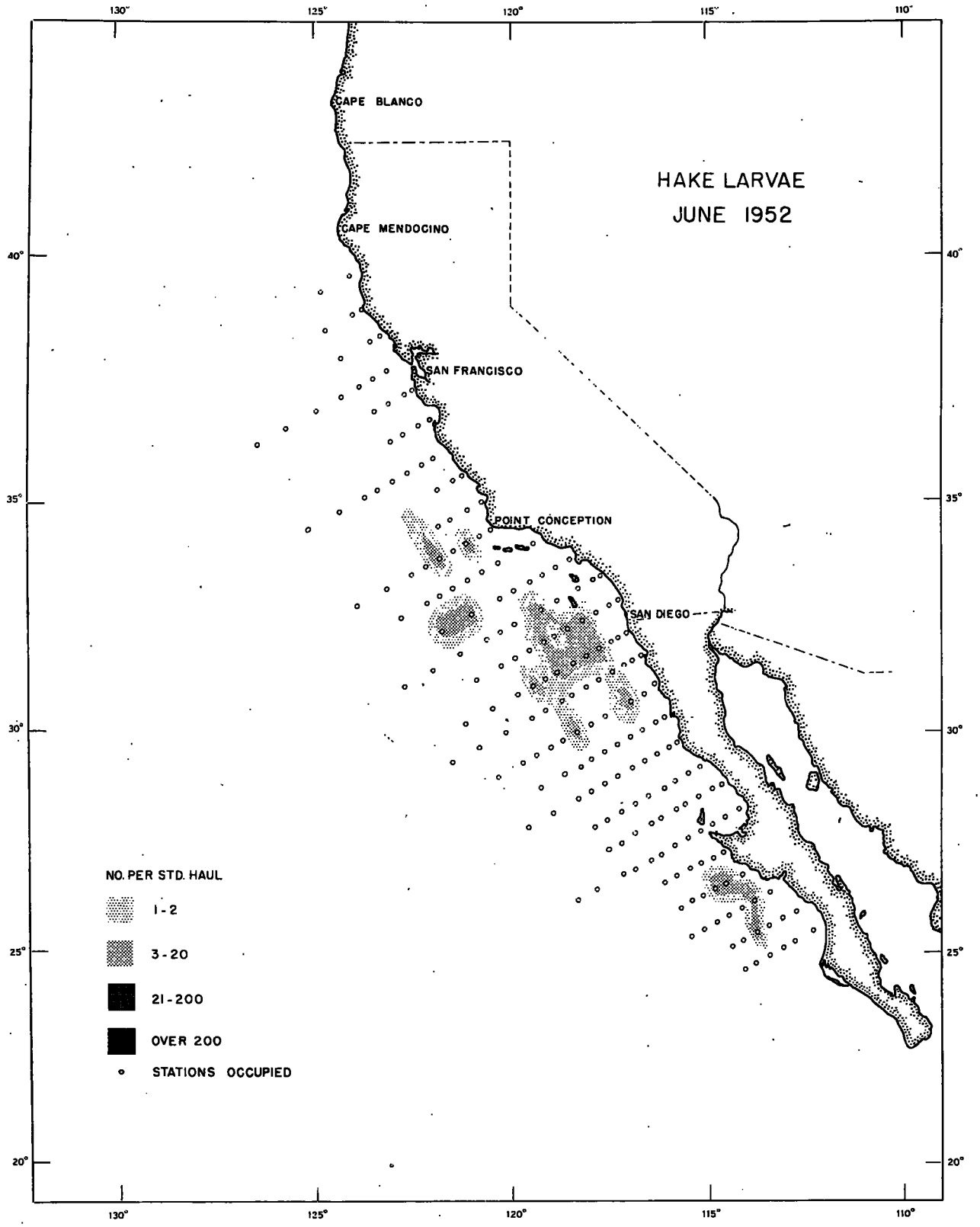

FIGURE 25.—Distribution and abundance of hake larvae during June 1952.

Relation to temperature.—The temperature range over which hake larvae were taken at station 94.80 was between 10.8° and 14.3° C., and in the other depth-distribution series it was between 11.0° and 15.4° C., with most larvae occurring at temperatures between 11.5° and 14.3°. The largest concentrations of hake larvae occurred near to or within the thermocline.

With the limited information on hand about the depth distribution of hake larvae, it is difficult to relate the distribution of hake larvae taken on survey cruises to temperature. In making such a comparison, it is desirable that the temperature at each station be expressed as a single value. This value can be either the average of a depth zone (the stratum within which most larvae occur), or the temperature at a selected depth (preferably the depth at which the largest concentrations of larvae occur). A problem arises in selecting either a depth zone or a particular depth, for there is some evidence that the depth distribution as determined from special studies (tables 7 and 8) may not be typical of the general distribution of hake larvae. The yearly catch of hake larvae was increased several fold when the average depth of hauls was increased from approximately 68 to 135 meters, indicating that a larger proportion of hake larvae occur between 68 and 135 meters deep than in the stratum above. Obviously, more work is needed to determine the usual depth zone within which hake occur, and the relation of the depth distribution to such features as thermocline depth and latitude. Consequently, we have not tried to obtain the average temperature of a depth zone.

In making temperature observations at a hydrographic station, thermometers are usually spaced at only four depths in the stratum between 50 and 150 meters, these depths being 50, 75, 100, and 150 meters. In selecting a level that will represent the usual concentration of hake larvae, and yet have a directly determined, rather than an interpolated, temperature value, one of these four depths should be used. We have selected the 75-meter level. The abundance of larvae in relation to the temperature at this depth is summarized in table 9. The large concentrations of hake larvae (1,001 or more per standard haul) were taken over a 4.5-degree temperature range, 10.6° to 15.0° C. This temperature range is very similar to that found at the depths where hake larvae were obtained during vertical distribution studies. The overall temperature range at all stations at which hake larvae were obtained was greater, being from 8.6° to 18.5° C. Only about 4 percent of the occurrences were at temperatures greater than 16° C., however.

TABLE 9.—*Relation between water temperature at 75-meter depth and abundance of hake larvae, 1951 and 1952*

Temperature at 75-meter level	Number of standard hauls that collected—				Total number of hauls
	1 to 10 larvae	11 to 100 larvae	101 to 1,000 larvae	1,001 or more larvae	
Centigrade					
8.6°–9.0°	4	0	0	0	4
9.1°–10.0°	37	29	4	0	70
10.1°–11.0°	56	30	16	1	103
11.1°–12.0°	41	42	24	6	113
12.1°–13.0°	38	18	17	9	82
13.1°–14.0°	28	20	19	4	71
14.1°–15.0°	27	27	23	7	84
15.1°–16.0°	13	16	5	0	34
16.1°–17.0°	9	5	1	0	15
17.1°–18.0°	5	2	0	0	7
18.1°–18.5°	2	0	0	0	2
Total	260	189	109	27	585

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ADDENDUM

The interesting paper on American hakes by Ginsburg (Whitings on the coasts of the American continents, U. S. Dept. Interior, Fish and Wildlife Service, Fish. Bull. 96, vol. 56, pp. 187–208) was not seen by the authors until the present paper was in page proof. Ginsburg reports two species of hake from off western North America, *Merluccius productus* and *M. angustimanus* Garman. Eight specimens of the latter species, collected between Del Mar, Calif., and Panama were examined by Ginsburg.

The meristic characters of the two species, as given by Ginsburg, are as follows:

	M. productus	*M. angustimanus*
First dorsal	10–12	11 or 12
Second dorsal	39–44	36–39
Anal	41–44	37–40
Pectoral	14–16	15–17
Gill rakers	4–5+13–18	3–5+12–14
Scales (lateral line)	147–166	130–149

Although not mentioned in the body of the paper, a careful examination was made of our collections of hake eggs and larvae to determine whether one or two species were represented. We could not find evidence of more than one species. All specimens on which the dorsal and anal fins were fully developed had 40 to 42 rays in the second dorsal and 40 to 43 rays in the anal. Thus, our specimens were outside the range given by Ginsburg for *M. angustimanus*, but within the range associated with *M. productus*. Apparently, *M. angustimanus* either does not spawn within the area routinely surveyed on cruises of the California Cooperative Oceanic Fisheries Investigations, or the spawning takes place at a deeper level than that sampled by the hauls.

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PINK SALMON TAGGING EXPERIMENTS IN ICY STRAIT AND UPPER CHATHAM STRAIT 1950

By CARL H. ELLING and PAUL T. MACY

FISHERY BULLETIN 100

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Although migration routes of pink salmon (*Oncorhynchus gorbuscha*) in Southeastern Alaska were generally defined as the result of tagging experiments in the 1920's and 1930's, a more critical examination of the racial composition of the various runs was needed. During the summer of 1950, 17,400 pink salmon were tagged in Icy Strait and Upper Chatham Strait to determine the timing and composition of the runs contributing to the fishery in those areas.

Recoveries of fish tagged in Icy Strait confirmed the findings of preceding experiments. Pink salmon were found to disperse easterly through Icy Strait, south into Chatham Strait, and then east and north into Frederick Sound and Stephens Passage. Smaller groups proceeded to Lynn Canal and Peril Strait. There was little movement to westerly areas of Chichagof Island and into and beyond Sumner Strait.

Recoveries of salmon tagged in Upper Chatham Strait showed a predominant southward movement through Chatham Strait, an easterly and northerly movement into Frederick Sound and Stephens Passage, and a northward migration toward Icy Strait.

Extensive stream recovery of tagged fish suggests that pink salmon bound for Stephens Passage, Chatham Strait, and Icy Strait streams passed through Icy Strait at about the same time. Icy Strait races were in evidence from July 25 to September 5, Upper Chatham Strait races from August 1 to September 5, and Stephens Passage races from July 25 to August 30. Recoveries from Upper Chatham Strait taggings of August 20 to September 3 were concentrated in Chatham Strait streams. A few recoveries were made in Stephens Passage, Frederick Sound, and Peril Strait.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

PINK SALMON TAGGING EXPERIMENTS IN ICY STRAIT AND UPPER CHATHAM STRAIT 1950

By Carl H. Elling and Paul T. Macy

FISHERY BULLETIN 100
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PINK SALMON TAGGING EXPERIMENTS IN ICY STRAIT AND UPPER CHATHAM STRAIT, 1950

By CARL H. ELLING and PAUL T. MACY, *Fishery Research Biologists*

Early in 1950 the United States Fish and Wildlife Service announced a new program designed to concentrate Alaska fishery research on the pink-salmon fishery of Southeastern Alaska. A series of tagging experiments at strategic points in the Alexander Archipelago was planned as part of this program. The purpose of these experiments was (1) to identify the racial composition of the runs of pink salmon (*Oncorhynchus gorbuscha*) in each of the major fishing areas of Southeastern Alaska during the course of the season, by tracing the fish from the point of tagging to the spawning streams, and (2) to gather all possible other data pertinent to rates of migration, routes of travel, and intensity of fishing.

Perpetuation of our salmon stocks at a commercially productive level depends on regulation of the catch so that enough salmon of each race reach their respective spawning grounds when water conditions are right for spawning. Once salmon have spawned successfully, development within the egg and growth of the fry after hatching depend on natural conditions over which man has little control. These conditions make it difficult to determine the direct relation between escapement (that is, those salmon successfully reaching spawning areas) and return (that is, those salmon surviving to enter the fishery 2 years later).

Regulation of the pink-salmon fishery in Southeastern Alaska is particularly complex because of the number of streams and the differing spawning times in the area. To provide the best distribution of spawners in as many streams as possible, a thorough knowledge of the spawning periods of the various races, their availability and movements, and the exploitation in the fishery is required. Tagging is one way by which the biologist may gain some information about the pink-salmon fishery in Southeastern Alaska.

Tagging experiments in Southeastern Alaska were inaugurated by Willis Rich and his associates in 1924. Through tagging and subsequent recovery of tagged fish by the commercial fishery, those investigators were able to define general routes of migration, and to some degree show the timing of various runs. Information from those programs found ready application in the management of the fishery.

In our recent experiments we have sought to supplement earlier tagging studies with specific data on racial composition and availability in the fishery. We have achieved this by extensive tagging over a 43-day period, followed by an equally extensive recovery program both in the fishery and on the spawning grounds.

We are particularly indebted to the Columbia River Packers Association for the use of their traps at Point Adolphus and Pleasant Island, to the Todd Packing Company for use of their Cube Point trap, and to the Superior Packing and P. E. Harris Companies for use of their False Bay traps. We are obliged to the many individuals who returned tags and who carefully noted the information on their recovery. The staff of the Fisheries Research Institute was especially helpful in making a number of stream recoveries. Our particular thanks go to the bookkeepers of the various canneries, who were frequently interrupted during their regular activities to record and make payment for tags. Without such valuable assistance the recovery program could not have attained the success that it did. We thank Elizabeth Vaughan for review of the statistics presented in this paper, and are indebted to the late R. F. Shuman for his helpful instruction and planning assistance during the early phases of the experiment. Others who contributed liberally to the review of this paper include Albert L. Tester, O. E. Sette, C. E. Atkinson, C. J. Burner, M. G. Hanavan, and R. P. Silliman.

AREA DESCRIPTION AND NATURE OF FISHERY

Southeastern Alaska is composed of a group of islands and a narrow mainland strip which together comprise an area approximately 400 miles

long and 125 miles wide. The streams on these islands and along the rugged mainland shore provide the spawning grounds for millions of pink salmon each year. The principal watercourses in the northern part of the area are Icy Strait, Chatham Strait, Tenakee Inlet, Peril Strait, Frederick Sound, Stephens Passage, and Lynn Canal (fig. 1). Through this extensive network of inland passageways the salmon migrate to reach their parent streams (figs. 2 and 3). Most of the fishery is centered in this series of waterways. A minor part of the catch is taken along the outlying westerly shores of Baranof and Chichagof Islands.

The pink salmon of this area can be broadly classified into three groups in accordance with the time they arrive on their spawning grounds: (1) The early runs, which appear in quantity during the latter part of July and early August, (2) the midseason runs, which reach their height in late August and early September, and (3) the late runs, which extend through September and into early October.

A number of streams along the mainland shore of Stephens Passage, some of those emptying into Seymour Canal, and several tributaries of Tenakee Inlet, are known from stream surveys to support most of the early-spawning pink salmon. Fishing regulations in 1948, 1949, and 1950 protected these early fish by delaying the opening day of the fishing season until mid-August. This allowed many of the early spawners to escape all or nearly all of the fishery and reach the spawning grounds.

The late opening date of fishing has placed the heaviest fishing on the midseason- and late-spawning salmon. These fish, with a few exceptions, are shown by stream surveys to be produced by streams in Chatham Strait, Frederick Sound, and Peril Strait, and the few streams on the western shores of Baranof and Chichagof Islands. The Icy Strait area supports races which are relatively early and others which appear throughout the balance of the season.

The two principal types of gear used in Southeastern Alaska are the fish trap and the purse seine. Nearly all traps are the floating type, constructed of a sturdy framework of native spruce logs. They are towed to locations before the beginning of each season and each trap is fastened in position by a series of anchors and a lead cable which runs from the shore to the outer face of the trap. If any part of the trap is in 100 feet or more of water at mean high tide, this "lead" must not exceed 900 feet in length. Chicken-wire mesh extends downward from the lead to a maximum depth of about 48 feet, forming a barrier to the passage of salmon moving along the shoreline. In attempting to find a way around this barrier, the salmon swim into a series of trap compartments known as the jigger, heart, pot, and spiller. A single tunnel, tapering from a wide to a comparatively narrow opening, leads into each of these compartments. During the weekend closure of 36 hours, the wire-mesh heart walls are dropped and the pot tunnel is closed to allow the fish to pass out around the lead and through the trap. Most traps have a small cabin that houses a watchman while the trap is in operation. At the end of each season the trap anchors are lifted, the lead cable is released, and the trap framework is towed to a sheltered bay or cove, where it is stored until it is needed in the following season.

The other principal gear type is the purse seine which has been in use for many years in the Alaska salmon fishery. Although seine boats have gone through considerable development since the early days of the fishery, keel length is limited to 50 feet by law. In addition to this, the present law states that a seine used in Southeastern Alaska must not exceed 250 fathoms in length or 19½ fathoms in depth, nor be less than 150 fathoms in length and 8½ fathoms in depth. The standard mesh size in use is a 3½-inch stretch measure webbing.

TAGGING EQUIPMENT AND PROCEDURE

Metal strap tags, commonly used in all early salmon-tagging experiments in Southeastern Alaska (Rounsefell and Kask 1945), were easily applied to the fish but were not always easily detected, particularly in streams. To facilitate stream recovery of tagged salmon, we used the Petersen-disk-type tag, now almost universally used for tagging salmon. The two white plastic disks, $\frac{5}{16}$-inch in diameter, were attached one on each side of the fish by a 2-inch nickel pin inserted through the fleshy part of the back just below the dorsal fin.

In preparation for the tagging work, we constructed several tagging boxes like those developed and used by R. F. Shuman and P. R. Nelson in their investigations on the Karluk River, Kodiak

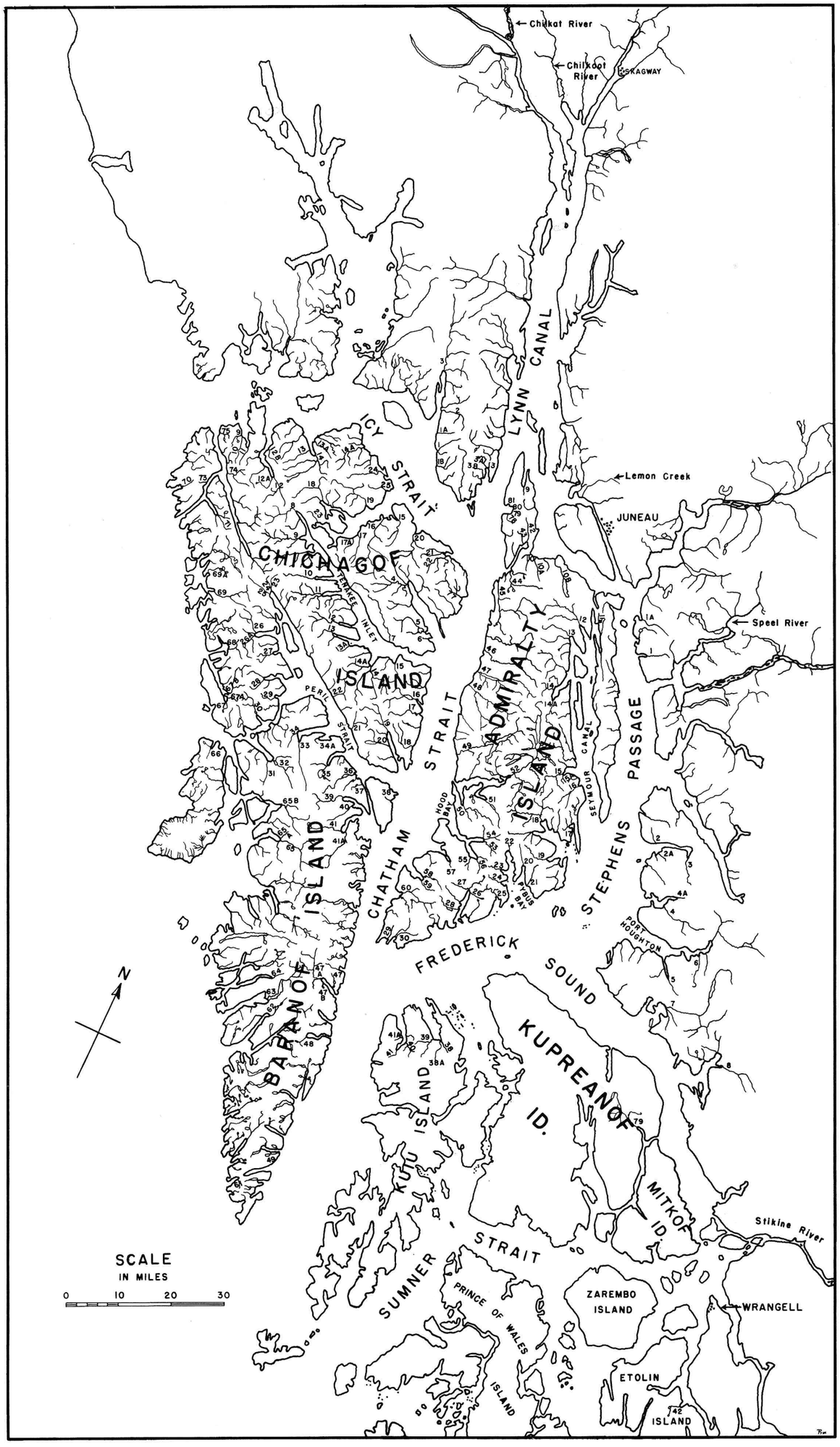

FIGURE 1.—Stream reference map of northern section of Southeastern Alaska.

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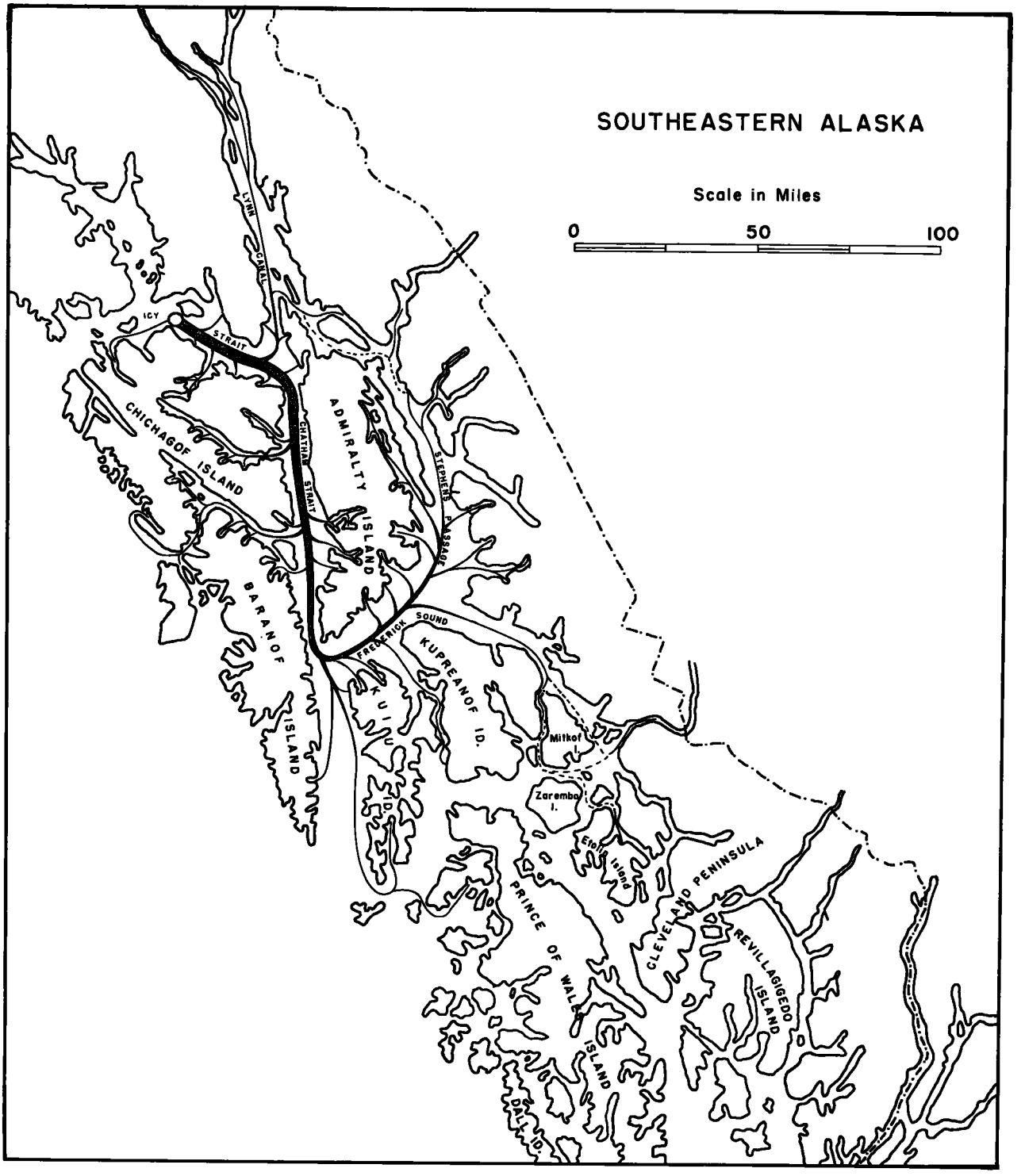

FIGURE 2.—Distribution of pink salmon tagged in Icy Strait, 1950, as indicated by commercial and stream tag recoveries.

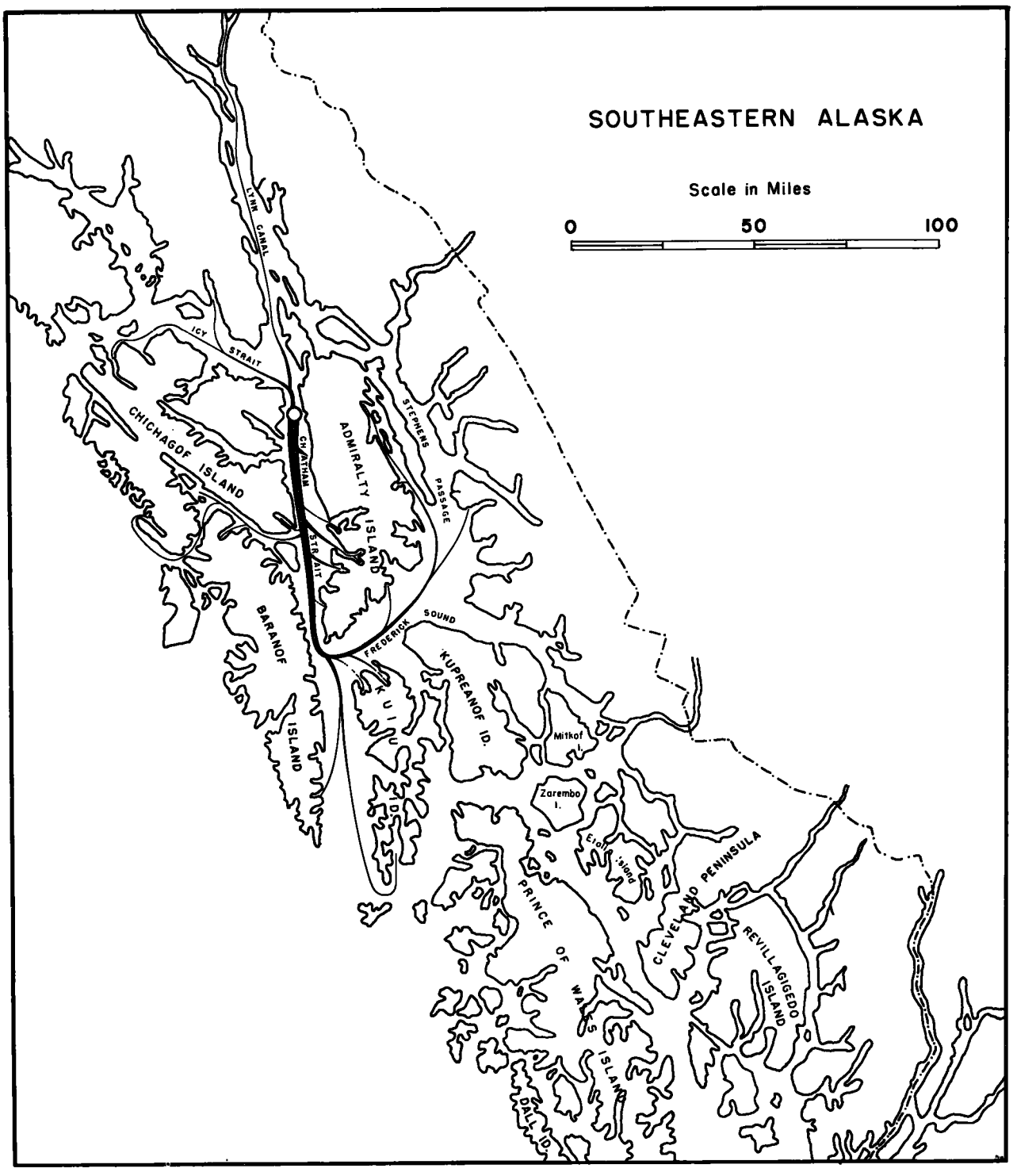

FIGURE 3.—Distribution of pink salmon tagged in Upper Chatham Strait, 1950, as indicated by commercial and stream tag recoveries.

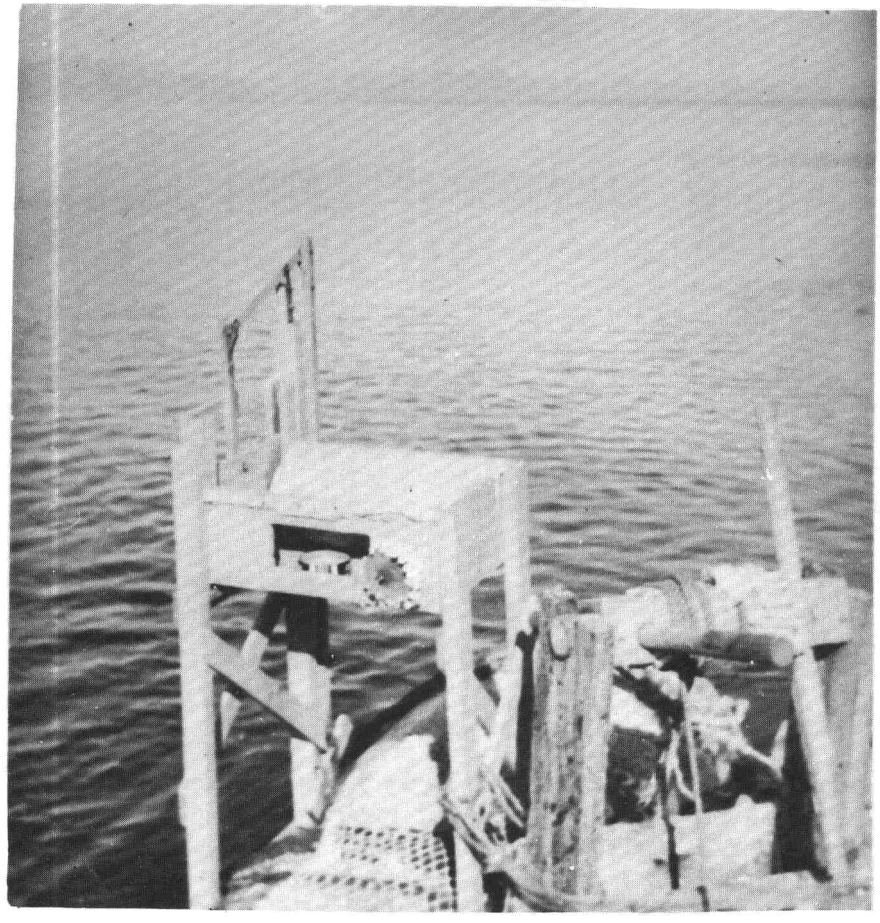

FIGURE 4.—Tagging box in position on head log of fish trap. Note tags and pins inserted in purse-seine cork. The metal container in box opening holds unnumbered disks.

Island. The simple mechanical features incorporated in the box (fig. 4) made it ideal for our use in tagging from floating fish traps. It is essentially a rectangular cradle, 24 by 15 by 8 inches, with V-shaped side walls mounted on 4-foot legs so that the fish are at waist-high level for tagging. The inner walls are lined with padding covered with heavy canvas to afford adequate protection against excessive bruising of the fish in handling. A sliding door, operated by a foot lever, opens at the outer end of the box to facilitate a quick, harmless release of the tagged fish. The tagger's side of the box is equipped with a rotating cork in which 100 pins with serially numbered disks are inserted. A pin is plucked from the cork as each successive fish is tagged. A convenient container, placed in a slot on the side of the box, holds unnumbered disks. The tagger generally puts 20 or so of these disks in his mouth, picking them one at a time from his lips and placing them on the pin as it is inserted through the fish. After 100 fish are tagged, the empty cork is replaced by one containing the next series of numbered disks.

Each day, preparatory to tagging, our crews pursed the trap spiller webs, confining the captured salmon to a narrow area at the head log of the fish trap (fig. 5). If the spiller contained several thousand salmon, care was taken to avoid crowding the fish excessively. Despite these efforts some smothering did occur. In this respect we found that pink salmon could stand far more abuse than could the other four species of salmon taken in the traps.

After the spiller web was pursed, we set the tagging boxes on the head log of the fish trap and arranged the tag series to be used for the day. By this time the trapped salmon had quieted

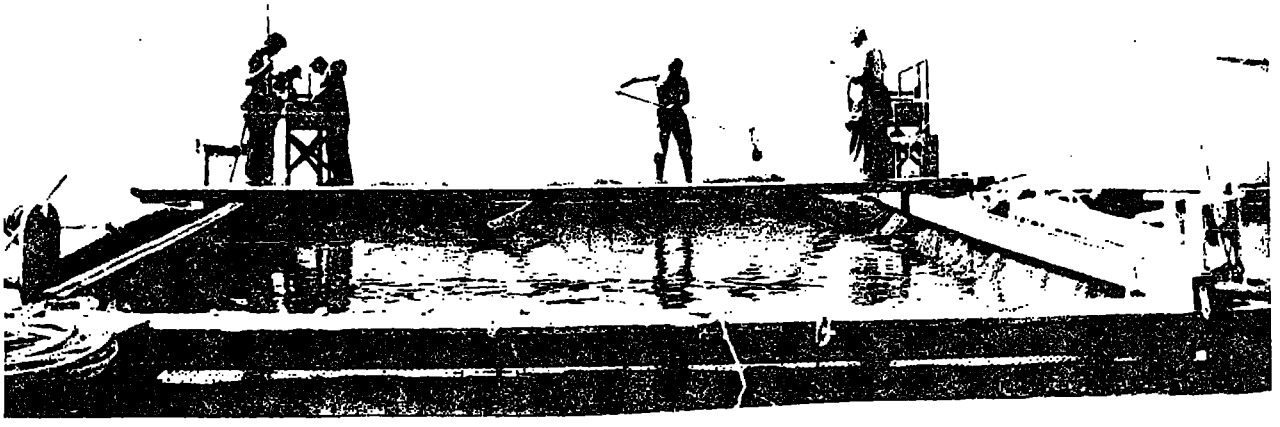

FIGURE 5.—Ideal tagging conditions at Point Adolphus, Alaska. Trap spiller has been lifted to confine fish in restricted area at head log of trap.

down enough to permit moderate handling of the fish while tagging.

Each of our tagging teams was composed of three men. One man dipped the fish from the trap spiller into the tagging box, placing the head of the salmon toward the outer end of the box. Another held the fish firmly in position with the dorsal side up by placing one hand over the head and the other around the caudal peduncle. Using long-nosed pliers, the tagger forced the nickel pin, strung with a numbered disk, through the fish, placing a blank tie-in disk on the opposing side. He then clipped off all but about ¾ inch of the pin and bent this remaining portion in circular fashion over the hole in the blank disk, taking care to fit the tag firmly but not too tightly. His assistant then opened the box door and released the fish into the open water. The whole operation was completed in less than a minute. Under favorable conditions, each team could tag from 800 to 1,000 fish a day.

TAGGING

Icy Strait

Two tagging sites, approximately 8 miles apart, were selected about midway in Icy Strait, one on each side of the channel (fig. 6). Our purpose here was to determine whether pink salmon in this area exhibited similar migratory patterns when tagged on opposite shorelines, to detect random movements between the two locations, and to give us a duplicate check on the movements of all fish tagged in this locality. The sites were picked for their proximity to the open ocean and their desirability as "calm water" tagging points. Several traps further west were avoided because of their exposure to ocean disturbances. As it was our desire to tag as continuously as possible, the locations selected were those that we felt would assure a reasonably uninterrupted operation.

The 1950 Icy Strait taggings differed from former experiments in Southeastern Alaska in that they were initiated fully 3 weeks before the start of the general commercial fishing season. Tagging commenced on July 25 at Point Adolphus trap No. 4 of the Columbia River Packers Association. Two days later our second crew began tagging at that company's Pleasant Island trap No. 2. Tagging progressed daily through August 14, the day before the opening of the commercial fishing season. During this time, 14,534 pink salmon were tagged—approximately all the pink salmon entering these two traps.

During the fishing season, tagging was con-

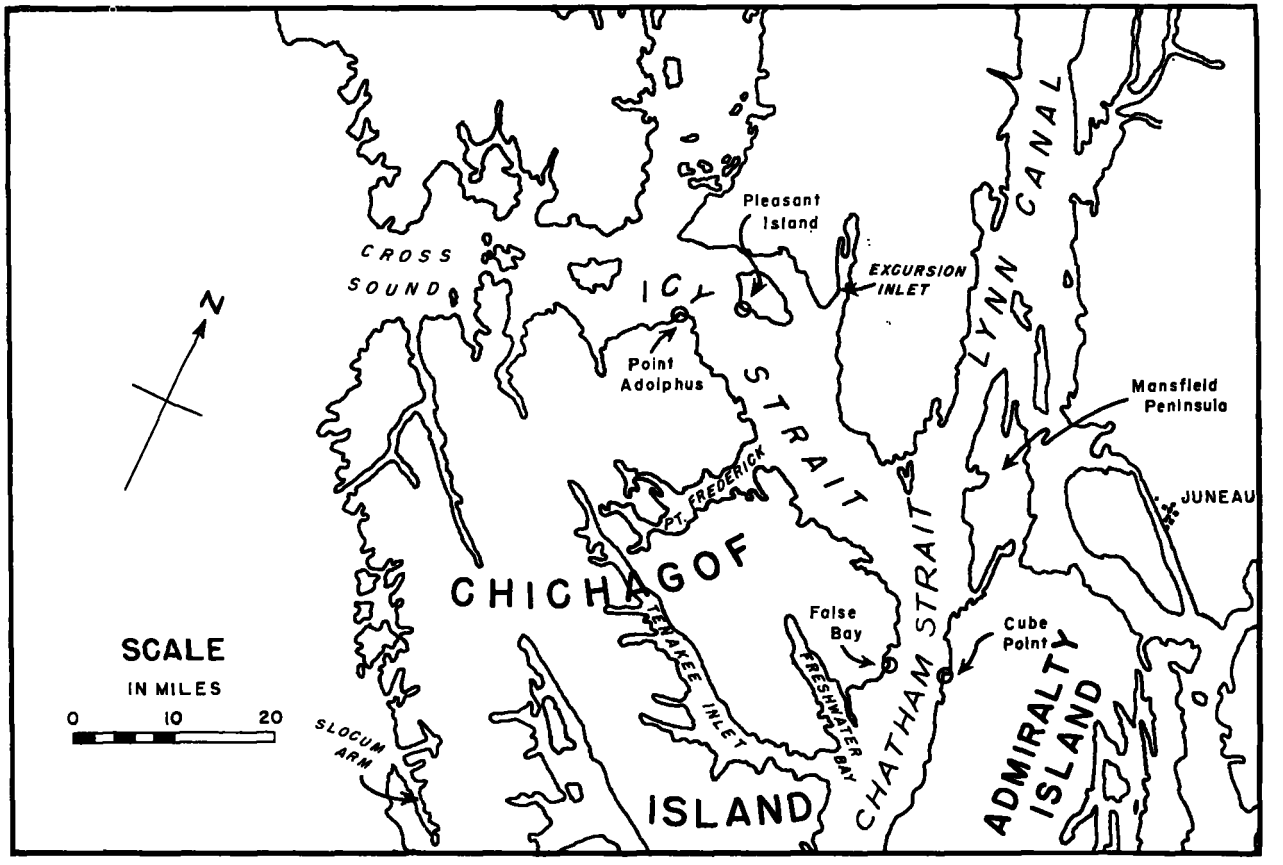

FIGURE 6.—Tagging locations in Icy Strait and Upper Chatham Strait.

ducted at Pleasant Island on August 27 and 30 and September 5 and at Point Adolphus on September 4. The total number of pink salmon tagged during these experiments was 1,061.

In all, 15,595 pink salmon were tagged in Icy Strait in the 43 days from July 25 to September 5.

Upper Chatham Strait

Tagging experiments in Upper Chatham Strait during the weekly closed periods of the regular fishing season included releases at the Todd Packing Company's Cube Point trap on August 20 and September 3, at the Superior Packing Company's False Bay trap on August 21, and at P. E. Harris's False Bay trap on September 3. Most of the 1,805 pinks tagged at these traps were taken at the Cube Point location on August 20.

COMMERCIAL RECOVERIES

Recovery effort

Before considering the returns within the commercial fishery, it is important to discuss in some detail the fishing effort which was instrumental in effecting the recovery of these tags. The length of season and the amount and distribution of gear brought into play are especially important in assessing the value of returns made from a particular tagging experiment.

Almost the entire commercial recovery[1] of tagged salmon began with the start of the general season at 6 a. m. on August 15. The few tags taken by trollers and gill netters before this date are negligible in relation to the total return. The fishing season continued until 6 p. m., September 2, with the usual 36-hour weekend closures. A 3-day extension was subsequently granted for the period of 6 a. m., September 7, to 6 p. m., September 9. The total fishing time was 432 hours.

Complete data on the quantity of mobile gear operated in this area and the time it was fished are lacking, but we do have figures on the number of traps used in each area. Since they were instrumental in making the majority of recoveries, their distribution by areas is given to indicate

[1] Commercial recoveries are those made in salt water, in contrast to stream recoveries, which are those made within stream channels.

the intensity of fishing effort in the various localities in which tags were recovered:

	Number of traps
Icy Strait	17
Lynn Canal	2
Upper Chatham Strait	31
Lower Chatham Strait	5
Frederick Sound	18
Stephens Passage [1]	0

[1] No traps were permitted in Stephens Passage during the 1950 season, nor were purse-seine vessels allowed to operate on the mainland shore of this area.

As the 1950 run of pink salmon in Icy Strait was one of the smallest on record, the daily volume of pinks entering the traps at which we were operating was never more than we could handle. Consequently, almost every pink salmon captured in these traps during our experiments was tagged, and a rather large number of tagged salmon were distributed in a relatively meager catch. We believe the combination of these two factors resulted in an unusually complete recovery. Had a similar number of tags been distributed in a large catch, the possibility of tags being overlooked probably would have been greater.

To effect the return of tags, a 50-cent reward was offered for each recovery with information pertinent to its capture. Placards announcing the tagging program and the reward for the return of tags with capture information were posted at strategic points in the fishing area. Information desired with the tag returns included date of capture, location, and type of gear. Tag-return booklets providing for simple listing of the above data were distributed to canneries, fish buyers, fishermen, and others likely to encounter tagged salmon.

Since tags were to be recovered both in the commercial fishery and on the spawning grounds, the most practical means of achieving an effective return in all areas depended on properly deploying our personnel and securing all possible help from outside sources. From the outset we decided that it would be impractical for our crews to attempt a thorough recovery program both in the commercial fishery and on the streams. Consequently, commercial recoveries and returns were left almost solely to fishermen and cannery personnel, while Service personnel concentrated on the capture of tagged salmon in streams.

For the most part this procedure was satisfactory. Since by far the greatest part of the commercial recovery came from traps, the matter of capture and return was largely the work of trap watchmen and tendermen. Cannery bookkeepers aided in recording the pertinent information on the tag-recovery forms which had been provided them and also made reward payments for return of the tags. (Companies honoring tag recoveries were reimbursed by the Fish and Wildlife Service.)

The occasional errors and omissions that appeared on the tag-return forms are understandable since first-hand data were not always available to those recording the facts of capture. Cannery tenders generally have several traps to service in the course of a day's run, and if tags are not immediately accounted for at each trap their specific identity can very well be lost by the time they reach the cannery bins. Had it been possible for us to station Service personnel aboard the tenders and at the canneries, the accuracy of recovery information undoubtedly could have been improved, but it is doubtful whether total recovery would have increased measurably. The fact that almost 6,500 tags were returned to us by canneries and fishermen, with virtually no assistance from our personnel, is ample proof of the cooperation given us by the fishing industry.

Of all tags returned by the commercial fishery, traps accounted for 88 percent, purse seines 8.5 percent, gill nets 2 percent, and trollers 0.5 percent. One percent came from unknown sources.

Returns from Icy Strait tagging

Tables 1 and 2 summarize the recoveries from the tagging at Pleasant Island and Point Adolphus. The elapsed time represents the number of days from date of tagging to date of capture. Tag returns are listed by major geographical subdivisions in which capture was made. Chatham Strait recoveries are divided into two sections, the upper portion including the area from the junction of Icy and Chatham Straits at Rocky Island to a line crossing Chatham Strait at Point Gardner (southern tip of Admiralty Island), and the lower section including all headlands and waters south of this line.

About 7 percent of all the returns could not be listed according to specific headland, bay, or inlet, because information on the tag-return forms was inadequate. Whenever the data were sufficient to designate the general area of recovery, they were listed accordingly under Icy Strait, Chatham Strait, or Frederick Sound. All recoveries credited to Chatham Strait were identified as having been made in the upper section of the strait.

TABLE 1.—*Commercial recoveries of pink salmon tagged at Pleasant Island, Icy Strait, 1950*

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	July 27–28 (50 tagged)				July 30 (361 tagged)				July 31 (480 tagged)				Aug. 1–2 (178 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove																
Inian Island																
Point Adolphus																
Point Gustavus																
Eagle Point																
Porpoise Island																
Whitestone																
Spasski																
Excursion Inlet					1			19	2	15	19	17				
Port Frederick									1			15				
Icy Strait									2			24	1			23
Total	0 (0%)				1 (0.3%)				5 (1.0%)				1 (0.6%)			
Lynn Canal area:																
Naked Island					1			23								
Funter																
Eldred Rock																
Chilkat Inlet									1			19	1			17
Chilkoot Inlet									2			11				
Lutak Inlet									1			17				
Total	0 (0%)				1 (0.3%)				4 (0.8%)				1 (0.6%)			
Upper Chatham Strait area:																
Hawk Inlet–Funter									1			24	2	15	20	18
Square Cove																
False Bay					1			27	1			16	1			16
Cube Point					1			18	1			21				
Point Hepburn	1			22					2			25				
Gypsum																
South Passage Point													1			13
Fishery Point					1			16	1			15				
Marble Bluff									3	16	24	19	2			13
Marble Cove																
Basket Bay	1			22	1			19								
Killisnoo					1			17	1			17				
Point Thatcher					1			20	1			16				
Peninsula Point									1			16				
Hood Bay					1			18								
Distant Point																
Eagle Point																
Chaik Bay					2	26	40	33	2	17	18	18				
Point Caution	2			21	1			18	2	15	18	17				
Point Turbot																
Wilson Cove									1			16				
Chatham Strait									3	21	26	24				
Total	4 (8.0%)				10 (2.8%)				20 (4.2%)				6 (3.4%)			
Lower Chatham Strait area:																
Red Bluff Bay					1			18					1			14
Kingsmill–Point Ellis	1			22	2	17	22	20	1			24				
Tebenkof Bay																
Gedney Harbor									1			23				
Total	1 (2.0%)				3 (0.8%)				2 (0.4%)				1 (0.6%)			
Frederick Sound–Stephens Passage area:																
Carroll Island																
Benson Cove																
Security Bay																
Saginaw Bay					1			25								
Point Brightman									1			16				
Point Cornwallis					1			17	1			26				
Deepwater Point																
Herring Bay									1			19				
Point McCartney																
Hamilton Bay																
Port Camden									1			18				
Cape Bendel																
Point Napean					1			19								
Pybus Bay					3	16	20	18	5	17	18	18	4	13	24	19
Pinta Point									1			23				
Gambier Bay																
Young Bay									2	15	19	17				
Taku Inlet	1			?	5			17	7	16	23	20	2			?
Portland Island																
Shelter Cove																
Frederick Sound																
Total	1 (2.0%)				11 (3.0%)				19 (4.0%)				6 (3.4%)			
Other areas:																
Tenakee Inlet																
Hoonah Sound					1			20	1			32				
Slocum Arm																
Affleck Canal																
Wrangell Narrows																
Warren Cove																
Total	0 (0%)				1 (0.3%)				1 (0.2%)				0 (0%)			
Unknown	0 (0%)				1 (0.3%)				4 (0.8%)				2 (1.0%)			
Grand total	6 (12.0%)				28 (7.8%)				55 (11.4%)				17 (9.6%)			

TABLE 1.—*Commercial recoveries of pink salmon tagged at Pleasant Island, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	Aug. 3 (258 tagged)				Aug. 4 (115 tagged)				Aug. 5 (729 tagged)				Aug. 6 (572 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove					1			13								
Inian Island													1			11
Point Adolphus									1			?				
Point Gustavus																
Eagle Point																
Porpoise Island																
Whitestone																
Spasski									2			14				
Excursion Inlet	1			16	1			12	3	11	13	12	5	9	16	13
Port Frederick	1			29												
Icy Strait	1			14	1			20	1			35	4	10	18	13
Total	3 (1.2%)				3 (2.6%)				7 (0.9%)				10 (1.8%)			
Lynn Canal area:																
Naked Island	1			14									2	10	11	11
Funter																
Eldred Rock																
Chilkat Inlet	1			14									2	8	19	13
Chilkoot Inlet	1			?					4	10	25	15	3	10	11	10
Lutak Inlet	1			?					3	7	12	10	3	8	16	10
Total	4 (1.5%)				0 (0%)				7 (0.9%)				10 (1.8%)			
Upper Chatham Strait area:																
Hawk Inlet–Funter	1			37					7	10	19	12	8	9	12	10
Square Cove									3	14	20	17	1			9
False Bay	1			14									3	12	23	18
Cube Point	3	12	14	13	1			13	8	10	25	12	10	9	17	11
Point Hepburn									5	11	20	16	1			10
Gypsum																
South Passage Point	2	12	15	14					2	11	13	12	3	9	11	10
Fishery Point									2	11	12	12	5	9	15	10
Marble Bluff					2	11	13	12	6	10	13	12	4	9	12	10
Marble Cove	1			14					1			?	1			10
Basket Bay					1			12	5	12	16	13	4	9	11	11
Killisnoo					1			13	3	12	36	28	3	11	12	12
Point Thatcher									3	12	14	13	5	10	20	13
Peninsula Point									3	11	12	12	2			10
Hood Bay									2	11	28	20	2			11
Distant Point					1			13	1			12	1			11
Eagle Point																
Chaik Bay									1			20				
Point Caution	3	12	16	15					5	10	17	14	7	10	16	12
Point Turbot									1			16				
Wilson Cove									1			13	1			12
Chatham Strait									19	10	21	13	8	9	13	12
Total	11 (4.2%)				6 (5.2%)				78 (10.7%)				69 (12.0%)			
Lower Chatham Strait area:																
Red Bluff Bay									1			18	2	12	13	12
Kingsmill-Point Ellis									8	13	24	16	9	9	26	15
Tebenkof Bay					1			20								
Gedney Harbor									1			18				
Total	0 (0%)				1 (0.9%)				10 (1.4%)				11 (1.9%)			
Frederick Sound–Stephens Passage area:																
Carroll Island									1			10	2	11	18	15
Benson Cove									2			11				
Security Bay									1			12				
Saginaw Bay	1			13					2			12	1			17
Point Brightman	1			15	1			26	3	13	17	15				
Point Cornwallis									1			10				
Deepwater Point					1			17	9			?	2	12	16	14
Herring Bay	1			19					4	11	25	16	1			13
Point McCartney					1			18								
Hamilton Bay																
Port Camden																
Cape Bendel	2	13	16	14					1			21	3	11	13	12
Point Napean	1			14					1			13				
Pybus Bay	4	12	15	14	1			15	21	10	20	13	11	10	16	13
Pinta Point													1			17
Gambier Bay	1			?												
Young Bay	3	12	16	15					3			14	2			13
Taku Inlet	3			14					2			5	2			12
Portland Island																
Shelter Cove																
Frederick Sound													1			10
Total	17 (6.6%)				4 (3.5%)				51 (7.1%)				26 (4.5%)			
Other areas:																
Tenakee Inlet																
Hoonah Sound	1			16					2			21				
Slocum Arm	1			13												
Affleck Canal													1			13
Wrangell Narrows	1			18												
Warren Cove																
Total	3 (1.2%)				0 (0%)				2 (0.3%)				1 (0.2%)			
Unknown	3 (1.2%)				3 (2.6%)				11 (1.5%)				12 (2.1%)			
Grand total	41 (15.9%)				17 (14.8%)				166 (22.8%)				139 (24.3%)			

TABLE 1.—*Commercial recoveries of pink salmon tagged at Pleasant Island, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	Aug. 7 (811 tagged)				Aug. 8 (290 tagged)				Aug. 9 (202 tagged)				Aug. 10 (399 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove					1			10					1			7
Inian Island	1			8	1			31								
Point Adolphus	2			8					1			13				
Point Gustavus													2	6	8	7
Eagle Point					1			18	1			9				
Porpoise Island																
Whitestone																
Spasski	2			15									1			3
Excursion Inlet	8	8	19	11	8	7	15	11	1			7	7	5	23	9
Port Frederick	3	8	25	19	1			24	1			23				
Icy Strait	1			13	2	9	25	17					1			6
Total	17 (2.1%)				14 (4.8%)				4 (2.0%)				12 (3.0%)			
Lynn Canal area:																
Naked Island	4	9	12	10	2	9	14	12					1			6
Funter					1			30					1			4
Eldred Rock																
Chilkat Inlet													1			13
Chilkoot Inlet	3	9	12	10	1			?					5	6	20	13
Lutak Inlet	8	7	15	10	2	6	10	8	1			7	1			6
Total	15 (1.8%)				6 (2.1%)				1 (0.5%)				9 (2.3%)			
Upper Chatham Strait area:																
Hawk Inlet–Funter	14	5	19	9	5	7	10	8	8	6	10	7	8	5	16	6
Square Cove	4	10	18	14									1			11
False Bay	1			11					3	6	16	10	2	5	15	10
Cube Point	17	8	18	11	6	7	13	9	10	6	13	8	7	5	11	6
Point Hepburn	9	10	19	16	1			9	2	7	14	11	3	6	9	8
Gypsum	2	8	12	10												
South Passage Point	2	8	10	9	3	9	16	12	2	8	15	12	4			7
Fishery Point	7	8	10	9	1			8	2	8	9	8	3	5	11	8
Marble Bluff	17			10	3	8	9	8	3	6	7	7	9	5	8	6
Marble Cove	3	9	10	9	2	8	9	8					1			6
Basket Bay	4	9	11	10	3	9	10	10	3			7	7	6	9	7
Killisnoo	9	8	34	12	1			8					3			7
Point Thatcher	8	9	12	10	4	8	9	8	1			17	9	6	16	10
Peninsula Point	4	9	12	10									2			12
Hood Bay	2			24	2			15					1			28
Distant Point	7	8	11	9									3	5	7	6
Eagle Point	4	9	14	10									1			9
Chalk Bay	1			10									2	20	29	24
Point Caution	8	8	12	10	5	8	10	9	1			17	4	6	12	8
Point Turbot									1			10				
Wilson Cove	6	11	12	11	1			10					2			6
Chatham Strait	24	8	22	12	9	9	22	13	6	6	15	9	17	5	20	9
Total	153 (18.9%)				46 (15.9%)				42 (20.8%)				89 (22.3%)			
Lower Chatham Strait area:																
Red Bluff Bay									1			12	1			28
Kingsmill–Point Ellis	14	9	19	15	7	9	25	13	5	7	15	10	5	6	19	11
Tebenkof Bay	3			?					3	9	20	15	1			8
Gedney Harbor	1			16					1			14				
Total	18 (2.2%)				7 (2.4%)				10 (4.9%)				7 (1.8%)			
Frederick Sound–Stephens Passage area:																
Carroll Island	1			12	2			8					1			9
Benson Cove																
Security Bay					1			15								
Saginaw Bay													1			7
Point Brightman	2	11	12	12	1			10					1			8
Point Cornwallis	1			9					1			7	2	6	8	7
Deepwater Point	4	9	15	10	2	10	13	12	3	9	13	12	7	7	15	8
Herring Bay	5	11	32	16	2	10	11	10					1			7
Point McCartney	7	10	14	12	3	13	14	13					2	9	15	12
Hamilton Bay																
Port Camden	1			17					1			10				
Cape Bendel	6	9	12	10	4	8	11	8	1			7	2	6	7	6
Point Napean	3	10	16	14					2	7	17	12				
Pybus Bay	27	9	15	11	4	10	11	11	5	9	10	10	8	5	12	9
Pinta Point	1			19									1			13
Gambier Bay																
Young Bay																
Taku Inlet																
Portland Island	1			3												
Shelter Cove																
Frederick Sound	4	9	11	10	1			9	2			7	3	8	12	10
Total	63 (7.8%)				20 (6.9%)				15 (7.4%)				29 (7.3%)			
Other areas:																
Tenakee Inlet	1			12												
Hoonah Sound	3			24												
Slocum Arm													1			14
Affleck Canal	1			17												
Wrangell Narrows																
Warren Cove																
Total	5 (0.6%)				0 (0%)				0 (0%)				1 (0.2%)			
Unknown	23 (2.8%)				10 (3.4%)				7 (3.5%)				12 (3.0%)			
Grand total	294 (36.2%)				103 (35.5%)				79 (39.1%)				159 (39.9%)			

TABLE 1.—*Commercial recoveries of pink salmon tagged at Pleasant Island, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	Aug. 11 (380 tagged)				Aug. 12 (942 tagged)				Aug. 13 (994 tagged)				Aug. 14 (739 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove	1			7	1			6	4			5	1			4
Inian Island													3			2
Point Adolphus					1			3	3	2	11	5				
Point Gustavus									2			5	3	2	4	3
Eagle Point					1			6	3	5	10	7	5	4	9	5
Porpoise Island																
Whitestone									1			11	1			10
Spasski					2	5	7	6	7	3	4	3	14	2	3	3
Excursion Inlet	3	4	10	6	26	3	9	4	33	2	20	5	118	1	27	3
Port Frederick	1			21					1			2	1			18
Icy Strait	1			5	7	4	26	10	3			2	21			3
Total	6 (1.6%)				38 (4.0%)				57 (5.8%)				167 (22.6%)			
Lynn Canal area:																
Naked Island	1			5	9	3	10	4	14	3	12	4	3	2	18	6
Funter									1			5				
Eldred Rock													1			8
Chilkat Inlet					1			4								
Chilkoot Inlet					2	11	13	12	3	9	12	10	3	9	16	13
Lutak Inlet	1			4	3	3	10	6	2	5	8	6	1			4
Total	2 (0.5%)				15 (1.6%)				20 (2.0%)				8 (1.1%)			
Upper Chatham Strait area:																
Hawk Inlet–Funter	14	4	13	6	40	3	12	5	78	2	18	4	47	1	10	3
Square Cove	1			8	3			5	13	2	4	3	24	1	9	4
False Bay	2	5	15	10	4	5	17	10	8	3	13	4	10	2	3	2
Cube Point	6	4	11	6	26	3	9	4	52	2	19	4	38	1	15	3
Point Hepburn	4	8	15	10	8	3	13	7	16	3	12	9	19	2	15	5
Gypsum	2	4	8	6	2	5	6	6	1			?	1			5
South Passage Point	7	4	8	6	6	4	13	6	4	2	11	5				
Fishery Point					9	3	12	5	15	2	8	2	7	2	7	4
Marble Bluff	8	5	8	6	15	3	14	6	21	2	9	3	28	1	10	3
Marble Cove					5	4	5	4	4			4	5	2	3	3
Basket Bay	5	5	7	6	15	3	9	6	8	2	8	5	4	1	7	4
Killisnoo	2	6	10	8	13	4	29	8	13	2	14	4	3	9	27	21
Point Thatcher	3			5	18	4	7	4	12	3	4	3	6	5	12	9
Peninsula Point	3	5	8	6	7	4	10	6	1			9	2	5	8	6
Hood Bay	4	6	28	13	1			28	2			18	3	18	26	22
Distant Point	2	7	13	10	10	3	6	5	7	3	4	3	5	1	6	3
Eagle Point	1			10	2	4	5	4	2			8				
Chalk Bay	3	9	28	19	1			20	5	5	19	14				
Point Caution	5	6	12	7	22	3	12	6	16	3	10	5	6	4	12	5
Point Turbot					2			9								
Wilson Cove	2	7	8	8	7	4	6	6	7	3	12	6	2			5
Chatham Strait	21	4	19	6	51	3	17	8	80	2	27	5	49	2	26	6
Total	95 (25.0%)				267 (28.3%)				365 (36.7%)				259 (35.1%)			
Lower Chatham Strait area:																
Red Bluff Bay	2	10	13	12	3	10	11	11	2			8	1			9
Kingsmill-Point Ellis	15	5	20	10	20	3	17	9	18	3	20	10	9	4	26	12
Tebenkof Bay					1			12	2	10	17	14	1			16
Gedney Harbor					4	11	16	14								
Total	17 (4.5%)				28 (3.0%)				22 (2.2%)				11 (1.5%)			
Frederick Sound–Stephens Passage area:																
Carroll Island	3	6	12	8	7	5	12	7	5	4	11	7	3	5	9	6
Benson Cove					1			5					1			16
Security Bay																
Saginaw Bay					3	9	12	11	2			?				
Point Brightman	3	5	8	6	3	6	20	10	3	5	17	9	2	5	18	10
Point Cornwallis	2			4	2	6	18	12	2			5	1			12
Deepwater Point	5	7	8	7	8	4	10	8	8	5	13	8	2	5	8	6
Herring Bay	1			7	5	5	18	8	6	5	16	8	5	4	25	10
Point McCartney					2	6	10	8	2			6				
Hamilton Bay									2	8	13	10				
Port Camden					1			8								
Cape Bendel	1			8	2			4	2			6				
Point Napean	1			10					2	4	5	4	4	5	9	7
Pybus Bay	16			11	25	3	14	8	12	5	15	8	3	2	5	3
Pinta Point	3			7	2	6	14	10					1			8
Gambier Bay																
Young Bay																
Taku Inlet									1			?				
Portland Island																
Shelter Cove									1			19	1			18
Frederick Sound					6	4	10	9	5	3	27	10				
Total	35 (9.2%)				67 (7.1%)				53 (5.3%)				23 (3.1%)			
Other areas:																
Tenakee Inlet																
Hoonah Sound	1			29	5	9	28	14	1			27				
Slocum Arm													1			2
Affleck Canal																
Wrangell Narrows																
Warren Cove																
Total	1 (0.2%)				5 (0.5%)				1 (0.1%)				1 (0.1%)			
Unknown	6 (1.6%)				27 (2.9%)				16 (1.6%)				9 (1.2%)			
Grand total	162 (42.6%)				447 (47.4%)				534 (53.7%)				478 (64.7%)			

TABLE 1.—*Commercial recoveries of pink salmon tagged at Pleasant Island, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—												Total recoveries (8,278 tagged)
	Aug. 27 (96 tagged)				Aug. 30 (306 tagged)				Sept. 5 (376 tagged)				
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean	
Icy Strait area:													
Gull Cove													10
Inian Island													5
Point Adolphus					1			5					9
Point Gustavus	2			4	5			1					15
Eagle Point	2			2	2			3					15
Porpoise Island					1			8					1
Whitestone													2
Spasski									1			2	29
Excursion Inlet	16	1	6	3	44	1	11	4	6	2	4	3	283
Port Frederick	2			2	1			2					13
Icy Strait	4	1	5	3	5	3	11	5					55
Total	26 (27.1%)				59 (19.3%)				7 (1.9%)				437 (5.3%)
Lynn Canal area:													
Naked Island									1			2	39
Funter													3
Eldred Rock													1
Chilkat Inlet													7
Chilkoot Inlet													27
Lutak Inlet													27
Total	0 (0%)				0 (0%)				1 (0.3%)				104 (1.2%)
Upper Chatham Strait area:													
Hawk Inlet-Funter	2			4	5	1	9	4	1			?	241
Square Cove					1			8	5			2	56
False Bay					2	1	10	5	1			4	40
Cube Point	1			2	4	1	9	4	11	3	8	5	202
Point Hepburn	1			2	2			3	4	2	4	2	78
Gypsum					2			2	2			2	12
South Passage Point													36
Fishery Point									1			3	54
Marble Bluff	1			2	1			?	1			2	124
Marble Cove									1			?	24
Basket Bay													61
Killisnoo													53
Point Thatcher									1			3	72
Peninsula Point													25
Hood Bay					3	8	10	9					23
Distant Point													37
Eagle Point													10
Chalk Bay													17
Point Caution													87
Point Turbot													4
Wilson Cove													30
Chatham Strait	20	2	11	4	27	1	10	4	33	2	10	3	367
Total	25 (26.0%)				47 (15.4%)				61 (16.2%)				1,653 (20.0%)
Lower Chatham Strait area:													
Red Bluff Bay													15
Kingsmill-Point Ellis					1			11					115
Tebenkof Bay													12
Gedney Harbor													8
Total	0 (0%)				1 (0.3%)				0 (0%)				150 (1.8%)
Frederick Sound-Stephens Passage area:													
Carroll Island													25
Benson Cove													4
Security Bay													2
Saginaw Bay													11
Point Brightman													21
Point Cornwallis													14
Deepwater Point													51
Herring Bay					2			10					34
Point McCartney													17
Hamilton Bay													2
Port Camden									2			?	6
Cape Bendel													24
Point Napean													15
Pybus Bay					1			?					150
Pinta Point													10
Gambier Bay													1
Young Bay													10
Taku Inlet													23
Portland Island													1
Shelter Cove													2
Frederick Sound													22
Total	0 (0%)				3 (1.0%)				2 (0.5%)				445 (5.4%)
Other areas:													
Tenakee Inlet													1
Hoonah Sound													15
Slocum Arm													3
Affleck Canal													2
Wrangell Narrows													1
Warren Cove					1			?					1
Total	0 (0%)				1 (0.3%)				0 (0%)				23 (0.3%)
Unknown	2 (2.1%)				5 (1.6%)				1 (0.3%)				154 (1.8%)
Grand total	53 (55.2%)				116 (37.9%)				72 (19.2%)				2,966 (35.8%)

TABLE 2.—*Commercial recoveries of pink salmon tagged at Point Adolphus, Icy Strait, 1950*

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	July 25–Aug. 2 (263 tagged)				Aug. 3 (526 tagged)				Aug. 4 (458 tagged)				Aug. 5 (133 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove																
Point Gustavus	1			?												
Point Adolphus, No. 6																
North Island																
Pleasant Island																
Eagle Point																
Port Frederick									1			28				
Spasski									1			?				
Whitestone																
Excursion Inlet					3	2	19	12	3	12	17	15	1			11
Icy Strait	1			20					1			14				
Total	2 (0.8%)				3 (0.6%)				6 (1.3%)				1 (0.8%)			
Lynn Canal area:																
Funter													1			14
Naked Island																
Chilkat Inlet																
Chilkoot Inlet					2	7	13	10								
Lutak Inlet									1			13				
Total	0 (0%)				2 (0.4%)				1 (0.2%)				1 (0.8%)			
Upper Chatham Strait area:																
Hawk Inlet-Funter	1			10	5	4	14	10	7	11	13	12	1			11
Square Cove													1			10
False Bay									3	12	22	15				
Cube Point	3	17	22	20	2	13	14	14	4	11	15	12				
Point Hepburn									3	12	21	15				
Gypsum									1			14	1			10
South Passage Point	1			15	2			12	2			11	1			11
Fishery Point					1			14	2	11	12	12				
Marble Bluff					5	12	22	15	2	11	21	16	1			14
Marble Cove					3	13	14	14								
Basket Bay									3	12	14	13				
Danger Point																
Killisnoo					1			15	6	12	20	14	1			13
Point Thatcher					2			13	3	13	22	20				
Peninsula Point					1			13	1			13	1			11
Hood Bay																
Distant Point	1			14	1			13	2	11	12	12	4	11	12	11
Chalk Bay					2	14	36	25								
Point Caution					2	12	15	14	4	11	15	12	1			11
Eagle Point					1			15	1			12				
Point Turbot					1			18	1			15	1			21
Wilson Cove									1			15				
Chatham Strait					7	12	18	14	5	12	29	20				
Total	6 (2.3%)				36 (6.8%)				51 (11.1%)				13 (9.7%)			
Lower Chatham Strait area:																
Red Bluff Bay					1			14	2	15	17	16				
Kingsmill-Point Ellis					3	14	16	15	3	16	25	19	2	11	19	15
Tebenkof Bay					2	15	21	18	2	13	19	16				
Gedney Harbor																
Total	0 (0%)				6 (1.1%)				7 (1.5%)				2 (1.5%)			
Frederick Sound-Stephens Passage area:																
Carroll Island					3	13	15	14								
Benson Cove									2			11				
Security Bay					1			14	1			13				
Saginaw Bay					1			14					1			12
Point Brightman																
Point Cornwallis									1			22				
Deepwater Point					3	14	15	14	3	14	17	16	1			?
Herring Bay	1			20	1			16								
Point McCartney									1			17				
Hamilton Bay																
Port Camden					1			14								
Cape Bendel					1			14	3	13	15	15				
Point Napean					1			12	1			17				
Pybus Bay	5	15	20	18	15	13	23	16	15	11	22	16	5	11	16	12
Pinta Point																
Gambier Bay																
Young Bay					2			16								
Taku Inlet	4			10	1			?	2	11	38	24				
Frederick Sound					4	15	36	20					1			35
Total	10 (3.8%)				34 (6.5%)				29 (6.4%)				8 (6.0%)			
Other areas:																
Tenakee Inlet																
Hoonah Sound																
Salisbury Sound	1			17												
Slocum Arm	1			30												
Warren Cove									1			16				
Stikine Flats																
Tokeen																
Affleck Canal																
Total	2 (0.8%)				0 (0%)				1 (0.2%)				0 (0%)			
Unknown	1 (0.3%)				4 (0.8%)				3 (0.7%)				0 (0%)			
Grand total	21 (8.0%)				85 (16.2%)				98 (21.4%)				25 (18.8%)			

TABLE 2.—*Commercial recoveries of pink salmon tagged at Point Adolphus, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	Aug. 6 (525 tagged)				Aug. 7 (335 tagged)				Aug. 8 (905 tagged)				Aug. 9 (149 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove									1			9				
Point Gustavus																
Point Adolphus, No. 6																
North Island																
Pleasant Island																
Eagle Point					1			11								
Port Frederick					2			25								
Spasski					2			12	4	8	11	9				
Whitestone																
Excursion Inlet	1			9					3	8	10	8				
Icy Strait									4	13	25	16				
Total	1 (0.2%)				5 (1.5%)				12 (1.3%)				0 (0%)			
Lynn Canal area:																
Funter																
Naked Island	1			11	2	9	10	10	3	8	14	10	2	10	20	15
Chilkat Inlet									2	14	16	15				
Chilkoot Inlet	3	8	10	9					6	8	15	10				
Lutak Inlet	1			11	3	11	12	11	4	1	8	6				
Total	5 (1.0%)				5 (1.5%)				15 (1.6%)				2 (1.3%)			
Upper Chatham Strait area:																
Hawk Inlet-Funter	3	9	11	10	7	8	18	10	5	7	8	8	2	6	7	6
Square Cove	1			16	1			14	2	7	14	10				
False Bay	2	10	11	10	1			9	3	7	18	12	1			7
Cube Point	8	9	12	10	5	8	15	10	16	7	13	8	2	8	19	14
Point Hepburn	3	13	19	18	1			9	9	8	17	10				
Gypsum	1			12	1			10	2	7	10	8	1			8
South Passage Point	5	9	15	10	4	8	10	9	4	10	17	12	2	8	15	12
Fishery Point	4	9	10	10	2	10	14	12	2	7	8	8	2			6
Marble Bluff					4			8	15	7	17	9	2	6	8	7
Marble Cove	1			10					6	8	9	9	1			7
Basket Bay	5	10	12	11	3	9	10	10	10	8	13	9	2			7
Danger Point					1			1								
Killisnoo	3	10	11	10	2	8	9	8	10	7	16	10	2	6	8	7
Point Thatcher	7	10	20	15	3	9	12	10	12	8	18	11				
Peninsula Point	2	10	11	10					3			8				
Hood Bay	2	25	26	26	1			15	3			13	1			23
Distant Point	3	11	34	20	3	9	10	10	2	9	14	8	1			8
Chalk Bay	2	11	33	22					5	17	25	20				
Point Caution	5	10	17	13	3	10	17	15	18	7	16	10	6	6	17	9
Eagle Point					1			9	2			9	1			7
Point Turbot					1			14	2	11	13	12	1			12
Wilson Cove	1			12					3			10				
Chatham Strait	6	9	16	12	4	9	34	18	23	7	32	12	2	7	15	11
Total	64 (12.2%)				48 (14.3%)				158 (17.5%)				29 (19.5%)			
Lower Chatham Strait area:																
Red Bluff Bay	4	10	19	15					2			30	1			7
Kingsmill-Point Ellis	10	9	16	13	7	14	19	16	22	8	21	11	5	7	15	10
Tebenkof Bay					1			11	2	15	16	16	1			15
Gedney Harbor																
Total	14 (2.6%)				8 (2.4%)				26 (2.9%)				7 (4.7%)			
Frederick Sound-Stephens Passage area:																
Carroll Island					1			17	6	7	16	11	1			7
Benson Cove	1			11	3	8	9	8	1			7				
Security Bay									1			9				
Saginaw Bay	1			?	1			16								
Point Brightman	3	10	12	11	1			26	3	8	22	14				
Point Cornwallis	2	9	24	16	3	11	23	15	1			7				
Deepwater Point	4	11	12	11	2	8	14	11	6	9	16	12	1			6
Herring Bay	5	10	16	12	2			11	1			10				
Point McCartney	2	12	15	14	1			11	1			10				
Hamilton Bay													1			17
Port Camden	1			12									1			10
Cape Bendel	2	10	11	10	3	9	10	10	5	8	11	9				
Point Napean																
Pybus Bay	19	10	20	13	11	9	15	12	33	7	18	12	2	7	9	8
Pinta Point																
Gambier Bay					1			12								
Young Bay					1			12								
Taku Inlet																
Frederick Sound	2	10	12	11	1			11	5	7	10	8				
Total	42 (8.0%)				31 (9.2%)				83 (7.0%)				6 (4.0%)			
Other areas:																
Tenakee Inlet	1			10												
Hoonah Sound									1			32				
Salisbury Sound																
Slocum Arm	1			18												
Warren Cove					1			13	1			12				
Stikine Flats									1			16				
Tokeen									1			16				
Affleck Canal																
Total	2 (0.4%)				1 (0.3%)				4 (0.4%)				0 (0%)			
Unknown	8 (1.5%)				4 (1.2%)				24 (2.7%)				1 (0.7%)			
Grand total	136 (25.9%)				102 (30.4%)				302 (33.4%)				45 (30.2%)			

TABLE 2.—*Commercial recoveries of pink salmon tagged at Point Adolphus, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—															
	Aug. 10 (1,110 tagged)				Aug. 11 (623 tagged)				Aug. 12 (996 tagged)				Aug. 13 (667 tagged)			
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)		
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean
Icy Strait area:																
Gull Cove					1			7	2			6	3			4
Point Gustavus	3			6	2	5	12	8					3			5
Point Adolphus, No. 6													1			4
North Island									1			3				
Pleasant Island									3	3	25	10	7			2
Eagle Point									3			6	3	5	12	7
Port Frederick	1			5												
Spasski	1			6	2	5	11	8	8	4	17	6	7	3	4	4
Whitestone													1			11
Excursion Inlet	6	6	19	11	7	5	8	7	23	3	21	6	24	2	10	3
Icy Strait	7	6	19	10	3	5	9	7	4	4	5	5	11	3	15	7
Total	18 (1.6%)				15 (2.4%)				44 (4.4%)				60 (9.0%)			
Lynn Canal area:																
Funter																
Naked Island	10	6	12	7	7	5	11	6	12	4	13	6	12	3	9	5
Chilkat Inlet																
Chilkoot Inlet	2	6	13	10	1			?	6	11	18	14				
Lutak Inlet	5	5	12	8	1			8	3	6	7	6				
Total	17 (1.5%)				9 (1.4%)				21 (2.1%)				12 (1.8%)			
Upper Chatham Strait area:																
Hawk Inlet-Funter	19	5	14	7	19	4	15	7	31	3	11	4	54	2	13	3
Square Cove	5	7	19	13	2			8	10	3	11	6	19	2	8	3
False Bay	4	7	16	9	4	5	18	9	5	4	13	6	9	3	13	5
Cube Point	31	5	20	6	25	4	18	6	40	3	17	4	50	2	16	3
Point Hepburn	9	6	16	11	6	5	15	10	9	4	13	8	13	3	12	6
Gypsum	3	5	8	6	1			7	1			7	2			2
South Passage Point	12	5	14	8	4	4	13	7	2	3	6	4	3	2	8	4
Fishery Point	9	5	7	6	6	4	6	5	15	3	10	6	5	2	3	2
Marble Bluff	9	5	14	7	9	4	13	6	19	3	14	6	23	2	4	3
Marble Cove	3			6	1			5	4			5	4	4	5	4
Basket Bay	11	5	11	7	11	5	10	7	12	4	9	6	4	2	4	3
Danger Point																
Killisnoo	19	5	14	8	9	5	30	12	9	4	9	5	5	5	13	7
Point Thatcher	10	6	9	7	4	5	8	6	6	4	14	10	8	3	13	9
Peninsula Point	6	6	13	8	4	5	15	7	6	5	10	8	1			4
Hood Bay	4	7	12	9	4	4	26	13	3	3	28	10				
Distant Point	8	6	8	7	9	4	13	6	13	3	7	4	11	2	20	5
Chaik Bay	5	15	30	20	2	14	28	21	5	13	20	17				
Point Caution	21	5	14	8	13	4	12	6	21	3	12	6	9	3	6	4
Eagle Point	2	6	7	6	4	5	8	6	1			9	1			8
Point Turbot	1			11	2			10								
Wilson Cove	3	6	8	7	3	5	7	6	3	6	13	7	3	3	5	4
Chatham Strait	39	5	30	9	27	4	19	7	53	3	14	6	50	2	15	4
Total	233 (21.0%)				169 (27.1%)				268 (26.9%)				274 (41.1%)			
Lower Chatham Strait area:																
Red Bluff Bay	5	11	14	12	5	8	18	11	8	5	11	9	4	4	9	6
Kingsmill-Point Ellis	38	6	15	10	30	5	22	10	34	4	18	8	11	3	13	9
Tebenkof Bay	7	12	20	16	4	7	13	11	7	11	18	13	2	10	17	14
Gedney Harbor					1			12	1			11				
Total	50 (4.5%)				40 (6.4%)				50 (5.0%)				17 (2.5%)			
Frederick Sound–Stephens Passage area:																
Carroll Island	2	6	8	7	2			13	7			6	3	4	6	5
Benson Cove	5	6	20	15					3			5				
Security Bay	1			7	1			12	1			5	1			4
Saginaw Bay	2			14	1			6	1			12	1			11
Point Brightman	5	8	12	9	7	5	22	10	2	6	18	12	2	9	17	13
Point Cornwallis	9	5	20	10	4	7	15	9	6	3	6	4				
Deepwater Point	11	7	16	10	3	6	10	8	12	5	14	7	4	4	8	6
Herring Bay	9	6	11	8	5	6	19	14	8	4	10	8	1			17
Point McCartney	5	7	11	9					5	9	10	10	3	5	9	6
Hamilton Bay													1			13
Port Camden	3	8	11	10	1			8	2	6	10	8				
Cape Bendel	7	6	9	8	6	5	11	6	1			5	4	4	6	4
Point Napean	6	7	12	10	1			6	1			10	1			9
Pybus Bay	33	6	16	9	18	4	15	10	19	4	14	9	8	8	13	11
Pinta Point	1			12	4	11	15	12	5	6	11	8	2			10
Gambier Bay																
Young Bay																
Taku Inlet																
Frederick Sound	7	6	12	8	6	5	7	6	4	4	6	5	1			5
Total	106 (9.5%)				59 (9.5%)				77 (7.8%)				32 (4.8%)			
Other areas:																
Tenakee Inlet																
Hoonah Sound	2	11	30	20	3	8	20	16	3	7	18	12				
Salisbury Sound					2	8	11	10	1			7	1			5
Slocum Arm																
Warren Cove									1			8	1			7
Stikine Flats																
Tokeen									1			11				
Affleck Canal													1			11
Total	2 (0.2%)				5 (0.8%)				6 (0.6%)				3 (0.4%)			
Unknown	35 (3.2%)				14 (2.3%)				16 (1.6%)				16 (2.4%)			
Grand total	461 (41.5%)				311 (49.9%)				482 (48.4%)				414 (62.0%)			

TABLE 2.—*Commercial recoveries of pink salmon tagged at Point Adolphus, Icy Strait, 1950*—Continued

[Does not include tagged fish recovered at point of tagging]

Recovered in—	Recoveries of fish tagged in period—												Total recoveries (7,317 tagged)
	Aug. 14 (344 tagged)				Sept. 4 (203 tagged)				Sept. 4 (80 tagged) [1]				
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean	
Icy Strait area:													
Gull Cove	1			4					1			4	9
Point Gustavus	3	2	4	3									12
Point Adolphus, No. 6													1
North Island													1
Pleasant Island					5	1	3	1	1			1	16
Eagle Point													7
Port Frederick	1			1									5
Spasski	5	2	3	2									30
Whitestone													1
Excursion Inlet	33	1	5	2	6	3	5	4	1			5	111
Icy Strait	11	2	10	3	2			5					44
Total	54 (15.7%)				13 (6.4%)				3 (3.7%)				237 (3.2%)
Lynn Canal area:													
Funter	3	4	6	5	1			2					4
Naked Island	3	2	8	4									53
Chilkat Inlet													2
Chilkoot Inlet	1			12									21
Lutak Inlet													18
Total	7 (2.0%)				1 (0.5%)				0 (0%)				98 (1.3%)
Upper Chatham Strait area:													
Hawk Inlet–Funter	19	2	12	3	1			4					174
Square Cove	10	1	9	3	2			3	1			5	55
False Bay	4	2	3	2									36
Cube Point	16	1	8	2	5	3	4	3					207
Point Hepburn	12	2	11	4	1			3					66
Gypsum													14
South Passage Point	2	2	7	4					1			3	45
Fishery Point	4	2	7	4									52
Marble Bluff	7	1	15	5	1			?					97
Marble Cove	2	2	3	2									25
Basket Bay	2	4	7	6									63
Danger Point													1
Killisnoo	3	5	27	16									70
Point Thatcher	2	2	5	4									57
Peninsula Point	3	3	8	6									28
Hood Bay													18
Distant Point	4	1	10	4									62
Chalk Bay	3	11	14	13									24
Point Caution	5			5									108
Eagle Point													14
Point Turbot													10
Wilson Cove	1			4									18
Chatham Strait	23	2	12	5	6	3	5	4	2	2	5	4	247
Total	122 (35.5%)				16 (7.9%)				4 (5.0%)				1,491 (20.4%)
Lower Chatham Strait area:													
Red Bluff Bay													32
Kingsmill–Point Ellis	6	4	12	8	4			5					175
Tebenkof Bay	1			8									29
Gedney Harbor													2
Total	7 (2.0%)				4 (2.0%)				0 (0%)				238 (3.2%)
Frederick Sound–Stephens Passage area:													
Carroll Island	1			4									26
Benson Cove													15
Security Bay													7
Saginaw Bay													9
Point Brightman													23
Point Cornwallis													28
Deepwater Point													50
Herring Bay	1			5									34
Point McCartney	1			5									19
Hamilton Bay													2
Port Camden													9
Cape Bendel													32
Point Napean	2	5	9	7	1			4					14
Pybus Bay	2	2	8	5									185
Pinta Point	1			9									13
Gambier Bay													1
Young Bay													3
Taku Inlet													7
Frederick Sound	3	4	9	7									34
Total	11 (3.2%)				1 (0.5%)				0 (0%)				509 (7.0%)
Other areas:													
Tenakee Inlet													1
Hoonah Sound	1			16									10
Salisbury Sound													5
Slocum Arm													2
Warren Cove	1			6									6
Stikine Flats													1
Tokeen													2
Affleck Canal													1
Total	2 (0.6%)				0 (0%)				0 (0%)				28 (0.4%)
Unknown	6 (1.8%)				3 (1.4%)				2 (2.5%)				137 (1.9%)
Grand total	209 (60.8%)				38 (18.7%)				9 (11.2%)				2,738 (37.4%)

[1] Tagging at Columbia River Packers Association Point Adolphus trap No. 6; all other tagging at their Adolphus trap No. 4.

Those recoveries listed as "Unknown" include the returns with insufficient data.

The recoveries show that fish tagged on opposite sides of Icy Strait follow similar migratory routes and do not necessarily follow along the shoreline from which they were originally tagged. Total recovery of fish tagged at Pleasant Island was 35.8 percent, and of those tagged at Point Adolphus 37.4 percent. By treating only the comparable data (July 27, 28, and 31, and August 1 through 14), a comparison of numbers tagged and recovered suggests that the two groups of fish were subjected to similar fishing intensities (chi square=1.274, d.f. 1, $0.2<P<0.3$).

The returns imply that the migratory routes (fig. 2) are similar to those found by earlier investigators (Rich 1926, Rich and Suomela 1927, Rich and Morton 1929): that pink salmon, after appearing in Icy Strait, distribute eastward through Icy Strait, southward into Chatham Strait, and then eastward into Frederick Sound and Stephens Passage. Minor runs go into Lynn Canal, Peril Strait, and South Chatham Strait.

Most of the fishery is east of the point of tagging. To determine direction of movement of the fish, we examined tag returns from traps in Icy Strait and Cross Sound. The data show that, although fishing intensities of the selected traps in the areas to the east and to the west of the point of tagging were nearly equal, 85.7 percent of the tag returns came from areas to the east of the point of tagging.

In examining recoveries for evidence of random movement of the salmon, the number of tags recovered west of the tagging point was compared with the number recovered east of that point. Seven traps to the west of Pleasant Island took a total of 36,846 pink salmon, while 6 traps to the east took 26,740. Thirty-five tags were recovered in the western section, and 213 tags in the eastern section (see table 3). Assuming a random movement of the fish, one would expect 144 tags $\left(\frac{248}{63,586}\times 36,846\right)$ from the western section and 104 tags $\left(\frac{248}{63,586}\times 26,740\right)$ from the eastern section. Comparing these expected recoveries with the actual gives a chi-square value of 196 with one degree of freedom. Thus, the hypothesis of random movement of the fish must be rejected at any reasonable level of significance.

A similar computation for the returns from the Point Adolphus tagging yields a chi-square value of 41 with one degree of freedom, and again the hypothesis of random movement must be rejected at any usual level of significance. Clearly, then, the predominant movement of pink salmon in Icy Strait is in an easterly direction.

In interpreting these data, it should be noted that they account only for the movement of salmon from point of release to point of capture. As most of the Icy Strait tagging was done before the start of the fishing season, many of the tagged fish enjoyed a week or more of freedom before they were intercepted by the fishery. We can only

TABLE 3.—*Comparison of easterly and westerly dispersion of pink salmon in Icy Strait as indicated by tag recoveries at 13 fish traps operating full time in this area*

[Returns from Point Adolphus and Pleasant Island tagging for period July 25 through August 30]

Tag returns west of tagging points	Tags recovered	Tag returns east of tagging points	Tags recovered
From Pleasant Island tagging (total pink salmon catch, 36,846), taken at—		From Pleasant Island tagging (total pink salmon catch, 26,740), taken at—	
Point Gustavus	15	Eagle Point	10
Point Adolphus, No. 4	8	North Village Point	69
Point Adolphus, No. 6	1	Village Point	34
Gull Cove	10	Rocky Point	63
Inian Island	1	Hawk Inlet, No. 9	7
North Island	0	Spasski	30
Three Hill Island	0		
Total	35	Total	213
From Point Adolphus tagging (total pink salmon catch, 25,935), taken at—		From Point Adolphus tagging (total pink salmon catch, 37,551), taken at—	
Point Gustavus	12	Pleasant Island	10
Point Adolphus, No. 6	1	Eagle Point	7
Gull Cove	8	North Village Point	19
Inian Island	0	Village Point	19
North Island	1	Rocky Point	35
Three Hill Island	0	Hawk Inlet, No. 9	5
		Spasski	30
Total	22	Total	125
Total returns west of tagging points	57	Total returns east of tagging points	338

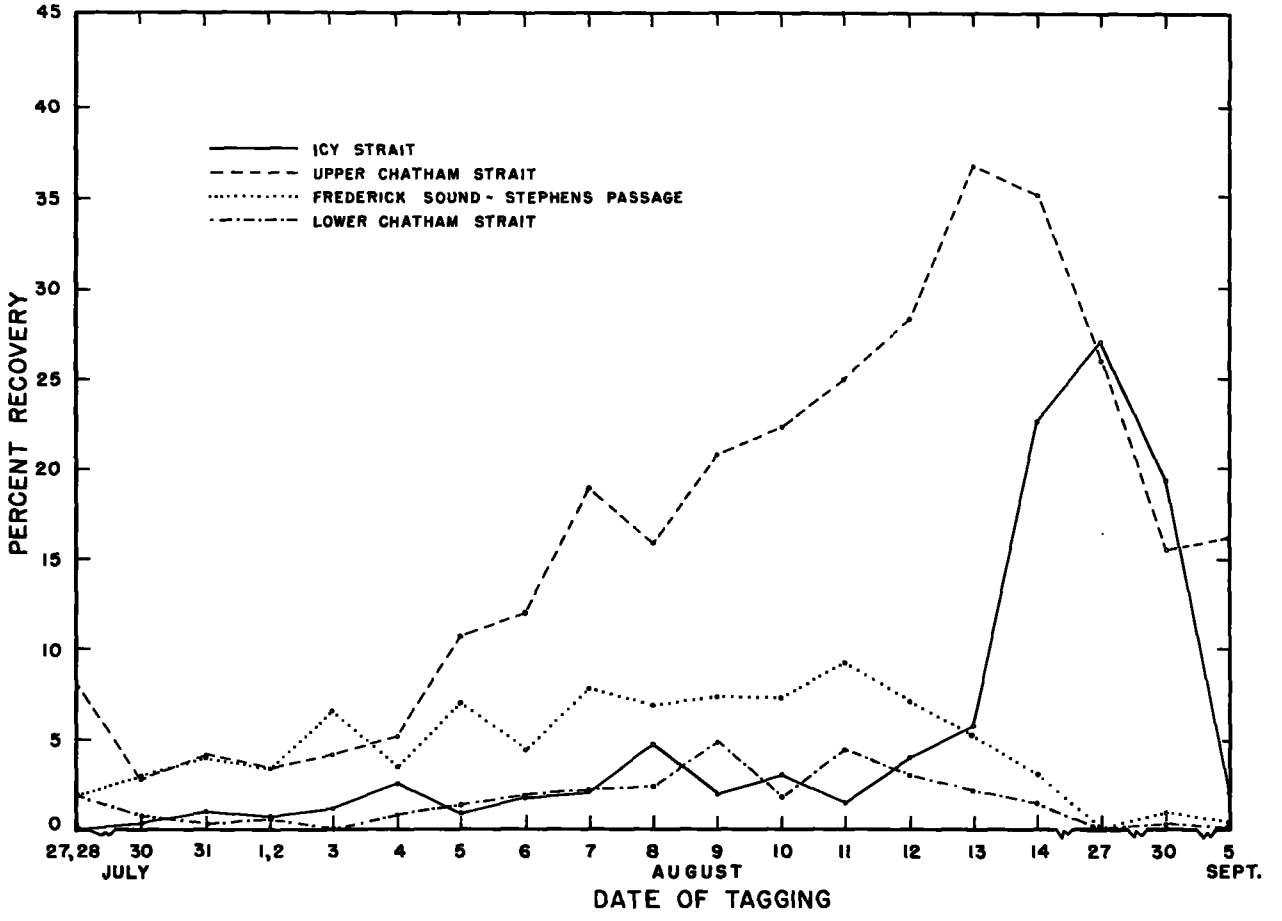

FIGURE 7.—Pleasant Island tagging, 1950: Percentage commercial recovery, by date of tagging and principal areas of recovery.

postulate as to their specific movements during this period, but the fish may well have traveled in a "to and fro" manner as described by Verhoeven (1952). Nevertheless, the prevailing movement appears to have been easterly, toward the inner channels where the more important spawning areas are located.

Seasonal distribution of tag returns by areas (figs. 7 and 8) indicate that the majority of the fish entering Icy Strait from July 25 to August 12 were not taken by the fishery in Icy Strait which opened on August 15. There are two possible explanations: (1) Early races destined for Icy Strait streams had already moved into or near their parent streams, and (2) those fish destined for more distant streams did not linger in Icy Strait but moved rapidly on. The sharp rise in Icy Strait recoveries of those fish tagged immediately before the opening of the commercial season is good evidence that migration through Icy Strait is comparatively rapid. This is clearly evident in the returns from the Pleasant Island tagging of August 13 and 14. Of those fish tagged 2 days before the opening of the commercial season, 5.8 percent were captured in Icy Strait. Of these fish tagged just a day before the opening of fishing, 22.6 percent were recovered in Icy Strait, showing an increase of about 4 times over the percentage returned from the previous day's tagging.

The recovery pattern in Upper Chatham Strait does not follow the trend evidenced in Icy Strait. Here there was a strikingly uniform increase in the percentage of recoveries made from each day's tagging as the date of tagging approached the opening day of the commercial season. The drop in percentage recovery from the tagging of August 13 to that of August 14 could be attributed to the marked increase in recovery in Icy Strait from the corresponding day's tagging. Recoveries of

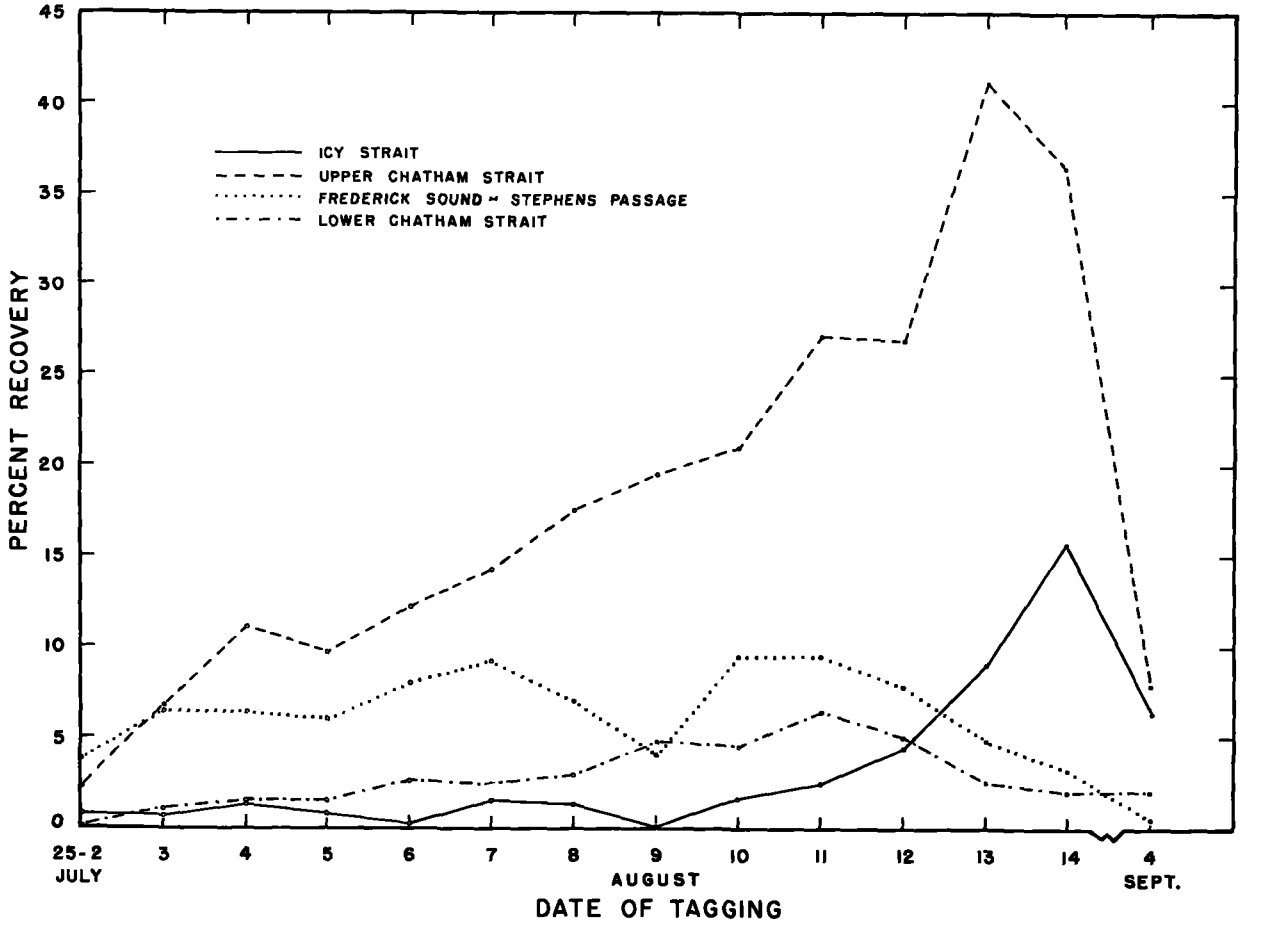

FIGURE 8.—Point Adolphus tagging, 1950: Percentage commercial recovery, by date of tagging and principal areas of recovery.

almost 19 percent were made in the Upper Chatham Strait area from fish tagged as early as August 7, indicating that a far greater percentage of the early tagged fish was susceptible to capture in this area than in Icy Strait.

For both Frederick Sound and Lower Chatham Strait, the percentages of commercial recoveries from the tagging after August 11 show a decline. There are two explanations for this: (1) Opening of the fishing season on August 15 increased the chances of capture near the point of tagging, and (2) increasing numbers of the fish tagged during the latter period were moving to streams less distant from the point of tagging. Those runs moving to the more distant streams, thus being subjected to capture over a considerable distance, will naturally show declines in their escapements as the fishery begins to draw upon them along the entire route of their migration. Whether these declines are entirely the result of fishing effort is not always easily determined.

Rate of exploitation.—Commercial recoveries from the tagging at Point Adolphus and at Pleasant Island showed a surprisingly uniform increase in the percentage recovery from each day of tagging as the date of the tagging approached the opening date of the fishing season on August 15. Regression lines obtained by plotting percentage recovery on the date of tagging at Point Adolphus and Pleasant Island are almost identical, with slopes of 3.547 and 3.630, respectively. The corresponding correlation coefficients of 0.963 and 0.974 are highly significant. Those fish tagged just before the opening of the season are exposed the longest and have the highest rate of recapture; those tagged earlier are progressively less likely to be taken since some will have had time to migrate into waters outside the fishing area.

The length of time a particular race of salmon is subject to capture by the fishery is determined by the distance and the speed it travels to reach its parent stream. The maximum elapsed time (from

date of tagging to date of capture) that we have on record for the 1950 season is 40 days, and the greatest distance is a recovery from Olive Cove (Etolin Island), about 225 miles from point of tagging.

Tagging in Icy Strait during the fishing season was limited to four experiments conducted between August 27 and September 5. Recoveries from each showed similar straight-line relations to dates of tagging. The percentage recovery decreased as the date of tagging approached the closing date of the fishing season. There was comparatively little decline in the percentage recovery between the tagging of August 14 and that of August 27. Recoveries from the Pleasant Island tagging of August 14 amounted to 64.7 percent. When tagging was resumed on August 27, recoveries amounted to 55.2 percent—a drop of slightly less than 10 percent.

On the basis of recoveries from the tagging of August 14, we assume that fishing mortality in salmon available to the fishery in Icy Strait during the fishing period probably remained between 60 and 65 percent, dropping below this rate only during the last few days of the commercial season. This estimate is based on the assumption that little or no tagging mortality occurred, that all tags recovered were returned, and that few tags were lost or shed. If any of these factors are of greater consequence than assumed, then our estimate of 60 to 65 percent is minimal.

Returns from Upper Chatham Strait tagging

A list of the returns from the tagging at Cube Point and False Bay (fig. 6) is given in table 4. Although the pattern of migration from these Chatham Strait points indicates a continuation of the migration route exhibited by fish tagged in Icy Strait, returns from the Chatham experiments also show a northward migration toward Mansfield Peninsula and Icy Strait. Of the 1,805 individuals tagged, 770 (42.6 percent) were recovered. Of this recovery, 112, or 14.5 percent, were recovered north of the point of tagging. If the percentage recovery to the north of the point of tagging were weighted to compensate for unequal amounts of fishing effort to the north and south (25 traps operated north of the point of tagging and 42 to the south), this figure would approach 20 percent. As well as we were able to determine, all recoveries listed under "Chatham Strait—General" were made south of the point of tagging. If some of these were possibly taken north of the tagging points, the proportion moving northward could have been even higher than 20 percent. The northward movement shown by the recoveries corresponds with earlier findings of tagging at Parker Point in 1926 and 1927 (Rich and Suomela 1927, Rich and Morton 1929).

Returns from the Upper Chatham Strait tagging of August 20 show that a considerably higher recovery was made in the Frederick Sound-Stephens Passage area than resulted from the nearest comparable tagging in Icy Strait on August 14 (9.0 to 3.1 percent). This is readily explained by the fact that the route from Icy Strait to Frederick Sound and Stephens Passage is longer and makes the fish pass more gear than does the route from Chatham Strait. Thus, a fish tagged in Icy Strait would be expected to have less chance of reaching Frederick Sound than one tagged in Chatham Strait.

STREAM RECOVERIES

Recovery effort

Stream recovery of tagged salmon is one of the means by which the researcher can differentiate the specific races that comprise the runs in any one major fishing area at any one time. With this phase of the study in mind, our crew put considerable effort into the survey of streams that were believed to be likely contributors to the Icy Strait run. Although only a portion of the total potential spawning area could be covered, the surveys were extensive enough to explore all possible areas of major distribution of salmon tagged in the Icy Strait area.

In some areas, effective coverage was not always achieved because of the impossibility of timing all the surveys to coincide with periods of peak escapement in the various stream systems. For example, in our surveys of the west coast of Chichagof Island during the latter part of August, eight streams were examined without revealing a single tagged salmon. Unfortunately, only four of these streams contained pink salmon at this time and these only in limited number. Presumably, the visits were several weeks in advance of the peak escapement into this area. However, if the negative evidence obtained from these surveys is combined with the limited tag recovery

TABLE 4.—*Commercial recoveries of pink salmon tagged in Upper Chatham Strait, 1950*

Recovered in—	Recoveries of fish tagged at—																		Total recoveries (1,805 tagged)
	Cube Point Aug. 20 (1,448 tagged)				False Bay Aug. 21 (33 tagged)				Cube Point Aug. 30 (125 tagged)				Cube Point Sept. 3 (185 tagged)				False Bay Sept. 3 (14 tagged)				
	Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			Number recovered	Elapsed time (days)			
		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean		Min.	Max.	Mean	
Icy Strait area:																					
Gull Cove	2			?																	2
Point Gustavus	1			?					1			1									2
Eagle Point	3	3	9	6																	3
Excursion Inlet	9	3	12	7	2	12	17	15	5	2	10	5									16
Spasski	2			5	1			4													3
Icy Strait—General	8	1	12	6																	8
Total	25 (1.7%)				3 (9.1%)				6 (4.8%)				0 (0%)				0 (0%)				34 (1.9%)
Lynn Canal area:																					
Naked Island	6	2	18	7	1			9	1			3									8
Funter Bay	2			18																	2
Total	8 (0.6%)				1 (3.0%)				1 (0.8%)				0 (0%)				0 (0%)				10 (0.6%)
Upper Chatham Strait area:																					
Hawk Inlet to Funter	54	1	6	1	1			?	2			3									57
Square Cove	10	1	2	1	1			?													11
Point Hepburn	49	2	9	4	1			4	5	1	3	1									55
Gypsum					1			0					1			4					2
Fishery Point	29	1	4	1																	29
Marble Bluff	32	2	9	4																	32
Marble Cove	29			?																	29
Basket Bay	1			1																	1
False Bay	9	1	9	5									1			5					10
Peninsula Point	3			2					1			1									4
South Passage Point	6	1	5	3																	6
Point Thatcher	8			6					3	1	2	1									11
Point Caution	53	1	6	3																	53
Hood Bay	16	11	13	12					4	9	10	10	5			6					25
Distant Point	11	4	9	7																	11
Killisnoo Island	18	1	21	8					1			11									19
Point Turbot	4	3	6	4																	4
Eagle Point	2			1																	2
Chalk Bay	16	3	13	9					1			2	1			?					18
Wilson Cove	8			5																	8
Chatham Strait—General	110	1	20	4	2	1	4	2	6	1	10	4									118
Total	468 (32.3%)				6 (18.2%)				23 (18.4%)				8 (4.3%)				0 (0%)				505 (28.0%)
Lower Chatham Strait area:																					
Kingsmill to Point Ellis	36	1	20	4									1			6					37
Red Bluff Bay	8	2	9	6																	8
Tebenkof Bay	7			10									1			?					8
Gedney Harbor	4	3	8	6																	4
Total	55 (3.8%)				0 (0%)				0 (0%)				2 (1.1%)				0 (0%)				57 (3.1%)
Frederick Sound–Stephens Passage area:																					
Point Brightman	10	1	13	8																	10
Point Cornwallis	1			10																	1
Deepwater Point	27	1	6	3									1			?					28
Carroll Island	17	3	4	3																	17
Herring Bay	12	2	19	6									1			6					13
Saginaw Bay	3			4																	3
Pybus Bay and vicinity	41	1	13	5																	41
Point McCartney	4	1	2	2																	4
Point Napean	11	3	6	3																	11
Cape Bendel	4	2	6	4																	4
Security Bay									1			?									1
Frederick Sound—General													1			4					1
Total	130 (9.0%)				0 (0%)				1 (0.8%)				3 (1.6%)				0 (0%)				134 (7.4%)
Other areas:																					
Hoonah Sound	4	10	11	10																	4
Affleck Canal	1			10																	1
Slocum Arm	1			4																	1
Unknown	22												2								24
Total	28 (1.9%)				0 (0%)				0 (0%)				2 (1.1%)				0 (0%)				30 (1.6%)
Grand total	714 (49.3%)				10 (30.3%)				31 (24.8%)				15 (8.1%)				0 (0%)				770 (42.6%)

made by purse-seine vessels operating in this area, the data do indicate there is little movement of pink salmon from Icy Strait to streams on the ocean side of Chichagof Island.

Survey crews of the *Heron* and *Sablefish* examined 98 streams. Field parties of the Fisheries Research Institute (1950) covered an additional 15 streams while making their annual escapement counts in the area. Other Service personnel and local residents participated in stream recovery and gave particularly close coverage to three streams—Humpback Creek, Game Creek, and Mole River. Altogether, approximately 125 streams were checked for tagged salmon in that part of Southeastern Alaska north of Sumner Strait. Table 5 gives a complete list of all streams covered by our survey parties and the relative amount of effort expended in this phase of the 1950 program.

Many of the streams in Southeastern Alaska, unnamed or with several local names, are identified by a numbering system devised by the Fish and Wildlife Service several years ago. Wherever possible, we have used these numbers to designate our surveys. These stream locations and numbers are shown in figure 1.

While an extensive survey of streams in Sumner Strait and areas to the southward was not undertaken by our group, many streams in the southern portion of Southeastern Alaska were inspected by Service personnel and Fisheries Research Institute workers making annual escapement counts. These surveys disclosed that there was no appreciable movement of tagged salmon into the streams of this area.

Recovery techniques

Our stream-survey crews tried several implements to capture tagged salmon in streams. Among these were the rifle, dip net, gaff, and spear. A spear made of three shark hooks welded together in pitchfork fashion and fastened to a pole approximately 10 feet long proved to be by far the most efficient tool used. A similar spear had previously been used by workers of the Fisheries Research Institute and found to be most satisfactory for the work.

We found that the ultimate success of a stream tag-recovery program is dependent upon a number of factors. Some of the more important are size of stream, weather, character of stream, individual adeptness in the capture of fish, time spent in capturing fish, condition of tagged fish, and time of stream survey.

TABLE 5.—*Stream tag recoveries by survey crews of the* Heron *and* Sablefish

Area and stream	Date of survey	Man-hours [1]	Pinks found [2]	Tags noted	Tags recovered	Distance covered
Icy Strait area:						*Miles*
Idaho Inlet, No. 12A	8/25	1.00	0	0	0	½
Idaho Inlet, No. 12	8/25	1.00	0	0	0	¾
Mud Bay, No. 14	8/26	1.50	0	0	0	1½
Neka Bay, stream on right side	8/31	.50	0	0	0	⅛
Neka Bay, No. 18	8/31	1.50	300	10	2	¼
Do	9/1	4.00	300	8	1	¼
Port Frederick, No. 17B	8/31	.50	4	1	1	⅛
Seagull Creek, No. 17A	8/31	3.00	200	11	10	¾
Do	8/31	1.50	150	7	4	½
Spasski Creek, No. 20	8/16	3.00	75	4	0	1¼
Do	8/26	1.50	15	1	0	¼
Do	8/29	3.50	269	12	5	1½
Game Creek, No. 16	8/29	6.00	424	6	0	2½
Whitestone Harbor, west stream	8/16	2.00	0	0	0	½
Whitestone Harbor, south stream	8/16	2.00	20	0	0	1
Do	8/29	2.50	117	9	1	1¼
Point Carolus, stream 1 mi. inside	9/3	1.50	0	0	0	1¼
Homeshore, No. 1	9/2	5.00	600	40	11	¼
Do	9/5	6.00	600	30	15	⅛
Homeshore, stream right of No. 1	9/2	3.50	100	11	8	⅛
Do	9/5	1.00	100	4	1	⅛
Homeshore, No. 1B	9/5	.83	0	0	0	⅛
Total		52.83		154	59	153¼
Lynn Canal area:						
Funter Bay, No. 78	9/6	2.00	32	3	2	⅛
Funter Bay, small stream right of No. 78	9/6	.50	5	0	0	¼
Funter Bay, Coot Cove Creek, No. 80	9/6	.50	0	0	0	⅛
Point Howard, ⅛ mi. left of No. 3A	9/6	.25	0	0	0	¼
Point Howard, No. 3A	9/6	1.00	70	6	3	¼
Howard Bay, Cove Creek, No. 3	9/5	1.33	360	6	4	½
Total		5.58		15	9	1¾
Upper Chatham Strait area:						
False Bay, No. 77	8/17	2.00	30	0	0	1
Freshwater Bay, stream head of bay	8/30	1.83	59	4	0	¾
Freshwater Bay, No. 4, head of bay	8/17	2.66	1,270	3	0	1¼
Sitkoh Bay, No. 19	9/18	2.00	75	0	0	1
Sitkoh Bay, No. 20	9/18	5.00	1,606	12	9	2
Greens Creek, No. 44, Hawk Inlet	8/16	1.16	0	0	0	¾
Wheeler Creek, Game Cove, No. 45	8/16	2.16	76	0	0	¾
Hood Bay, No. 54	9/16	1.83	250	3	1	1
Hood Bay, No. 56	9/17	2.16	1,432	12	1	1
Chalk Bay, No. 57	9/17	2.50	1,342	11	6	1
Total		23.30		45	17	10½
Tenakee Inlet area:						
Corner Bay, east stream No. 14A	8/17	2.25	4	0	0	1¼
Do	8/31	2.16	13	1	0	¾
Kadashan Bay, east side of bay	8/31	3.33	621	3	3	1½
Kadashan Bay, right side of bay	8/17	.66	18	0	0	⅛
Seal Bay, No. 11	8/18	3.33	7,940	0	0	¾
Long Bay, No. 10	8/18	4.66	12,200	1	0	1⅞
Do	9/1	3.50	1,321	5	0	1¼
East Goose Bay, No. 9A	8/18	2.00	271	0	0	1
Goose Bay, No. 9	8/18	2.83	233	0	0	1½
Tenakee Inlet, stream at head	9/1	1.33	0	0	0	¾
Total		26.05		10	3	11

See footnote at end of table.

TABLE 5.—*Stream tag recoveries by survey crews of the* Heron *and* Sablefish—Continued

Area and stream	Date of survey	Man-hours [1]	Pinks found [2]	Tags noted	Tags recovered	Distance covered
Frederick Sound-Stephens Passage area:						*Miles*
Barlow Cove, left side, end of cove	9/6	0.83	2	0	0	½
Barlow Cove, right side, end of cove	9/6	.50	0	0	0	¼
Barlow Cove, ½ mile from end, right side	9/6	.50	0	0	0	⅛
Seymour Canal, No. 11	9/10	.83	0	0	0	⅛
Seymour Canal, No. 13	9/10	2.33	2,050	29	19	½
Seymour Canal, ⅛ mi. south of No. 13	9/10	.66	44	0	0	⅛
Windfall Harbor, 1½ mile North of No. 14	9/10	1.33	108	4	4	⅛
Windfall Harbor, No. 14	9/9	3.50	105	3	1	1
Mole River, No. 15	9/9	4.00	1,219	25	20	1
Mole Harbor, No. 15A	9/11	.33	0	0	0	⅛
Gambier Bay, ½ mi. north of No. 17	9/11	1.33	180	5	5	½
Gambier Bay, No. 17	9/11	1.33	182	4	4	¼
Gambier Bay, No. 19	9/12	1.66	103	1	0	1
Pybus Bay, No. 21	9/12	1.33	300	2	0	¾
Pybus Bay, No. 20	9/12	2.00	383	5	1	1
Pybus Bay, No. 22	9/12	0.83	132	1	0	¾
Pybus Bay, No. 24	9/13	0.66	7	0	0	¼
Bay South of Pybus Bay, No. 25	9/14	4.50	234	2	1	2
Eliza Harbor, No. 26	9/14	0.50	0	0	0	⅛
Eliza Harbor, stream bet. Nos. 26 and 27	9/14	1.16	204	2	0	⅜
Eliza Harbor, No. 27	9/14	0.66	5	0	0	¼
Eliza Harbor, No. 28	9/14	0.83	10	0	0	⅛
Limestone Inlet, No. 1	9/11	6.00	2,000	40	21	½
Windham Bay, No. 2	9/12	4.00	3,250	30	18	1
Windham Bay, stream opp. No. 2 at 150°	9/12	2.00	3,600	15	11	¾
Hobart Bay, No. 4A	9/13	2.00	285	6	3	1¼
Hobart Bay, stream right of 4A	9/13	0.50	0	0	0	¼
Port Houghton, No. 5	9/13 9/14	8.00	5,200	24	21	4½
Portage Bay, left stream	9/21	1.00	0	0	0	⅜
Portage Bay, right corner	9/21	0.66	0	0	0	¼
Saginaw Bay, No. 38 (?)	9/18	1.33	113	0	0	¾
Saginaw Bay, main stream No. 38A or 39	9/18	2.16	1,246	6	3	1¼
Security Bay, No. 40 (?)	9/19	1.16	773	0	0	½
Security Bay, main stream east end	9/20	1.33	196	0	0	¾
Security Bay, No. 40A (?)	9/19	1.00	108	1	0	½
Total		62.74		205	132	25⅜
Peril Strait area:						
Patterson Bay, No. 26	9/16	6.00	1,510	8	4	½
Patterson Bay, No. 26A	9/16	0.50	35	0	0	⅛
Ushk Bay, No. 27	8/22	1.50	4	0	0	¾
Ushk Bay, No. 28	8/22	1.50	0	0	0	1
Poison Cove, No. 29	8/22	1.66	0	0	0	½
Deep Bay, No. 30	9/16	2.00	82	1	0	1
Appleton Cove, No. 34A	9/17	1.00	25	0	0	½
Rodman Bay, No. 34	9/17	0.50	2	0	0	¼
Rodman Bay, No. 33A	9/17	4.00	2,515	12	5	⅝
Fish Bay, No. 32	9/15	0.50	260	0	0	½
Fish Bay, No. 31	9/15	0.50	40	0	0	½
Total		19.66		21	9	6¾
West coast Chichagof Island:						
Lisianski Inlet, No. 52	8/24	2.00	130	0	0	1¼
Stag Bay, No. 50	8/24	1.50	7	0	0	⅛
Goulding Harbor, stream at head	8/24	2.50	0	0	0	¾
Black Bay, No. 45	8/24	1.50	0	0	0	¾
Black River, No. 44	8/24	2.50	574	0	0	1⅛
Waterfall Cove, No. 40	8/23	1.00	117	0	0	¾
Flat Cove, Slocum Arm	8/23	0.73	0	0	0	⅛
Slocum Arm, No. 37	8/23	2.00	0	0	0	½
Total		13.73		0	0	6
Other streams:						
Petersburg Creek	9/22	4.00	0	0	0	1¼
Stream left of mouth of Petersburg Creek	9/22	1.00	0	0	0	¼
Stream on right, near mouth of Petersburg Creek	9/22	1.00	0	0	0	¼
St. John Harbor (right corner) Zarembo Island	9/23	2.00	6	0	0	½

TABLE 5.—*Stream tag recoveries by survey crews of the* Heron *and* Sablefish—Continued

Area and stream	Date of survey	Man-hours [1]	Pinks found [2]	Tags noted	Tags recovered	Distance covered
Other streams—Continued						
St. John Harbor (left corner) Zarembo Island	9/23	1.00	0	0	0	½
Total		9.00		0	0	2¾
Grand total		212.89		450	229	80

[1] Includes only time of upstream survey where no tags were noted; time spent recovering tags is included.
[2] Includes both live and dead fish.

The typical stream in Southeastern Alaska is generally one that is easily waded in the summer months and has numerous shallow riffles in which the fish are readily accessible. Occasionally we did encounter large streams containing a number of spawners that were difficult to approach and capture. Weather also affects the completeness of recovery—bright days are generally the best for observation purposes. Heavy rains result in very poor recovery conditions because of reduced visibility and high water. Some streams may have a series of deep holes in which most of the salmon lie preparatory to moving into the shallower spawning riffles. Recovery of tagged fish in these large deep pools is almost impossible.

The time spent in searching a stream obviously affects the total recovery of tags in that stream. Since the magnitude of the area we had to survey precluded any possibility of spending more than half a day on one stream, we frequently recovered less than 50 percent of the tags sighted in the larger streams.

The general physical condition of the salmon at time of survey has some bearing on the number of recoveries made. Green fish, those just in from the sea, are far more difficult to capture than are the spawners and spent fish. Approximately a sixth of all tags recovered were taken from dead fish. Here the recovery was largely the result of keen observation on the part of the survey crews, involving a thorough examination of all carcasses in the stream bed and on high ground.

The most important of all the factors affecting the success of stream recovery of tagged salmon is the time of the survey. This should be shortly after the peak of spawning activity, since it is then that the majority of individuals migrating to a particular stream are available. In practice, time

limitations made it impossible for our crews to visit all streams at the most desirable time.

In evaluating these factors it must be remembered that while the number of tags recovered in any one stream may be evidence of the stream's importance to the tagged population, a comparison between streams should be made with caution, since the recoveries are closely associated with the effort placed on each stream. Thus, the four streams showing the highest number of recoveries—Humpback Creek, Game Creek, Chaik Bay stream No. 57, and Mole River—were also subject to the most intensive observation. Humpback Creek has a Fish and Wildlife Service weir near its mouth, permitting daily observation. Game Creek, a short distance from the village of Hoonah, was under constant surveillance by the local native population. Chaik Bay No. 57 and Mole River recoveries were largely the result of an intensive coverage by local residents.

Returns from Icy Strait tagging

Tables 6 and 7 summarize, by date of tagging, all stream recoveries made from those fish released at Pleasant Island and Point Adolphus. Although our initial experiments were in progress fully 3 weeks before the start of the general fishing season, the presence of schools of pink salmon in the vicinity of streams with early runs of salmon in Tenakee Inlet and Stephens Passage indicated that some fish were already approaching these spawning grounds at the time our experiments were commencing. This was particularly true of the early runs in Tenakee Inlet. Stream-survey reports of the Fisheries Research Institute reveal that Seal Bay, Kadashan Bay, and Long Bay streams all contained pink salmon at the time tagging operations were initiated in late July. By mid-August the escapement into these streams was very near its peak; yet among the thousands of fish observed at this time only one tag was seen by our survey parties. A few tags were eventually recovered in this area, but in relation to the size of the escapement it is obvious that our experiments included only a minor portion of the early Tenakee races. Apparently most of these pink salmon either passed through Icy Strait before July 25 or made their way to Tenakee Inlet through channels other than Icy Strait.

A similar situation prevailed in some of the early-run streams of the Stephens Passage area. There, the number of recoveries indicates that our tagging included a far greater portion of the runs than was evident in Tenakee Inlet. Returns from Port Houghton stream No. 5, for example, cover a tagging period from July 25 to August 13. Similarly, returns from Limestone Creek cover a period from July 29 to August 13. Records on Mole River in Seymour Canal show recoveries from July 26 to August 13. All these streams were reported to contain some pink salmon at the time tagging started, indicating a considerable chronological spread in the migration to these spawning grounds.

The distribution of stream recoveries, when recovery on a percentage basis by area is discounted, is very similar to that shown by the commercial recoveries in tables 1 and 2. Virtually every area in which commercial recoveries were made is similarly represented in the tables listing stream recoveries. Only on the west coast of Chichagof Island, where a few commercial recoveries were made, is there an absence of stream recoveries. Possible explanation for this has been given previously in the text.

Returns from Upper Chatham Strait tagging

It is apparent from an examination of table 8 that the majority of fish tagged in Upper Chatham Strait from August 20 to September 3 were bound for streams in Chatham Strait. The percentage destined for Stephens Passage and Frederick Sound may have been slightly higher than is shown by the stream returns, since these races were subject to fishing pressure over a longer distance than those bound for the Chatham Strait area.

The stream recoveries follow the pattern shown by the commercial recoveries in table 4 with one possible exception: while some commercial recoveries were made in Icy Strait, no stream recoveries were made in this area. A possible explanation would be that the movement into Icy Strait was not great (approximately 2 percent commercial recovery), and that stream-recovery effort in this area during September was not sufficient to locate the few tags which may have reached the streams.

Additional stream observations of tagged fish

Tagged salmon were recovered in 61 streams in an area extending from Taiya River at Skagway to Snake Creek in Olive Cove, Etolin Island.

TABLE 6.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*

Recovered in—	Number recovered from tagging of—																				Total recoveries (8,278 tagged)
	July 27 (23 tagged)	July 28 (27 tagged)	July 30 (361 tagged)	July 31 (480 tagged)	Aug. 1 (99 tagged)	Aug. 2 (79 tagged)	Aug. 3 (258 tagged)	Aug. 4 (115 tagged)	Aug. 5 (729 tagged)	Aug. 6 (572 tagged)	Aug. 7 (811 tagged)	Aug. 8 (290 tagged)	Aug. 9 (202 tagged)	Aug. 10 (399 tagged)	Aug. 11 (380 tagged)	Aug. 12 (942 tagged)	Aug. 13 (994 tagged)	Aug. 14 (739 tagged)	Aug. 27 (96 tagged)	Aug. 30 (306 tagged)	Sept. 5 (376 tagged)	
Icy Strait area:																					
Humpback Creek			3	6	1		2		6	5	5	3		2	2	3	1	2				41
Game Creek			1	3			2		5	1	2	1		2	2	5	2	2		7	1	35
Homeshore, No. 1			1	1					2	1	3		2		1	2						13
Homeshore right of No. 1									1	1	1				1	1		1				6
Seagull Creek, No. 17A							1		1		2		1	1								6
Spasski Creek, No. 20			2						1	2	1											6
Neka Bay, No. 18				1			1			1							1					4
Idaho Inlet, No. 12									1													1
Port Frederick, No. 17B											1											1
Whitestone Harbor, south stream				1																		1
Total			7	11	1		6		17	11	15	4	3	5	6	11	4	5		7	1	114
Lynn Canal area:																					
Howard Cove, No. 3										1	1					1						3
Chilkoot River									1								1					2
Funter Bay, No. 78															1	1						2
Howard Cove, No. 3A													1					1				2
Chilkat River									1													1
Total									2	1	1		1		1	2	1	1				10
Upper Chatham Strait area:																					
South Arm Hood Bay							1				3					1	1		1			7
Favorite Bay Stream										1	2			2		1	2					8
Chalk Bay, No. 57																1	3					4
Sitkoh Bay, No. 20																			2	1	1	4
North Arm Hood Bay, Nos. 53 or 54					1					1						1	1			1	1	5
Bear Creek, Hood Bay																				1	1	2
Clear River, Kelp Bay																1	1					2
Wilson Cove, No. 60																				1		1
Total					1		1			2	5			2		5	8		3	3	3	33
South Chatham Strait area: Lover's Cove stream																	1					1
Frederick Sound–Stephens Passage area:																						
Mole River, No. 15			5	3			2	2	6	2	7	2		1		4						34
Limestone Creek, No. 1			2	4	1	1	1			2	2					1						14
Port Houghton, No. 5				1			1	3	2	2	1						1					11
Seymour Canal, No. 13			1							2	4	2					1					10
Windham Bay, No. 2									3							1	2	1	1	1		9
Saginaw Bay, No. 39															1			2			1	4
Security Bay, No. 40															1	1	1			1		4
Stream, 150° opposite Windham Bay, No. 2							1		1		2						1					5
Hobart Bay, No. 4A										1	1											2
Speel River, Port Snettisham			1		1																	2
Gambier Bay, ½ mile north of No. 17																1						1
Lemon Creek, Juneau																1						1
Port Houghton, No. 6			1																			1
Pybus Bay, No. 20																	1					1
Point McCartney stream																	1					1
Windfall Harbor, 1½ m. north of No. 14																1						1
Total			10	8	2	1	5	5	12	9	17	4		1	2	10	8	3	1	2	1	101

Tenakee Inlet area:																						
Eaton Creek	1		1	1		1										1						5
Crab Bay, No. 13A				3																		3
Kadashan Bay, No. 14				1	1									1								3
Seal Bay, No. 11			1	1																		2
Long Bay, No. 10			1																			1
Total	1		3	6	1	1								1		1						14
Peril Strait area:																						
Patterson Bay, No. 26 creek														1		1						2
Rodman Bay, No. 33 creek													1				1					2
Paradise Flats creek, Saook, No. 35										1												1
Total										1			1	1		1	1					5
Other streams:																						
Petersburg Creek														1								1
Snake Creek, Olive Cove Weir, Etolin Island												1										1
Twin Creek, Mitkof Island, Wrangell Narrows									1													1
Total									1			1		1								3
Grand total	1 (4.3%)	0 (0%)	20 (5.5%)	25 (5.2%)	5 (5.0%)	2 (2.5%)	12 (4.6%)	5 (4.3%)	32 (4.4%)	24 (4.2%)	38 (4.7%)	9 (3.1%)	5 (2.5%)	11 (2.7%)	9 (2.4%)	30 (3.2%)	23 (2.3%)	9 (1.2%)	4 (4.2%)	12 (3.9%)	5 (1.3%)	281 (3.4%)

TABLE 7.—*Stream recoveries of pink salmon tagged at Point Adolphus, 1950*

Recovered in—	Number recovered from tagging of—																			Total recoveries (7,317 tagged [2])
	July 25 (29 tagged)	July 26 (53 tagged)	July 27 (28 tagged)	July 28 (48 tagged)	July 29 (26 tagged)	July 31 (39 tagged)	Aug. 2 (38 tagged)	Aug. 3 (626 tagged)	Aug. 4 (458 tagged)	Aug. 5 (133 tagged)	Aug. 6 (525 tagged)	Aug. 7 (335 tagged)	Aug. 8 (905 tagged)	Aug. 9 (149 tagged)	Aug. 10 (1,110 tagged)	Aug. 11 (623 tagged)	Aug. 12 (996 tagged)	Aug. 13 (667 tagged)	Aug. 14 (344 tagged)	Sept. 4 (284 tagged [1])	
Icy Strait area:																					
Humpback Creek					1			4	1	2	4	5	12	1	5	2	2	1			40
Game Creek								4	2		3	2	6	2	3			1			23
Seagull Creek, No. 17A									1		3		2			1			1		8
Neka Bay, No. 18									1		1		2								4
Homeshore, No. 1								1		1	2		1		3	3	1	2			13
Spasski Creek, No. 20												1	1		2						3
Stream right of No. 1															1				1		4
Chicken Creek																				1	1
Total					1			9	5	3	13	8	24	3	14	6	3	4	2	1	96
Lynn Canal area:																					
Point Howard, No. 3A											1										1
Howard Cove, No. 3															1						1
Chilkoot River																	2	1			3
Total											1				1		2	1			5
Upper Chatham Strait area:																					
South arm Hood Bay, No. 55								2		1			1		3	1	6	1			15
Clear River, Kelp Bay								1							1	1					3
Bear Creek, Hood Bay									1								1	1			3
Chalk Bay, No. 57												1					4			1	6
North arm Hood Bay, Nos. 53 or 54													1		1		1	1	1		5
Favorite Bay stream													3		4	2	2		3		14
Calin Creek, Hood Bay															1						1
Sitkoh Bay, No. 20																	2				2
Total								3	1	1		1	5		10	4	16	3	4	1	49
South Chatham Strait area: Lover's Cove Stream							1										1			1	3
Frederick Sound-Stephens Passage area:																					
Port Houghton, No. 6	1																				1
Port Houghton, No. 5	1			1				2	2						3	1	1				11
Mole River, No. 15		1						4	3	1	4	2	6		3	1	1	2			28
Limestone Creek, No. 1					1			1	1	1	1		1	1	2	2	1	1			13
Windham Bay, No. 2													1		1		1	1	1		5
Stream 150° opposite No. 2								1	1	1		1	1		1						6
Windfall Harbor, No. 14								1													1
Seymour Canal, No. 13		1						2			1			1	1	1					7
Gambier Bay, No. 17									1				1		1	1					4
Gambier Bay, ½ mile north of No. 17															2			1	1		4
Security Bay, No. 40													3								3
Windfall Harbor, 1½ miles north of No. 14													1			1	1				3
Hobart Bay, No. 4A															1						1
Stream right of Sweetheart Lake Creek																	1				1
Saginaw Bay, No. 39																	1		1		2
Total	2	2		1	1			11	8	3	6	3	14	2	15	7	7	5	3		90
Tenakee Inlet area:																					
Kadashan Bay, No. 14				1				1				1	1								4
Seal Bay, No. 11								2													2
Crab Bay, No. 13A								1													1
Eaton Creek								1													1
Total				1				5				1	1								8

Peril Strait area:																						
Rodman Creek, No. 33									1			2			1	1		1				6
Patterson Bay, No. 26																	1	1				2
Poison Cove, No. 29															1							1
Total									1			2			2	1	1	2				9
Other streams:																						
Stikine River								1								1						2
Petersburg Creek											1											1
Total								1			1					1						3
Grand total	2 (6.9%)	2 (3.8%)	0 (0%)	2 (4.2%)	2 (7.7%)	0 (0%)	1 (2.6%)	29 (5.5%)	15 (3.3%)	7 (5.3%)	21 (4.0%)	15 (4.5%)	44 (4.9%)	5 (3.4%)	42 (3.8%)	19 (3.0%)	30 (3.0%)	15 (2.2%)	9 (2.6%)	3 (1.1%)	263 (3.6%)	

[1] Includes 80 fish tagged at Point Adolphus trap No. 6 of the Columbia River Packers Association.
[2] Includes 2 fish tagged August 1.

TABLE 8.—*Stream recoveries of pink salmon tagged in Upper Chatham Strait, 1950*

[Column heading indicates tagging location, date, and number tagged]

Recovered in—	Cube Point Aug. 20 (1,448)	Cube Point Aug. 30 (125)	Cube Point Sept. 3 (185)	False Bay Aug. 21 (33)	False Bay Sept. 3 (14)	Total recoveries (1,805 tagged)
Lynn Canal area: Dyea River, Skagway	1					1
Upper Chatham Strait area:						
Chalk Bay, No. 57	33	1				34
Favorite Bay stream	2					2
Hood Bay, No. 55	8					8
Sitkoh Bay, No. 20	2		1			3
Hood Bay, No. 56	1					1
Fishery Creek, No. 48		1				1
Wilson Cove, No. 60			1		1	2
Bear Creek, Hood Bay			1			1
Total	46	2	3		1	52
South Chatham Strait area: Lover's Cove stream	2	1				3
Frederick Sound–Stephens Passage area:						
Mole River, No. 15	3					3
Security Bay, No. 40	1					1
Windham Bay, No. 2	5					5
Seymour Canal, No. 13	2					2
Bay S. of Pybus, No. 25	1					1
Saginaw Bay, No. 39	2					2
Total	14					14
Peril Strait area: Rodman Creek, No. 33	1			1		2
Grand total	64 (4.4%)	3 (2.4%)	3 (1.6%)	1 (3.0%)	1 (7.1%)	72 (4.0%)

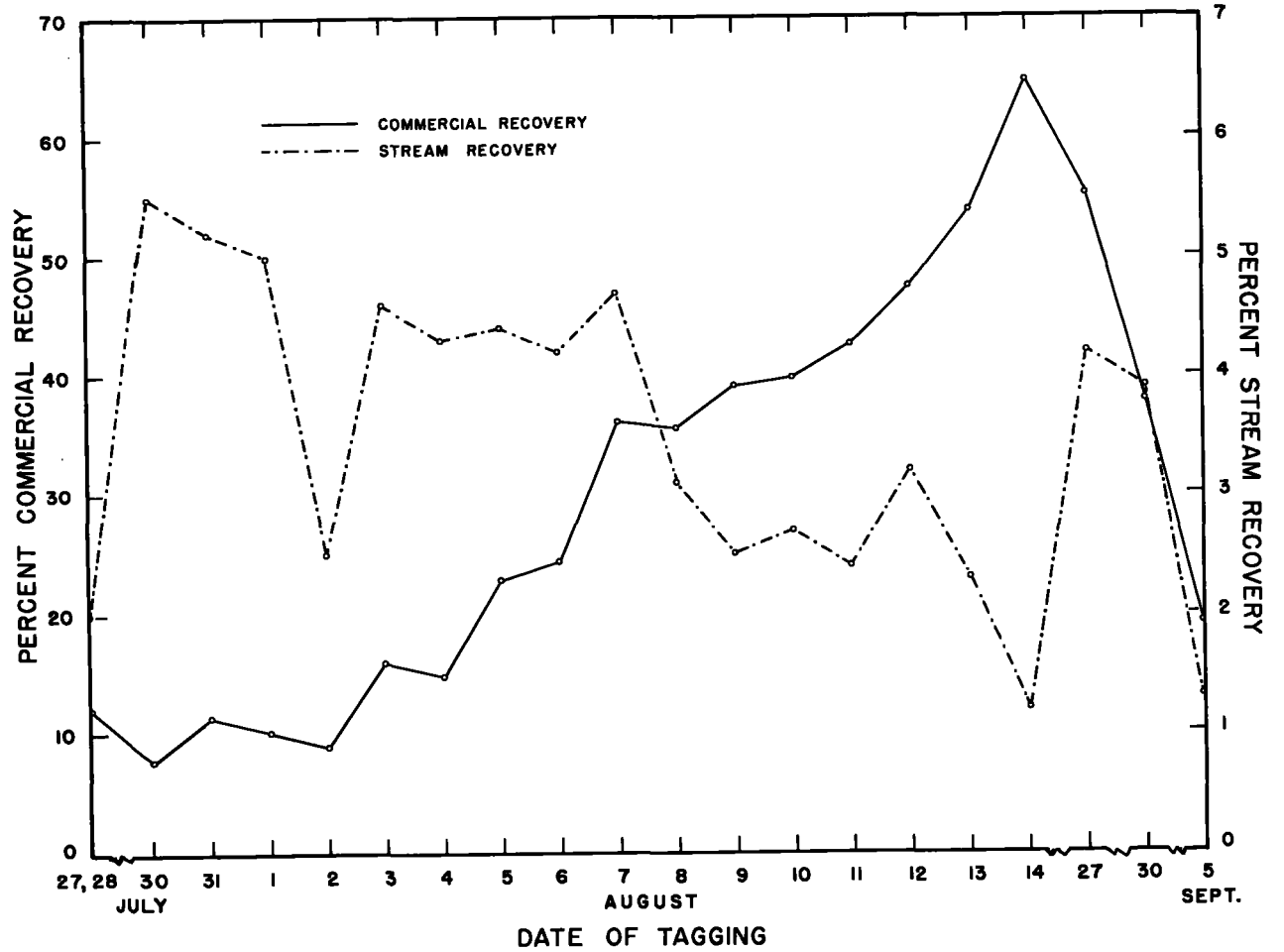

FIGURE 9.—Pleasant Island tagging, 1950: Comparison of stream and commercial recoveries, by date of tagging

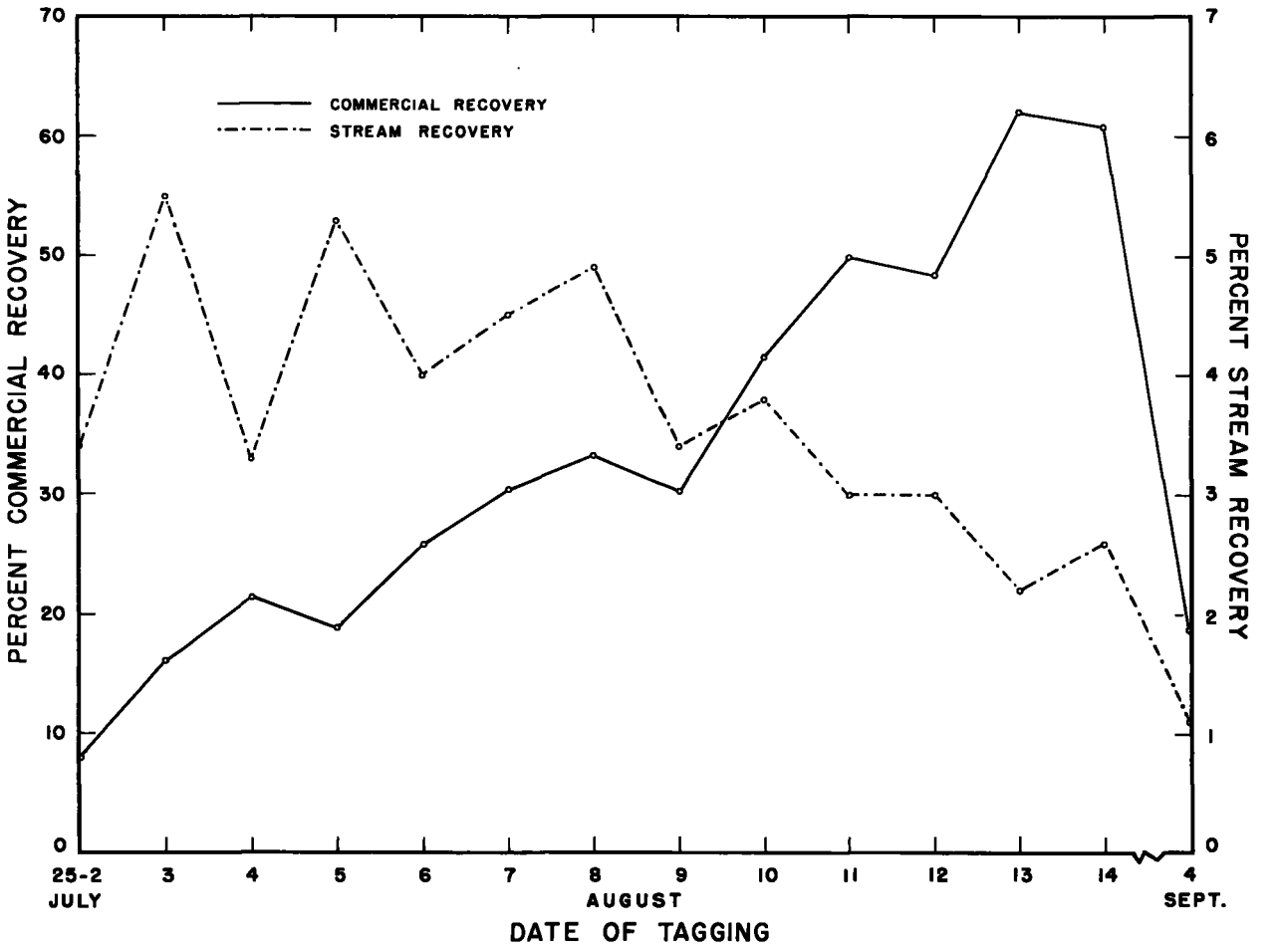

FIGURE 10.—Point Adolphus tagging, 1950: Comparison of stream and commercial recoveries, by date of tagging.

In addition, tagged fish were positively identified in 13 other streams where capture was not possible. These streams, and the dates on which tagged salmon were observed, were as follows:

Stream at head of Freshwater Bay	Aug. 17 and 30
West stream, Corner Bay, Tenakee Inlet	Aug. 31
Gambier Bay, No. 19	Sept. 12
Pybus Bay, No. 22	Sept. 12
Pybus Bay, No. 21	Sept. 12
Eliza Harbor, between No. 26 and No. 27	Sept. 14
Deep Bay, No. 30, Peril Strait	Sept. 16
Tunehean Creek, Kupreanof Island	Aug. 23
Jackson Hole stream, Kuiu Island	Aug. 23
Elena Bay, No. 44C	Sept. 2
Pleasant Harbor, No. 16	Aug. 27
Shuck River	Aug. 22
Gambier Bay, No. 18	Aug. 29

There is no way of determining the exact point at which these fish were tagged, but by process of elimination we may assume that virtually all those observed in August were tagged in Icy Strait. The tagged fish observed in September may have been tagged either in Icy Strait or in Upper Chatham Strait.

Comparison of stream and commercial recovery with respect to date of tagging

About 3.5 percent of all fish tagged at Pleasant Island and Point Adolphus were recovered in streams, the recovery ranging from approximately 5 to 7 percent on fish tagged at the beginning of the experiment to about 1 to 2 percent on those tagged just before the opening of commercial fishing. As might be expected, the stream recovery decreases as the corresponding commercial recovery increases (figs. 9 and 10). The noticeable drop in stream recoveries of fish tagged on the last days of the experiment was probably caused by adverse weather conditions which hampered stream-recovery efforts. It is also possible that a number of fish tagged in September were not yet in the streams at the time our recovery surveys ended on September 23.

Time of passage of major geographical races in Icy Strait

We have previously mentioned the similarity of the commercial returns from the two Icy Strait tagging points. Examination of the stream-recovery data in tables 6 and 7 likewise showed an apparent agreement in the corresponding stream returns from these tagging points. Applying the Brandt-Snedecor method to the data, we found that in general there were no significant differences in the returns from the two points of tagging among the various recovery localities: Icy Strait, Lynn Canal, Tenakee Inlet, Upper Chatham Strait, Peril Strait, Frederick Sound, and Stephens Passage (chi square=10.23, d.f. 6, $0.1<P<0.2$). In view of this suggested homogeneity of returns, the Point Adolphus and Pleasant Island returns were combined and are given in table 9. The combination of this material is particularly advantageous since it yields a total of 544 stream recoveries upon which to base our inferences on the presence of the various races in Icy Strait according to time.

A graphic presentation of the time of occurrence of the major geographical groups of races in Icy Strait is shown in figure 11. The total stream recoveries for each date of tagging by area of recovery are taken from table 9. One of the more important features suggested by this graph is that the three major groups represented, Icy Strait, Upper Chatham Strait, and Stephens Passage, were all available in Icy Strait over quite comparable periods of time. Stephens Passage races were in evidence from July 25 to August 30, Icy Strait races from July 29 to September 5, and Upper Chatham Strait races from August 1 to September 5.

Recoveries in Frederick Sound, Peril Strait, Tenakee Inlet, and Lynn Canal indicate that these races were available for shorter periods of time. The efforts of our crews and of those of the Fisheries Research Institute were sufficient to give adequate coverage in each section with respect to the corresponding number of spawners. The limited recovery in Tenakee Inlet has been discussed and, as mentioned, this recovery may be related to the time of sampling in Icy Strait or to migration from areas other than Icy Strait.

Inspection of figure 9 suggests the possibility of selecting peak times of passage of the various racial groups in Icy Strait on the basis of numbers recovered in each area. However, since no tagging was conducted during the period August 15 to 26, we have no way of determining the true pattern of availability during this period. Furthermore, a thorough interpretation of racial peaking as depicted in figure 9 should account for such factors as (1) the relation of numbers tagged to the numbers available each day, (2) possible varying degrees of fishing intensity on the various races with respect to time, and (3) varying amounts of recovery effort in the different streams. While it would be possible to consider items 1 and 3, it would be difficult indeed to determine the necessary adjustments involved in item 2. Consequently, we do not feel that our returns alone offer conclusive evidence of the peak time of passage of the racial groups in Icy Strait.

Speed of migration from tagging point to stream

It is difficult to obtain a true measure of the elapsed time involved in the movement of a salmon from the time it was tagged until it entered the stream, since in most instances we have no accurate way of determining when the fish actually entered the stream. One approach to the problem is to calculate the time in days from the date of tagging to the date of recovery, using only recoveries of live fish and making no allowance for the stage of maturity of the fish. Such an analysis was made for the elapsed time from Icy Strait tagging points to the four principal areas of recovery. These times, in days, are as follows:

To—	*Average from Pleasant Island*	*Average from Point Adolphus*	*Range*
Icy Strait	25. 3	25. 5	6 to 41
Tenakee Inlet	25. 4	25. 6	16 to 36
Upper Chatham Strait	28. 8	30. 9	12 to 46
Stephens Passage–Seymour Canal	33. 0	33. 0	8 to 46

These figures are, in all probability, somewhat in excess of the true elapsed times, since it is very unlikely that all of the tagged fish were captured immediately or shortly after their entrance into the various streams. Indeed, if we are to consider the wide area examined for tagged salmon, it is quite possible that many fish spent considerable time on the spawning ground before their capture. The elapsed time, then, is undoubtedly influenced by the date on which the survey was conducted and therefore may not correctly represent the

TABLE 9.—*Combined stream recoveries of pink salmon tagged at Pleasant Island and Point Adolphus, 1950*

Recovered in—	Number recovered from tagging of—												
	July 25 (29 tagged)	July 26 (53 tagged)	July 27 (51 tagged)	July 28 (75 tagged)	July 29 (26 tagged)	July 30 (361 tagged)	July 31 (519 tagged)	Aug. 1 (101 tagged)	Aug. 2 (117 tagged)	Aug. 3 (784 tagged)	Aug. 4 (573 tagged)	Aug. 5 (862 tagged)	Aug. 6 (1,097 tagged)
Icy Strait area:													
Humpback Creek, No. 19					1	3	6	1		6	1	8	9
Game Creek, No. 16						1	2			5	2	5	4
Seagull Creek, No. 17A										1	1	1	3
Port Frederick, No. 17B													
Neka Bay, No. 18							1			1	1		2
Spasski Creek, No. 20						2						2	2
Homeshore, No. 1						1	1			1		2	3
Homeshore, rt. of No. 1												1	1
Chicken Creek, No. 14A													
Idaho Inlet, No. 12												1	
Whitestone Harbor, south stream							1						
Total					1	7	11	1		15	5	20	24
Lynn Canal area:													
Funter Bay, No. 78													
Howard Cove, No. 3A													1
Howard Cove, No. 3													1
Chilkat River												1	
Chilkoot River												1	
Total												2	2
Tenakee Inlet area:													
Kadashan Bay, No. 14				1			1	1		1			
Crab Bay, No. 13A							3			1			
Eaton Creek			1			1	1		1	1			
Seal Bay, No. 11						1	1			2			
Long Bay, No. 10						1							
Total			1	1		3	6	1	1	5			
Upper Chatham Strait area:													
South arm Hood Bay, No. 55										3		1	
North arm Hood Bay, No. 53 *or* No. 54								1					1
Bear Creek, Hood Bay											1		
Calin Creek, Hood Bay													
Favorite Bay stream													1
Sitkoh Bay, No. 20													
Clear River, Kelp Bay										1			
Chalk Bay, No. 57													
Wilson Cove, No. 60													
Total								1		4	1	1	2
Peril Strait area:													
Saook Bay, No. 35													1
Rodman Creek, No. 33											1		
Patterson Bay, No. 26													
Poison Cove No. 29													
Total											1		1
Frederick Sound area:													
Point McCartney stream													
Pybus Bay, No. 20													
Saginaw Bay, No. 39													
Security Bay, No. 40													
Total													
Stephens Passage area:													
Gambier Bay, No. 17											1		
Half mile north of Gambier Bay, No. 17													
Port Houghton, No. 5	1			1			1			3	5	2	2
Port Houghton, No. 6	1					1							
Hobart Bay, No. 4A													1
Windham Bay, No. 2												3	
Windham Bay, No. 2A										2	1	2	
Mole River, No. 15		1				5	3			6	5	7	6
Windfall Harbor, No. 14										1			
Stream 1½ mi. north No. 14													
Seymour Canal, No. 13		1				1				2			3
Speel River, Port Snettisham						1		1					
Limestone Creek, No. 1					1	2	4	1	1	2	1	1	3
Stream, rt. of Sweetheart Creek													
Lemon Creek, Juneau													
Total	2	2		1	1	10	8	2	1	16	13	15	15
South Chatham Strait area: Lover's Cove stream									1				
Other areas:													
Stikine River										1			
Petersburg Creek, No. 79													1
Snake Creek, No. 42													
Twin Creek, Mitkof Island												1	
Total										1		1	1
Grand total	2 (6.9%)	2 (3.8%)	1 (2.0%)	2 (2.7%)	2 (7.7%)	20 (5.5%)	25 (4.8%)	5 (5.1%)	3 (2.6%)	41 (5.2%)	20 (3.5%)	39 (4.5%)	45 (4.1%)

TABLE 9.—*Combined stream recoveries of pink salmon tagged at Pleasant Island and Point Adolphus, 1950*—Continued

Recovered in—	Number recovered from tagging of—												Total recoveries (15,595 tagged)
	Aug. 7 (1,146 tagged)	Aug. 8 (1,195 tagged)	Aug. 9 (351 tagged)	Aug. 10 (1,509 tagged)	Aug. 11 (1,003 tagged)	Aug. 12 (1,938 tagged)	Aug. 13 (1,061 tagged)	Aug. 14 (1,083 tagged)	Aug. 27 (96 tagged)	Aug. 30 (306 tagged)	Sept. 4 (283 tagged)	Sept. 5 (376 tagged)	
Icy Strait area:													
Humpback Creek, No. 19	10	15	1	7	4	5	2	2					81
Game Creek, No. 16	4	7	2	5	2	5	3	2		7		1	58
Seagull Creek, No. 17A	2	2	1	1	1			1					14
Port Frederick, No. 17B	1												1
Neka Bay, No. 18		2					1						8
Spasski Creek, No. 20	1			2									9
Homeshore, No. 1	3	1	2	3	4	3	2						26
Homeshore, rt. of No. 1	2	1		1	1	1		2					10
Chicken Creek, No. 14A											1		1
Idaho Inlet, No. 12													1
Whitestone Harbor, south stream													1
Total	23	28	6	19	12	14	8	7		7	1	1	210
Lynn Canal area:													
Funter Bay, No. 78					1	1							2
Howard Cove, No. 3A			1					1					3
Howard Cove, No. 3	1			1		1							4
Chilkat River													1
Chilkoot River						2	2						5
Total	1		1	1	1	4	2	1					15
Tenakee Inlet area:													
Kadashan Bay, No. 14	1	1		1									7
Crab Bay, No. 13A													4
Eaton Creek						1							6
Seal Bay, No. 11													4
Long Bay, No. 10													1
Total	1	1		1		1							22
Upper Chatham Strait area:													
South arm Hood Bay, No. 55	3	1		3	1	7	2		1				22
North arm Hood Bay, Nos. 53 or 54		1		1		2	2	1				1	10
Bear Creek, Hood Bay						1	1			1		1	5
Calin Creek, Hood Bay				1									1
Favorite Bay stream	2	3		6	2	3	2	3					22
Sitkoh Bay, No. 20						2			2	1		1	6
Clear River, Kelp Bay				1	1	1	1						5
Chalk Bay, No. 57	1					5	3				1		10
Wilson Cove, No. 60										1			1
Total	6	5		12	4	21	11	4	3	3	1	3	82
Peril Strait area:													
Saook Bay, No. 35													1
Rodman Creek, No. 33	2		1	1	1		2						8
Patterson Bay, No. 26				1		2	1						4
Poison Cove, No. 29				1									1
Total	2		1	3	1	2	3						14
Frederick Sound area:													
Point McCartney stream							1						1
Pybus Bay, No. 20							1						1
Saginaw Bay, No. 39					1	1		3				1	6
Security Bay, No. 40		3			1	1	1			1			7
Total		3			2	2	3	3		1		1	15
Stephens Passage area:													
Gambier Bay, No. 17		1		1	1								4
Half mile north of Gambier Bay, No. 17				2		1	1	1					5
Port Houghton, No. 5	1			3	1	1	1						22
Port Houghton, No. 6													2
Hobart Bay, No. 4A	1			1									3
Windham Bay, No. 2		1		1		2	3	2	1	1			14
Windham Bay, No. 2A	3	1		1			1						11
Mole River, No. 15	9	8		4	1	5	2						62
Windfall Harbor, No. 14													1
Stream 1½ mi. north, No. 14		1			1	2							4
Seymour Canal, No. 13	4	2	1	1	1		1						17
Speel River, Port Snettisham													2
Limestone Creek, No. 1	2	1	1	2	2	2	1						27
Stream, rt. of Sweetheart Creek						1							1
Lemon Creek, Juneau						1							1
Total	20	15	2	16	7	15	10	3	1	1			176
South Chatham strait area:													
Lover's Cove Stream						1	1				1		4
Other areas:													
Stikine River					1								2
Petersburg Creek, No. 79				1									2
Snake Creek No. 42		1											1
Twin Creek, Mitkof Island													1
Total		1		1	1								6
Grand total	53 (4.6%)	53 (4.4%)	10 (2.8%)	53 (3.5%)	28 (2.8%)	60 (3.1%)	38 (2.3%)	18 (1.7%)	4 (4.2%)	12 (3.9%)	3 (1.1%)	5 (1.3%)	544 (3.5%)

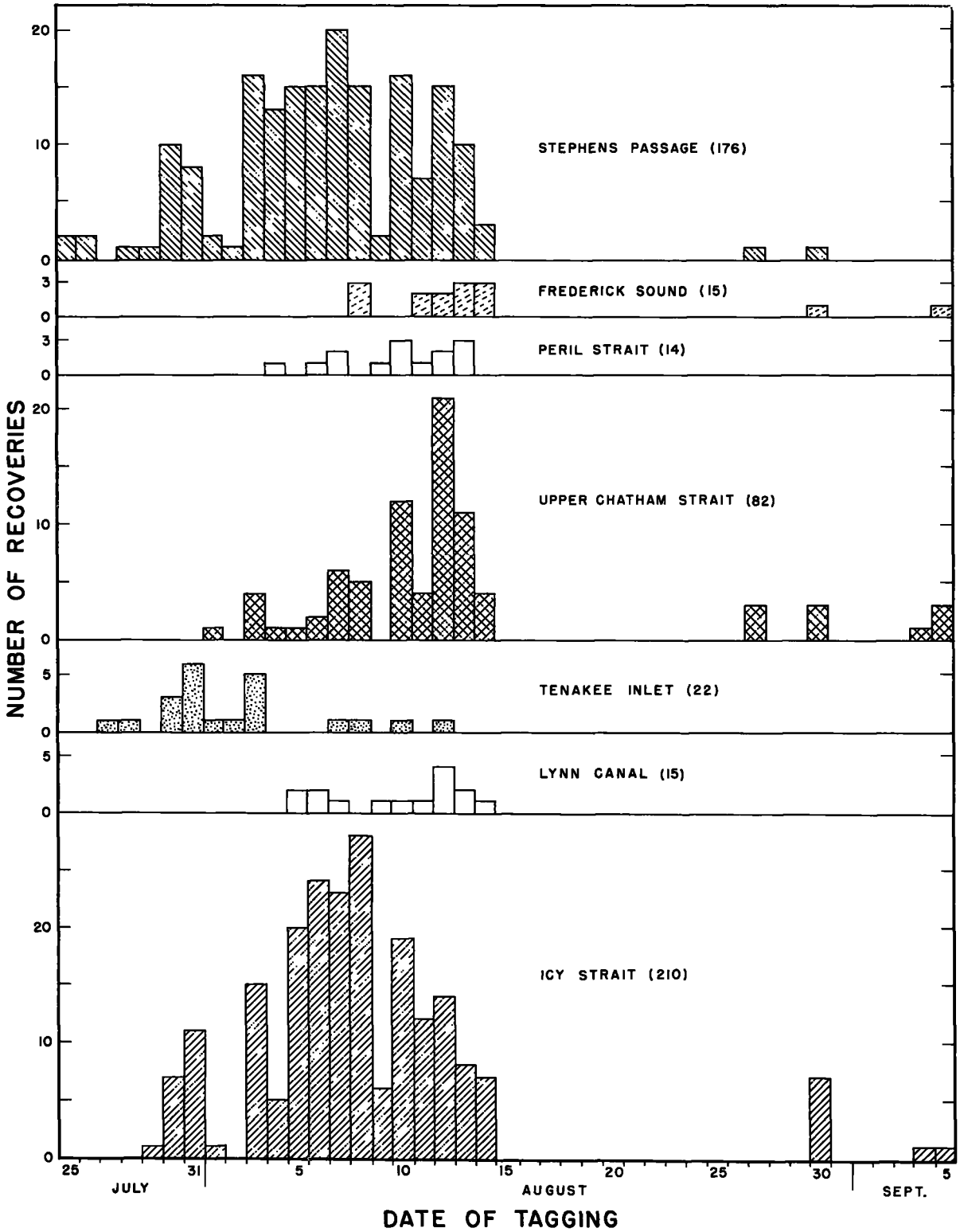

FIGURE 11.—Racial composition of Icy Strait pink salmon run, 1950, as indicated by number of stream recoveries made from each tagging for period July 25 to September 5, inclusive. Numbers in parentheses indicate total stream recovery in each area. No tagging was conducted during period August 15 to 26, inclusive.

actual time taken by the fish to travel between the indicated points.

A particularly interesting indication of variation in rate of migration is found in the comparison of two stream recoveries made in Lover's Cove Stream on southeast Baranof Island. A fish tagged and released in Icy Strait on August 2 arrived on the spawning grounds at approximately the same time as did a fish tagged and released in Icy strait on September 4. These fish were recovered by Service personnel conducting intertidal-zone spawning experiments at Lover's Cove, Big Port Walter. Few pink salmon entered this stream before September 10, and as the grounds were under constant observation throughout the spawning period it is certain that these two recoveries were made within a very short time after the salmon entered the stream.

SUMMARY

A total of 17,400 pink salmon were tagged in Icy Strait and Upper Chatham Strait in the period July 25 to September 5, 1950. Of this number, 6,478, or 37.2 percent, were recovered by the commercial fishery. The highest recovery of a single day's tagging was 64.7 percent, which came from the Pleasant Island tagging of August 14, the day before the fishing season opened. Recoveries of tagged salmon released within the fishing season suggest that fishing mortality on these fish probably remained above 50 percent throughout most of season, dropping below this only during the last week.

Commercial recovery by principal tagging points was as follows:

Tagged at—	*Number tagged*	*Number recovered*	*Percent recovered*
Pleasant Island	8,278	2,966	35.8
Point Adolphus	7,317	2,738	37.4
Cube Point	1,758	760	43.2
False Bay	47	10	21.3
Unknown (tags broken)		4	
All points	[1] 17,400	6,478	37.2

[1] Does not include tagged fish captured at original point of tagging.

Pink salmon tagged in Icy Strait were found to migrate east through Icy Strait and south into Chatham Strait, and then east and north into Frederick Sound and Stephens Passage. Smaller segments of the main run branched into Lynn Canal and South Chatham Strait. There was little movement to western areas of Chichagof Island. Returns from the daily tagging in Icy Strait showed that recoveries increased at the rate of 3.6 percent a day as the day of tagging approached the opening day of the commercial season. While tagging within the fishing period was limited to four experiments during the latter part of the season, the returns indicate a progressive decline as the date of tagging approaches the closing date of fishing. No significant differences were noted in the returns from the tagging at Point Adolphus and those from the tagging at Pleasant Island.

Recoveries from the tagging in Upper Chatham Strait indicate a major southward movement through Chatham Strait and then eastward into Frederick Sound and Stephens Passage. There is also evidence of a smaller but significant northward migration.

A total of 616 tags, or 5.6 percent, of the 10,922 tags not recovered commercially, were recovered in 61 streams. Approximately 125 streams north of 56° 30′ in Southeastern Alaska were examined for tagged salmon. Stream recoveries from each point of tagging were as follows:

Tagged at—	*Number tagged*	*Number recovered*	*Percent recovered*
Pleasant Island	8,278	281	3.4
Point Adolphus	7,317	263	3.6
Upper Chatham Strait	1,805	72	4.0
All points	17,400	616	3.5

Stream recoveries illustrate very clearly the great mixing of races which occurs on the commercial fishing ground. For example, from the 1,110 individuals tagged at Point Adolphus on August 10, recoveries were made in 22 streams. Analysis of stream returns indicated that there was very little difference in the length of time the major racial groups were present in Icy Strait: Stephens Passage races were found to be present from July 25 to August 30, Icy Strait races from July 29 to September 5, and Chatham Strait races from August 1 to September 5.

While some tag recoveries were made in Tenakee Inlet, there are indications that either the tagging did not adequately sample this run or the main part of it reached Tenakee Inlet through areas other than Icy Strait.

Stream recoveries from the tagging in Upper Chatham Strait indicate that the majority of these fish were bound for streams in Chatham Strait and Stephens Passage. The average rate of migration from point of tagging to the streams was not readily determined, although evidence of considerable variability in rate of movement was obtained.

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APPENDIX

Complete lists of stream recoveries by point of release are included in tables 10, 11, and 12. Personnel of the Fish and Wildlife Service and Fisheries Research Institute made approximately 70 percent of these recoveries, while local residents and others accounted for the remaining 30 percent.

TABLE 10.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Eaton Creek, Tenakee Inlet	7/27	9/1	x		36
Long Bay, No. 10	7/30	8/26	x		27
Mole River, No. 15	7/30	9/10	x		42
Game Creek, No. 16	7/30	8/27	x		28
Port Houghton, No. 6	7/30	8/20	x		21
Limestone Inlet, No. 1	7/30	8/23	x		24
Speel River, Port Snettisham	7/30	8/9	x		10
Homeshore, No. 1	7/30	9/5	x		38
Limestone Inlet, No. 1	7/30	9/11	x		43
Spasski Creek, No. 20	7/30	8/29	x		30
Mole River, No. 15	7/30	9/9	x		41
Do	7/30	9/9	x		41
Do	7/30	9/9	x		41
Do	7/30	9/9	x		41

TABLE 10.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Seymour Canal, No. 13	7/30	9/10	x		42
Eaton Creek, Tenakee Inlet	7/30	9/1	x		33
Humpback Creek, No. 19	7/30	8/31	x		32
Do	7/30	9/3	x		35
Do	7/30	9/4	x		36
Seal Bay, No. 11	7/30	9/3	x		35
Spasski Creek, No. 20	7/30	8/19	x		20
Seal Bay, No. 11	7/31	8/24	x		24
Kadashan Bay, No. 14 Creek	7/31	8/27	x		27
Mole River, No. 15	7/31	9/10	x		41
Game Creek, No. 16	7/31	9/7	x		38
Do	7/31	8/31	x		31
Limestone Inlet, No. 1	7/31	8/23	x		23
Do	7/31	8/23	x		23
Neka Bay stream, No. 18	7/31	9/1	x		32
Homeshore stream, No. 1	7/31	9/2	x		33
Limestone Creek, No. 1	7/31	9/11	x		42
Do	7/31	9/11	x		42
Port Houghton, No. 5	7/31	9/14		x	45
Whitestone Harbor, No. 22	7/31	8/29	x		29
Mole River, No. 15	7/31	9/9	x		40
Do	7/31	9/9	x		40
Crab Bay, No. 13A	7/31	8/16	x		16
Do	7/31	8/16	x		16
Do	7/31	8/16	x		16
Eaton Creek, Tenakee Inlet	7/31	9/1	x		32
Humpback Creek, No. 19	7/31	8/20		x	20
Do	7/31	8/20		x	20
Do	7/31	8/24	x		24
Do	7/31	8/26	x		26
Do	7/31	8/26	x		26
Do	7/31	9/14		x	45
Kadashan Bay Creek, No. 14	8/1	8/27	x		26
Limestone Inlet, No. 1	8/1	8/23	x		22
Speel River, Port Snettisham	8/1	8/9	x		8
Hood Bay Nos. 53 or 54	8/1	9/16	x		46
Humpback Creek, No. 19	8/1	8/27	x		26
Limestone Inlet, No. 1	8/2	9/11	x		40
Eaton Creek, Tenakee Inlet	8/2	9/1	x		30
Mole River, No. 15	8/3	9/10	x		38
Do	8/3	9/10	x		38
Game Creek, No. 16	8/3	9/5	x		33
Limestone Inlet Creek, No. 1	8/3	8/23	x		20
Hood Bay, No. 55	8/3	9/17	x		45
Humpback Creek, No. 19	8/3	8/12	x		9
Seagull Creek, No. 17A	8/3	8/31	x		28
Neka Bay, No. 18 Stream	8/3	8/31	x		28
Windham Bay, opposite No. 2	8/3	9/12	x		40
Port Houghton, No. 5	8/3	9/14	x		42
Game Creek, No. 16	8/3	8/22	x		19
Humpback Creek, No. 19	8/3	9/3	x		31
Mole River, No. 15	8/4	9/10	x		37
Port Houghton, No. 5	8/4	9/14		x	41
Do	8/4	9/14	x		41
Do	8/4	9/14	x		41
Mole River, No. 15	8/4	9/9	x		36
Spasski Creek, No. 20	8/5	9/2	x		28
Chilkoot River	8/5	9/21	x		50
Twin Creek, Mitkof Isl., Wrangell Narrows	8/5	9/10		x	36
Mole River, No. 15	8/5	9/10	x		36
Do	8/5	9/10	x		36
Do	8/5	9/12	x		38
Do	8/5	9/13	x		39
Game Creek, No. 19	8/5	9/4	x		30
Do	8/5	9/4	x		30
Do	8/5	9/5	x		31
Do	8/5	9/4	x		30
Sophia Creek, Windham Bay, No. 2	8/5	8/21	x		16
Idaho Inlet, No. 12	8/5	9/6	x		32
Seagull Creek, No. 17A	8/5	9/1	x		27
Homeshore Stream, No. 1	8/5	9/2	x		28
Stream to rt. of Homeshore No. 1	8/5	9/2	x		28
Homeshore stream, No. 1	8/5	9/5	x		31
Windham Bay stream, No. 2	8/5	9/12		x	38
Do	8/5	9/12		x	38

See footnotes at end of table.

TABLE 10.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Stream opposite No. 2, Windham Bay	8/5	9/12	x		38
Port Houghton, No. 5	8/5	9/13		x	39
Do	8/5	9/14		x	40
Mole River, No. 15	8/5	9/9	x		35
Do	8/5	9/9	x		35
Game Creek, No. 16	8/5	8/22	x		17
Humpback Creek, No. 19	8/5	8/28		x	23
Do	8/5	8/30	x		25
Do	8/5	9/1		x	27
Do	8/5	9/3	x		29
Do	8/5	9/4		x	30
Do	8/5	9/13		x	39
Chilkat River	8/5	8/29	x		24
Spasski Creek, No. 20	8/6	9/2	x		27
Paradise Flats Creek, Saook, No. 35	8/6	8/28	x		22
Mole River, No. 15	8/6	9/18	x		43
N. arm Hood Bay, Nos. 53–54	8/6	9/7	x		32
Favorite Bay stream	8/6	9/10	x		35
Game Creek, No. 16	8/6	8/31	x		25
Neka Bay, No. 18	8/6	9/3	x		28
Homeshore stream, No. 1	8/6	9/2	x		27
Homeshore, stream right of No. 1	8/6	9/2	x		27
Limestone Creek, No. 1	8/6	9/11	x		36
Do	8/6	9/11	x		36
Hobart Bay, No. 4A	8/6	9/13	x		38
Port Houghton, No. 5	8/6	9/14		x	39
Do	8/6	9/14		x	39
Spasski Creek, No. 20	8/6	8/29	x		23
Howard Cove Creek, No. 3	8/6	9/5	x		30
Mole River, No. 15	8/6	9/9	x		34
Seymour Canal, No. 13	8/6	9/10	x		35
Do	8/6	9/10	x		35
Humpback Creek, No. 19	8/6	8/26	x		20
Do	8/6	8/26	x		20
Do	8/6	8/30	x		24
Do	8/6	8/30	x		24
Do	8/6	9/5		x	30
Mole River, No. 15	8/7	9/10	x		34
Do	8/7	9/11	x		35
Do	8/7	9/11	x		35
Do	8/7	9/11	x		35
Favorite Bay stream	8/7	9/10	x		34
Game Creek, No. 16	8/7	9/4	x		28
Do	8/7	8/16	x		9
S. arm Hood Bay, No. 55	8/7	9/7	x		31
Do	8/7	9/10	x		34
Do	8/7	9/17	x		41
Port Frederick, No. 17B	8/7	8/31	x		24
Seagull Creek, No. 17A	8/7	8/31	x		24
Do	8/7	8/31	x		24
Homeshore stream, No. 1	8/7	9/2	x		26
Do	8/7	9/2	x		26
Homeshore, stream to right of No. 1	8/7	9/2	x		26
Homeshore, No. 1	8/7	9/5	x		29
Limestone Inlet, No. 1	8/7	9/11	x		35
Do	8/7	9/11	x		35
Stream opp. Windham Bay, No. 2	8/7	9/12	x		36
Do	8/7	9/12	x		36
Hobart Bay, No. 4A	8/7	9/13	x		37
Port Houghton, No. 5	8/7	9/14		x	38
Spasski Creek, No. 20	8/7	8/29	x		22
Howard Cove, No. 3	8/7	9/5	x		29
Mole River, No. 15	8/7	9/9	x		33
Do	8/7	9/9	x		33
Do	8/7	9/9		x	33
Seymour Canal, No. 13	8/7	9/10	x		34
Do	8/7	9/10	x		34
Do	8/7	9/10	x		34
Do	8/7	9/10	x		34
Humpback Creek, No. 19	8/7	8/29		x	22
Do	8/7	8/30	x		23
Do	8/7	9/5		x	29
Do	8/7	9/7		x	31
Do	8/7	9/7		x	31
Favorite Bay stream	8/7	9/12		x	36
Mole River, No. 15	8/8	9/10	x		33
Do	8/8	9/12	x		35
Game Creek, No. 16	8/8	8/31	x		23
Etolin Island, Snake Creek	8/8	8/26	x		18
Seymour Canal, No. 13	8/8	9/10	x		33
Do	8/8	9/10	x		33
Humpback Creek, No. 19	8/8	8/26	x		18
Do	8/8	8/28		x	20
Do	8/8	9/13		x	36

TABLE 10.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Rodman Bay, No. 33	8/9	9/16	x		38
Seagull Creek, No. 17A	8/9	9/1	x		23
Homeshore stream, No. 1	8/9	9/2	x		24
Do	8/9	9/5	x		27
Stream No. 3A, Port Howard	8/9	9/6	x		28
Kadashan Bay Creek, No. 14	8/10	8/27	x		17
Petersburg Creek	8/10	9/10	x		31
Mole River, No. 15	8/10	9/12	x		33
Favorite Bay stream	8/10	9/10	x		31
Game Creek, No. 16	8/10	9/5	x		26
Do	8/10	9/15	x		36
Seagull Creek, No. 17A	8/10	8/31	x		21
Patterson Bay, No. 26	8/10	9/16	x		37
Humpback Creek, No. 19	8/10	8/28		x	18
Do	8/10	9/4		x	25
Favorite Bay stream	8/10	9/12		x	33
Game Creek, No. 19	8/11	9/8		x	28
Do	8/11	9/7		x	27
Security Bay, No. 40	8/11	9/18		x	38
Saginaw Bay, No. 39	8/11	9/19	x		39
Homeshore stream to right of No. 1	8/11	9/2	x		22
Homeshore stream, No. 1	8/11	9/5	x		25
Funter Bay, No. 78	8/11	9/6	x		26
Humpback Creek, No. 19	8/11	8/30	x		19
Do	8/11	9/13		x	33
Mole River, No. 15	8/12	9/11	x		30
Do	8/12	9/11	x		30
Do	8/12	9/12	x		31
Do	8/12	9/12	x		31
Game Creek, No. 16	8/12	9/12	x		31
Do	8/12	9/9	x		28
Do	8/12	9/5	x		24
Do	8/12	9/5	x		24
Do	8/12	9/15	x		34
Lemon Creek, Juneau	8/12	9/9	x		28
Security Bay, No. 40	8/12	9/18	x		37
N. arm Hood Bay, Nos. 53–54	8/12	9/8	x		27
Hood Bay, No. 55	8/12	9/11	x		30
Clear River, Kelp Bay	8/12	9/9	x		28
Homeshore stream, No. 1	8/12	9/2	x		21
Stream right of Homeshore, No. 1	8/12	9/2	x		21
Homeshore stream, No. 1	8/12	9/5	x		24
Funter Bay, stream No. 78	8/12	9/6	x		25
Limestone Creek, No. 1	8/12	9/11	x		30
Windham Bay, No. 2	8/12	9/12	x		31
Patterson Bay, No. 26	8/12	9/16	x		35
Howard Cove Creek, No. 3	8/12	9/5	x		24
Windfall Harbor, 1½ Mi. N. of No. 14	8/12	9/10	x		29
Gambier Bay, ½ mile N. of No. 17	8/12	9/11	x		30
Eaton Creek, Tenakee Inlet	8/12	9/1	x		20
Humpback Creek, No. 19	8/12	8/27	x		15
Do	8/12	9/4		x	23
Do	8/12	9/7		x	26
Favorite Bay stream	8/12	9/12		x	31
Chalk Bay Stream, No. 57	8/12	9/10	x		29
Do	8/13	9/10	x		28
Do	8/13	9/10	x		28
Favorite Bay stream	8/13	9/10	x		28
Game Creek, No. 16	8/13	9/15	x		33
Do	8/13	9/15	x		33
Security Bay, No. 40	8/13	9/18	x		36
Hood Bay, No. 55	8/13	9/11	x		29
Do	8/13	9/17	x		35
Clear River, Kelp Bay	8/13	9/9	x		27
Rodman Bay, No. 33	8/13	9/16	x		34
Neka Bay, No. 18	8/13	9/3	x		21
Point McCartney stream	8/13	9/3	x		21
Windham Bay, No. 2	8/13	9/12	x		30
Do	8/13	9/12	x		30
Stream opp. No. 2, Windham Bay	8/13	9/12	x		30
Port Houghton, No. 5	8/13	9/14	x		32
Seymour Canal, No. 13	8/13	9/10	x		28
Pybus Bay, No. 20	8/13	9/12	x		30
Chalk Bay, No. 57	8/13	9/17	x		35
Humpback Creek, No. 19	8/13	9/1		x	19
Chilkoot River	8/13	10/1		x	49
Lover's Cove stream	8/13	9/13	x		31
Favorite Bay stream	8/13	9/12		x	30
Game Creek, No. 16	8/14	9/4	x		21
Do	8/14	9/15	x		32

See footnotes at end of table.

TABLE 10.—*Stream recoveries of pink salmon tagged at Pleasant Island, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Saginaw Bay, No. 39	8/14	9/19	x		36
Stream to rt. of No. 1, Homeshore	8/14	9/5	x		22
Stream No. 3A, Point Howard	8/14	9/6	x		23
Windham Bay, No. 2	8/14	9/12	x		29
Saginaw Bay, main stream	8/14	9/18	x		35
Humpback Creek, No. 19	8/14	9/4		x	21
Do	8/14	9/7		x	24
Windham Bay, No. 2	8/27	9/12	x		16
Sitkoh Bay, No. 20	8/27	9/18	x		22
Do	8/27	9/18	x		22
Hood Bay, No. 55	8/27	10/10		x	44
Game Creek, No. 16	8/30	9/9	x		10
Do	8/30	9/9	x		10
Do	8/30	9/9	x		10
Do	8/30	9/9	x		10
Do	8/30	9/12	x		13
Do	8/30	9/12	x		13
Do	8/30	9/5	x		6
Security Bay, No. 40	8/30	9/18	x		19
Wilson Cove, No. 60	8/30	9/10	x		11
Windham Bay, No. 2	8/30	9/12	x		13
Sitkoh Bay, No. 20	8/30	9/18	x		19
Bear Creek, Hood Bay	8/30	Oct.		x	
Game Creek, No. 16	9/5	9/15	x		10
Saginaw Bay, No. 39	9/5	9/19	x		14
Hood Bay, No. 55	9/5	9/17	x		12
Sitkoh Bay, No. 20	9/5	9/18	x		13
Bear Creek, Hood Bay	9/5	Oct.		x	
All streams			237	44	

[1] Condition of fish at time of recovery.
[2] From date of release to date of capture.

TABLE 11.—*Stream recoveries of pink salmon tagged at Point Adolphus, 1950*

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Port Houghton, No. 6	7/25	8/20	x		26
Port Houghton, No. 5	7/25	9/13		x	50
Mole River, No. 15	7/26	8/25	x		30
Seymour Canal, No. 13	7/26	9/10	x		46
Port Houghton, No. 5	7/28	8/20	x		23
Kadashan Bay, No. 14	7/28	8/31	x		34
Limestone Creek, No. 1	7/29	8/23	x		25
Humpback Creek, No. 19	7/29	8/20		x	22
Lover's Cove stream	8/2	9/20	x		49
Seal Bay, No. 11	8/3	8/24	x		21
Do	8/3	9/3	x		31
Mole River, No. 15	8/3	9/10	x		38
Do	8/3	9/10	x		38
Do	8/3	9/10	x		38
Do	8/3	9/9	x		37
Game Creek, No. 16	8/3	9/5	x		33
Do	8/3	9/5	x		33
Do	8/3	8/30	x		27
Do	8/3	8/31	x		28
S. arm Hood Bay, No. 55	8/3	9/7	x		35
Do	8/3	9/10	x		38
Clear River, No. 41	8/3	9/9	x		37
Homeshore, No. 1	8/3	9/5	x		33
Stikine River	8/3	8/19	x		16
Limestone Creek, No. 1	8/3	9/11		x	39
Windham Bay, opp. No. 2	8/3	9/12	x		40
Port Houghton, No. 5	8/3	9/13		x	41
Do	8/3	9/14	x		42
Kadashan Bay, No. 14	8/3	8/31	x		28
Windfall Harbor, No. 14	8/3	9/9	x		37
Seymour Canal, No. 13	8/3	9/10	x		38
Do	8/3	9/10	x		38
Crab Bay, No. 13A	8/3	8/22	x		19
Eaton Creek, Tenakee	8/3	9/1	x		29
Humpback Creek, No. 19	8/3	8/24	x		21
Do	8/3	8/30	x		27
Do	8/3	9/3	x		31
Do	8/3	9/5		x	33

TABLE 11.—*Stream recoveries of pink salmon tagged at Point Adolphus, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Mole River, No. 15	8/4	9/10	x		37
Do	8/4	9/10	x		37
Do	8/4	9/10	x		37
Game Creek, No. 16	8/4	8/31		x	27
Do	8/4	9/4	x		31
Rodman Bay, No. 33	8/4	9/8	x		35
Neka Bay, No. 18	8/4	9/3	x		30
Seagull Creek, No. 17A	8/4	8/31	x		27
Limestone Creek, No. 1	8/4	9/11	x		38
Windham Bay, Opp. No. 2	8/4	9/12	x		39
Port Houghton, No. 5	8/4	9/13		x	40
Do	8/4	9/14		x	41
Gambier Bay, No. 17	8/4	9/11	x		38
Bear Creek, Hood Bay	8/4	Oct.		x	
Humpback Creek, No. 19	8/4	8/26	x		22
Do	8/5	9/2	x		28
Hood Bay, No. 55	8/5	9/10	x		36
Limestone Creek, No. 1	8/5	9/11		x	37
Windham Bay, opp. No. 2	8/5	9/12		x	38
Spasski Creek, No. 20	8/5	8/29	x		24
Mole River, No. 15	8/5	9/9	x		35
Humpback Creek, No. 19	8/5	9/5		x	31
Petersburg Creek	8/6	9/17		x	42
Mole River, No. 15	8/6	9/10	x		35
Do	8/6	9/10	x		35
Do	8/6	9/10	x		35
Do	8/6	9/10	x		35
Game Creek, No. 16	8/6	9/4	x		29
Do	8/6	8/30	x		24
Seagull Creek, No. 17A	8/6	8/31	x		25
Do	8/6	8/31	x		25
Do	8/6	9/1	x		26
Neka Bay, No. 18	8/6	8/31	x		25
Homeshore, No. 1	8/6	9/5	x		30
Do	8/6	9/5	x		30
Point Howard, No. 3A	8/6	9/6	x		31
Limestone Creek, No. 1	8/6	9/11	x		36
Seymour Canal, No. 13	8/6	9/10	x		35
Game Creek, No. 16	8/6	9/3	x		28
Humpback Creek, No. 19	8/6	8/27	x		21
Do	8/6	8/31	x		25
Do	8/6	9/7		x	32
Do	8/6	9/13		x	38
Kadashan Bay, No. 14	8/7	8/27	x		20
Mole River, No. 15	8/7	9/10	x		34
Do	8/7	9/11	x		35
Humpback Creek, No. 19	8/7	9/10	x		34
Game Creek, No. 16	8/7	9/4	x		28
Do	8/7	9/4	x		28
Stream right of No. 1, Homeshore	8/7	9/2	x		26
Windham Bay, opposite No. 2	8/7	9/12	x		36
Rodman Bay, No. 33	8/7	9/17	x		41
Do	8/7	9/16	x		40
Chalk Bay, No. 57	8/7	9/17	x		41
Humpback Creek, No. 19	8/7	8/28		x	21
Do	8/7	8/31	x		24
Do	8/7	9/3	x		27
Do	8/7	9/13		x	37
N. arm Hood Bay, Nos. 53-54	8/8	9/17		x	40
Mole River, No. 15	8/8	9/10	x		33
Do	8/8	9/10	x		33
Do	8/8	9/10	x		33
Do	8/8	9/10	x		33
Do	8/8	9/9	x		32
Do	8/8	9/9	x		32
Favorite Bay stream	8/8	9/10	x		33
Do	8/8	9/10	x		33
Do	8/8	9/10	x		33
Game Creek, No. 16	8/8	9/4	x		27
Do	8/8	8/30	x		22
Do	8/8	8/30	x		22
Do	8/8	8/30	x		22
Do	8/8	9/5	x		28
Do	8/8	9/4	x		27
Security Bay, No. 40	8/8	9/18	x		41
Do	8/8	9/18	x		41
Do	8/8	9/18	x		41
S. arm Hood Bay, No. 55	8/8	9/7	x		30
Neka Bay, No. 18	8/8	9/3	x		26
Do	8/8	9/3	x		26
Seagull Creek, No. 17A	8/8	8/31	x		23
Do	8/8	8/31	x		23
Homeshore, No. 1	8/8	9/2	x		25
Stream right of Homeshore No. 1	8/8	9/2	x		25

See footnotes at end of table.

TABLE 11.—*Stream recoveries of pink salmon tagged at Point Adolphus, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Limestone Creek, No. 1	8/8	9/11		x	34
Windham Bay, No. 2	8/8	9/12	x		35
Windham Bay, opposite No. 2	8/8	9/12	x		35
Kadashan Bay, No. 14	8/8	8/31	x		23
Windfall Harbor, 1½ Mi. N. No. 14	8/8	9/10	x		33
Gambier Bay, No. 17	8/8	9/1	x		34
Humpback Creek, No. 19	8/8	8/28		x	20
Do	8/8	8/28		x	20
Do	8/8	8/28		x	20
Do	8/8	8/29		x	21
Do	8/8	8/29		x	21
Do	8/8	8/30	x		22
Do	8/8	9/2		x	25
Do	8/8	9/3	x		26
Do	8/8	9/7		x	30
Do	8/8	9/13		x	36
Do	8/8	9/13		x	36
Do	8/8	9/13		x	36
Game Creek, No. 16	8/9	9/7	x		29
Do	8/9	9/4	x		26
Limestone Creek, No. 1	8/9	9/11		x	33
Seymour Canal, No. 13	8/9	9/10	x		32
Humpback Creek, No. 19	8/9	8/30	x		21
Gambier Bay, ½ mi. N. No. 17	8/10	9/11	x		32
Do	8/10	9/11	x		32
Spasski Creek, No. 20	8/10	9/2	x		22
Mole River, No. 15	8/10	9/9	x		30
Do	8/10	9/9	x		30
Do	8/10	9/11	x		32
Favorite Bay stream	8/10	9/10	x		31
Do	8/10	9/10	x		31
Do	8/10	9/11	x		32
Do	8/10	9/12	x		33
Game Creek, No. 16	8/10	9/9	x		30
Do	8/10	9/4	x		25
Do	8/10	8/31	x		21
Poison Cove, Peril Strait	8/10	9/14	x		35
S. arm Hood Bay, No. 55	8/10	9/7	x		28
Do	8/10	9/7	x		28
Do	8/10	9/7	x		28
N. arm Hood Bay, Nos. 53-54	8/10	9/8	x		29
Clear River, Kelp Bay	8/10	9/9	x		30
Stream right of Homeshore, No. 1	8/10	9/2	x		23
Homeshore, No. 1	8/10	9/5	x		26
Do	8/10	9/5	x		26
Do	8/10	9/5	x		26
Limestone Creek, No. 1	8/10	9/11	x		32
Do	8/10	9/11	x		32
Windham Bay, No. 2	8/10	9/12	x		33
Windham Bay, opp. No. 2	8/10	9/12	x		33
Hobart Bay, No. 4A	8/10	9/13	x		34
Port Houghton, No. 5	8/10	9/13		x	34
Do	8/10	9/14	x		35
Do	8/10	9/14	x		35
Rodman Bay, No. 33	8/10	9/17	x		38
Spasski Creek, No. 20	8/10	8/29	x		19
Howard Cove, No. 3	8/10	9/5	x		26
Seymour Canal, No. 13	8/10	9/10	x		31
Gambier Bay, No. 17	8/10	9/11	x		31
Humpback Creek, No. 19	8/10	8/30	x		20
Do	8/10	8/30	x		20
Do	8/10	9/5		x	26
Do	8/10	9/13		x	34
Do	8/10	9/13		x	34
Culin Creek, Hood Bay	8/10	Oct.		x	
Mole River, No. 15	8/11	9/10	x		30
S. arm Hood Bay, No. 55	8/11	9/10	x		30
Clear River, Kelp Bay	8/11	9/9	x		29
Seagull Creek, No. 17A	8/11	8/31	x		20
Homeshore, No. 1	8/11	9/2	x		22
Do	8/11	9/2	x		22
Do	8/11	9/5	x		25
Limestone Creek, No. 1	8/11	9/11	x		31
Do	8/11	9/11	x		31

TABLE 11.—*Stream recoveries of pink salmon tagged at Point Adolphus, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Port Houghton, No. 5	8/11	9/14		x	34
Rodman Bay, No. 33	8/11	9/17	x		37
Windfall Harbor 1½ mi. N. No. 14	8/11	9/10	x		30
Seymour Canal, No. 13	8/11	9/10	x		30
Gambier Bay, No. 17	8/11	9/11	x		31
Humpback Creek, No. 19	8/11	8/28		x	17
Do	8/11	8/31	x		20
Stikine River	8/11	8/25	x		14
Favorite Bay stream	8/11	9/11		x	31
Do	8/11	9/12		x	32
Chaik Bay, No. 57	8/12	9/10	x		29
Do	8/12	9/10	x		29
Do	8/12	9/17	x		36
Do	8/12	9/17	x		36
Favorite Bay stream	8/12	9/10	x		29
Do	8/12	9/12		x	31
Gilbert Bay, Str. to Rt. of Sweetheart L. Cr	8/12	8/23	x		11
Saginaw Bay, No. 39	8/12	9/19	x		38
N. Arm Hood Bay, Nos. 53 or 54	8/12	9/8	x		27
S. arm Hood Bay, No. 55	8/12	9/10	x		29
Do	8/12	9/7	x		26
Do	8/12	9/10	x		29
Do	8/12	9/10	x		29
Do	8/12	9/10	x		29
Do	8/12	9/24	x		43
Homeshore, No. 1	8/12	9/2	x		21
Limestone Creek, No. 1	8/12	9/11	x		30
Windham Bay, No. 2	8/12	9/12	x		31
Port Houghton, No. 5	8/12	9/14		x	33
Patterson Bay, No. 26	8/12	9/16	x		35
Sitkoh Bay, No. 20	8/12	9/18	x		37
Do	8/12	9/18	x		37
Mole River, No. 15	8/12	9/9	x		28
Windfall Harbor, 1½ mi. N. No. 14	8/12	9/10	x		29
Humpback Creek, No. 19	8/12	8/27		x	15
Do	8/12	9/7		x	26
Chilkoot River	8/12	10/1		x	50
Do	8/12	10/1		x	50
Lover's Cove stream	8/12	9/20	x		39
Bear Creek, Hood Bay	8/12	Oct.		x	
Mole River, No. 15	8/13	9/12	x		30
Do	8/13	9/12	x		30
Game Creek, No. 16	8/13	9/23	x		41
S. arm Hood Bay, No. 55	8/13	9/7	x		25
N. arm Hood Bay, Nos. 53 or 54	8/13	9/8	x		26
Rodman Bay, No. 33	8/13	9/16	x		34
Homeshore, No. 1	8/13	9/5		x	23
Do	8/13	9/5		x	23
Limestone Creek, No. 1	8/13	9/11	x		29
Windham Bay, No. 2	8/13	9/12	x		30
Patterson Bay, No. 26	8/13	9/16	x		34
Gambier Bay, ½ Mi. N. No. 17	8/13	9/11	x		29
Humpback Creek, No. 19	8/13	9/14		x	32
Chilkoot River	8/13	10/1		x	49
Bear Creek, Hood Bay	8/13	Oct.		x	
N. arm Hood Bay, Nos. 53-54	8/14	9/10		x	27
Saginaw Bay, No. 39	8/14	9/19	x		36
Seagull Creek, No. 17A	8/14	9/1	x		18
Homeshore, right of No. 1	8/14	9/2	x		19
Windham Bay, No. 2	8/14	9/12	x		29
Gambier Bay, ½ mi. N. No. 17	8/14	9/11	x		28
Favorite Bay stream	8/14	9/12		x	29
Do	8/14	9/11		x	28
Do	8/14	9/11		x	28
Chicken Creek No. 14A	9/4	9/14	x		10
Lover's Cove stream	9/4	9/16	x		12
Chaik Bay, No. 57	9/4	9/17	x		13
All streams			208	55	

[1] Condition of fish at time of recovery.
[2] From date of release to date of recovery.

TABLE 12.—*Stream recoveries of pink salmon tagged at Cube Point, 1950*

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Mole River, No. 15	8/20	9/11	x		22
Do	8/20	9/11	x		22
Do	8/20	9/11	x		22
Chaik Bay, No. 57	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/10	x		21
Favorite Bay, stream	8/20	9/10	x		21
Do	8/20	9/10	x		21

TABLE 12.—*Stream recoveries of pink salmon tagged at Cube Point, 1950*—Continued

Stream name and FWS number	Date tagged	Date recovered	Condition [1]		Elapsed time [2]
			Alive	Dead	
					Days
Security Bay, No. 40	8/20	9/18	x		29
Hood Bay, No. 55	8/20	9/10	x		21
Do	8/20	9/10	x		21
Do	8/20	9/17	x		28
Do	8/20	9/11	x		22
Do	8/20	9/17	x		28
Do	8/20	9/17	x		28
Do	8/20	9/11	x		22
Do	8/20	9/11	x		22
Dyea River mouth, Lynn Canal	8/20	8/30	x		10
Windham Bay, No. 2	8/20	9/12	x		23
Do	8/20	9/12	x		23
Do	8/20	9/12	x		23
Do	8/20	9/12	x		23
Do	8/20	9/12	x		23
Rodman Bay, No. 33	8/20	9/17	x		28
Sitkoh Bay, No. 20	8/20	9/18	x		29
Do	8/20	9/18	x		29
Seymour Canal, No. 13	8/20	9/10	x		21
Do	8/20	9/10	x		21
Bay South of Pybus, No. 25	8/20	9/14	x		25
Hood Bay, No. 56	8/20	9/17	x		28
Saginaw Bay, No. 39	8/20	9/18	x		29
Do	8/20	9/18	x		29
Lover's Cove stream	8/20	9/20	x		31
Do	8/20	9/27	x		38
Do	8/30	9/27	x		28
Fishery Creek, No. 48	8/30	9/11	x		12
Chalk Bay, No. 57	8/30	9/17	x		18
Wilson Cove, No. 60	9/3	9/17	x		14
Sitkoh Bay, No. 20	9/3	9/18	x		15
Bear Creek, Hood Bay	9/3	Oct.		x	
All streams			69	1	

[1] Condition of fish at time of recovery.
[2] From date of release to date of recovery.

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FACTORS ASSOCIATED WITH FLUCTUATIONS IN ABUNDANCE OF HUDSON RIVER SHAD

BY GERALD B. TALBOT

FISHERY BULLETIN 101

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

A study of the Hudson River shad (*Alosa sapidissima*) was undertaken during 1950 and 1951 as part of a shad investigation carried out by the Fish and Wildlife Service to supply information to the Atlantic States Marine Fisheries Commission for fishery regulation along the Atlantic coast. Catch and effort statistics were obtained for the years 1915 through 1951, from various sources, for the gill-net fishery which catches more than 95 percent of the shad in the Hudson River. A tagging program during 1951 gave estimates of the total shad population entering the river that year. The total run and the escapement (since the catch was known) were then calculated for each year from 1915 through 1950. Age analysis of a sample of the catch of 1950 and 1951 showed that most shad returned as adults to the river at 4 and 5 years of age. Also, about 50 percent of the fish had previously spawned.

It was shown that about 85 percent of the variation in size of the run between 1920 and 1951 could be attributed to the size of the escapement from the fishery. No correlation was found between the size of the run each year and such factors as stream flow, water temperatures, channel improvements, ship traffic, or hatchery operations. No evidence of natural cycles of abundance was found. Catches of Hudson River shad in waters outside the river were shown to be large, and these catches may affect the expected size of the run. Using the methods outlined, the size of run can be predicted 1 year in advance, and by controlling the fishing efforts, the desired number of shad can be allowed to escape so that future runs can produce maximum sustained yields of shad from this river.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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FACTORS ASSOCIATED WITH FLUCTUATIONS IN ABUNDANCE OF HUDSON RIVER SHAD

By Gerald B. Talbot, *Fishery Research Biologist*

The commercial yield of Atlantic-coast shad (*Alosa sapidissima*) reached a peak of 50 million pounds in 1896 and thereafter declined until in 1950 it was less than a sixth of the 1896 catch. Alarmed by the continued decline of this valuable food fish, the Atlantic States Marine Fisheries Commission initiated action which resulted in special Congressional appropriations for a 6-year study of shad in the Atlantic Coast States. The Fish and Wildlife Service, as the primary research agency of the Commission, began this study in 1950. The basic purposes of the investigation were to discover the underlying causes of the decline, to determine conditions favoring recovery, and to provide basic information for scientific management of the fishery to obtain a maximum sustained yield.

Since funds and personnel were not sufficient for a study of all the major shad runs simultaneously, it was necessary to limit the field work each year to small areas. Work was begun on the Hudson River in the spring of 1950 and was continued in 1951. Plans were formulated to study other areas simultaneously and in succeeding years. This report covers only the studies made on the Hudson River.

The following members of the Fish and Wildlife Service assisted in this project: R. A. Fredin, to whom special acknowledgements are due for his help in the statistical analyses, C. E. Atkinson, J. P. Cating, R. H. Eggleston, J. H. Finucane, B. A. Lehman, John Parkin, T. Penny, C. L. Perkins, Jr., J. E. Sykes, and C. H. Walburg, of the Beaufort Fishery Laboratory staff, as well as Henry Bearse and R. H. Wilson of the Market News Service, Branch of Commercial Fisheries.

We are also grateful to W. C. Senning, J. R. Greeley, A. W. Bromley, J. Skain, Cecil Heacox, Alfred Tucker, and J. R. Westman (now with Rutgers University) of the New York Conservation Department, to F. W. Gilcreas and B. F. Pfeil, of the New York Department of Health, and to A. Heaton Underhill, A. E. Sullivan, and H. P. Hartmann, of the New Jersey Department of Fish and Game, for their help and cooperation during this study.

In addition, we greatly appreciate the help of the fish wardens of both States and the many commercial fishermen who helped us in every way possible to ensure success of our project.

DESCRIPTION OF THE RIVER AND ITS SHAD FISHERY

The Hudson River has its source in the Adirondack Mountains, flows generally southward about 300 miles, and empties into Upper New York Bay at the Battery, New York City. The river is tidal from its mouth upstream to Troy, a distance of about 160 miles (fig. 1). A dam at Troy is the upper limit of shad migration. The original wooden dam at Troy was finished in 1826, and this was later replaced by a masonry structure. From the dam at Troy to Peekskill the river ranges from 200 yards to 2,500 yards in width. Below this it broadens into Haverstraw Bay where the width ranges from 3 to 4 miles. The lower section of the river, from Dobbs Ferry to the Battery, averages about a mile in width.

The fresh-water section of the river extends downstream to a few miles below Poughkeepsie, where the intrusion of salt water begins. The degree of salinity at any particular place, and the position of the division between fresh and brackish water depends upon the tide and river run-off. The average weekly surface salinity at Bear Mountain Bridge (about 25 miles below Poughkeepsie) from July through October 1951 was 0.69‰ with a maximum of 2.39‰ and a minimum of 0.0‰. At Piermont Pier, about 20 miles below Bear Mountain Bridge, the average of the weekly samples for the same period was 6.81‰, with a maximum of 8.50‰ and a mini-

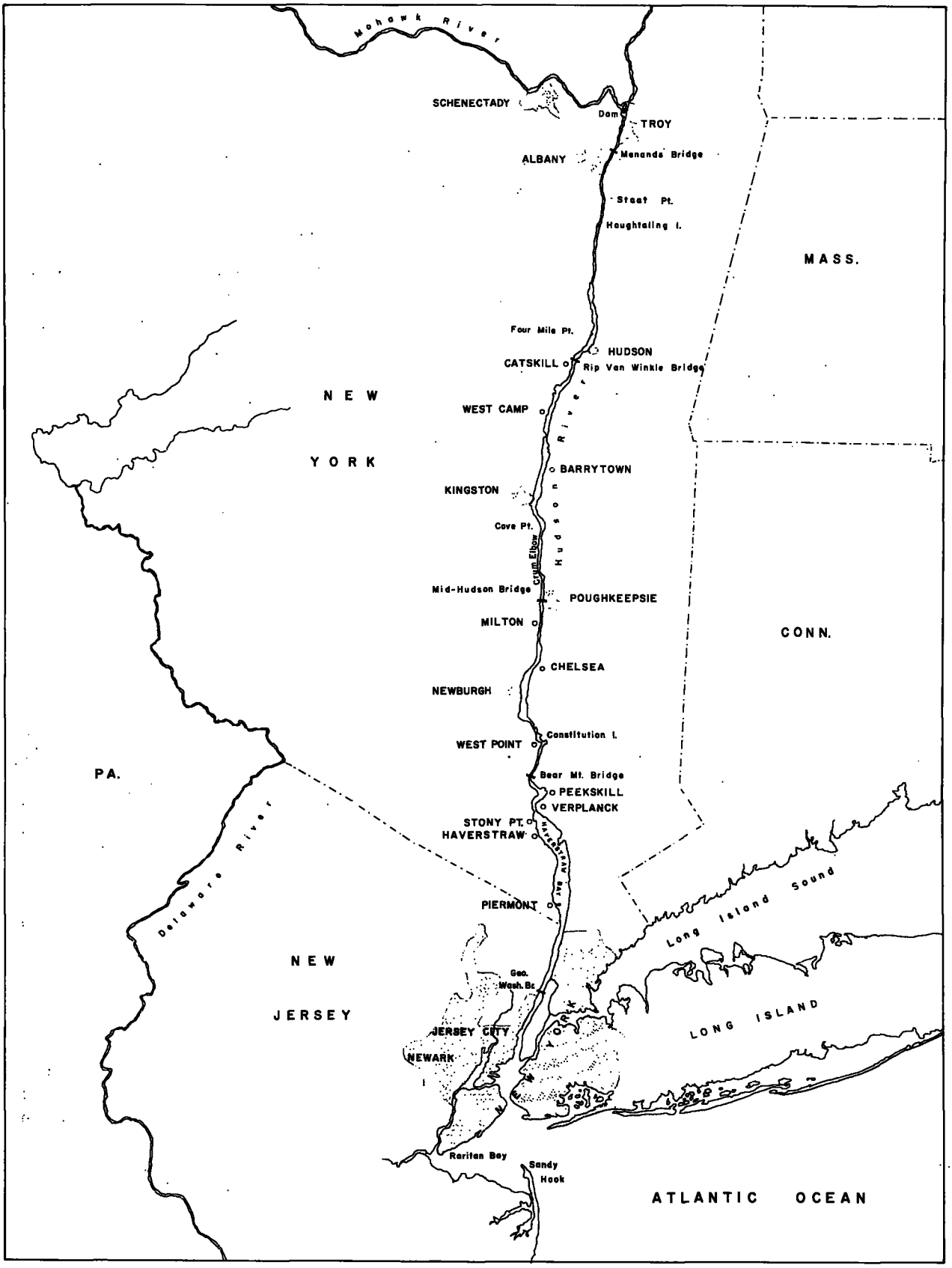

FIGURE 1.—Hudson River from Troy to the Atlantic Ocean.

mum of 2.09°/₀₀ (unpublished data, U. S. Fish and Wildlife Service and New York Department of Health).

The shad is the largest member of the family Clupeidae in the United States. It is anadromous, usually ascending streams in the spring of the year to spawn. Shad begin their run into the Hudson River the last of March or the first of April, and the run is usually over by the end of June. The bulk of the catch is made in a 6- or 7-week period. The adult shad normally do not die after spawning, and if they survive natural and fishing hazards they return to spawn in successive years.

The average number of eggs laid per female is approximately 250,000 (Lehman 1953). Eggs are about 3 mm. in diameter, are nonadhesive, and are deposited free in the water. After the eggs absorb water, their specific gravity is slightly greater than that of water and they sink to the bottom and are carried along by river and tidal currents.

On the basis of egg sampling by Cable (New York Conservation Department, 1943), the present major spawning area in the Hudson River appears to be between Port Ewen and Coxsackie, with the greatest concentration of eggs occurring just below the town of Catskill. The eggs hatch into a larval stage in 6 to 8 days at 17° C., and in another 4 or 5 days at the same temperature develop into their final form (Leim 1924). The young shad stay in the river until October or November, attaining a length of from 3 to 5 inches, and then migrate to sea.

The shad fishery in the Hudson was at a low level of production during the early years of the century (fig. 2) and continued at a low level until 1934. Then, contrary to the general trend of the shad fishery along the Atlantic coast, production increased tremendously and for the next 10 years the catches equaled those of the best years on record. After 1945 a decline set in, and at the present time the catch is nearing the previous low level of production.

Gill nets are the principal type of commercial gear used in the Hudson River shad fishery. Haul seines and other miscellaneous gear account for small catches, but these are inconsequential compared to the gill-net landings. There is no sport fishery.

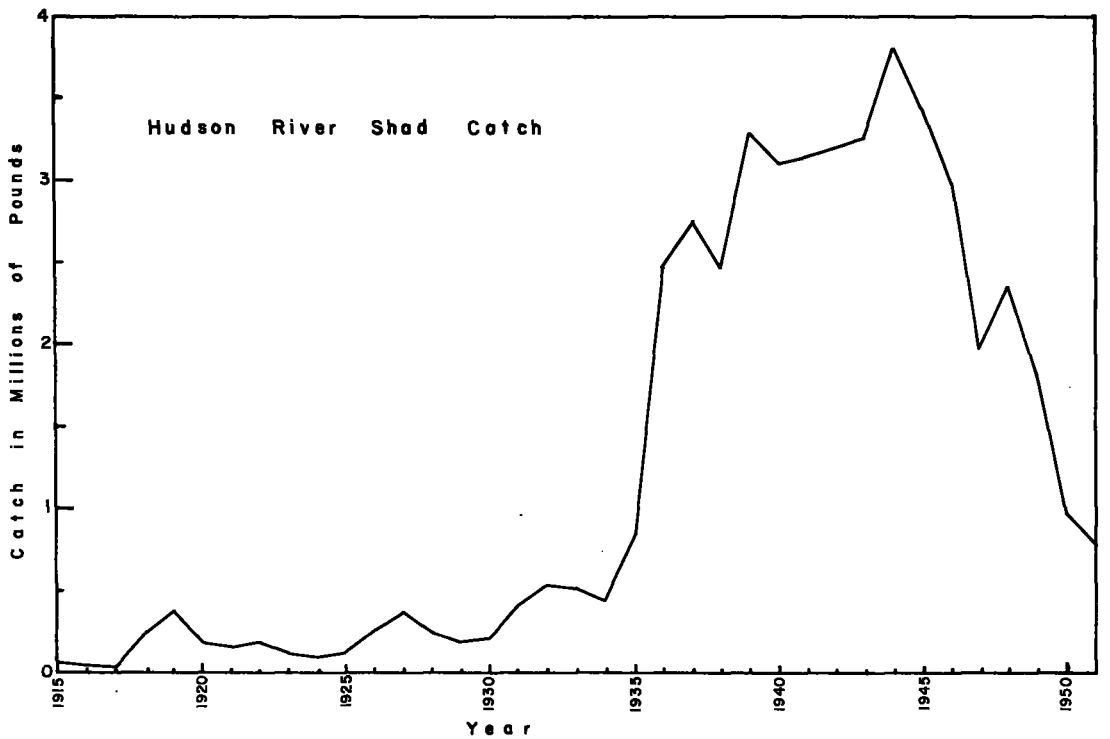

FIGURE 2.—Hudson River shad catch, 1915 through 1951. (Statistics from U. S. Fish and Wildlife Service, 1915–49; from New York and New Jersey conservation agencies, 1950–51.)

The gill nets are operated as drift nets and stake nets, and because of the physical character of the river the fishery can be divided into three natural classifications, New Jersey stake-net, New York stake-net, and New York drift-net areas. In the lower section of the river, which is bounded by both New York and New Jersey, stake gill nets are used almost exclusively. Nearly all of these are set and operated from the New Jersey side of the river and are licensed by the State of New Jersey. For an occasional net that extends beyond the middle of the river into New York waters, a license from New York is required for that portion of the net in New York.

The nets in this area are suspended from long poles, spaced about 30 feet apart, which are driven into the river bottom. These nets are usually fished only on the flood tide. The fish are removed just before high slack water, and the net is removed or fastened above water level until the next low slack water occurs. Because of navigational difficulties in the lower part of the river, the U. S. Army Corps of Engineers since 1940 has designated areas and lengths of nets that can be used so that channels for shipping are unobstructed. These nets are installed and operated during the shad season only.

In Haverstraw Bay, shad fishing is accomplished mainly by means of stake gill nets. These are set in shallow areas of the bay. Since the river velocity is not so great here as in the lower part, the nets in Haverstraw Bay can be fished on both the flood and ebb tides. Because of the greater width of the river, however, stake nets in Haverstraw Bay occupy a smaller proportion of the river width than the stake nets below, and catch fewer fish per net.

Above Haverstraw Bay and extending to the city of Hudson, the fishing is done almost entirely by drift gill nets. These are placed in the river during flood or ebb tides from skiffs usually carrying two men, and are set so that the net will not encounter snags or other obstructions during the drift. The nets are usually removed from the water at slack tide and hauled into the skiffs. Fishing is carried out at night if the water is clear,

TABLE 1.—*Hudson River shad catch and units of gear fished annually in New York, 1915–49*

[Data from U. S. Fish and Wildlife Service]

Year	Drift gill nets			Stake gill nets			Haul seines			Caught incidentally		Total New York catch	
	Number of nets	Catch		Number of nets	Catch		Number of nets	Catch		Number of fish	Pounds	Number of fish	Pounds
		Number of fish	Pounds		Number of fish	Pounds		Number of fish	Pounds				
1915	79	11,333	47,333				2	62	298	211	933	11,606	48,564
1916	76	7,536	31,670				3	191	1,008	60	245	7,787	32,923
1917	213	9,535	34,420				13	1,080	3,924			10,615	38,344
1918	272	61,583	214,196				15	1,821	6,406			63,404	220,602
1919	359	75,060	296,259				12	1,441	5,047			76,501	301,306
1920	190	37,821	150,658				10	1,871	7,057			39,692	157,715
1921	159	27,991	101,465				5	747	2,603	210	815	28,948	104,883
1922	133	34,763	123,469				5	1,348	4,855			36,111	128,324
1923	110	27,245	93,503				2	669	2,100	722	2,260	28,636	97,863
1924	95	22,002	70,159				2	625	1,760	187	600	22,814	72,519
1925	90	32,509	104,063	13	1,144	3,644	4	825	2,375	90	277	34,568	110,359
1926	96	61,625	184,059	11	4,544	14,443	8	6,963	20,102			73,312	219,183
1927	123	85,174	283,041				5	4,337	15,023	473	1,629	89,984	299,693
1928	118	53,477	169,557	16	4,100	14,291	2	2,350	6,640	1,152	3,693	61,079	194,181
1929	104	43,430	149,328	10	2,550	8,567						45,980	157,895
1930	105	44,817	148,372	14	3,979	15,298				445	1,334	49,241	165,004
1931	104	92,353	303,563	15	9,975	33,795	2	1,270	3,815	445	1,438	104,043	342,611
1932	110	107,753	347,354	10	13,032	48,950	2	535	1,350	38	100	121,358	397,754
1933	118	96,411	314,693	14	8,300	31,293	2	576	1,670	1,655		105,287	347,656
1934	126	102,281	302,900	14	1,142	3,500	10	1,020	3,000		4,800	106,098	314,200
1935	281	137,487	434,500				28	3,592	10,200	2,898	8,600	143,977	453,300
1936	124	253,562	683,800	551	42,299	133,100	14	7,884	16,800	269	700	304,014	834,400
1937	185	279,780	932,600	26	7,110	23,700	15	5,900	19,700			292,790	976,000
1938	232	283,700	946,000	301	4,470	14,900	18	3,480	11,600			291,650	972,500
1939	230	442,291	1,442,600	139	4,302	14,200	13	18,062	59,600			464,655	1,516,400
1940	145	270,390	865,400	380	130,446	416,400	12	4,970	15,900			405,806	1,297,700
1941	146	257,112	822,800	129	156,603	513,600	6	1,422	4,600			415,137	1,341,000
1942	125	275,463	805,200	353	166,416	485,600	8	995	2,900	381	1,100	443,255	1,294,800
1943	155	368,786	1,032,600	78	219,481	592,000	13	4,223	11,400	1,331	4,000	593,821	1,640,000
1944	128	351,500	1,056,000	317	188,700	566,900	12	9,400	28,300			549,600	1,651,200
1945	173	358,315	1,072,700	122	314,535	941,200	10	16,633	48,800	9,507	28,600	698,990	2,091,300
1946	189	283,500	849,600	155	192,000	574,000	18	7,700	23,300			483,200	1,446,900
1947	231	162,000	602,800	148	82,917	307,100	35	11,590	42,900	1,242	4,600	257,749	957,400
1948	223	203,178	612,400	155	147,396	443,700	37	22,010	65,500			372,584	1,121,600
1949	191	135,694	441,500	102	71,835	264,000	43	13,030	43,300			220,559	748,800

but if the water is turbid, fishing is also done during the day. All the river above the New Jersey stake-net area is entirely within New York State, and licenses are issued by that State for shad fishing in Haverstraw Bay and above. In recent years little or no fishing has been done between the city of Hudson and the dam at Troy.

Most of the shad catch in the New York section of the river is made by fishermen holding special shad licenses good only for the legal shad-fishing season extending from March 15 to June 15 each year. A small part of the catch is made by fishermen holding regular gill-net licenses which are valid throughout the year for other species of fish in addition to shad.

STATISTICS OF THE FISHERY

The U. S. Fish and Wildlife Service and its predecessor, the Bureau of Fisheries, have published yearly statistics of the Hudson River shad fishery in Fishery Statistics of the United States and in Fishery Industries of the United States. From 1915 through 1949, these reports give the numbers and pounds of shad caught, as well as the amount and kinds of gear making the catch. The data are presented in tables 1 and 2.

Also available are the New York Conservation Department's annual reports listing the total shad catches made by New York fishermen in the Hudson River, the number of licenses and catch by special stake and drift gill net licenses first issued in 1924, and the number of regular gill-net licenses issued each year. There is no way of determining at the present time how many of the regular gill-net licenses were used to fish for shad or what their shad catches were. We have therefore presented here only the data for the special gill-net licenses. These are shown in table 3. These data were furnished by the New York Conservation Department from original material in files and contain several corrections of small errors found in previously published data.

TABLE 2.—*Hudson River shad catch and units of gear fished annually in New Jersey, and total catch for New York and New Jersey, 1915–49*

[Data from U. S. Fish and Wildlife Service]

Year	Drift gill nets			Stake gill nets			Total New Jersey catch		Total Hudson River catch, New York and New Jersey	
	Number of nets	Catch		Number of nets	Catch		Number of fish	Pounds	Number of fish	Pounds
		Number of fish	Pounds		Number of fish	Pounds				
1915				7	4,249	20,104	4,249	20,104	15,855	68,668
1916				3	1,500	7,250	1,500	7,250	9,287	40,173
1917				2	1,400	5,040	1,400	5,040	12,015	43,384
1918				1	3,999	14,000	3,999	14,000	67,403	234,602
1919				14	13,800	73,668	13,800	73,668	90,301	374,974
1920				10	9,623	42,129	9,623	42,129	49,315	199,844
1921				8	6,500	25,920	6,500	25,920	35,448	130,803
1922				8	12,225	46,862	12,225	46,862	48,336	175,186
1923				5	6,450	23,865	6,450	23,865	35,086	121,728
1924				4	5,980	21,850	5,980	21,850	28,794	94,369
1925				4	4,300	13,975	4,300	13,975	38,868	124,334
1926				4	11,150	46,237	11,150	46,237	84,462	265,420
1927				7	20,300	58,362	20,300	58,362	110,284	358,055
1928				7	17,950	52,050	17,950	52,050	79,029	246,231
1929				5	10,500	38,850	10,500	38,850	56,480	196,745
1930				7	12,200	41,500	12,200	41,500	61,441	206,504
1931				4	21,900	72,000	21,900	72,000	125,943	414,611
1932				6	38,000	132,000	38,000	132,000	159,358	529,754
1933	1	150	524	13	49,000	170,500	49,150	171,024	154,437	518,680
1934				14	35,360	123,800	35,360	123,800	141,458	438,000
1935				26	116,003	394,100	116,003	394,100	259,980	847,400
1936				672	393,211	1,633,500	393,211	1,633,500	697,225	2,467,900
1937	1	1,000	3,000	87	584,400	1,753,200	585,400	1,756,200	878,190	2,732,500
1938	1	70	200	65	420,079	1,494,500	420,149	1,494,500	711,799	2,467,000
1939	1	1,014	5,000	47	517,597	1,549,300	518,511	1,754,200	983,166	3,270,700
1940	4	11,941	49,700	55	512,525	1,767,000	524,466	1,816,700	930,272	3,114,400
1941	2	812	3,100	55	517,609	1,789,400	518,421	1,792,500	933,558	3,133,500
1942	2	1,293	4,800	47	580,651	1,886,300	581,944	1,891,100	1,025,199	3,185,900
1943	2	2,123	7,450	40	525,493	1,577,900	527,616	1,585,350	1,121,437	3,225,350
1944	3	2,318	8,700	41	640,203	2,149,500	642,521	2,158,200	1,192,121	3,809,400
1945	4	(1)	8,700	84	(1)	1,377,200	(1)	1,385,900		3,477,200
1946				182	437,689	1,525,243	437,689	1,525,243	920,889	2,972,143
1947				154	282,121	1,024,392	282,121	1,024,392	539,870	1,981,792
1948	6	500	1,500	92	338,513	1,231,300	339,013	1,232,800	711,597	2,354,400
1949	14	16,865	51,156	161	257,678	917,414	274,543	978,570	495,102	1,727,370

(1) Not available.

TABLE 3.—*Number of licenses issued and shad catch for special gill nets in New York State, 1924–51*

Year	Number of licenses	Catch in pounds	Year	Number of licenses	Catch in pounds
1924	97	55, 546	1938	261	922, 285
1925	[1] 98	87, 700	1939	254	1, 384, 527
1926	99	165, 920	1940	216	1, 268, 723
1927	136	226, 388	1941	231	1, 322, 521
1928	129	146, 241	1942	220	1, 278, 064
1929	122	100, 798	1943	230	1, 606, 751
1930	121	91, 025	1944	263	2, 025, 811
1931	120	195, 293	1945	242	2, 167, 540
1932	123	246, 995	1946	357	1, 749, 193
1933	146	224, 582	1947	366	1, 021, 617
1934	144	249, 174	1948	357	1, 229, 641
1935	140	425, 332	1949	315	1, 064, 854
1936	162	623, 122	1950	295	471, 068
1937	200	901, 585	1951	215	423, 473

[1] No record; estimated.

Since 1940 the New York Conservation Department has differentiated between the numbers and catches by special drift-net licenses and special stake-net licenses. These are presented in table 4.

Beginning in 1937, the New Jersey Board of Fish and Game Commissioners, later the Division of Fish and Game, has published in its annual report various data relating to the Hudson River shad fishery. These data include the number and pounds of shad landed, the number of nets and boats used, and the number of men engaged in the fishery. The shad landings agree closely with those shown for New Jersey in table 2. Unfortunately, the data given for the number of nets used in the fishery in the New Jersey reports refer to number of nets owned by the fishermen (since 1947, number licensed) and not to the actual number of stake nets fished during the season; hence they cannot be used for determining fishing effort.

TABLE 4.—*Special drift and stake net licenses issued, and catch by each type of net in New York State, 1940–51*

Year	Total number of licenses	Drift gill nets		Stake gill nets	
		Number of licenses	Catch, in pounds	Number of licenses	Catch, in pounds
1940	216	153	917, 665	63	351, 058
1941	231	146	822, 778	85	499, 743
1942	220	132	804, 687	88	473, 377
1943	230	133	1, 015, 137	97	591, 614
1944	263	159	1, 110, 155	104	915, 656
1945	242	150	1, 080, 188	92	1, 087, 352
1946	357	231	891, 885	126	857, 308
1947	366	235	571, 130	131	450, 487
1948	357	219	661, 333	138	568, 308
1949	315	189	403, 521	126	661, 333
1950	295	172	239, 866	123	231, 202
1951	215	125	280, 020	90	143, 453

An analysis of the data in tables 1 and 2 for the purpose of combining catch and effort data for all gear for all parts of the river has disclosed some irregularities which we have been unable to reconcile with known facts. Beginning with 1936, the numbers of stake gill nets operating in New York, as shown in table 1, are unusually high on alternate years. The numbers of special gill-net licenses issued by New York during the same period, as shown in table 3, do not show these fluctuations, and neither do the total number of licenses issued for regular and special gill-net licenses as shown in the New York Conservation Department's annual reports.

In addition to these discrepancies, the number of stake nets operated in New Jersey in 1936 is listed as 672. Since the area in which stake nets can be set in that part of the Hudson River bounded by New Jersey is only about 16 miles in length, and since by law the nets must be 1,500 feet apart, there can be a maximum of approximately 56 stake nets in the river at any one time. It is probable that the figure of 672 is a typographical error, but the numbers listed for the New Jersey stake nets for 1937 and from 1945 through 1948 also are unreasonably large. It may be possible that the figures for the latter years were erroneously recorded as the number of nets owned, rather than the number of stake nets set in the river. Since none of the original data are available from which to check these figures, we have viewed the data in tables 1 and 2 with suspicion, especially for the amount of gear used after 1935.

During the field seasons of 1950 and 1951 there was ample opportunity to observe the various types of gear and their operation. It was found that the few drift gill net operators in the New Jersey area fished very irregularly and hence no measure of their fishing effort was available for past years. The same was true of the haul seines operated in the New York area. On the other hand, the special drift gill net and stake gill net operators in New York, and the stake gill net operators in New Jersey, usually fished all season, or at least through the peak of the season, if they fished at all. It was therefore necessary to limit this study to those types of gear. As these nets usually catch more than 95 percent of all the shad caught in the Hudson, little error is introduced by disregarding the catch and effort of the other types of gear.

In compiling a table of catch and effort data for the Hudson River shad fishery we have used the U. S. Bureau of Fisheries and the U. S. Fish and Wildlife Service statistics as shown in tables 1 and 2, for the years 1915 through 1935 for the

State of New Jersey, and for 1915 through 1923 for New York State, since these are the only data available. From 1924 through 1951 we have used the New York special gill-net license and catch data for New York State since these appeared to be the most accurate. The number of special gill-net licenses issued in 1925 was not available, so this was estimated.

The total number of stake nets operated in the New Jersey section of the Hudson River in 1935 is listed as 26 in Fishery Industries of the United States (U. S. Bureau of Fisheries, 1938). In the breakdown by counties, however, the number of stake nets listed for Bergen County is 15 and there is none listed for Hudson County (the only other county bordering the Hudson River), and so we have used 15 stake nets as perhaps being more nearly correct. For the years 1936 through 1951 there are no published records of the number of stake nets operating in the New Jersey area of the river. Fortunately, the Corps of Engineers has made a survey of this fishery each year since 1938 in connection with the regulation of the channels of the Hudson River, and through correspondence they have supplied us with the number of nets operating each year from 1938 through 1951. We have used these data along with the catches of shad given in reports of the Fish and Wildlife Service (tables 1 and 2), since they agree closely with data for the same period obtained from the New Jersey Fish and Game Department. The numbers of stake nets fished in New Jersey in 1950 and 1951 were verified by our field crew while working on the river. The only years for which usable effort data were not available for New Jersey were 1936 and 1937. We have estimated these as indicated in table 5, after talking with fishermen, fish buyers, and others, and believe that they are approximately correct figures. These data, taken from the several sources mentioned, as shown in table 5 are the Hudson River catch and effort statistics used in the analyses in this report.

Since 1915, New York has instituted closed weekends, also called "lift periods," as a conservation measure, during which shad fishing is not permitted. From 1915 through 1917 the weekly closure was 2½ days, but the closure applied only to fishing downriver as far as Verplanck Point. After 1917 it included all the river under the supervision of New York. We have assumed that fishing effort was uniform throughout the New York part of the Hudson River and have corrected the closure on a geographical basis by using only 2 days of closure for the first 3 years to make these closures more comparable to those after 1917. The State of New Jersey did not establish closed days until 1940, and since then by cooperative action the number of closed days each year in the two States has been uniform. The number of days of closure each year by each State is shown in table 5.

TABLE 5.—*Hudson River shad catch, units of gear, and closed days for drift and stake gill nets, by years, 1915–51*

[Data from various sources]

Year	New York			New Jersey			Total catch, in pounds
	Number of gill nets	Catch, in pounds	Closed days per week	Number of stake gill nets	Catch, in pounds	Closed days per week	
1915	79	47,333	[2] 2	7	20,104	0	67,437
1916	76	31,670	[2] 2	3	7,250	0	38,920
1917	213	34,420	[2] 2	2	5,040	0	39,460
1918	272	214,196	2½	1	14,000	0	228,196
1919	359	296,259	2½	14	73,668	0	369,927
1920	190	150,658	2½	10	42,129	0	192,787
1921	159	101,465	2½	8	25,920	0	127,385
1922	133	123,469	2½	8	46,862	0	170,331
1923	110	93,503	2½	5	23,865	0	117,368
1924	97	55,546	2½	4	21,850	0	77,396
1925	[1] 98	87,700	2½	4	13,975	0	101,675
1926	99	165,920	2½	4	46,237	0	212,157
1927	136	226,388	2½	7	58,362	0	284,750
1928	129	146,241	2½	7	52,050	0	198,291
1929	122	100,798	2½	5	38,850	0	139,648
1930	121	91,025	2½	7	41,500	0	132,525
1931	120	195,293	2½	4	72,000	0	267,293
1932	123	246,995	2½	6	132,000	0	378,995
1933	146	224,582	2½	13	170,500	0	395,082
1934	144	249,174	2½	14	123,800	0	372,974
1935	140	425,332	2½	15	394,100	0	819,432
1936	162	628,122	2½	[1] 36	1,633,500	0	2,256,622
1937	200	901,585	2½	[1] 36	1,753,200	0	2,654,785
1938	261	922,285	2½	52	1,494,500	0	2,416,785
1939	254	1,348,527	2½	43	1,754,300	0	3,102,827
1940	216	1,268,723	1½	46	1,767,000	1½	3,035,723
1941	231	1,322,521	1½	46	1,789,400	1½	3,111,921
1942	220	1,278,064	1½	48	1,886,300	1½	3,164,364
1943	230	1,606,751	0	32	1,577,900	0	3,184,651
1944	263	2,025,811	0	38	2,149,500	0	4,175,311
1945	242	2,167,540	1½	35	1,377,200	1½	3,544,740
1946	357	1,749,193	1½	52	1,525,243	1½	3,274,436
1947	366	1,021,617	1½	52	1,024,392	1½	2,046,009
1948	357	1,229,641	1½	44	1,231,300	1½	2,460,941
1949	315	1,064,854	1½	46	972,857	1½	2,037,711
1950	295	471,068	1½	40	520,958	1½	992,026
1951	215	423,473	3	25	331,523	3	754,996

[1] No record; estimated.
[2] In 1915, 1916, and 1917, the 2½ days closure extended only down to Verplanck Point; see text.

In this study the catches are listed in pounds of fish caught rather than numbers of fish because most of the landings are recorded in pounds. Where numbers of fish are given in published records these have usually been empirically converted to pounds by some such figure as 2.5 pounds each for male shad and 3.5 pounds for females. Since many of the published landings do not list the weight by sexes, it is impossible at this time to

calculate the numbers of each sex for all years with the data available. While it might be more desirable to have the figures in numbers of fish rather than pounds, the magnitude of the changes in the catch would not differ greatly, because the conversion factors remain about the same.

TAGGING STUDIES

During the shad runs of 1950 and 1951, shad were tagged at the mouth of the Hudson River to estimate the total shad population entering the river. Captures of shad for tagging were made by drifting a commercial gill net below the New Jersey stake-net area. Fishing was carried out uniformly throughout the season in 1951, so that as nearly as possible the tags were affixed in proportion to the number of shad migrating upstream. Petersen disk tags were used and were affixed just below the dorsal fin. During the fishing season the shad fishermen were interviewed each week to collect the tags they had recovered and to obtain a record of their daily catches. Catch-record or log books were furnished to a representative number of those fishermen who normally kept no records of their shad catch. With few exceptions, the fishermen cooperated wholeheartedly in this study.

In 1950 the tagging experiment was late in getting started, and it was not possible to canvass all of the fishermen for tag returns. For this reason a sample was selected to provide an estimate of the ratio of tagged fish to fishermen's total catch. This ratio in turn was applied to the total catch reported to the State agencies to obtain estimates of the fishing rate and total population in pounds. This appears to be a valid method since the log-book records showed that fishing effort was uniform throughout the 6- or 7-week season when the bulk of the catch is made. The information obtained is as follows:

FIGURE 3.—Tagging shad near the mouth of the Hudson River.

Number of shad tagged at mouth of river, 1950	242
Number of tagged shad recovered by sample fishermen	57

Quantity of shad caught by sample fishermen ---------- pounds--	355,000
Total quantity of shad caught by all fishermen (C) ---------- pounds--	992,000
Estimated number of tagged fish recovered by all fishermen $\left(=57\times\frac{992{,}000}{335{,}000}\right)$ ----------	159
Estimated fishing rate $\left(=\frac{159}{242}\right)$ ----- percent--	65.7
Estimated total size run $\left(N=\frac{C}{0.657}\right)$ pounds-	1,510,000
Limits of confidence (95 percent) pounds----[1]	1,383,000 to 1,619,000
Estimated escapement (E) -------- pounds----	518,000

[1] Chapman 1948; Schaefer 1951.

During the shad run of 1951, shad were tagged throughout the fishing season. The fishermen were fully aware of our program and were canvassed regularly, and in almost every instance cooperated enthusiastically. We were able to use the total catch and total tags recovered, in our analysis, and hence we feel that the 1951 experiment gave us more reliable information than was obtained in 1950. The data from the 1951 experiment are as follows:

Number of shad tagged at mouth of river------	524
Number of tagged shad recovered in entire river fishery----------	241
Best estimate of fishing rate $\left(=\frac{241}{524}\right)$ percent-	46
Total catch (C) ---------- pounds--	755,000
Estimated size of run (N) ---------- do----	1,641,000
Limits of confidence (95 percent) pounds----[1]	1,530,000 to 1,740,000
Estimated escapement (E) -------- pounds----	886,00

[1] Chapman 1948; Schaefer 1951.

In a study of shad on the Umpqua River, Gharrett (1950) found that Petersen-disk type tags made the tagged fish more susceptible to capture because the tag became entangled in the gear; hence, a disproportionate number of tags were returned, and a correction for tag selectivity was necessary. We have examined this matter of tag selectivity in our tagging program by comparing the proportion of tags recovered in the New Jersey fishing area with that in the New York area. It can be reasoned that if the tagged fish were more susceptible to capture than untagged fish, there should be a higher proportion of tagged shad in the New Jersey catch than in the New York catch. Chi-square tests of the actual and expected numbers of tags returned from each area disclosed that there was no significant difference between the proportions of tagged fish in the catches of the two areas in either year. We have therefore concluded that a correction for tag selectivity was not necessary in our tagging experiment.

The reason for the difference between Gharrett's results and ours probably can be ascribed to the fact that in the Umpqua River the legal minimum stretched-mesh size of nets is 6 inches while in the Hudson River the stretched-mesh size ranges from 5 inches to 5¾ inches and averages about 5½ inches. An examination of shad caught in the Hudson River showed that in most cases the fish were gilled just behind the head, and only rarely did the mesh slip back to the dorsal fin where the tag might be a factor in retention of the fish by the net. The reverse was probably true in the Umpqua River where the mesh size was larger.

Other known sources of error which may affect the accuracy of population estimates based on tagging experiments are mortality of shad resulting from the tagging operations, shedding of the tags before capture, and natural mortality by predation, disease, or other hazard. Since our experiments were of such short duration, errors caused by predation and disease should be small. Mortalities attributable to the tagging procedure were considered, but are difficult to determine. During the tagging operations the condition of the shad after tagging was noted on the tagging records. When shad were caught during rough weather they were in extremely poor condition as a result of being jerked up and down in the gill net by wave action. Because of this it was thought at the time that all fish caught and tagged on some days would surely die after being returned to the water. No difference in the percentage or time of return was found in these tagged shad, however, when compared with tagged shad which appeared to be in good condition when returned to the river. Although proof is lacking, it appeared from these comparisons that Hudson River shad had remarkably good recuperative ability and that mortality from the tagging operations was not great. It is of course possible that some delayed action such as fungus growths on the fish from handling might have caused equal mortality on both groups of fish, but evidence of such was not found on any of the tagged fish examined after capture. In any event we have used the results of the tagging data as the best estimates of the populations available.

COMPARISON OF GEAR EFFICIENCY

The number of net-fishing days fished each season by New York and New Jersey fishermen was calculated by multiplying the number of nets fished by the number of days of fishing in a 6-week season each year (table 6). In these calculations we have limited the season to 6 weeks, since about 90 percent of the fish are caught during that period and practically all of the fishermen are fishing regularly. At the beginning and end of the season, fishing is done by only a few fishermen, and some of them fish intermittently, but when the run arrives in volume almost all of the fishermen fish consistently until the run diminishes.

From the records of catches made by the New York special drift and stake gill nets (table 4), it would appear that these two types of gear may not be comparable, so far as capturing shad is concerned. The stake nets caught slightly more shad per net on the average than did the drift nets. This may result because the stake nets get their catch first, while the drift nets fish on what is left. Since records for numbers and catch by each type are not available for the years before 1940, in this study the two types of gear are combined.

To obtain the total fishing-effort figure for the whole river, it is necessary to combine the fishing effort of both the New York and the New Jersey fishing gear. It can be seen from table 5 that the New Jersey nets catch more shad per net than do the New York nets. Actually, they average about six times as much per net. Part of this difference undoubtedly results from the fact that the New Jersey nets are located nearer the mouth of the river than the New York nets, which fish only on those shad that escape the New Jersey fishery. It is necessary, therefore, to determine whether the greater catches by New Jersey gear reflect a greater fishing power by that gear.

It can be seen that theoretically the first net set in the river has a better chance of catching fish than the next one upstream, and the second net a better chance than the third. In this paper, however, we are concerned only with the average fishing power of the New Jersey nets as compared with the average fishing power of the New York nets.

We are able to estimate the average fishing power of nets fished in New Jersey and New York by using a technique described by Fredin (1954). A comparison of the fishing powers of the nets enables us to standardize fishing effort. First, we will define "fishing power" to mean the ability of 1 unit of gear to capture a certain fraction of the fish present in the river in 1 day's fishing. We will call this fraction p, and it should be constant for a given type of gear in a given location within a season and between seasons provided (1) there is no change in design or manipulation of the nets to make them more or less efficient as a means of catching shad, (2) fishing effort is uniform in a given season, and (3) the migration pattern of shad is similar each year.

Stevenson's description of the Hudson River shad fishery illustrates that fishing was carried out in the same manner in 1896 as is done now. The use of outboard motors rather than oars has lessened the work of the fishermen in later years, but the time and manner in which the nets are fished and the nets themselves appear to have changed little. Nylon nets rather than linen were used by so few fishermen in 1950 and 1951 that our results would not be biased because of them, should nylon prove to be more efficient.

Since the shad-fishing season is short, most of the fishermen earn their livelihood by other occupations and either take their vacations or lay off work to fish. Once the run begins, they usually fish every legal day possible during the short season. Fishing effort, therefore, tends to be uniform during the main part of the run. Since there is no evidence that the shad, once in the river, behave or migrate differently in different seasons, it has been assumed that the above-listed provisions hold for the Hudson River shad fishery.

All the shad which enter the river are susceptible to capture by the New Jersey nets. If we consider the run as a whole and denote its size by N, the number of pounds of shad removed in 1 net-day's fishing in the New Jersey area is pN. The number of pounds remaining after 1 net-day's fishing is qN, where $q=1-p$. The fish escaping the first net-day are susceptible to capture the second net-day during which pqN are removed. The number of pounds removed and the number remaining after successive net-days are as follows:

Fishing period:	*Pounds removed*	*Pounds remaining*
First net-day	pN	qN
Second net-day	pqN	q^2N
Third net-day	pq^2N	q^3N
Fourth net day	pq^3N	q^4N
...	.	.
...	.	.
...	.	.
$n-1$ net-day	$pq^{n-2}N$	$q^{n-1}N$
nth net-day	$pq^{n-1}N$	q^nN

After the nth net-day of fishing by the New Jersey nets, there remain q^nN pounds of fish. This represents the escapement from the New Jersey nets. From our tagging experiment of 1951, we found that the total population (N) entering the river was 1,641,000 pounds. The catch (C) by the New Jersey nets as shown in table 5 was 332,000 pounds (to the nearest thousand pounds); hence the escapement (E) from the New Jersey nets was 1,309,000 pounds. Now, since the escapement (E) equal q^nN, as shown above, $q^n=\frac{E}{N}$, and since there were 600 net-days fished in New Jersey in 1951 (table 6), we have for the New Jersey nets:

$$q^{600}=\frac{1{,}309{,}000}{1{,}641{,}000}$$

from which we find that $q=0.999623$ and therefore $p=0.000377$. This is an estimate of the average fishing power of a New Jersey net that fishes 1 day. In 1 net-day of fishing a New Jersey net removes an average of 0.0377 percent of the fish available.

TABLE 6.—*Net-days fished in 6-week season for New York and New Jersey, and total catch, by years, 1915–51*

Year	Number of nets fished		Number of fishing days		Number of net-days		Total catch, in thousands of pounds
	New York	New Jersey	New York	New Jersey	New York	New Jersey	
1915	79	7	30	42	2,370	294	67
1916	76	3	30	42	2,280	126	39
1917	213	2	30	42	6,390	84	39
1918	272	1	27	42	7,344	42	228
1919	359	14	27	42	9,693	588	370
1920	190	10	27	42	5,130	420	193
1921	159	8	27	42	4,293	336	127
1922	133	8	27	42	3,591	336	170
1923	110	5	27	42	2,970	210	117
1924	97	4	27	42	2,619	168	77
1925	98	4	27	42	2,646	168	102
1926	99	4	27	42	2,673	168	212
1927	136	7	27	42	3,672	294	285
1928	129	7	27	42	3,483	294	198
1929	122	5	27	42	3,294	210	140
1930	121	7	27	42	3,267	294	133
1931	120	4	27	42	3,240	168	267
1932	123	6	27	42	3,321	252	379
1933	146	13	27	42	3,942	546	395
1934	144	14	27	42	3,888	588	373
1935	140	15	27	42	3,780	630	819
1936	162	36	27	42	4,374	1,512	1,257
1937	200	36	27	42	5,400	1,512	2,655
1938	261	52	27	42	7,047	2,184	2,417
1939	254	43	27	42	6,858	1,806	3,103
1940	216	46	33	33	7,128	1,518	3,036
1941	231	46	33	33	7,623	1,518	3,112
1942	220	48	33	33	7,260	1,584	3,164
1943	230	32	42	42	9,660	1,344	3,185
1944	263	38	42	42	11,046	1,596	4,175
1945	242	35	33	33	7,986	1,155	3,545
1946	357	52	33	33	11,781	1,716	3,274
1947	366	52	33	33	12,078	1,716	2,046
1948	357	44	33	33	11,781	1,452	2,461
1949	315	46	33	33	10,395	1,518	2,038
1950	295	40	33	33	9,735	1,320	992
1951	215	25	24	24	5,160	600	755

The shad that escape the New Jersey nets are available to the New York nets. We can determine the fishing power of a net that fishes in the New York area by the same method that we used for determining p for the New Jersey nets. Of the 1,309,000 pounds of shad available to the New York nets, 423,000 pounds were removed in 5,160 net-days (tables 5 and 6). The escapement from the New York nets as shown in the 1951 tagging data was 886,000 pounds which is the total escapement from the entire Hudson River fishery in 1951.[1] From these data:

$$q^{5160}=\frac{886{,}000}{1{,}309{,}000}$$

from which $q=0.999924$ and $p=0.000076$.

The estimated fishing power (p) of an average New Jersey net was found to be 0.000377. Dividing this by 0.000076 (the fishing power of an average New York net) gives:

$$\frac{0.000377}{0.000076}=4.96$$

Or in other words, the fishing power of an average New Jersey stake net is 4.96 times that of an average New York net.

Now that a measure of the fishing power of the nets in each area has been obtained, it is possible to convert the total fishing effort for the Hudson River to standard units. A standard-fishing-unit (s. f. u.) day will be defined as 1 New York net that fishes 1 day. A New Jersey net-day, therefore, is equivalent to 4.96 standard-fishing-unit days, or about 5 s. f. u. days. The second column of table 7 has been computed by multiplying the total net-days in New Jersey (table 6) by 5 and adding the net-days for New York (table 6). These are entered in table 7 as total s. f. u. days for each year. The catch is also given in thousands of pounds and the catch per unit of effort for each year is given as catch per s. f. u. day in pounds. These data are shown graphically in figure 4.

It can be seen that fishing effort, with the exception of that for 1919, was comparatively low

[1] Strictly speaking, the spawning population may be slightly larger than this, since some fish may spawn, or partially spawn, before being caught, but these are few in number, as the fishermen usually stop fishing when many spawned-out fish are caught, since they have low market value.

between 1915 and 1936. In 1936 the large catches attracted more fishermen, and fishing effort increased that year and remained high until 1950. Since it was apparent in the latter year that the shad runs had declined from their previous abundance, both New York and New Jersey increased the closed period to 3 days (table 5) as a conservation measure to reduce fishing intensity. This in itself greatly reduced the fishing effort, and the restriction to 4 days' fishing per week discouraged

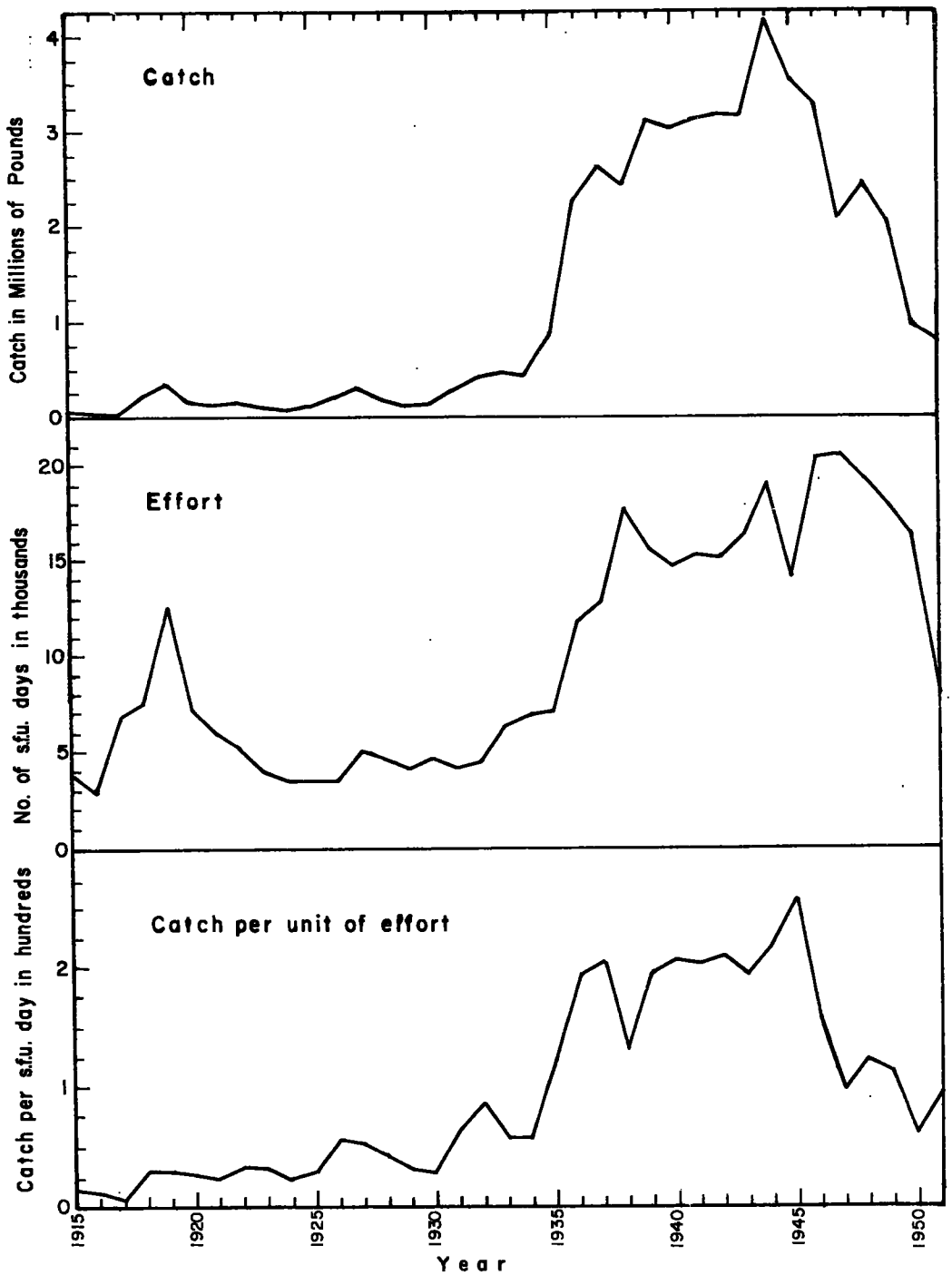

FIGURE 4.—Hudson River shad catch, total fishing effort of New York special gill nets and New Jersey stake nets, and catch per unit of effort, from 1915 through 1951.

some fishermen from operating that year. As a result the fishing effort in 1951 dropped to half that of the previous year.

The 1950 tagging experiment, although starting after the fishing season began and not carried out in as comprehensive a manner as in 1951, and therefore not considered to be so accurate, does give an independent estimate of the fishing power of the nets in the two areas. In that experiment the total population was estimated at 1,510,000 pounds, of which New Jersey caught 521,000 pounds (table 5), and the escapement from the New Jersey nets was 989,000 pounds. As shown in table 6, the number of New Jersey net-days of fishing in 1950 was 1,320, thus,

$$q^{1320}=\frac{989,000}{1,510,000}$$

and $q=0.999679$ and $p=0.000321$.

TABLE 7.—*Total fishing effort, total catch, and catch per unit of effort, by years, 1915–51*

Year	Total s. f. u. days	Total catch	Catch per s. f. u. day
		1,000 pounds	*Pounds*
1915	3,840	67	17
1916	2,910	39	13
1917	6,810	39	6
1918	7,554	228	30
1919	12,633	370	29
1920	7,230	193	27
1921	5,973	127	21
1922	5,271	170	32
1923	4,020	117	29
1924	3,450	77	22
1925	3,486	102	29
1926	3,513	212	60
1927	5,142	285	55
1928	4,953	198	40
1929	4,344	140	32
1930	4,737	133	28
1931	4,080	267	65
1932	4,581	379	83
1933	6,672	395	59
1934	6,828	373	55
1935	6,930	819	118
1936	11,934	2,257	189
1937	12,960	2,655	205
1938	17,967	2,417	134
1939	15,888	3,103	195
1940	14,718	3,036	206
1941	15,213	3,112	204
1942	15,180	3,164	208
1943	16,380	3,185	194
1944	19,026	4,175	219
1945	13,761	3,545	258
1946	20,361	3,274	161
1947	20,658	2,046	99
1948	19,041	2,461	129
1949	17,985	2,038	113
1950	16,335	992	61
1951	8,160	755	92

As before, the fish that escaped the New Jersey nets were available to the New York nets. In 9,735 net-days of fishing, the New York nets took 471,000 pounds of shad, and the escapement from the New York nets, which is the ultimate spawning population, was 518,000 pounds. From this,

$$q^{9735}=\frac{518,000}{989,000}$$

from which $q=0.999934$ and $p=0.000066$. In 1950 the relative power of an average New Jersey net as compared with an average New York net was $\frac{0.000321}{0.000066}=4.86$. This figure is less than the figure obtained from the 1951 tagging data, but as previously mentioned our field work was late in starting in 1950 and we therefore place more reliance on the 1951 estimate. The two estimates, however, are not widely divergent, and the two years, 1950 and 1951, represent extremes both in the amount of fishing effort expended and in weather conditions which might have affected the movements of fish. We have therefore felt justified in using the numeral 5 to relate the efficiency of the New Jersey stake gill nets to the New York gill nets.

Since the fishing power of a New York gill net was taken as the standard unit of measure of fishing effort, the fraction of fish that is removed in 1 standard-fishing-unit day is the same as that previously found for the fishing power of the New York gill net, that is, $p=0.000076$. The total standard-fishing-unit days, by seasons from 1915 through 1950, have been calculated (table 7). Now pN is the number of pounds of shad removed in the first s. f. u. day, pqN is the number of pounds removed the second s. f. u. day, pq^2N is the number of pounds removed the third s. f. u. day, and so forth. It can be seen that in any season the total catch is as follows:

$$C=pN+pqN+pq^2N+pq^3N+\cdots\cdots+pq^{n-1}N$$

Factoring,

$$C=pN(1+q+q^2+q^3+\cdots\cdots q^{n-1})$$

Since the expression in the parentheses is a geometric progression, its sum can be expressed by the formula

$$\frac{1-q^n}{1-q}.$$

Substituting, we have:

$$C=pN\frac{(1-q^n)}{(1-q)}$$

and, therefore,

$$N=\frac{C}{p\left(\frac{1-q^n}{1-q}\right)}$$

or, since

$$p=(1-q),$$

$$N=\frac{C}{1-q^n}.$$

Since p and q are assumed constant from year to year, and C (catch) and n (s. f. u. days) are known (table 7), we can estimate the total population for each year from 1915 through 1950, by the above formula. These estimates, along with the estimated annual fishing rate and escapement, are shown in table 8. In figure 5 the total population, catch, and escapement (spawning population) are shown graphically.

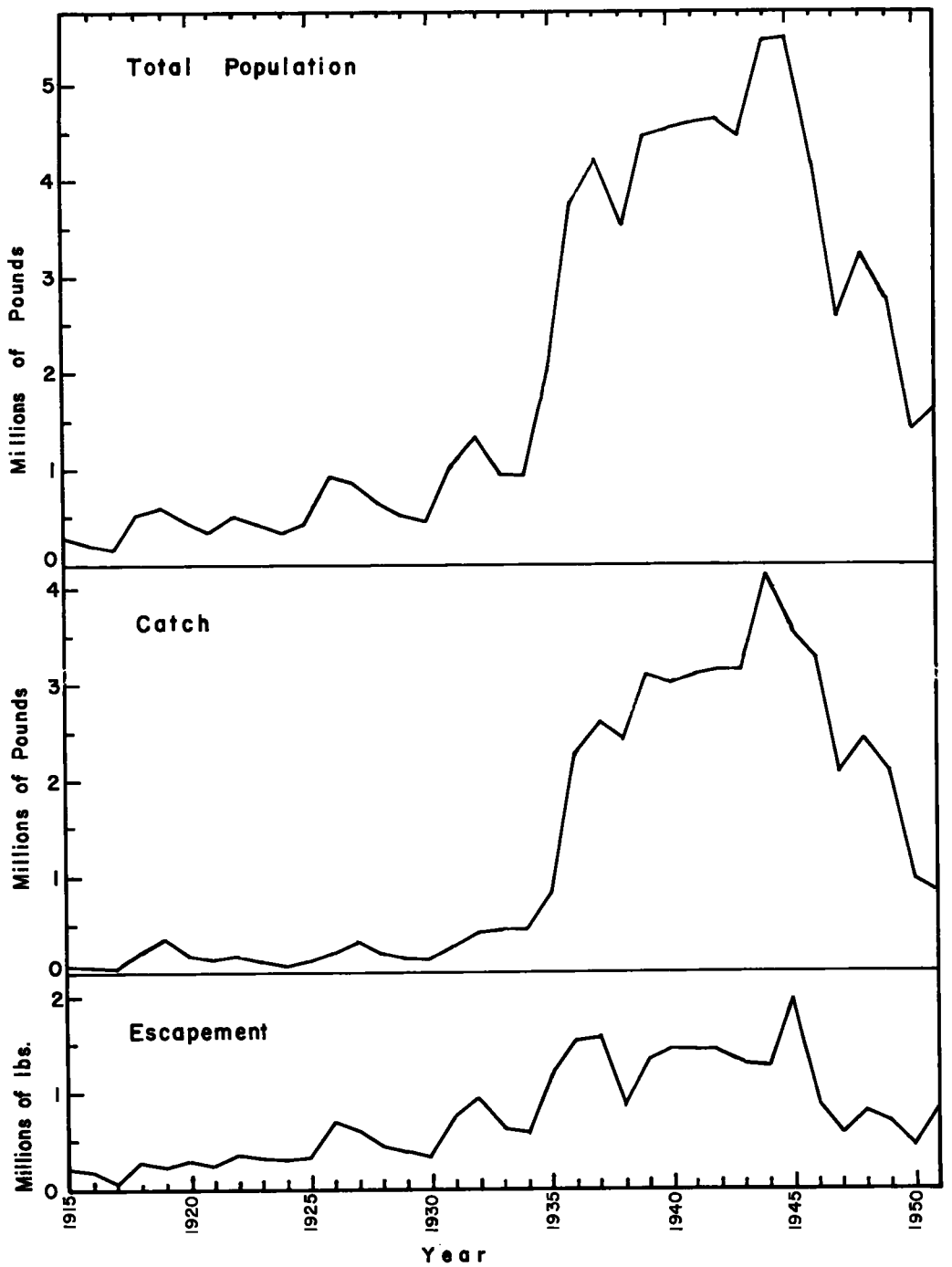

FIGURE 5.—Total calculated Hudson River shad population, catch, and escapement from fishery, from 1915 through 1951.

CALCULATION OF POPULATIONS, 1915–50

It has been demonstrated by several authors that under certain conditions it is possible to estimate the total population present for one of two years, provided the total population is known for the other year and total catch and effort are known for both (Baranov 1918; Ricker, 1940, 1944, 1948). It is possible to use the method presented by these authors, using instantaneous fishing rates (Ricker 1948), to calculate the total Hudson River shad population for each year from 1915 through 1950 with the data presented in table 7 and the 1951 tagging data. As has been shown by Fredin (1954) it is also possible to estimate total populations for years for which fishing effort and catch are available, if the total population and effort are known for one year, by the procedure used here to determine the fishing power of the New York and New Jersey nets. We have used Fredin's method since it does not involve the concepts of instantaneous mortality rates, the theory of which is more difficult for many readers to follow. The results using either method will be practically identical.

TABLE 8.—*Catch, effort, fishing rate, and calculated total population and escapement of shad in the Hudson River, by years, 1915–51*

Year	Catch	Effort	Fishing rate	Total population	Escapement
	1,000 pounds	*s. f. u. days*	*Percent*	*1,000 pounds*	*1,000 pounds*
1915	67	3,840	25.2	266	199
1916	39	2,910	19.8	197	158
1917	39	6,810	40.2	97	58
1918	228	7,554	43.5	524	296
1919	370	12,633	61.5	601	231
1920	193	7,230	42.1	458	265
1921	127	5,973	36.3	349	222
1922	170	5,271	32.9	517	347
1923	117	4,020	26.2	446	329
1924	77	3,459	23.0	334	257
1925	102	3,486	23.2	440	338
1926	212	3,513	23.3	908	696
1927	285	5,142	32.2	884	599
1928	198	4,593	31.2	634	436
1929	140	4,344	28.0	500	360
1930	133	4,737	30.1	442	309
1931	267	4,080	26.6	1,006	739
1932	379	4,581	29.3	1,294	915
1933	395	6,672	39.6	997	602
1934	373	6,828	40.3	925	552
1935	819	6,930	40.8	2,008	1,189
1936	2,257	11,934	59.4	3,796	1,539
1937	2,655	12,960	62.5	4,249	1,594
1938	2,417	17,967	74.3	3,253	836
1939	3,103	15,888	69.9	4,437	1,334
1940	3,036	14,718	67.2	4,521	1,485
1941	3,112	15,213	68.4	4,552	1,440
1942	3,164	15,180	68.3	4,634	1,470
1943	3,185	16,380	71.0	4,484	1,299
1944	4,175	19,026	76.3	5,473	1,298
1945	3,545	13,761	64.7	5,480	1,935
1946	3,274	20,361	78.6	4,107	893
1947	2,046	20,658	79.0	2,588	542
1948	2,461	19,041	76.3	3,225	764
1949	2,038	17,985	74.3	2,741	703
1950	992	16,335	70.9	1,398	406
1951	755	8,160	46.0	1,639	884

It should be noted that in calculating the population and fishing rate for 1950 by the above method, the estimated fishing rate is 70.9 percent, whereas from our tagging experiment the fishing rate was estimated to be 65.7 percent. The population calculated from the 70.9-percent fishing rate is well within the limits of confidence as shown previously in the 1950 tagging data, and considering the limited nature of the tagging work the agreement appears about as good as might be expected.

FACTORS ASSOCIATED WITH FLUCTUATIONS IN HUDSON RIVER SHAD RUNS

Many factors have been suggested as the cause of the decline of the Hudson shad fishery at the turn of the century, its subsequent dramatic recovery beginning in 1936, and the decline beginning in 1945. These include ship traffic in the river, pollution, hatchery operations, dredging, overfishing, and weather. These are difficult to evaluate on the basis of catch data alone (the only figures previously available) since it is known that the total catches of fish depend not only upon the number of fish present, but also upon the amount of effort expended to catch the fish. The calculations in the previous section permit a direct comparison between factors suspected of affecting the runs and the total populations entering the river each year.

Before any relations can be evaluated we must take into account the age of the fish in the run, since the effect of a factor that influences the spawning population, eggs, or young shad of any one year will not appear until the fish of that year-class return to the river as adults and enter the fishery.

Scales were taken from a sample of the commercial catch of shad during the field work in 1950 and in 1951. These were read for total age, age at first spawning, and number of times the fish had previously spawned, for each sex, using the method developed by Cating (1953). The results are shown in table 9. The readings for the two years were then combined by weighting each year's catch in numbers according to sex and gear used. The results are expressed in percentages in table 10. It can be seen that shad which are 4, 5, 6, and 7 years old make up the bulk of the catch, that these fish enter the river for the first time predominantly at 4 and 5 years of age, and that during

TABLE 9.—*Distribution, by age at capture, by age at first spawning, and by number of times previously spawned, as read from scale samples, of shad caught in the New Jersey stake nets and the New York special gill nets in 1950 and 1951*

Group	Number of specimens							
	New Jersey stake nets				New York special gill nets			
	1950 sample [1]		1951 sample [2]		1950 sample [3]		1951 sample [4]	
	Females	Males	Females	Males	Females	Males	Females	Males
Total age at capture:								
2 years	0	1	0	0	1	7	0	0
3 years	2	3	3	1	5	20	1	10
4 years	43	12	89	53	66	17	141	70
5 years	70	18	58	49	130	53	117	109
6 years	31	18	37	45	89	87	80	184
7 years	6	11	24	61	32	56	51	212
8 years	2	5	15	29	10	8	19	88
9 years	2	2	9	8	5	4	5	17
Over 9 years	7	0	9	0	3	0	3	1
Total	163	70	244	246	341	252	417	691
Age at first spawning:								
2 years	0	1	0	0	1	9	0	5
3 years	4	8	3	4	9	44	5	104
4 years	66	32	103	126	124	128	256	440
5 years	74	22	89	88	177	61	135	123
6 years	17	7	41	28	30	10	18	18
Over 6 years	2	0	8	0	0	0	3	1
Total	163	70	244	246	341	252	417	691
Number of times previously spawned:								
None	108	28	166	91	177	48	231	108
1 time	34	12	35	41	98	72	59	97
2 times	9	24	18	56	50	82	80	179
3 times	5	4	15	42	6	43	38	199
4 times	1	1	5	13	6	6	6	86
5 times	5	1	2	3	2	1	2	20
6 times	0	0	1	0	1	0	1	1
7 times	1	0	2	0	1	0	0	1
Total	163	70	244	246	341	252	417	691

[1] Total 1950 catch: 152,216 females, 74,712 males.
[2] Total 1951 catch: 85,145 females, 58,511 males.
[3] Total 1950 catch: 36,625 females, 42,601 males.
[4] Total 1951 catch: 35,625 females, 59,375 males.

this period at least 49 percent of the shad in our sample were entering the river for the first time. Most of the shad caught that were over 5 years old entered the river for the first time as 4- or 5-year-olds and escaped the fishery until caught in later years.

It would be highly desirable to have representative scale samples from each year's catch so that the age compositions could be determined and age classes could be assigned to the year of their origin. Scale samples were not available for all the years covered by this study, so it was necessary to use the averages shown in table 10 as the best estimate obtainable of the age classes, or groups that make up the catch for each year.

TABLE 10.—*Percentage distribution, by age at capture, by age at first spawning, and by number of times previously spawned, as read from scale samples, of 2,424 shad in the commercial catch of 1950 and 1951*

[Weighted according to catch by sex, gear, and year]

Group	Percentage in group
Total age at capture:	
3 years	2
4 years	23
5 years	29
6 years	22
7 years	14
8 years	6
9 years	2
Over 9 years	2
Total	100
Age at first spawning:	
2 years	+
3 years	6
4 years	47
5 years	36
6 years	10
Over 6 years	1
Total	100
Number of times previously spawned:	
None	49
1 time	19
2 times	18
3 times	10
4 times	2
5 times	2
6 times	+
7 times	+
Total	100

FISHING EFFORT

Many men connected with the shad fishery of the Hudson River, including the fishermen themselves, believe that overfishing is the cause of the recent decline in the Hudson River catches. The drift netters in the upper fishing areas blame the stake-net operators in the lower areas. The

New York stake-net operators blame the New Jersey stake-net operators below them, while the New Jersey operators blame the ocean pound nets or the New York drift netters because the latter fish on the spawning grounds. If the fish are caught before they spawn, and nearly all of them are, it makes no difference where they are caught. The run is diminished by the same amount.

In table 8 the estimated spawning escapement for each year is listed, as well as the total population entering the river each year. As previously shown, the catchable population of shad each year appears to be made up mainly of the progeny of shad which spawned 4 and 5 years earlier. The fish that escaped the fishery the previous year are very important (table 10), since 51 percent of the shad sampled had spawned previously. The effect that the escapement 5 years earlier, 4 years earlier, or 1 year earlier has on the population of any one year can be evaluated by multiple-regression analysis. This has been done.

TABLE 11.—*Regression of calculated populations* Y (N_i) *and escapement 5 years earlier* X_1 (E_{i-5}) *and 4 years earlier* X_2 (E_{i-4}) *and 1 year earlier* X_3 (E_{i-1})

Year i	X_1 (E_{i-5})	X_2 (E_{i-4})	X_3 (E_{i-1})	Y (N_i)	Year i	X_1 (E_{i-5})	X_2 (E_{i-4})	X_3 (E_{i-1})	Y (N_i)
1920...	199	158	231	458	1936...	739	915	1,189	3,796
1921...	158	58	265	349	1937...	915	602	1,539	4,249
1922...	58	296	222	517	1938...	602	552	1,594	3,253
1923...	296	231	347	446	1939...	552	1,189	836	4,437
1924...	231	265	329	334	1940...	1,189	1,539	1,334	4,521
1925...	265	222	257	440	1941...	1,539	1,594	1,485	4,552
1926...	222	347	338	908	1942...	1,594	836	1,440	4,634
1927...	347	329	696	884	1943...	836	1,334	1,470	4,484
1928...	329	257	599	634	1944...	1,334	1,485	1,299	5,473
1929...	257	338	436	500	1945...	1,485	1,440	1,298	5,480
1930...	338	696	360	442	1946...	1,440	1,470	1,935	4,167
1931...	696	599	309	1,016	1947...	1,470	1,299	893	2,588
1932...	599	436	739	1,294	1948...	1,299	1,298	542	3,225
1933...	436	360	915	997	1949...	1,298	1,935	764	2,741
1934...	360	309	602	925	1950...	1,935	893	703	1,398
1935...	309	739	552	2,028	1951...	893	542	406	1,639

$$\hat{Y}=-558.18326-0.06055X_1+1.55549X_2+2.07915X_3$$

Tests of significance of regression coefficients:

$t_{b_1}=-0.1467$ d. f.=28 $p>0.5$

$t_{b_2}=3.678$ d. f.=28 $p<0.01$

$t_{b_3}=5.865$ d. f.=28 $p<0.01$

Analysis of variance

Source	d. f.	SS	MS
Total	32	264,197,481	
Means	1	165,524,464	165,524,464
Regression	3	83,838,733	27,946,244
Error	28	14,834,284	529,796

$F=\frac{27,946,244}{529,796}=52.749$ with 3 and 28 d. f. $P<0.01$

$R^2=1-\frac{14,834,284}{264,197,481-165,524,464}=0.8497=85$ percent

$R=0.92$ $P<0.01$

In table 11, the total estimated population (N) for each year (i) from 1920 to 1951 has been entered in column 5, and this is designated as Y. In the second column the estimated escapement 5 years earlier or E_{i-5} is listed; this column is designated as X_1. Columns 3 and 4 are similar except that they are the escapements 4 years earlier and 1 year earlier; they are designated as X_2 and X_3 respectively. Also shown in table 11 are the regression equation, an analysis of variance for the multiple regression, and the multiple correlation coefficient R. Both the F value and R value are highly significant at the 1-percent level, and it can be inferred that 85 percent of the variations in total populations studied can be accounted for by changes in the escapement 5 years, 4 years, and 1 year earlier.

It can be seen in table 11 that the regression coefficient for the escapement 5 years earlier (b_1) does not differ significantly from zero, while the other two are highly significant. This indicates that the escapement 1 year earlier and 4 years earlier produce the high correlation value shown. This is not what might be expected from the age analysis of the scales. Since the proportion of 4- and 5-year-old fish in the catch may vary in different years, especially with changes in fishing intensity, the data in table 10 were divided into two parts. These were the period from 1920 through 1934, when the population sizes were gradually increasing and fishing effort was comparatively low, and the period from 1935 through 1951, when population sizes increased rapidly and then declined, and fishing intensity for most of the years was high. Multiple-regression analyses were calculated for each of these sets of data. The regression equations, tests of significance of the regression coefficients, analyses of variance for the multiple regressions, and the multiple-correlation coefficients R, are as follows:

1920–34 data:

$$\hat{Y}=97.670+0.95366X_1+0.04262X_2+0.58702X_3$$

$t_{b_1}=2.078$ d. f.=11 $p\sim0.06$

$t_{b_2}=0.104$ d. f.=11 $p>0.50$

$t_{b_3}=0.106$ d. f.=11 $p\sim0.06$

Analysis of Variance

Source	d. f.	SS	MS
Total	15	8,112,492	
Mean	1	6,860,049	
Regression	3	856,613	285,538
Error	11	395,830	35,984

$F=7.935$ d. f.=3 and 11 $p<0.01$

$R^2=0.684$

$R=0.827$ $p<0.01$

1935–51 data:

$\hat{Y} = -742.061 - 0.59115X_1 + 1.16810X_2 + 1.90983X_3$

$t_{b_1} = -0.894$ d. f. = 13 $p \sim 0.40$

$t_{b_2} = 1.962$ d. f. = 13 $p \sim 0.075$

$t_{b_3} = 3.761$ d. f. = 13 $p < 0.01$

Analysis of Variance

Source	d. f.	SS	MS
Total	17	256, 185, 929	.....
Mean	1	230, 994, 248	.....
Regression	3	15, 223, 774	5, 074, 591
Error	13	9, 967, 907	766, 762

$F = 6.618$ d. f. = 3 and 13 $p < 0.01$

$R^2 = 0.604$

$R = 0.772$ $p < 0.01$

It can be seen from the two sets of data that for both periods there is a highly significant correlation value R. Of further interest, however, is the fact that for the early set of figures the regression coefficient for the escapement 5 years earlier approaches significance at the 5-percent level, while that for the escapement 4 years before is not significant. The data for the later period show that the regression coefficient for the escapement 4 years earlier approaches significance while that for the escapement 5 years earlier does not. In other words the escapements the year before and 5 years before produced the high correlation for the early data while the escapements the year before and 4 years before produced the high correlation for the later data. This is what might be expected since, when the fishing effort is low and the runs are increasing, the catch of fish tends to be of older stock than when the fishing effort is high. Obviously, what is needed to prove the point for this particular case is scale samples from both periods. As was previously mentioned, samples are only available for some of the years during the latter period. We felt justified, therefore, in using the data in table 10, since these data are the best available, keeping in mind that more accurate analyses can be made when scale samples are available for every year.

Using the appropriate escapement data in the regression equation in table 11, we have predicted the total population for each year from 1920 through 1951. The predicted populations based on escapements are shown in table 12, along with the population estimates from table 8, which were calculated from catch and effort data and the tagging studies. These data are shown graphically in figure 6 which shows also the percentage difference between the two population estimates. The deviations from regression shown in table 12 and figure 6 represent changes in the total populations not accounted for by escapements. In other words, they reflect the effects of other factors.

TABLE 12.—*Comparison of calculated total runs with runs predicted from regression equation, by years. 1920–51*

Year	Calculated run N_i	Predicted run $\hat{Y}$	Deviation $N_i - \hat{Y}$	Year	Calculated run N_i	Predicted run $\hat{Y}$	Deviation $N_i - \hat{Y}$
1920	458	156	302	1936	3, 796	3, 292	504
1921	349	73	276	1937	4, 249	3, 523	726
1922	517	360	157	1938	3, 253	3, 578	−325
1923	446	505	−59	1939	4, 437	2, 996	1, 441
1924	334	524	−190	1940	4, 521	4, 537	−16
1925	440	305	135	1941	4, 552	4, 916	−364
1926	908	671	237	1942	4, 634	3, 640	994
1927	884	1, 380	−496	1943	4, 484	4, 522	−38
1928	634	1, 067	−433	1944	5, 473	4, 533	940
1929	500	858	−358	1945	5, 480	4, 290	1, 190
1930	442	1, 252	−810	1946	4, 167	5, 664	−1, 497
1931	1, 006	974	32	1947	2, 588	3, 230	−642
1932	1, 294	1, 620	−326	1948	3, 225	2, 509	716
1933	997	1, 878	−881	1949	2, 471	3, 962	−1, 221
1934	925	1, 152	−227	1950	1, 398	2, 175	−777
1935	2, 008	1, 720	288	1951	1, 639	1, 075	564

Records of the shad catches previous to 1915 are sketchy and will be discussed later. The figures that are available for the early years show good catches during the period from 1879 through 1901, after which there was a drastic decline.

Unfortunately, the only year for which we know the amount of gear used in making the catches is 1896—in the report of Stevenson (1899). In that paper the number of stake nets is listed as individual nets hung between poles rather than in rows of nets set in the river as has been done since 1915. In New Jersey there were 1,518 individual stake nets listed, and Stevenson states that on the average there were 25 or 30 stake nets to the row. On the basis of 30 nets to the row, there were about 50 rows of nets in the New Jersey section of the Hudson River similar to the nets listed for recent years. In addition, there were 12 rows of pole nets which are the same as stake nets except that the webbing is in one piece. This makes a total of approximately 62 nets equivalent to the stake nets used in recent records.

For New York, Stevenson lists 337 drift nets fishing for shad in the Hudson River and 1,099 of the individual stake nets. No figure is given of the number of nets to the row for the stake nets, but using the figure of 30 as given for the New Jersey stake nets, there would be about 33 stake nets in New York. In addition to these there were 2 pole nets, giving a total of 35 stake nets equivalent to those we have used in our previous calculations.

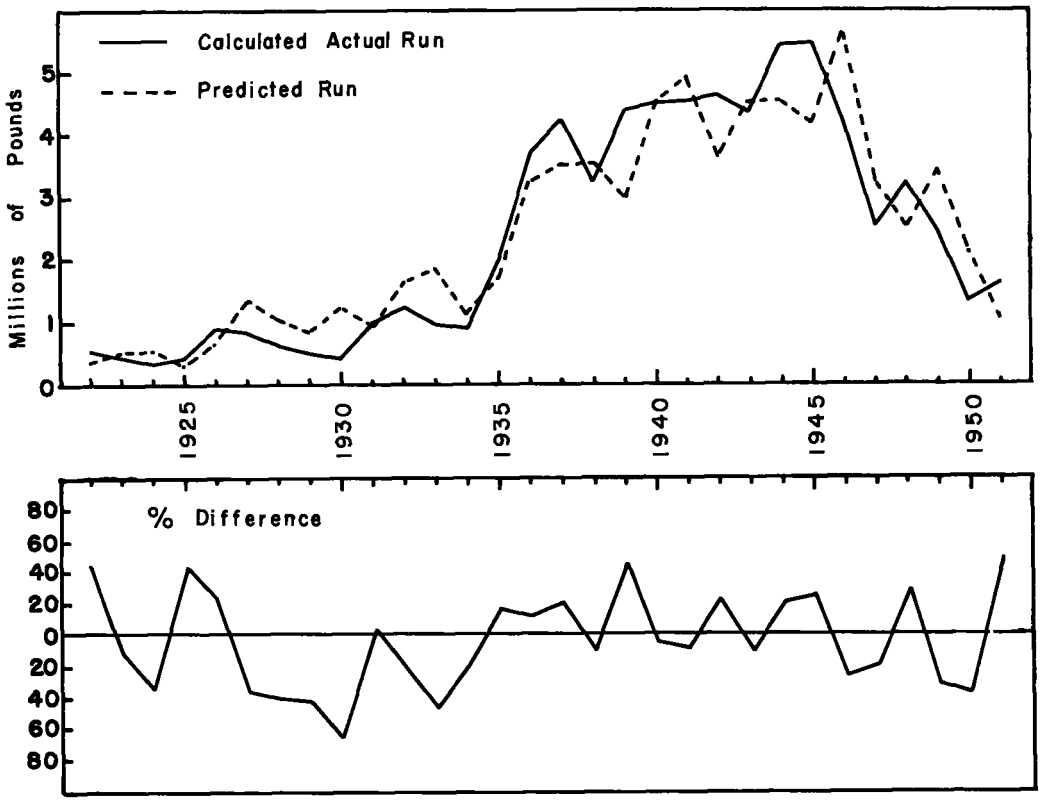

FIGURE 6.—Comparison of calculated actual Hudson River shad runs and predicted shad runs, and percentage difference between them.

The fishing power of the New Jersey stake nets has been shown to be equivalent to approximately 5 New York drift gill or stake nets. Therefore, there was a total of 722 ($62\times5+377+35$) standard fishing units of gear operating in the Hudson River in 1896. Stevenson states that fishing was closed 1½ days each week; therefore, 33 days were available for fishing during the 6-week season upon which we have based our calculations. This gives a total of 23,826 s. f. u. days for the fishing season. The catch by this gear was 519,853 shad which averaged about 4 pounds each (U. S. Fish and Wildlife Service, Fishery Statistics for 1945, p. 166) which gives a catch of approximately 2,079,412 pounds. Using the methods previously employed, the total population of shad in 1896 was estimated to have been 2,490,000 pounds, leaving a spawning population of 411,000 pounds. The fishing rate was therefore 83.5 percent.

The calculations for 1896 may be slightly in error since the conversion to gear equivalent to that used presently may not be strictly correct. The error should not be great, however, and the fishing rate of 83.5 percent is higher than any during the past 37 years as shown in table 8. If it is indicative of the fishing intensity at the turn of the century, the low productivity during the early 1900's probably resulted from too few shad being allowed to spawn.

It would appear from available data that the most important factor in the fluctuations in shad runs during the past 37 years, and possibly during earlier years, was the number of shad escaping to spawn each year. Other factors were investigated during the present study, however, to determine whether they had any influence on the shad runs, or whether they were the cause of the deviations from regression as shown in table 12.

STREAM FLOW

The water-discharge records of the Hudson River were examined to determine whether there was any correlation between stream flow and the size of shad runs. Discharge data were compiled for the Hudson River at Troy for each year from 1919 to 1948 from the records of the U. S. Geologi-

cal Survey. These were computed by adding the Hudson River discharge at Mechanicville to the discharge of the Mohawk River which drains into the Hudson below Mechanicville. The Mohawk River discharges were recorded at Crescent Dam from 1919 to 1925, and at Cohoes from 1925 to 1948. Beginning in October 1948, the Hudson discharges at Troy were obtained directly from a gage at Green Island, just above the Troy Dam.

Figure 7 is a composite graph showing the water discharge for the Hudson River at Troy for the years 1919 to 1948. The discharges each year fluctuated greatly almost every month of the year except July, August, and September. In general, most of the high discharges occurred in March and April, but relatively high discharges occurred every month but August.

For a river the size of the Hudson, the most unusual situation brought out by an examination of the water records was the low flows occurring during the summer months. Every year, flows below 5,000 second-feet were recorded for part of the season, and during 1941 the flow was below 2,000 second-feet for 24 days. In this respect the Hudson River below Troy is not a river in the truest sense of the word, but a river valley into which the sea has been admitted by subsidence of the land, or an estuary. Tidal action, particularly during low flows, has more effect on the river velocity than does runoff.

It was considered that fluctuations in water discharge might directly affect the eggs or young shad while they were in the river, or indirectly affect them in some manner such as diluting or flushing out the pollutants in the river. To examine this possibility, multiple-regression analyses were made between the size of run of shad each year and the peak water discharges 4 and 5 years earlier for each of the months of April, May, and June for the years 1924 through 1951. No significant correlations were found. Similar multiple-regression analyses were made between the size of run each year and the average monthly discharges 4 and 5 years earlier for each of the months of May through July. Again no significant correlations were found. As previously shown, the size of run each year depends on the escapement of the previous year as well as on the progeny of the runs 4 and 5 years earlier. This would tend to obscure any correlation should it exist. It is not possible to make corrections in these calculations for the escapement in the previous year until scale samples are available for the years being checked so that the age composition of the runs can be determined. It was concluded that if variations in river discharge have

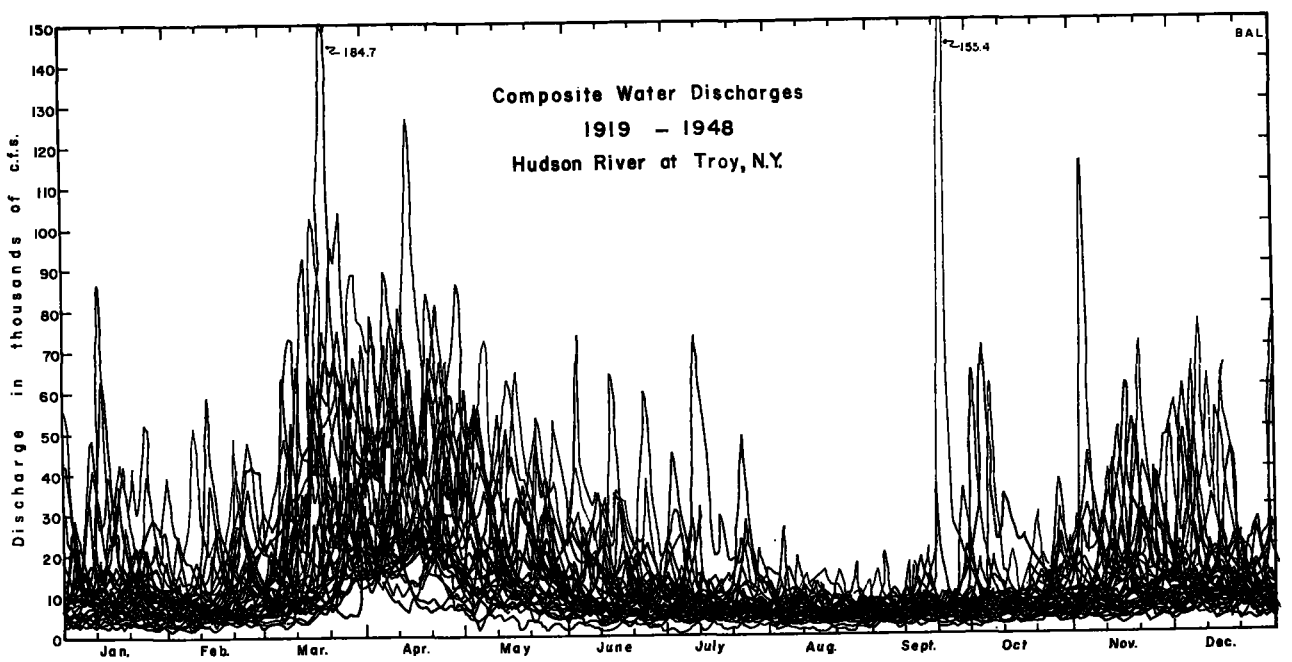

FIGURE 7.—Composite of Hudson River discharges at Troy, 1919 through 1948.

any effect on the shad runs the effect is obscured by other factors.

WATER TEMPERATURES

Water temperatures of the Hudson River at Poughkeepsie have been recorded for many years by the water works department of that city, which utilizes the Hudson River for its water supply. These temperatures are taken each day at 8 a. m. Many of the early records have been lost, but we were able to obtain the mean monthly temperatures from 1908 through 1919, and from March 1929 through 1949, from Thomas Cole, who was superintendent of the water-treatment plant before his retirement in 1949. The 1950 records were obtained at the Poughkeepsie water-treatment plant and are shown in figure 8. The monthly mean temperatures from March 1929 through 1950 are shown in table 13. The means of the monthly temperatures for these years are shown in figure 9, and the approximate time that the adults and young shad are in the river is also indicated.

The temperatures shown in table 13 and figures 8 and 9 are lower than mean daily temperatures since they were taken at 8 a. m. each day. Maximum and minimum daily temperatures were taken from April through August of 1951 and it was found that the greatest difference between maximum and minimum daily temperatures during this time was 7° F., while the average difference was 3.1° F. The average differences between the temperatures taken at 8 a. m. and the daily average of maximum and minimum was 1.4° F. It is probable that the mean temperatures as shown in table 13 and figures 8 and 9 during spring and summer should be approximately 1.4° higher to represent the average daily temperatures.

The shad runs in the Hudson River usually start around the first of April (fig. 9), at which time the interpolated average water temperature at 8 a. m. is about 40° F. In 1950, the temperature was 38° F. on April 1 (fig. 8). According to individual records of fishermen and landing reports (U. S. Fish and Wildlife Service, Fishery Products Report, 1938–51), the peak of the run, as judged from the catch, occurs between the middle of April and the middle of May, at which time the temperature averages 45° F. to 57° F. (table 13), but the temperature was colder than this in April 1950 (43° F. to 56° F., fig. 8). No conclusive data were obtained during this study as to the specific dates of spawning, but these probably occur primarily during the month of May in the Hudson River, at which time the fishermen obtain ripe fish and a few spawned-out fish. During this period the average 8 a. m. temperatures were between 51° F. and 62° F. (fig. 9). In 1950, they ranged between 45° F. and 60° F., and in 1951 (not shown) they were between 51° F. and 63° F. The daily average temperatures were probably

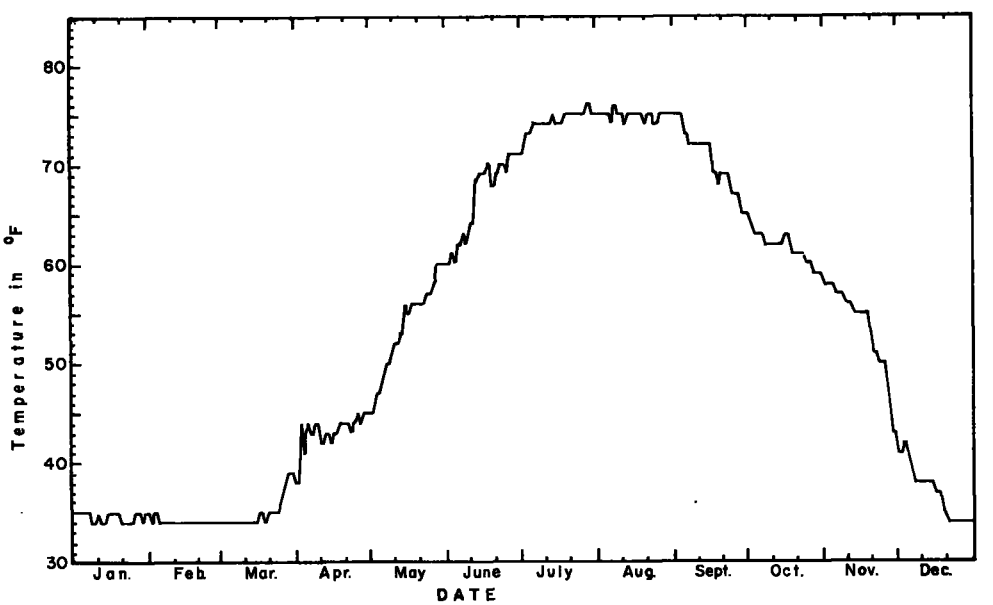

FIGURE 8.—Hudson River water temperatures at 8 a. m. at Poughkeepsie, for 1950.

about 1.4° F. higher than those listed, as previously explained. Massman (1952) has shown that in Virginia streams the greatest catches of shad eggs in plankton nets were at temperatures between 12° C. and 20° C. (53.6° F. and 68° F.). Cable (unpublished data) made good catches of shad eggs in plankton nets in the Hudson River at temperatures ranging from 57° F. to 68° F. during the last of May and first week of June in 1940 and 1941. Spawning had probably begun before she started sampling, and since she sampled during the afternoon and evening, the temperatures recorded may be near maximum for the day rather than average.

It is conceivable that variations in water temperature might affect the survival of eggs, larvae, or juveniles, and hence affect the size of the run 4 and 5 years later. No trends in water temperature could be found, however, which might have accounted for the great fluctuations in shad production, nor were any variations in average temperatures found that might have caused the devia-

TABLE 13.—*Monthly mean water temperatures of the Hudson River at Poughkeepsie, 1929–50*

[Temperatures in ° F.]

Year	January	February	March	April	May	June	July	August	September	October	November	December
1929				44.0	54.0	67.0	74.0	73.0	70.0	59.0	48.0	37.0
1930	33.0	33.0	36.0	43.5	55.0	65.0	74.0	75.8	71.7	63.7	50.4	34.9
1931	32.6	32.6	35.3	48.5	57.1	68.5	76.6	77.9	73.0	65.6	52.7	35.0
1932	34.3	33.6	34.2	42.7	56.1	67.3	73.3	75.8	72.5	60.5	46.3	34.5
1933	36.6	35.5	36.6	45.6	57.8	69.9	73.9	76.0	70.2	61.0	41.8	35.0
1934	33.0	33.0	33.0	42.6	55.5	65.8	72.2	71.5	66.4	57.8	46.4	35.0
1935	33.0	33.0	34.7	43.5	56.5	66.6	74.8	75.7	68.3	56.6	49.5	35.0
1936	33.0	33.0	36.6	43.4	58.8	68.9	75.6	77.4	71.2	60.5	44.0	34.0
1937	33.7	33.0	34.4	41.0	58.3	67.9	70.7	76.2	68.2	54.9	40.9	35.0
1938	33.0	34.0	36.5	47.0	59.9	68.3	74.1	76.8	68.0	56.2	49.2	35.6
1939	33.0	33.0	32.9	42.3	56.4	70.9	75.5	77.4	71.4	60.9	45.0	34.9
1940	33.0	33.0	34.0	40.0	58.0	70.0	75.0	77.0	70.0	61.0	47.0	37.0
1941	33.5	32.9	33.3	46.8	60.4	67.6	74.8	76.5	72.0	64.2	50.9	36.0
1942	33.6	34.0	37.0	45.4	59.0	70.4	75.6	77.1	72.1	59.2	47.3	35.6
1943	33.0	33.0	35.0	41.0	54.0	70.2	76.8	77.9	72.4	60.6	47.7	35.4
1944	33.4	35.1	36.0	40.4	57.7	68.9	76.1	78.2	73.2	62.1	48.6	35.3
1945	34.0	34.1	38.8	50.8	55.2	64.2	73.9	73.9	71.1	54.4	43.6	35.0
1946	33.4	33.2	38.6	47.8	55.4	64.5	73.2	74.1	71.3	63.2	52.9	39.5
1947	34.1	34.2	35.7	45.3	54.4	64.1	73.0	76.3	74.5	60.1	49.9	35.8
1948	33.0	33.0	35.6	47.1	55.4	64.3	75.0	76.2	74.5	62.9	52.1	41.8
1949	34.4	34.2	36.2	48.4	59.5	68.4	76.8	78.2	73.2	64.2	52.7	37.0
1950	34.6	34.1	35.2	43.4	54.1	66.8	74.2	74.8	70.4	61.6	53.5	36.9
Mean	33.6	33.5	35.5	44.6	56.8	67.5	74.5	76.1	71.2	60.5	48.2	36.0

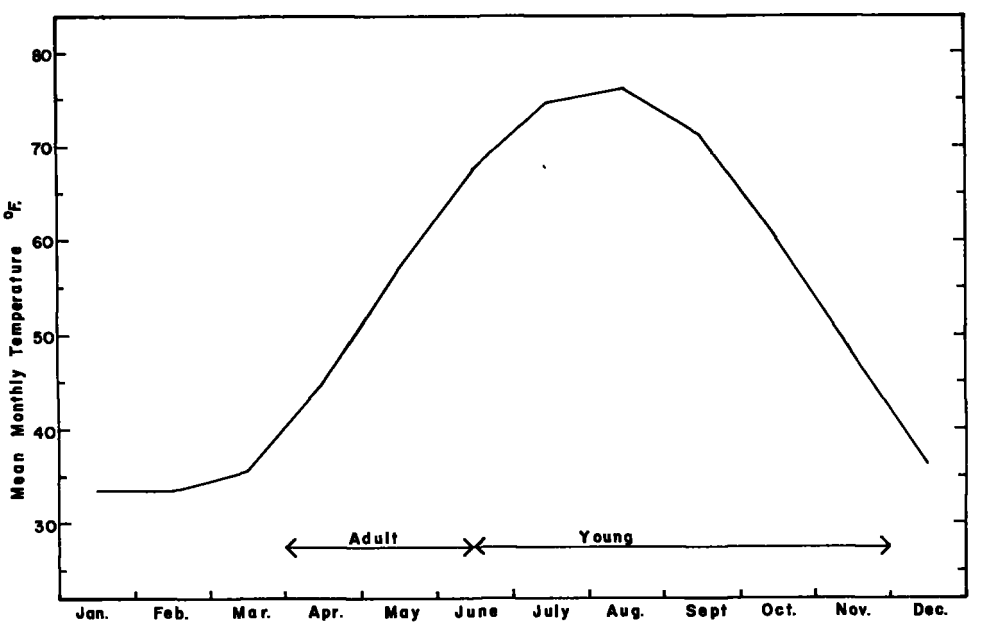

FIGURE 9.—Hudson River monthly mean water temperatures in °F., taken at 8 a. m., at Poughkeepsie, for 1929 through 1950, and periods when adult and young shad are in the river.

tions between predicted and calculated populations as shown in table 12. The only period of any duration when deviations from average water temperatures occurred was from June through October in the years 1939 through 1944. During this period 28 of the 30 monthly average temperatures shown in table 13 were above the mean for the monthly temperatures for 1929 through 1950. So far as could be determined, this had no effect on subsequent shad runs to the Hudson River. Variations in daily temperatures (records of which are not now available) may have occurred during critical periods of development of the eggs and larvae of the shad, which might have affected production. It is not likely, however, that they would have occurred in such a manner as to cause the fluctuations in total shad catches as shown in figure 2, but they might have been partially the cause of the deviations from predicted populations shown in table 12, either directly or indirectly as temperature affects other factors such as pollution. Since the only records available at this time are the mean monthly temperatures, which obscure daily variations, no examination can be made of this possibility.

Fishermen and others acquainted with the shad fishery believe that when a warm spring occurs the shad run is earlier than when cold weather prevails. To check on this statistically, a regression analysis was run using the mean water temperature for April from 1938 through 1951 and the week of peak catch in New York as measured by the landings in Fulton Market in New York City. The regression coefficient was not quite significant at the 5-percent level. In general, it can be said from an examination of the data that the Hudson River shad runs tend to be earlier when the spring is warmer than average, but the regression of time of the runs on water temperatures is not statistically significant. This same result has also been noted for the Columbia River shad runs (Talbot 1953). If better indexes than were used here were developed for water temperatures, and for time of run, a significant relation might be found.

CHANNEL IMPROVEMENTS

The Hudson River channel has undergone improvement for navigation purposes since 1789 (U. S. Army, Pt. I, 1920). Originally there was a 25-foot channel (with the exception of a few shoals which restricted the minimum depth to 19 feet) from New York City to Hudson. Above Hudson the river was obstructed by sandbars, making a tortuous and unstable channel. After partial improvement by the State of New York between 1797 and 1831, a narrow, crooked channel existed with a navigable depth of 3½ to 11 feet between Coxsackie and Waterford. From 1834 to 1892, improvement work was carried on by the State of New York in conjunction with the Federal Government, and legal control was given to the United States Government in 1891. A project initiated in 1899 called for a 12-foot channel from Coxsackie to Waterford. This was later increased to a projected depth of 27 feet between Hudson and Albany, as well as for the section between New York City and Hudson. By 1931 the river was dredged to minimum depths of 27 feet between New York City and Hudson and 26 feet to Albany. By the next year there was a 27-foot channel to Albany.

Deepening the channel has caused an increase in the mean tidal range in the upper part of the river between New Baltimore and Troy (U. S. Army, Pt. I, 1920). In 1831 the mean range of the tide at Albany was 2.09 feet. In 1910 the mean range was 2.9 feet, and the present project increased the mean range about 0.4 feet, or an increase in mean range of about 1.21 feet since 1831.

In addition to the change in tidal effect, many of the shallow sandbars have been removed in the upper section from areas which may have been former spawning grounds. What effect, if any, this may have had on the runs of earlier years cannot now be ascertained. Since the shad runs of the Hudson have made a dramatic recovery and again declined in recent years, the dredging records of the river were examined to determine whether the removal of this material has influenced the abundance of shad since 1920. Records of the amount of material in cubic yards removed from the upper Hudson for each year between 1920 and 1948 were obtained from the Corps of Engineers (U. S. Army, Pt. I, 1920–49). These amounts are shown in figure 10 and include both soft material and rock removed.

It can be seen in figure 10 that the greatest amount of material was removed between 1926 and 1934. The shad runs, however, increased in later years (1936–46) to somewhere near their greatest former abundance as shown in figure 15.

and since have declined. It must be concluded, therefore, that whatever effect the deepening of the upper reaches of the river has had on the shad runs, the fishery has still been able to produce at a high level, and the dredging operations in recent years have had no measurable adverse effect on the abundance of shad.

SHIP TRAFFIC

The Hudson River is one of the most important highways of commerce in the United States. It is open to navigation to Albany for a period of 8 to 10 months a year. During the past 10 or 15 years from 200 to 1,800 steam and motor vessels have visited the port of Albany each year, as well

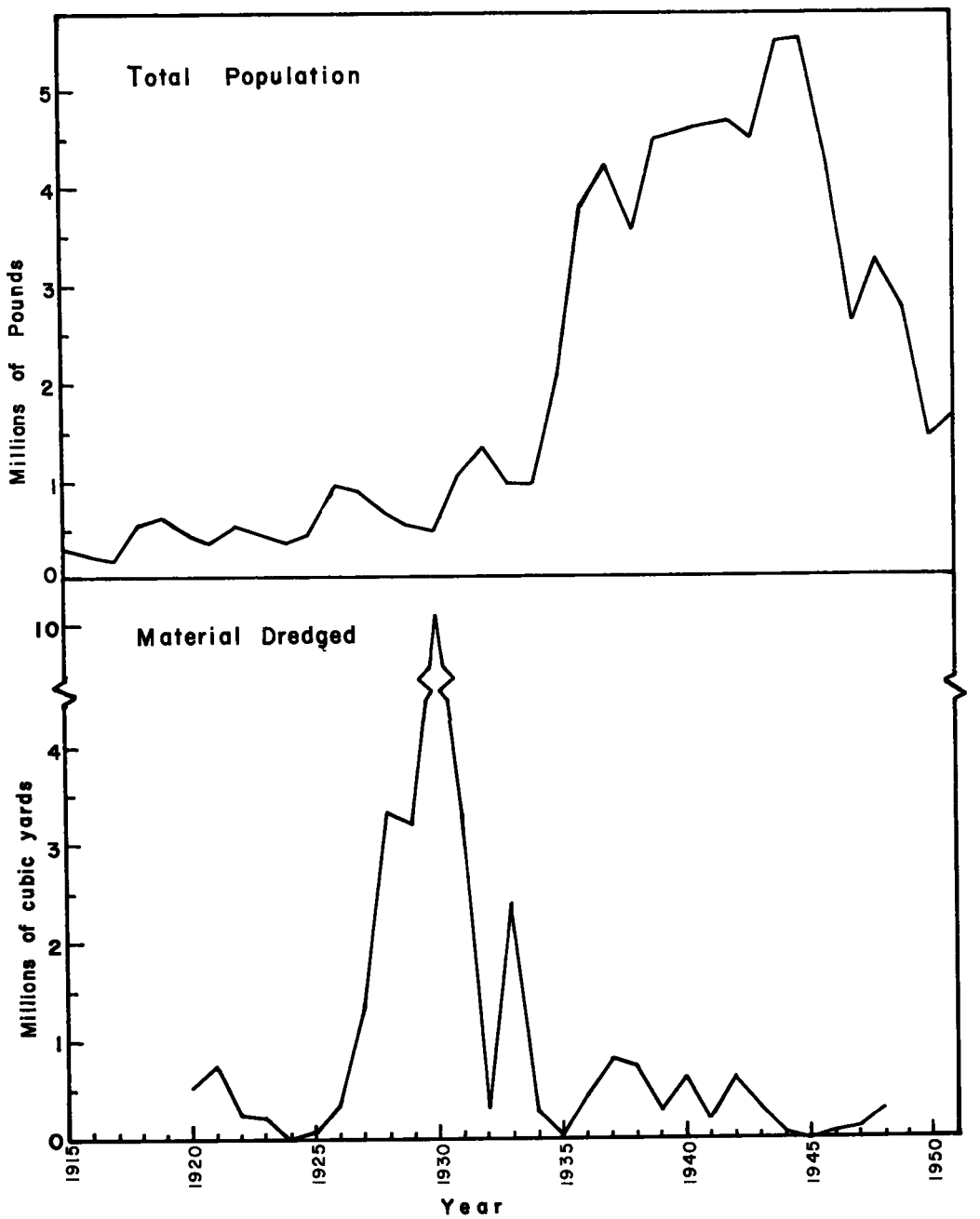

FIGURE 10.—Cubic yards of soft and hard material removed from Hudson River by dredging, 1920 through 1948, compared with total shad populations during the same years.

as approximately the same number of barges (U. S. Army, Pt. II, 1920–49). In addition, there is much traffic in the river that is bound for points below Albany. This congestion of shipping in the river represents a hazard to fishing operations, particularly to the drift-net fishermen in the upper fishing areas. Often the operators of the ships and barges make no effort to avoid either the fishermen's boats or their nets, as required by law, with the result that fishing is interrupted many times each season and loss of nets is common. In addition, the wakes of large ships cause large waves which make the anchoring of small boats difficult and cause damage to small wharves and boats along the shores.

Because of this, many fishermen are understandably antagonistic towards the captains or pilots of the ships and blame many of their difficulties on river traffic. During the course of our field work in 1950 and 1951, many fishermen informed us of the damage caused by shipping and also told of large numbers of eggs, presumably of shad, which had been washed up on the beaches by the waves caused by passing ships. In addition, some of the fishermen believe that the waves from passing ships and the turbulence caused by ships' propellers stir up shad eggs, sand, and silt from the river bottom, and that the eggs are smothered when all of these settle to the bottom again.

The hazards of ship traffic while shad fishing on the Hudson were experienced many times by the field crews working with the fishermen, but no evidence was ever found of shad eggs being washed ashore by the waves of passing ships. Nevertheless, records of ship traffic on the Hudson were examined in an attempt to determine whether variations in river traffic could be the cause of fluctuations in the shad populations.

Records of the numbers of trips made by ships and barges on the Hudson River are available from the report of the Chief of Engineers (U. S. Army, Pt. II, 1920–49), for various sections of the river. From these we have compiled the numbers of trips (one way only) by steamers and motor vessels between New York City and ports along the river to Waterford, for the years 1920 through 1949. The statistics for 1920 list all shipping above New York City. Between 1921 and 1933 the records are for trips between Tarrytown and Waterford, and after 1933 the records are for trips between Harlem River and ports along the river up to Waterford. These are shown in figure 11 (solid line) along with the estimated shad population 4 years later.

With the exception of the year 1923, when traffic was extremely high, there was a gradual though irregular decline in river traffic of steam and motor vessels from 1921 to 1944. During this time the shad population increased tremendously and then declined again. Obviously there is no correlation between the total number of trips made by steamers and motor vessels and shad production during this period.

On the assumption that larger ships could possibly do more damage than smaller ships, the number of trips (one way) by vessels of more than 20-foot draft between New York City and places along the Hudson River up to Waterford was compiled. These are shown as the broken line in figure 11, and depict a trend much different from that of all shipping on the river. The increase in traffic by larger and more heavily laden vessels beginning in the 1930's resulted, undoubtedly, from the deepening of the channel to 27 feet for the whole river between New York City and Albany in 1931 and 1932. The heavy ship traffic increased to a peak in 1939, but then decreased again to a low in 1942 because, as a result of World War II, the railroads handled most land freight, leaving the ships for ocean hauling. After 1945 the heavy hauling on the river again increased, reaching a peak in 1947. The peak of traffic by these vessels from 1935 to 1939 had no noticeable effect on the shad runs 4 and 5 years later, and the decrease in traffic during the war years and subsequent increase after the war compares with an overall decline during this time in the shad run 4 and 5 years later. We have concluded that, although shipping in the river is detrimental to fishing gear and constitutes a hazard to fishing, there is no evidence to show that it is detrimental to the shad runs.

HATCHERIES

For many years a shad hatchery was operated on the Hudson River in the vicinity of Catskill. In addition to the shad hatched at this station, the U. S. Fish and Fisheries Commission furnished shad fry for distribution in the Hudson River during the years between 1882 and 1904. More recently the practice of artificially hatching shad eggs has not received support, and the Hudson

River shad hatchery, along with many others on the Atlantic coast, has ceased operations.

Many fishermen and others associated with the fishing industry have insisted that the closure of the Hudson River hatchery has been the cause of the present decline in the Hudson River shad fishery. To examine this possibility, the records of shad eggs hatched or fry stocked each year have been compiled from available records (New York Fisheries Commission; New York Forests, Fish and Game Commission; New York Conservation Department; U. S. Fish Commission). These

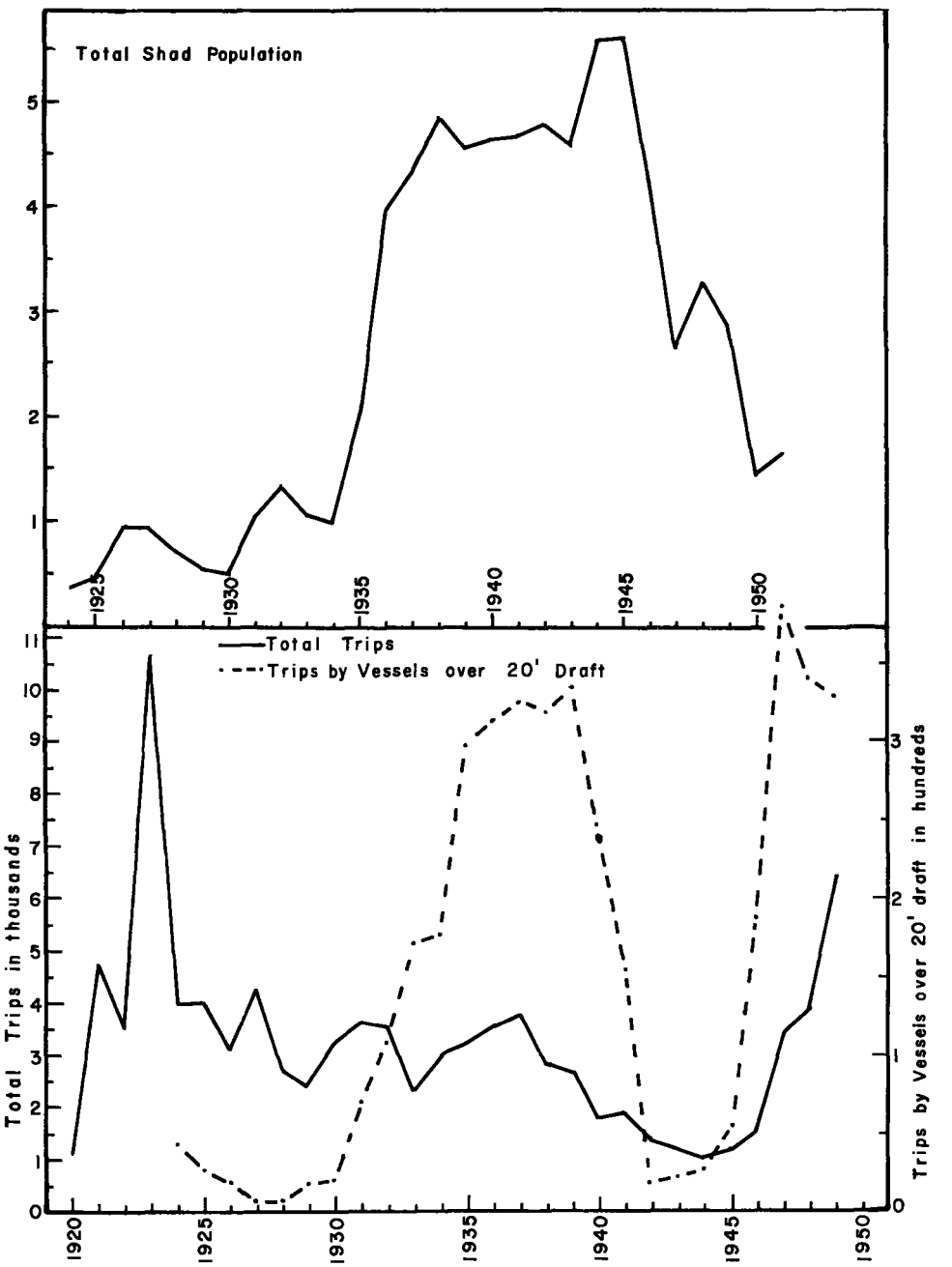

FIGURE 11.—Total number of 1-way trips by steam and motor vessels of more than 20-foot draft compared with total shad populations 4 years later.

show that artificially hatched fry were stocked in the Hudson almost every year from 1869 through 1944 (table 14 and fig. 12).

Early records of the shad catches from the Hudson River are fragmentary and will be discussed later, but it is known that the catches were large in some years between 1870 and 1902, and particularly between 1885 and 1901 (see fig. 15). These catches indicate large runs of shad, which appear to be reflected in the numbers of eggs that were obtained, hatched, and stocked each year. The greatest hatchery production occurred between 1887 and 1903. What part the hatchery played in shad production during early years is hard to assess at present, but it can be stated definitely that the peak hatchery production in 1899, 1900, and 1901 (fig. 12) did not maintain the runs, for the shad catch dropped from 3,432,472 pounds in 1901 (the peak year of hatchery production) to 573,399 pounds in 1904 (U. S. Bureau of Fsheries, 1907) and did not recover to anywhere near its former abundance until 32 years later, beginning in 1936.

TABLE 14.—*Hatchery shad released in Hudson River, 1869–1944*

Year	By U. S. Fish Commission	By New York State	Total
1869		15,000,000	15,000,000
1870		2,604,000	2,604,000
1871		8,295,000	8,295,000
1872		7,489,000	7,489,000
1873		5,041,000	5,041,000
1874		5,020,000	5,020,000
1875		4,580,000	4,580,000
1876		1,850,000	1,850,000
1877		3,584,000	3,584,000
1878		4,705,000	4,705,000
1879		6,459,000	6,459,000
1880		3,972,900	3,972,900
1881			
1882	963,000		963,000
1883	1,700,000	1,925,000	3,625,000
1884	1,477,000	1,467,000	2,944,000
1885	1,250,000	1,728,000	2,978,000
1886	2,412,000	2,279,000	4,691,000
1887	2,779,000	3,822,000	6,601,000
1888	4,200,000	3,924,500	8,124,500
1889	5,893,000	6,000,000	11,893,000
1890	6,366,000	2,025,000	8,391,000
1891	9,348,000	2,224,000	11,572,000
1892	5,199,000	2,436,000	7,635,000
1893	1,573,000	2,215,000	3,788,000
1894	5,414,000	190,000	5,614,000
1895	4,900,000	3,087,000	7,987,000
1896	4,595,000	4,095,000	8,690,000
1897	7,125,000	3,018,000	10,143,000
1898	5,500,000	6,579,400	12,079,400
1899	11,470,000	2,113,800	13,583,800
1900	10,280,000	2,870,200	13,150,200
1901	13,156,000	4,806,600	17,962,600
1902	2,123,000	3,911,150	6,034,150
1903		3,119,900	3,119,900
1904	3,000,000	1,518,500	4,518,500
1905		2,361,900	2,361,900
1906		400,000	400,000
1907		566,000	566,000
1908		881,000	881,000
1909		1,016,500	1,016,500
1910		6,126,500	6,126,500
1911		4,807,250	4,807,250
1912		6,603,695	6,603,695
1913		6,420,000	6,420,000
1914		1,403,000	1,403,000
1915		1,246,418	1,246,418
1916		1,411,000	1,411,000
1917		122,665	122,665
1918		2,054	2,054
1919		2,160,000	2,160,000
1920		1,776,279	1,776,279
1921		703,125	703,125
1922		1,056,875	1,056,875
1923		1,406,000	1,406,000
1924		1,282,500	1,282,500
1925		1,064,000	1,064,000
1926		2,014,722	2,014,722
1927		3,032,875	3,032,875
1928		2,455,750	2,455,750
1929		2,619,625	2,619,625
1930		1,781,250	1,781,250
1931		2,965,187	2,965,187
1932		2,755,000	2,755,000
1933		3,769,125	3,769,125
1934		3,075,625	3,075,625
1935		2,797,750	2,797,750
1936		2,999,625	2,999,625
1937		2,812,000	2,812,000
1938		3,222,875	3,222,875
1939		2,983,000	2,983,000
1940		[1] 1,000,000	[1] 1,000,000
1941		1,498,750	1,498,750
1942		997,500	997,500
1943			
1944		1,539,000	1,539,000

[1] Estimated.

Since the effect of hatchery operations on the 1936 to 1946 increase in shad production is of more immediate interest, because figures are available for both hatchery production and size of run each year, recent records have been examined closely. To determine whether hatchery production affects the size of runs in later years, a multiple-regression analysis was calculated between the size of the run each year from 1915 through 1946 and hatchery production 4 and 5 years before each year's run. No significant correlation was found. Here again the size of the escapement of the year before would tend to obscure any correlation that might exist, and there is no way possible at this time to make corrections for this factor.

It is not surprising that no correlation exists between the hatchery output and the sizes of subsequent runs. The average number of eggs obtained per female shad by fish culturists is between 20,000 and 30,000 (New York Fish. Comm. Rept. for 1899; Brice, 1898) but recently it has been shown (Lehman, 1953) that the actual number of eggs per female spawned naturally each season is between 100,000 and 500,000, depending on the age of the fish. Some of the eggs may be spawned in advance of stripping, but many are not ripe when the fish are stripped, and since the fish are usually killed in the process many of the eggs are lost. Since 1914, the number of eggs hatched artificially in the Hudson River hatchery each year has usually been between 1 and 3 million. From 40 to 120 female shad were stripped to obtain these eggs (at 25,000 per female), and if each of the females contained an average of 250,000 eggs it

is possible that between 10 million and 30 million eggs were wasted in the process. The added protection given artificially hatched eggs can hardly be expected to compensate for the waste of eggs inherent in the process.

In some cases, the eggs for hatchery operations were obtained from commercial fishermen who stripped ripe eggs from the fish before selling them. In these cases no wastage occurs, but in any event the number of eggs handled each year is comparatively very small. For instance, the eggs handled in 1914 are equivalent to the total production of only 4 or 5 averaged-sized female shad, and the greatest hatchery output in 1901 of almost 18 million eggs is equivalent to the total egg production of only about 72 fish. Furthermore, the lowest calculated escapement shown in table 8 was 58,000 pounds in 1917. If females made up half the poundage, there were 29,000 pounds of female shad, and converting pounds to fish by a factor of 4 pounds to the female gives a figure of over 7,000 female shad spawning naturally that year. The hatchery production in the same year (table 14) was only about half that produced by 1 average-sized fish. Similarly, the greatest hatchery production in recent years was in 1933 and is equivalent to the production of approximately 15 female shad. In that same year the calculated natural escapement was 602,000 pounds which, on the basis of a fifty-fifty sex ratio, and an average weight of 4 pounds, amounts to more than 75,000 females spawning naturally. Obviously, the number of eggs that it has been possible to obtain for hatchery operations is only an extremely small fraction of the amount spawned naturally, and the increased survival

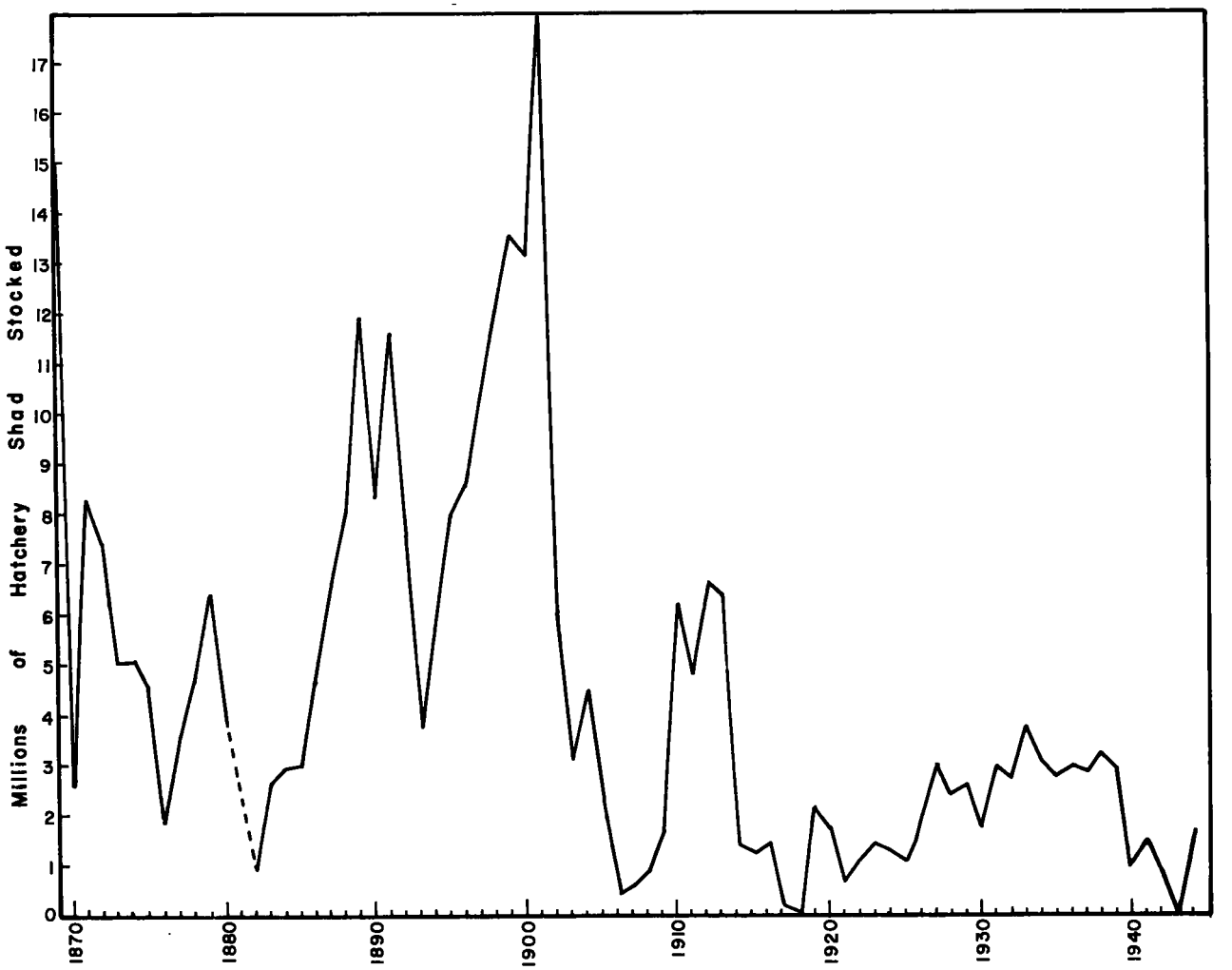

FIGURE 12.—Artificially hatched shad stocked in the Hudson River, 1869 through 1944.

rate, if any, resulting from current shad-hatchery practices has not produced, and cannot be expected to produce, an increase in shad production.

POLLUTION

Industrial and domestic pollution has been a serious problem in the Hudson River for many years, as a result of unrestricted discharge of raw sewage into the river for two centuries. Until recently very little was done about this situation, and then only in the lower reaches of the river. Complaints concerning the effects of pollution on the fisheries were voiced before the turn of the present century. Marshal McDonald in 1887 mentions that the Hudson fisheries were standing up remarkably well despite the gross pollution of the river by sewage, and the refuse of paper, calico, and other factories in operation along its banks.

In the eleventh annual report of the New York Forest, Fish and Game Commission (1906) there is mention of the serious pollution problem confronting the Commission. It is stated that, "Formerly, shad were caught up to the Troy Dam . . . It would seem as if, year after year, the run of fish was retarded by an invisible line which annually stretched further and further down the river and beyond which the fish would not pass . . . At present, the fish do not seem to run much above Hudson."

The annual report of the Torresdale hatchery (Pennsylvania Dept. Fish. 1914) states that at the Linlithgo hatchery on the Hudson River eggs are hatched in pond water since the Hudson River water is badly polluted.

One of the greatest difficulties in evaluating pollution data arises from the fact that there are no generally accepted standards of water quality which are recognized as constituting a good fish habitat. References dealing with this problem are almost innumerable. As pointed out by the California Water Pollution Control Board (1952), various investigators have been individualistic in their approaches to the problem, and the conditions under which they conducted their experiments varied widely and were seldom standardized. This has led to confusion and a lack of agreement in standards prescribed by different agencies dealing with water-quality criteria.

Listed in table 15 are standards for dissolved oxygen, biochemical oxygen demand (B. O. D.), and coliform-bacteria counts which have been adopted by several State or interstate agencies for water considered as a good fish habitat. While there is no overall agreement, it can be seen that these criteria call for an average for any month for dissolved oxygen of not less than between 6.0 p. p. m. and 6.5 p. p. m. The minimum for any day shall not be less than between 4.0 p. p. m. and 75-percent saturation (7.5 p. p. m. at 60° F.). The standards for these agencies for biochemical oxygen demand state that the average for any month shall not be more than between 1.5 to 2.5 p. p. m., and the maximum for any month shall not be more than between 3.0 to 3.5 p. p. m. Standards for coliform-bacteria counts range from 50 per 100 ml. to a maximum of 2,000 per 100 ml.

A great deal of work on water-quality problems is now in progress, and it is probable that more

TABLE 15.—*Dissolved oxygen, biochemical oxygen demand, and bacteria count standards of several States and agencies for water considered as good fish habitat*

[Data from California Water Pollution Board (1952)]

State or agency	Class	Dissolved oxygen p. p. m.		5-day B. O. D. at 20° C. p. p. m.		Most probable number of coliform bacteria per 100 ml.	
		Average any month not less than—	Minimum any month not less than—	Average any month not over—	Maximum any month not over—	Average any month, not over—	Maximum any sample not over—
Maryland Water Pollution Control Board	A	6.0	5.0	2.5	3.5	2,000	
West Virginia State Water Commission	A	6.5	5.0	2.5	3.5	1,000 or 2,000 in agricultural area.	
New York Dept. of Health, Water Pollution Control Board.	C		Trout waters 5.0; non-trout waters 4.0.				
Interstate Commission on the Potomac River Basin.	B	6.5	5.0	1.5	3.0	50 to 500	1,000.
Interstate Sanitation Commission New York, New Jersey and Connecticut.	A		50-percent saturation (5.0 at 60° C.).				100 in 50 percent of samples during bathing season only.
New England Interstate Water Pollution Control Commission.	C		(5 p. p. m.)				
New Hampshire Water Pollution Commission.	C		5.0				

definite and hence more uniformly acceptable standards based on standardized and controlled experiments will be formulated in the future for various types of waters and various species of fish. The above criteria, however, appear reasonable at present for judging the water quality of the Hudson River.

Very little continuous factual information concerning water quality of the Hudson River is available except for that portion of the river adjacent to New York City. Here, by the late 1800's, sewage disposal had overtaxed the capacity of the surrounding water to assimilate it, and beginning about 1900 the problems of sewage disposal were studied by various State and municipal bodies. In 1909 the Metropolitan Sewage Commission began making systematic dissolved-oxygen measurements and other water-quality determinations during the summer months (when conditions were at their worst) in the various waters surrounding the city, and these have been continued by other agencies until the present time. Dissolved-oxygen determinations were made at 5 stations in the Hudson River between Mount St. Vincent and the Battery. The annual (June through September) average and the minimum determination for the station opposite the Battery, where usually the lowest oxygen sag occurs, are shown in figure 13. These data were furnished by the New York City Department of Public Works. They show a downward trend from 1909 to 1926 and then a continuation of low levels averaging around 37 percent saturation of oxygen. The minimum oxygen saturation found throughout any season has been low since 1912, and since 1919 has averaged only 19 percent.

The dissolved-oxygen values as shown in figure 13 are indicative of gross pollution and are so far below any generally recognized minimum standard for fish life that shad could probably not survive to spawn, or the eggs and young could not survive, in water conditions such as those existing in this part of the river. These values, however, represent conditions during summer months, when low stream flows and high temperatures prevail, which cause fast oxidation of the sewage and subsequent lowering of the dissolved-oxygen content of the water. Fortunately, most of the adult shad migrate upstream to spawn and return to the ocean during April and May, when river discharge is

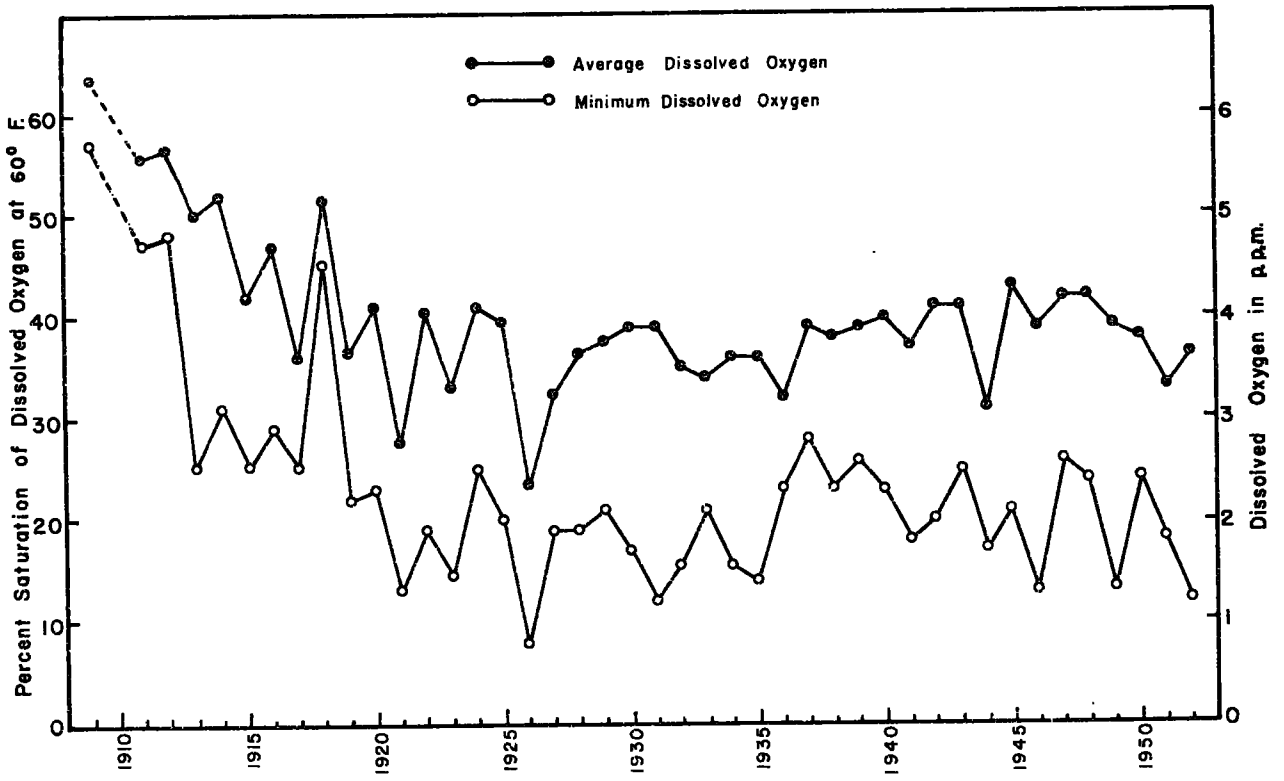

FIGURE 13.—Average dissolved oxygen and minimum dissolved oxygen in the Hudson River at the Battery, from 1909 through 1952.

greater and water temperatures lower than in the summer, and hence oxygen depletion is less severe; consequently, most adult shad probably escape the oxygen sags which have been observed in this area during the summer months. Similarly, the young shad leave the river in October or November, when cold weather again reduces oxygen depletion, and probably most of them do not encounter lethal conditions. While it is probable that during some years mortalities of late-migrating adults and early-migrating young may occur in this section of the river, they do not appear to have affected fluctuations in shad production, or at least there is no correlation between average oxygen content of the water as shown in figure 13 and shad production during the period between 1915 and 1951. Any effect that pollution in this area has had on the runs of shad may well have been uniform each year since about 1919, as there appears to be little overall change in water quality, as measured by oxygen content, since that time.

Since 1937, the Interstate Sanitation Commission, representing the States of New Jersey, New York, and Connecticut, has been working successfully to clean up the marine waters around New York City, Long Island, and the Hudson River to Bear Mountain Bridge. Good progress has been made, despite a setback during the war years, and sewage-treatment plants have been installed at Bear Mountain and in several communities located on Haverstraw Bay. No sewage-treatment plants have yet been constructed to eliminate pollution which New York City dumps into the Hudson River. These are contemplated in the near future, however, and by 1959 practically all pollution in the area under the jurisdiction of the interstate compact should be ended.

In 1951 the Fish and Wildlife Service in cooperation with the New York State Department of Health carried out a water-quality study of the Hudson River during the months of July through October. Weekly samples (except during the week of September 25–30 when a mechanical breakdown occurred) were taken at 5 locations at each of 17 stations located between Troy and Piermont. The stations chosen were those previously designated by the New York Health Department, plus two more below Bear Mountain Bridge. The positions of these stations are shown in table 16. The 5 locations at each station where samples were taken were also those designated by the New York Health Department and are: East shore, west shore, center of channel at 5-foot depth, center of channel at mid-depth, and center of channel 5-feet off bottom. The following determinations were made and recorded, with other data, from each sample: Color, odor, turbidity, temperature, pH, dissolved oxygen, B. O. D., and coliform-bacteria count.

TABLE 16.—*Hudson River sampling stations, 1951*

Station No.	Place	Miles above the Battery, New York City
00	Piermont Pier	25.0
0	Stony Point	39.5
1	Bear Mountain Bridge	48.0
2	Constitution Island (north end)	55.0
3	Breakneck Point, Storm King Mountain	57.5
4	Chelsea, Low Point, Roseton	67.0
5	Milton Railroad Station	74.5
6	North of Crum Elbow (200' north of Light 26)	83.0
7	Cave Point (½ mile south of Esopus Light)	89.0
8	Barrytown (Buoy 34A)	100.5
9	West Camp (Light 37)	111.0
10	Catskill (Light 50)	120.0
11	Four Mile Point (Light 59)	126.5
12	Houghtaling Island (Light 72)	135.5
13	Staat Point (Light 90)	146.0
14	Menands Bridge	157.0
15	Troy Lock	161.0

The average dissolved oxygen of the 5 samples at each station for each week during the course of the study are shown in table 17. Also shown are the monthly averages, season minimums, and dates of their occurrence for each station. As shown in this table, weekly averages of less than 5 p. p. m. of dissolved oxygen occurred at all stations one or more weeks during the sampling, and below 4 p. p. m. at 7 of the 17 stations. Season minimums below 4 p. p. m. were recorded at 10 of the 17 stations. All the minimum values were found during July and August when water temperatures were at their highest. The lowest values were found below the Troy, Rensselaer, and Albany area (stations 11, 12, and 13) and they undoubtedly result from the large amount of raw sewage dumped into the river by those cities. Below this, minimum values were somewhat higher, reaching 4.2 p. p. m. at station 7 located between Kingston and Poughkeepsie. At station 5, which is below Poughkeepsie, another oxygen sag is apparent resulting undoubtedly from raw sewage from that city. Below this, the minimum dissolved oxygen was somewhat better but dropped again at the two lowest stations.

In table 18 are shown the average biochemical oxygen demand (B. O. D.) determinations for the

TABLE 17.—*Dissolved oxygen at 17 stations in the Hudson River, by weeks, July–October 1951*

[Average, in parts per million, of samples from 5 locations at each station]

Week of—	At station No.—																
	00	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
July 2–6	7.0	4.5	5.6	5.6	5.7	5.0	4.2	4.1	4.4	3.8	3.8	3.6	4.1	5.0	6.2	7.0	7.6
July 9–13	7.6	5.8	5.6	6.1	6.1	5.8	4.2	4.3	5.6	6.6	6.5	8.2	7.2	4.5	5.8	7.4	7.6
July 16–20	5.5	4.8	5.0	5.2	5.2	4.3	4.0	4.0	4.8	4.3	4.5	5.4	6.1	5.4	5.6	6.0	6.7
July 23–27	6.1	5.2	4.6	4.5	4.6	4.8	3.8	4.0	4.6	4.2	5.1	6.3	5.5	4.7	4.4	5.8	7.0
Average for month	6.6	5.4	5.2	5.4	5.4	5.0	4.0	4.1	4.8	4.7	5.0	5.9	5.7	4.9	5.5	6.5	7.2
July 30—Aug. 3	4.8	4.2	4.8	5.0	5.1	4.2	3.3	4.1	5.1	5.1	4.3	4.1	4.1	3.3	4.3	6.1	6.8
August 6–10	5.0	5.6	4.8	5.9	6.1	5.5	4.1	4.5	5.3	5.6	5.0	3.9	3.7	2.2	2.6	4.8	7.0
August 13–17	4.5	4.6	5.0	5.7	6.0	5.2	4.2	5.2	6.0	5.7	5.3	3.4	2.9	2.3	1.3	4.3	4.9
August 20–24	4.9	5.4	5.4	5.7	5.8	5.1	4.8	5.4	5.6	4.2	4.7	4.8	4.4	3.0	4.8	6.7	7.7
August 27–31	7.0	5.8	5.0	5.5	6.0	5.2	4.8	5.2	5.8	5.3	5.5	4.8	4.4	3.8	4.2	6.0	6.8
Average for month	5.2	5.1	5.0	5.6	5.8	5.2	4.2	4.9	5.6	5.2	5.0	4.2	3.9	2.9	3.4	5.6	6.6
Sept. 3–7	5.1	5.1	5.1	5.8	5.9	5.9	4.9	4.8	5.3	5.2	4.6	3.6	4.1	4.9	4.9	7.1	8.2
Sept. 10–14	5.1	5.5	5.8	6.3	6.3	5.6	4.6	5.7	6.8	6.5	6.3	6.0	5.4	5.4	5.3	6.4	7.7
Sept. 17–22	6.3	5.8	6.2	6.6	6.6	5.9	5.2	6.3	6.6	7.2	5.5	4.4	4.7	3.2	3.6	5.9	7.0
Average for month	5.5	5.5	5.7	6.2	6.3	5.8	4.9	5.6	6.2	6.3	5.5	4.7	4.7	4.5	4.6	6.5	7.6
Oct. 1–5	6.5	6.4	6.1	6.7	7.1	6.2	5.9	6.2	7.0	7.1	7.1	4.9	4.5	3.8	4.5	7.3	7.9
Oct. 8–12	6.9	7.0	7.0	7.4	7.4	6.7	6.8	7.4	7.8	7.3	5.9	5.1	6.2	7.6	7.9	10.0	10.2
Oct. 15–19	7.5	7.3	7.4	7.7	7.8	7.7	7.6	8.1	8.0	9.0	8.1	8.2	8.6	8.4	8.1	9.7	10.2
Oct. 22–26	6.9	7.4	7.6	8.0	8.3	8.0	7.6	8.0	8.8	9.4	8.9	7.4	6.8	5.9	7.4	9.7	10.2
Average for month	7.0	7.0	7.0	7.4	7.6	7.2	7.0	7.4	7.9	8.2	7.5	6.4	6.5	6.4	7.0	9.2	9.6
Season minimum [1]	3.6 (Aug. 2)	4.0 (Aug. 2)	4.4 (July 24)	4.4 (July 24)	4.4 (July 24)	3.8 (Aug. 1)	3.2 (Aug. 1)	3.8 (July 25, July 31)	4.2 (July 4, July 31)	3.6 (July 3)	3.6 (July 3)	3.4 (July 3, Aug. 15)	2.6 (Aug. 15)	2.0 (Aug. 14)	1.2 (Aug. 14)	4.0 (Aug. 14)	4.2 (Aug. 14)

[1] Date in parentheses.

TABLE 18.—*Biochemical oxygen demand determinations at 17 stations in the Hudson River, by weeks, July–October 1951*

[Average, in parts per million, of determinations for 5 locations at each station]

Week of—	At station No.—																
	00	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
July 2–6	1.4	0.8	1.0	0.6	0.8	0.7									2.1	3.1	3.0
July 9–13	1.0	0.4	0.3	0.6	0.6	0.7			1.3	1.8	2.6	2.8	2.0		2.3	2.3	2.2
July 16–20	0.9	0.4	0.4	0.4	0.6	0.6	0.4	0.7	1.0	1.0	1.3	3.2	1.9	1.6	1.8	1.9	2.0
July 23–27	0.7	0.2	0.0	0.2	0.2	0.6	0.4	0.6	0.9	1.0	1.1	1.6	1.5	1.4	1.7	2.2	2.6
Average for month	1.0	0.4	0.4	0.4	0.5	0.6	0.4	0.6	1.1	1.3	1.7	2.5	1.8	1.5	2.0	2.4	2.4
July 30–Aug. 3	0.9	0.2	0.4	0.4	0.4	0.6	0.2	0.6	0.9	1.0	0.7	1.3	1.3	1.2	1.2	1.5	1.8
Aug. 6–10	0.7	0.7	0.5	0.7	0.8	0.7	0.4	0.4	0.7	0.8	0.8	1.0	1.0	1.2	2.0	3.5	2.8
Aug. 13–17	0.7	0.4	0.4	0.6	0.6	0.5	0.2	0.6	0.9	0.9	0.8	1.3	1.2	1.1	1.0	2.2	3.6
Aug. 20–24	0.5	0.7	0.5	0.5	0.6	0.7	0.3	0.7	0.9	1.0	1.2	1.4	1.3	1.0	2.1	3.4	2.9
Aug. 27–31	2.4	0.9	0.4	0.6	0.9	0.5	0.4	0.6	1.0	0.9	1.1	1.5	1.6		1.7	2.0	2.4
Average for month	1.0	0.6	0.5	0.6	0.7	0.6	0.3	0.6	0.9	0.9	0.9	1.3	1.3	1.1	1.6	2.5	2.7
Sept. 3–7	0.6	0.6	0.4	0.5	0.4	0.6	0.4	0.4	0.6	0.9	0.8	1.2	1.4	1.4	2.0	3.7	3.0
Sept. 10–14	0.6	0.2	0.4	0.4	0.5	0.6	0.6	0.7	1.2	1.0	1.0	1.4	1.4	1.6	2.5	2.9	2.4
Sept. 17–22	0.8	0.6	0.8	0.4	0.3	0.3	0.4	0.8	0.8	1.0	1.0	1.4	1.7	1.3	2.2	3.1	4.0
Average for month	0.7	0.5	0.5	0.4	0.4	0.7	0.5	0.6	0.9	1.0	0.9	1.3	1.5	1.4	2.2	3.2	3.5
Oct. 1–5	0.4	0.5	0.4	0.4	0.4	0.4	0.3	0.5	0.6	0.8	0.9	1.9	1.9	2.0	2.0	3.5	3.4
Oct. 8–12	0.7	0.6	0.4	0.4	0.5	0.5	0.4	0.5	0.7	1.0	1.7	2.0	1.7	2.0	3.7	1.7	1.4
Oct. 15–19	0.6	0.6	0.3	0.5	0.5	0.6	0.8	1.1	1.1	1.7	1.7	1.8	1.8	2.2	3.8	1.8	1.8
Oct. 22–26	0.7	0.5	0.4	0.4	0.5	0.7	0.8	1.1	1.1	1.0	1.7	1.4	1.5	2.1	4.0	4.0	3.4
Average for month	0.6	0.5	0.4	0.4	0.5	0.5	0.6	0.8	0.9	1.4	1.5	1.8	1.7	2.1	3.4	2.8	2.5
Individual sample maximum [1]	5.4 (Aug. 31)	1.4 (Aug. 31, Sept. 18)	3.0 (Sept. 18)	0.9 (Aug. 7)	1.2 (July 5, Aug. 31)	2.0 (July 10)	1.0 (Oct. 18, Oct. 23)	1.6 (Oct. 17)	1.8 (Sept. 12)	2.0 (July 11, Oct. 24)	2.8 (July 12)	3.0 (July 12)	2.4 (July 12)	2.2 (Oct. 2, Oct. 11, Oct. 16, Oct. 25)	4.2 (Oct. 25)	4.4 (Sept. 7)	4.2 (Sept. 22, Oct. 26)

[1] Date in parentheses.

5 locations at each of the 17 stations for each week of the water-quality study. In addition, the monthly averages and maximum B. O. D.'s for any individual sample are shown with the dates of occurrence. Individual B. O. D. determinations higher than those considered satisfactory for a good fish habitat (3.0 to 3.5 p. p. m.) were found at stations 00, 13, 14, and 15, where the determinations were 5.4, 4.2, 4.4, and 4.2 p. p. m., respectively. Monthly averages higher than those considered tolerable for a good fish habitat by the Interstate Commission on the Potomac River (1.5) were found at stations 9, 10, 11, 13, 14, and 15 in July; at stations 14 and 15 in August; at stations 13, 14, and 15 in September; and at stations 10 through 15 in October. Using the higher value of 2.5 p. p. m. as listed by Maryland and Virginia, averages considered too high were found at station 15 in August, stations 14 and 15 in September, and stations 13 and 14 in October.

Table 19 gives the average coliform-bacteria counts of the 5 samples taken at each station each week for the 17 stations. Also given are the monthly averages for each station and the maximum individual bacteria counts for each station with the dates of occurrence. The highest bacteria count considered as a good fish habitat from the criteria examined and shown in table 15 was that of Maryland which specifies a monthly average of not more than 2,000 coliform bacteria per 100 ml. The largest maximum individual count allowable is 1,000 as given by the Interstate Commission on the Potomac River Basin. Using these as a basis for examining the 1951 Hudson River bacteria counts shown in table 19, it can be seen from the maximum individual samples that every station sampled in the Hudson River had at some time during the season a coliform-bacteria count above that considered as a good fish habitat. Furthermore, every station, with the exception of stations 6, 7, 8, and 9, had above-allowable individual average bacteria counts every month throughout the season. The highest monthly average bacteria counts were found at stations 10 through 15 in the upper part of the river area studied, but individual determinations just as large were found at the two lowest stations.

Based on the limits set up in table 15 the pollution records indicate that the entire area of the Hudson River studied cannot be considered a good habitat for fishes. The section most polluted is that between the Albany-Troy-Schenectady metropolitan area and Hudson, N. Y. (stations 10–15). This section of the river at one time supported a considerable shad fishery (New York Fish. Comm., 1890) and probably was also a good spawning area. In recent years few if any shad have been caught above Hudson, and sampling for shad eggs by the New York Conservation Department (1943) in 1940, 1941, and 1942, and by our staff in 1951 showed that little if any of this area is now used by shad for spawning purposes.

The effect that pollution has had on shad production in the Hudson River is difficult to ascertain since no records comparable to those just presented are available for previous years. The New York Department of Health in 1949 made examinations of water samples from the same 5 locations at stations 1 through 15 during the week of August 22 to 26 and again during the week of November 14 to 18 (unpublished records). The minimum oxygen determinations during the week in August were lower than the season minimums for the 1951 survey at stations 13, 14, and 15, while at the other stations the minimums were somewhat higher than for those in 1951. Biochemical oxygen demand determinations and bacteria counts showed pollution conditions similar to those in 1951. Their survey made from November 14 to 18 showed conditions similar to those shown for the week of October 22 to 26 in 1951.

The only other water-quality survey covering this part of the Hudson River was that done by the New York Conservation Department in 1934 and 1936 (Faigenbaum, 1935, 1937) in connection with the Department's biological survey of the Mohawk-Hudson watershed in 1934 and the biological survey of the lower Hudson River in 1936. The water-quality studies on the Hudson River in 1934 covered that section of the river between the Troy Dam and Hudson from August 28 to September 6. The 1936 survey was carried out between Hudson and Yonkers from June 18 to September 5.

In this survey, samples were usually taken only once during the season at each location. The work was begun in the upper areas and was gradually shifted downstream as the season progressed; consequently, no direct comparisons between the 1934–36 survey and our 1951 survey are possible. In addition, the surface samples in

TABLE 19.—*Average of most probable number of coliform bacteria at 17 stations in the Hudson River, by weeks, July–October 1951*

[Average, in thousands per 100 ml., of counts at 5 locations at each station]

Week of—	At station No. —																
	00	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
July 2–6	3.5	2.6	1.7	2.7	2.9	1.5	0.9	0.2	0.7	0.4	0.6	2.1	3.8	2.6	12.4	32.3	39.2
July 9–13	0.4	1.4	0.5	4.4	2.8	1.3	3.1	0.8	0.4	0.5	1.0	1.7	1.4	6.0	50.0	22.5	16.9
July 16–20	6.3	3.9	0.7	1.3	4.1	1.3	1.4	3.8	0.4	0.4	0.9	5.0	5.4	1.7	18.1	18.7	11.4
July 23–27	3.0	1.0	0.6	2.9	2.6	2.2	2.4	1.2	0.3	0.8	1.0	5.1	8.0	3.5	54.4	32.8	23.8
Average for month	3.3	2.2	0.9	2.8	3.1	1.6	2.0	1.5	0.4	0.5	0.9	3.5	4.6	3.4	23.7	26.6	22.8
July 30–Aug. 3	0.7	1.3	0.3	1.1	0.9	2.3	4.1	0.5	0.3	0.2	1.4	25.6	2.7	3.7	26.2	32.8	18.1
Aug. 6–10	2.4	1.6	0.4	0.8	3.6	1.2	1.1	0.7	0.6	0.2	0.3	3.1	5.7	4.1	65.7	88.8	46.1
Aug. 13–17	14.0	35.8	0.9	3.4	3.7	1.5	8.4	0.4	0.4	0.4	0.8	2.9	5.6	1.9	20.2	13.8	24.9
Aug. 20–24	1.8	4.5	1.5	4.8	3.1	3.7	2.4	1.1	1.3	0.3	2.0	28.1	2.6	4.6	14.6	80.0	16.3
Aug. 27–31	55.3	13.4	1.7	8.6	5.1	1.6	12.5	0.8	0.3	0.6	0.4	2.1	13.6	8.2	31.1	31.0	43.8
Average for month	14.8	4.9	1.0	3.6	3.3	2.1	5.7	0.6	0.6	0.3	1.0	12.4	6.0	4.5	31.6	49.3	29.8
Sept. 3–7	2.6	192.5	2.3	25.4	4.2	9.7	1.9	0.5	0.3	0.2	0.7	6.6	2.7	5.1	67.2	76.0	10.2
Sept. 10–14	3.8	2.1	0.5	12.9	1.6	10.0	3.1	0.4	0.5	0.1	0.3	3.7	4.3	4.5	93.2	91.4	26.6
Sept. 17–22	0.9	3.0	0.8	2.3	2.3	3.7	3.7	0.2	0.4	0.1	0.6	13.5	30.4	5.2	3.5	58.8	41.7
Average for month	2.4	81.2	1.2	5.9	2.7	7.8	2.9	0.4	0.4	0.1	0.5	8.0	12.5	4.9	54.6	75.4	26.2
Oct. 1–5	0.6	1.4	1.7	2.4	1.7	0.6	2.7	6.9	0.2	1.0	0.4	4.1	11.4	4.9	80.9	31.0	79.8
Oct. 8–12	9.3	4.3	0.9	4.3	15.0	0.9	15.0	4.3	0.9	2.3	2.3	24.0	24.0	24.0	24.0	110.0	24.0
Oct. 15–19	9.5	2.3	4.3	6.4	9.3	4.3	4.3	4.3	0.4	2.3	4.3	4.6	4.6	110.0	110.0	110.0	110.0
Oct. 22–26	24.0	4.3	3.9	2.3	4.3	2.3	2.3	0.8	0.2	0.4	4.3	46.0	24.0	24.0	158.0	110.0	46.0
Average for month	10.8	3.1	2.7	3.8	7.6	4.1	6.1	4.1	0.5	1.5	2.8	30.0	26.4	40.7	95.2	90.2	65.0
Individual sample maximum [1]	[2] 240.0 (Aug. 31)	[2] 240.0 (Sept. 4)	4.3 (Sept. 5, Oct. 4, Oct. 18)	24.0 (Aug. 31)	15.0 (Oct. 9)	46.0 (Sept. 5)	24.0 (Aug. 16)	12.0 (Oct. 3)	4.3 (Aug. 23)	4.3 (Oct. 3)	4.3 (Aug. 23, Aug. 28, Oct. 17, Oct. 24)	110.0 (July 31, Aug. 23)	110.0 (Sept. 20)	110.0 (Oct. 16)	[2] 240.0 (Aug. 10, Oct. 1, Oct. 12, Oct. 25)	[2] 240.0 (Aug. 10, Sept. 17)	[2] 240.0 (Oct. 1)

[1] Date in parentheses.
[2] These samples were recorded as "greater than 240,000." The figure 240,000 was used in calculating averages.

the 1934–36 survey were taken just below the surface, and the bottom samples just off the bottom, while in the 1951 survey samples were taken 5 feet below the surface and 5 feet above the bottom.

No B. O. D. determinations or bacteria counts were made in the 1934–36 surveys; dissolved-oxygen determinations were made, however, and these are shown by the solid line in figure 14 for all mid-depth determinations made during the 1934–36 survey. These are given here because they are more comparable with the mid-depth samples taken in 1951 than are the top and bottom samples. Included in figure 14 are the season mid-depth minimum dissolved-oxygen determinations from the 1951 study for comparison. Both of these oxygen profiles show that gross pollution occurs in the area below Albany and that at least partial oxygen recovery takes place by the time the water reaches the city of Hudson. Both profiles indicate an increase in pollution around Poughkeepsie. The lower values shown for 1951 cannot be definitely interpreted to mean that pollution was worse in 1951 than during the 1934–36 survey, since the 1951 data are the mid-depth minimums of the season while the 1934–36 data are usually for one determination only at each location during the season. It is possible, however, that industrial pollution was somewhat less during the 1936 survey than in 1951, for the New York census of manufacturers for 1929, 1939, and 1947 (U. S. Bureau of the Census, 1929, 1939, 1947) shows that, based on the number of wage earners, industrial activity was greatly curtailed after 1929, undoubtedly as a result of the depression, and then increased again to even greater activity by 1947.

One source of serious pollution that none of the water-quality studies have taken into account is oil dumped in the river. As pointed out by Nelson (1925), "Oil is, gallon for gallon as thrown out, the most destructive to aquatic life of all foreign substances now entering our coastal waters." During our studies on the Hudson in 1950 and 1951, large quantities of oil were observed in several areas in the river, and traces of oil were in evidence almost everywhere. The boats and sam-

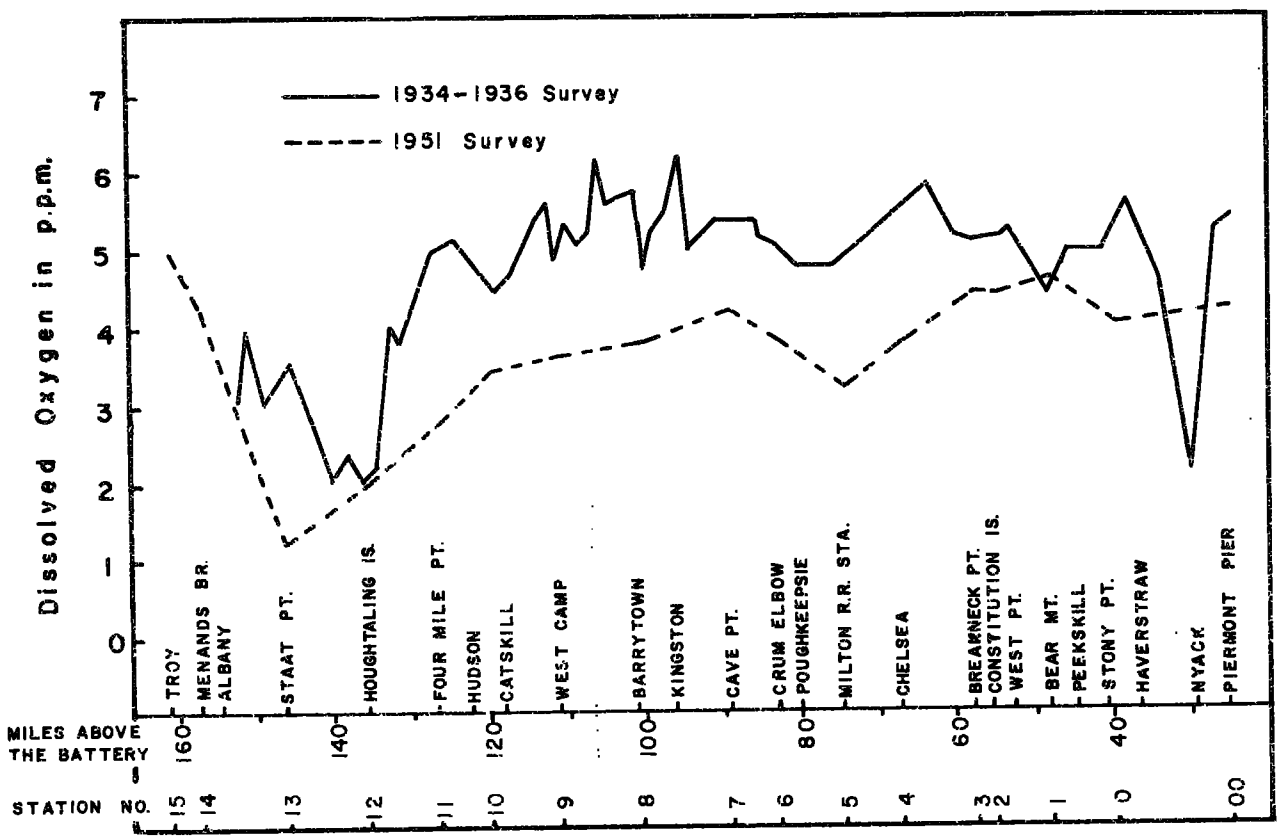

FIGURE 14.—Mid-depth minimum dissolved-oxygen determinations in 1951 and all mid-depth dissolved-oxygen determinations in 1934–36 at various stations between Troy and Piermont.

pling equipment became covered with it after short use in many areas, though not too evident visually. From observations made, it was apparent that some of this oil entered the water through spillage while oil tankers unloaded at shore installations, but most of it apparently came from tankers and oil barges illegally pumping their bilges and tanks into the river on the downstream run after delivering products, such as gasoline, lumber, fuel oil, and kerosene to upriver ports. In recent years the greatest percentage of freight transported on the Hudson River has been that of oil products, and the total tonnage hauled has increased tremendously. Pollution from this source, according to fishermen, sportsmen, and others, also has greatly increased during the past few years.

As pointed out by Chipman and Galtsoff (1949), the toxicity of oil in water has been demonstrated many times experimentally, using fishes and marine invertebrates, and these authors present data showing the toxicity of various oils to several forms of marine life. The toxic effect of oil appears to result from a substance or substances leached from the oil by water. Since no measure of this pollutant is available, it is not possible at this time to estimate its effect on the shad runs.

With the increase in oil pollution there have come many complaints about the flavor of shad from the Hudson River. Organoleptic tests by our field staff disclosed that these complaints were well founded. In 18 out of 20 shad tested there was a definite off flavor which could best be described as tasting like gasoline or kerosene. In some fish this was barely discernible, but in others it was strong, and in several the smell of kerosene was detected while cooking the fish. Apparently the off flavor of the resident fishes is worse than that of the anadromous shad, for Hudson River carp, catfish, perch, and some others are no longer acceptable on New York City markets.[2] Some fishermen transport Hudson River carp to freshwater ponds where they are artificially fed until the off flavor disappears before marketing. Obviously, if the Hudson River is to produce edible fish in quantity, regulations concerning oil pollution should be rigidly enforced, and failure to do so may not only curtail the run, but make the fish unsalable.

[2] Personal communication from Henry Bearse, Market News Service, U. S. Fish and Wildlife Service, New York City.

From the data available, it can be concluded that parts of the Hudson River used, or formerly used, by shad are grossly polluted and that all parts of the river used by shad are polluted to such an extent as to be considered a poor fish habitat. The effect of pollution on shad production cannot be determined because records are not available to show changes in pollution. It is known, however, that pollution in the river below Troy Dam has been severe enough to cause comment before the beginning of the present century and even fish kills are noted in recent years (New York Conservation Dept. 1942). It is possible, therefore, that variations in predicted and calculated shad production as shown in table 12 have occurred because of different degrees of pollution resulting from the pollution load itself, variations in river runoff, water temperatures, wind, and rain. It is probably safe to conclude, although factual proof is lacking, that productivity and certainly quality of the shad would increase if pollution were diminished in this river.

CATCHES OUTSIDE THE RIVER

Returns of tagged shad from our enumeration work in 1950 and 1951 after termination of the fishing season in the river, were received from Long Island, the coast of Massachusetts, and Maine. The spring after tagging, tags were returned from North Carolina, Virginia, Maryland, Delaware, and New Jersey. These were comparatively few, but indicate that Hudson River shad during their migrations may be captured at least from Maine to North Carolina. The greatest percentage of outside returns came from the fishery along the New Jersey coast in the spring.

The results of unpublished tagging experiments (Hollis, Fish and Wildlife Service) conducted along the New Jersey coast and Staten Island, indicate that a large proportion of the shad caught in this region as well as some caught off Long Island are bound for the Hudson River, while lesser numbers are headed for the Connecticut River, Chesapeake Bay, and elsewhere. Table 20 shows the pound-net catches from these areas. The shad catches shown for Long Island include only the unspawned fish caught before June. The spawned-out fish caught in June and July have no market value as edible fish and are not recorded. The volume of shad caught in these areas is large enough to noticeably affect the catches in the

Hudson River should most or a large proportion of them be Hudson River fish (table 20). Fluctuations in these catches, as well as changes in the percentage of Hudson River shad in them, and catches of Hudson shad made elsewhere in waters outside the river, may well have produced a large part of the differences between calculated and predicted populations as shown in table 12. A study of the outside catches, particularly those made along the coast of New Jersey, to determine the composition or racial origin of the fish will be necessary if a more precise measurement is desired of the shad production of the Hudson River than was obtained in this study.

TABLE 20.—*Shad catches by New Jersey pound nets, Staten Island pound nets, and pound nets off Long Island from Jones Beach to Bellport Coast Guard Station, Great South Bay, Gardiner Bay, and Peconic Bay*

[In pounds. Statistics for Staten Island and Long Island from Bureau of Marine Fisheries, New York Conservation Department; those for New Jersey from New Jersey Department of Fish and Game]

Year	New Jersey Coast and Raritan Bay	Staten Island	Long Island	Total
1946	499, 877	175, 555	119, 306	794, 738
1947	303, 081	253, 168	36, 009	592, 258
1948	572, 521	223, 637	47, 659	843, 817
1949	411, 314	94, 556	54, 972	560, 842
1950	480, 435	204, 631	8, 930	693, 996
1951	150, 617	36, 200	12, 534	199, 351

CYCLES OF ABUNDANCE

It has been suggested (Burkenroad 1946) that cyclical fluctuations in abundance of Hudson River shad have occurred which may not be associated with human activities or random in period. In an attempt to determine whether definite natural cycles of abundance have occurred, we have examined the population curve in figure 5 and the deviations from regression in table 12. Clearly, no periodic cycles of abundance are reflected in the population curve, and the deviations from regression appear to be randomly distributed. Since it has already been shown that about 85 percent of the fluctuation in size of runs since 1920 was a function of fishing effort and related spawning escapement, cyclical changes in population size, if any, must have been small and would be entirely obscured by changes in fishing effort and spawning escapements.

Since natural cycles of abundance may have occurred over a longer period than the past 37 years, we have attempted to obtain data for the years previous to 1915. Catch data are available for some years as far back as 1880, but no comparable effort data are available previous to 1915 except for 1896. Therefore, we are unable to construct a true population curve covering a greater period of time because the size of the catch depends on fishing effort as well as on the actual size of the population. As a result, catch data alone are often misleading and the formulation of cyclic theories therefrom is, to a considerable degree, pure speculation. For lack of better information, however, and because we wish to obtain some indication of the size of the shad runs for a long period of time in which natural cycles might be more evident, we shall use catch records and adjective estimates of the size of the catches available for some years as far back as 1834. These have been obtained from several sources (New York Fish Comm., 1869–96; New York Forest, Fish and Game Comm., 1895–1910; U. S. Comm. Fish and Fisheries, 1884–1905; U. S. Bur. Fish., 1907, 1921–41; U. S. Bur. of the Census, 1911; and Stevenson 1899). Devoe (quoted in Burkenroad 1946) noted the condition of the Hudson shad fishery as early as 1824, but his remarks pertain only to the fyke-net fishery in or near New York Harbor and not to the river as a whole.

Adjective estimates are a poor indication of the condition of the fishery, since a slight decline after several good years is usually referred to as a "poor" year, whereas a catch of the same magnitude after a series of worse years may be referred to as "average" or "good." Newspaper articles in 1948, for instance, reported that the Hudson shad run was the poorest in 50 years, and in 1951 the run was reported as the poorest on record. Neither of these statements is in agreement with the catch records (fig. 2). We have therefore used only those adjective estimates from publications having a particular interest in the Hudson River shad fishery, and these estimates we do not consider as irrefutable. Another source of error is the fact that for some of the early years the catch figures attributed to the Hudson include catches in New York Bay, or sometimes for the whole State of New York, whereas for other years only the catches actually made in the river are included. These errors are probably not great enough to obscure the general magnitude of the catches since almost all the shad caught in New York are from the Hudson River. The data collected are presented

in figure 15. Where actual figures for the size of the catch were available they were plotted according to the right-hand scale in pounds caught. When numbers rather than pounds of fish were given they were roughly converted to pounds by a factor of three. Where adjective estimates only were available they were plotted according to the adjective scale shown on the left of figure 15.

Two definite peaks of abundance are approximately centered in the years 1887 and 1942, which are 55 years apart. If the adjective estimate of 1855 is disregarded and it is assumed that the run was good for a period around 1832, it would appear that there might be evidence of a 55-year cycle of abundance of shad on the Hudson. The records indicate, however, that the run of 1855 was good. Furthermore, the records show that the runs were, in general, good between 1877 and 1901. The runs of 1881, 1884, and 1892, listed as "poor" during this period, were in all probability better than is shown in figure 15, since the reference "poor" probably inferred that the runs were poor compared with the years immediately previous which were good. In any event, there were a series of fairly good runs from 1877 through 1901, or for a period of 25 years. No records are available for a similar period around 1832, but the last period of abundance from 1936 to 1949 is only for 14 years. This is not what would be expected, if the runs were fluctuating at a regular 55-year natural cycle of abundance.

Since there is no reason for discarding the indicated "good" catch of 1855, there is no evidence from the available records to indicate that the Hudson River shad runs are following any natural cycle of abundance, or that cyclic fluctuations produce the deviations from regression as shown in table 11.

SUMMARY AND CONCLUSIONS

The shad fishery of the Hudson River was at a low level of production during the early years of this century until 1934. Then, unlike that of most shad streams along the Atlantic coast, its production increased tremendously, and for the next 12 years the catches almost equaled those of the best years on record. After 1945, a decline in catches occurred, and at present the catch is nearing the previous low level of production.

The Fish and Wildlife Service, acting as the primary research agency of the Atlantic States Marine Fisheries Commission, began a study of the Hudson shad fishery in 1950 as part of an investigation of the Atlantic-coast shad to seek the underlying causes of the decline, to determine

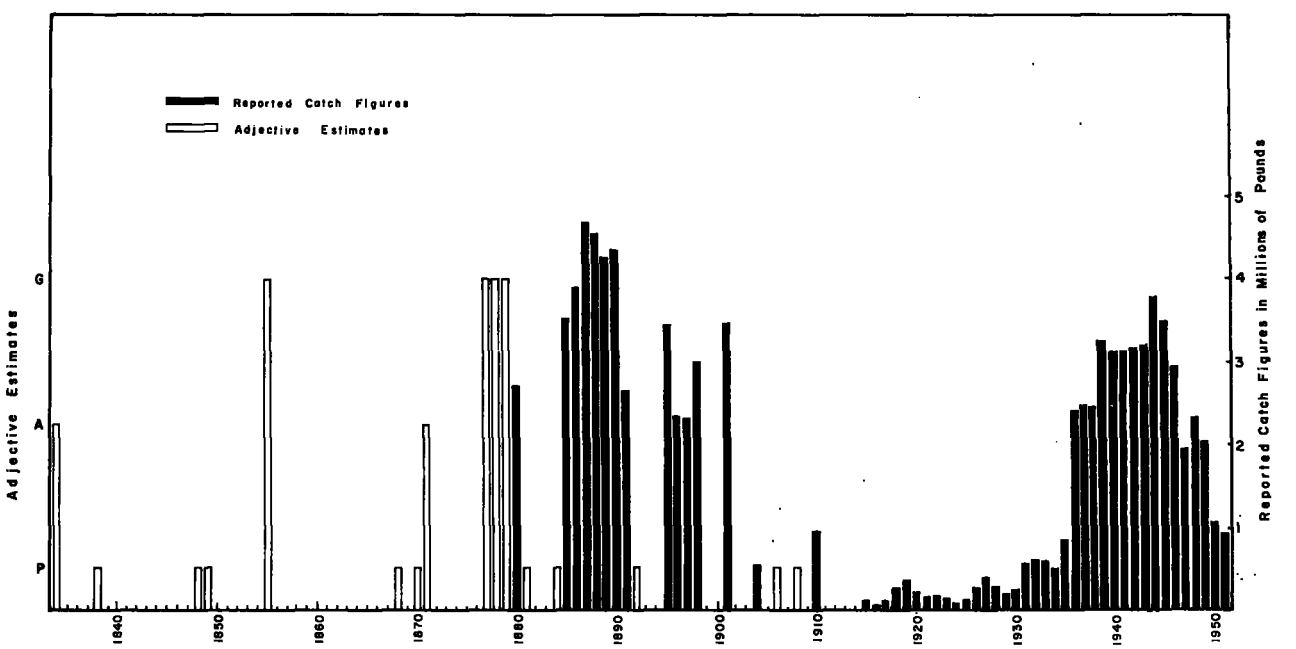

FIGURE 15.—Hudson River shad catches and adjective estimates for some years between 1834 and 1951. *G* indicates good catch, *A*, average catch, and *P*, poor catch.

conditions favoring recovery, and to provide basic information for proper scientific management of the fishery for obtaining a maximum sustained yield.

Catch statistics for the Hudson River shad fishery were compiled from all available sources. Only the drift and stake gill net fishermen in New York and the stake gill net fishermen in New Jersey fish consistently throughout the fishing season or through the peak of the season. The study of the Hudson shad fishery was therefore limited to these gears, and since effort data were available only for the nets fishing under special gill-net licenses in New York, only these were used for the New York fishery. Since these types of gear usually catch more than 95 percent of the shad caught in the Hudson, little validity is lost by the restriction. Catch and effort data were obtained for each year from 1915 through 1951. The total shad populations entering the river in 1950 and 1951 were enumerated by tagging experiments. Using the method developed by Fredin, the shad population and escapement for each year back to 1915 were calculated from the catch and effort data.

According to scale readings from a sample of the catch of 1950 and 1951, Hudson River shad spawn for the first time predominantly at 4 and 5 years of age. Of the shad caught, 51 percent had spawned previously; the ages of those caught were preponderantly 4, 5, and 6 years. Therefore, since the catch of any year depends on the progeny of the shad that spawn 4 and 5 years earlier and the fish that escape the fishery the year previous to any year's catch, the effect these have on the run of any year was evaluated by means of a multiple-regression analysis. This disclosed that approximately 85 percent of the fluctuation in the size of runs each year can be accounted for by changes in the escapement 5, 4, and 1 year earlier than the year of individual runs.

By using the regression equation, populations predicted from the escapements 5, 4, and 1 year earlier were calculated. The differences between these predicted populations and the actual populations calculated from catch and effort data illustrated the effect of factors other than escapement on the populations.

Several factors which have been blamed for the decline in shad production have been examined. No correlation was found between stream flows, water temperatures, channel improvements, ship traffic, hatchery operations and the production of shad.

From the available data there was no evidence that the shad runs fluctuated in natural cycles of abundance.

Pollution of the Hudson River is a serious problem and may be an important factor in shad production, but there are no records available to show changes in pollution on the spawning and rearing grounds so that cause-and-effect relations can be shown, if they exist.

Limited tagging studies have indicated that Hudson River shad are caught outside the river from Maine to North Carolina, but are taken in large numbers only along the New Jersey coast, and off Staten and Long Islands. A study of these fisheries is necessary to determine what percentage of the catch is Hudson River shad, if more precise data on Hudson River shad production is desired than has been presented here.

This study has shown that within the limits of the populations studied, the largest factor in the fluctuations of shad in the Hudson River is that of the number of shad escaping the commercial fishery to spawn. While pollution and catches outside the river may have an important effect on this fishery, on the average about 85 percent of the variations in the size of the run each year is dependent on the size of the escapement 5, 4, and 1 year earlier. By using the methods outlined in this paper it is possible to predict the size of the shad run one year in advance within desired confidence limits. By controlling the fishing effort with days closed to fishing, as has previously been done, the desired number of shad can be allowed to escape so that the size of future runs can be regulated to produce maximum sustained yields of shad.

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LIMNOLOGICAL EFFECTS OF FERTILIZING BARE LAKE, ALASKA

By PHILIP R. NELSON and W. T. EDMONDSON

FISHERY BULLETIN 102

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Bare Lake, an unstratified lake on Kodiak Island (Alaska), was fertilized with commercial inorganic fertilizers during 4 consecutive years. The rate of photosynthesis in 10-day periods following fertilizations increased by factors of from 2.5 to 7 as compared with 10-day periods before fertilization. The efficiency of utilization of sunlight by the phytoplankton was increased by fertilization. Following fertilization the phytoplankton population increased greatly, the water transparency decreased, and the pH increased. There is evidence that the egg production of some rotifers was accelerated. No progressive increase in the population of crustaceans occurred during the years of fertilization.

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LIMNOLOGICAL EFFECTS OF FERTILIZING BARE LAKE, ALASKA

By PHILIP R. NELSON and W. T. EDMONDSON,[1] *Fishery Research Biologists*

Karluk Lake on Kodiak Island is one of the world's most important red salmon systems. In the early years of the fishery (1888–95) the annual catch alone averaged 3 million red salmon. Since then, a continuous decline in the magnitude of the runs has occurred; in fact, during the period 1944–53 the average yearly run (catch plus escapement into the lake) has amounted to about 1,030,000 fish, just 34 percent of the catch in the early years.

Various explanations of the decline in population may be offered. It might be supposed for instance, that changes at sea may be reducing survival there. Nevertheless, there are good reasons for thinking that the cause of the decline is in the fresh-water phase of the life cycle. A reasonable hypothesis may be stated as follows: with large runs, great quantities of nitrogen, phosphorus, and other important elements were liberated into the lakes when the spawned-out salmon died and decayed. These nutrients were used by phytoplankton, which were fed on by the organisms eaten by young salmon. With intensive fishing, the supply of nutrients to the phytoplankton was greatly reduced, resulting indirectly in lowered production of food for the young fish during their fresh-water phase. The decrease in food supply is supposed to have resulted in increased mortality of salmon either before migrating, or at sea before returning. In the latter case, a decrease in food would probably mean that the migrants going to sea would be smaller, which would result in a higher ocean mortality. Such has been reported by Barnaby (1944), "A greater return, or survival, was found among the older and larger 4-year migrants than among the 3-year migrants." The reasons for developing this hypothesis may now be stated.

The juvenile red salmon spend from a few months to 4 years in the lake before migrating to the sea. During the fresh-water phase of their life history the greatest mortality occurs. Barnaby (1944, p. 294) states, "The mortality of Karluk River red salmon during the fresh-water stage of their life history is usually over 99 percent." While this may be greater than in most areas, it is clear that relatively small changes in mortality may have relatively large effects on survival.

At Karluk Lake the carcasses of spawned-out salmon can furnish a large amount of the phosphorus and nitrogen requirements of the phytoplankton. For example, during 4 years measurements were made of the phosphate at the mouths of tributary streams in the period when the salmon were decomposing in the streams, and on the same streams the phosphate content was determined above the salmon spawning areas, or at the stream outlets prior to the entrance of the fish. Results from this work show almost a fourfold increase (from 0.008 milligram/liter to 0.029 mgm./l.) in phosphate in the stream water during the spawning period of 2 to 3 months. This is a partial figure as it has been found that about one-third of the fish decompose in the stream water while the rest are either removed by animals and birds or washed into the lake before decomposing. Furthermore, it is estimated that 25 percent of the fish in the escapement, the group escaping the fishery and passing into the lake, spawn in the lake and decompose there.

An analysis of the mineral content of canned red salmon (*Oncorhynchus nerka* Walbaum), by Nilson and Coulson (1939), shows phosphorus to comprise 0.3364 percent of the wet weight. Shostrom, Clough, and Clark (1924) found that bone free samples of Karluk River red salmon ran 21.6 percent protein material (3.5 percent nitrogen).

[1] W. T. Edmondson, Department of Zoology, University of Washington, Seattle, Wash.

On the basis of these figures, the decomposition in Karluk Lake of a million spawned red salmon of approximately 4 pounds (1.8 kg.) average weight, approximately 6.7 tons (6,100 kg.) of phosphorus and 70 tons (63,500 kg.) of nitrogen would be liberated. To duplicate this amount in commercial fertilizers would require 37 tons (33,400 kg.) of phosphate at a cost of about $3,000, and nearly 420 tons (381,000 kg.) of sodium nitrate at a cost of nearly $25,000.

Although the size of escapements entering Karluk Lake in the early years is unknown, it may be assumed on the basis of the catch at that time, that prior to fishing, annual runs exceeded 3 million red salmon. In recent years, escapements of 700,000 fish annually account for less than one-quarter of the nutrients formerly supplied.

If this hypothesis states the true explanation for the decline of the salmon population, it can be tested by fertilizing a lake to bring the rate of supply of nutrients to the phytoplankton up to the level probably attained in prefishing years. It should be emphasized that it is not necessary to consider the economics of the conversion of fertilizer into fish flesh. Most growing is done at sea. What is required is merely to fertilize to such an extent that survival is increased significantly.

Although the Karluk fishery is the chief one with which we are concerned, Karluk Lake is so large (total area approximately 14½ square miles) that it appeared desirable to experiment on a small lake where the costs would not be excessive and the results could be accurately assessed. This work should give some indication of the feasibility of fertilizing elsewhere in large lakes.

In 1949, aerial and ground surveys were conducted to find a suitable small lake. Bare Lake, on the southwestern end of Kodiak Island about 15 miles from Karluk Lake, most nearly fulfilled the requirements. From 1950 to 1954 Bare Lake was treated on 7 different occasions with commercial nitrate and phosphate fertilizers.

Primarily, this investigation was designed to determine whether the addition of nutrients would increase the survival of the lake-resident red salmon prior to migration. Although there is evidence of an increase in the size of seaward migrants since fertilization, insufficient data make an analysis inconclusive at this time; a report on this aspect of the work will be made at a later date. The purpose of the present paper is to describe the immediate effects of fertilization on the plankton organisms which are important in the food chain leading to the fish. The bottom organisms, although important, are not treated in this paper.

We thank the men of the United Fishermen of Alaska at Kodiak for their interest and financial help in the work at Bare Lake. We are grateful to the following men for their work in enumerating and identifying plankton: Albert C. Jones, Jr., Robert J. Simon, Melvin R. Greenwood, and Carl E. Abegglen. Field workers who contributed materially in the collection of the data are Carl E. Abegglen, Robert C. Davison, Charles J. Hunter, Carl R. Schroeder, Alfred J. Schroeder, Ralph L. Swan, Robert T. Heg, and Paul H. Hatch. Dr. Phil E. Church of the University of Washington Department of Meteorology, supplied data used in calibrating the light meter. We are grateful to G. W. Whetstone and staff of the Water Resources Division, Geological Survey, at Palmer, Alaska, for making the analysis in table 3.

DESCRIPTION OF BARE LAKE

Bare Lake lies in latitude 57° 11′ N. and longitude 154° 19′ W. It occupies an oval-shaped basin, rather regular in outline (fig. 1). The main axis of the lake lies in a northwest direction and its maximum length is 1,222 meters (4,010 ft.); the maximum width is 495 meters (1,620 ft). The lake is approximately 49 hectares (120 acres) in area, and has a maximum depth of 7.5 meters, mean depth 4.0 meters. Bare Lake can be reached only by air at present.

The lake lies at an elevation of about 380 feet and is surrounded by mountains which rise to a height of more than 2,000 feet. The outlet, flowing from the north end of the lake, is a small stream with a mean discharge of about 6 cubic feet a second (170 l./sec.), which flows into Red River at a point 5 miles distant from the outlet. The lake is fed by one small inlet stream and several small springs.

Species of fish present, in decreasing order of abundance, are the threespine stickleback (*Gasterosteus aculeatus microcephalus* Girard), red salmon juveniles (*Oncorhynchus nerka* Walbaum), dolly varden trout (*Salvelinus malma*

Walbaum), coho salmon juveniles (*Oncorhynchus kisutch* Walbaum), bullhead (*Cottus aleuticus* Gilbert), steelhead trout (*Salmo gairdnerii gairdnerii* Richardson), and king salmon juveniles (*Oncorhynchus tschawytscha* Walbaum). Aquatic vegetation is rather sparse in the lake; water moss, *Fontinalis*, quill wort, *Isoëtes*, and water buttercup, *Ranunculus*, comprise the dominant forms.

METHODS AND EQUIPMENT

During the summers at Bare Lake, analyses of the water were made at the station designated in figure 1. A frame raft was anchored each year at the station to mark the location and from which to suspend bottles for photosynthesis determinations. Water samples were collected with a 3-liter Kemmerer water bottle. Each sample day, water was taken from the surface and from 3- and 6-meter depths.

Dissolved oxygen measurements were made by the Winkler method (American Public Health Association 1946) after tests for the presence of interfering substances proved to be negative.

Measurements of the rate of photosynthesis were made at the surface and at 3- and 6-meter depths. The method, which is becoming a common limnological procedure, was originally described by Gaarder and Gran (1927). These measurements were made by filling pairs of clear glass bottles of 250-ml. capacity with water from each depth. One bottle from each pair was covered with several layers of black cloth and the pairs of bottles were suspended from the raft at the depths from which the water in each was taken. The dissolved oxygen at each depth was measured. After four days the bottles were retrieved and the oxygen content in the light and dark bottles determined. The increase of oxygen in the light bottle (net photosynthesis) is a measure of the oxygen produced by photosynthesis less the amount consumed in respiration, which is measured by the decrease of oxygen in the dark bottle. The total amount produced for the period of exposure (gross photosynthesis) is found by adding the increase of oxygen in the light bottle to the decrease in the dark bottle, or more simply by subtracting the concentration in the dark bottle from that in the light bottle. The measurements are converted to rates by dividing by the time of exposure and are expressed in milligrams per liter of oxygen per day. To permit comparison between our figures and data from other lakes, the volumetric rates at three depths were averaged, each being weighted according to the amount of water at the depth represented, and the averages were converted to a unit area basis by determining the volume of water under 1 square centimeter of lake surface to the mean depth of the lake (4.0 meters).

Certain limitations of the method should be borne in mind. The rate of decrease of oxygen in the dark bottles is a measure of the respiration of the entire biota including the algae. The rate of increase of oxygen in the light bottle therefore is not a true measure of the net photosynthesis of the phytoplankton since there is non-algal as well as algal respiration in the light bottle. However, the rate of increase in the light bottle can be regarded as the net photosynthesis of the entire biota, and is a measure of the momentary balance between the producers and the consumers. Thus when the heterotrophic population becomes too large, oxygen may decrease in the light bottle even with adequate illumination, although it will decrease in the dark bottle faster. The difference is still a measure of algal photosynthesis.

Unfortunately, the rapid multiplication of bacteria in bottled water low in nutrients increases the respiration over that of free water (ZoBell and Anderson, 1936), and the net photosynthesis is underestimated. An assumption of the method is that respiration of all members of the population will be the same in the dark and in the light, as appears to be true for photosynthetic organisms (Brown 1953). While this assumption is not likely to be fully met by other organisms, the differences are probably small enough so that the method is still capable of giving meaningful measurements. Because of the absorption of a small amount of light by the glass of the bottles the rate of photosynthesis may be expected to be slightly underestimated under conditions in which light is at less than optimum intensity. As will be seen, this condition can have affected the present work slightly, since light was not consistently limiting.

Recently Steemann-Nielsen (1952, 1954) has expressed considerable distrust of the bottle technique for waters in which the rate of production was low, although Riley (1953) pointed out objections to the earlier paper. Steemann-Nielsen

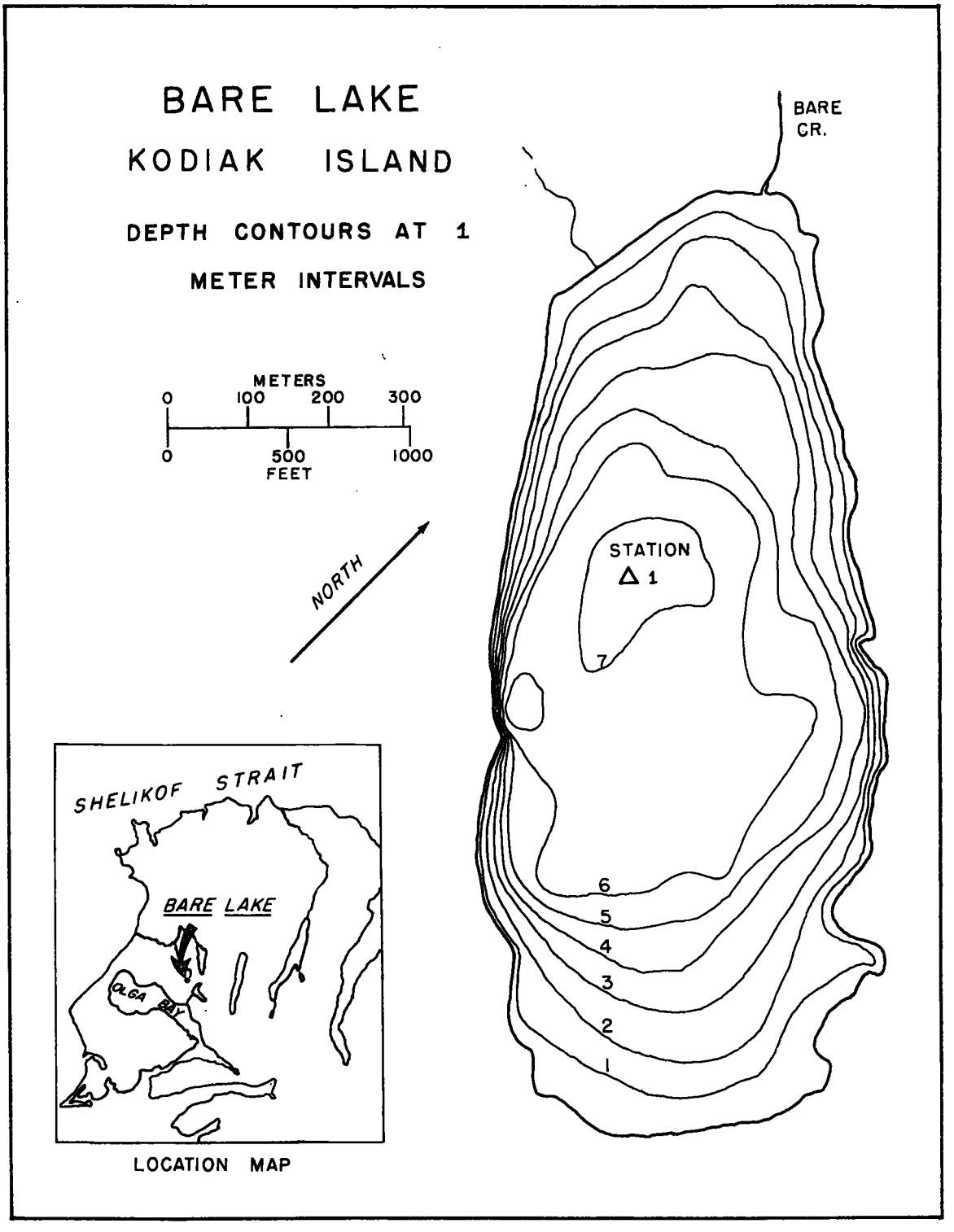

FIGURE 1.—Bare Lake, Kodiak Island, Alaska.

maintained that light has an inhibitory effect on bacteria in the light-bottle. At the moment of writing, a proper evaluation of the method has not been made. It should now be tested with bacteria-free cultures of algae, and cultures to which known quantities of bacteria have been added. In any case, Steemann-Nielsen agreed that useful results can be obtained when production is high. In the present work, greatest emphasis is placed on comparisons between rates before and after fertilization, not so much the absolute rates themselves.

Measurements of the pH were made by the use of a model 607A Hellige comparator.

Temperatures were taken with a Kahl reversing thermometer calibrated in tenths of a degree centigrade.

Free carbon dioxide and alkalinity measurements were both made by the titration methods (American Public Health Association 1946). To minimize the error of loss of CO_2 in the free carbon dioxide test, the method of stirring as described by Ellis and others (1948) was followed.

Soluble phosphorus measurements were made by the method described by Ellis and others (1948); however, one-half of the amount of ammonium molybdate was used (Wattenberg 1937). Measurements of the concentration were made by a 6-volt battery-operated Cenco photelometer which had been calibrated with solutions of known phosphate content. A 5-centimeter cell of 50-milliter capacity and a red filter were used. All determinations on the photelometer were made approximately 6 minutes after the addition of reagents, as the blue color fades with time. Concentrations expressed as mgm./l. of phosphate phosphorus are accurate for small concentrations to within 0.002 mgm./l.

Total phosphorus was determined with perchloric acid digestion, the excess acid being neutralized, and the resulting phosphate determined as described above (Robinson 1941).

Nitrate was determined by a modification of the method of Zwicker and Robinson (1944). Since chloride ions are required to develop the red color, 2 ml. of a 7.8 percent solution of NaCl was added to 4 ml. of lake water and thoroughly mixed before adding 2 ml. of strychnidine. Samples were read in the above described photelometer and the nitrate concentration determined from a plotted curve derived from a similar treatment of standards. For these determinations 1 cm. cells of 10 ml. capacity and a green filter were used. Results expressed in mgm./l. of nitrate nitrogen are accurate for small concentrations to within 0.01 mgm./l. Total nitrogen was determined by a semi-micro Kjeldahl method.

Water-transparency measurements were taken with a Secchi disc.

Intensity of incident light was measured by means of a photographic exposure meter which received reflected light from a white painted surface. The meter was placed within a cylindrical holder 30 cm. above the painted surface and received light from a circular surface having an area of 254.5 sq. cm. Readings were taken three times daily at 9 a. m., 12 noon, and 3 p. m. and are expressed in units of cal./cm.^{2}/min. The instrument, calibrated by comparison with an Eppley pyrheliometer under a variety of meteorological conditions at the University of Washington, proved to have a nearly linear response over the range in which it was used. A table was prepared to convert the reading to the Eppley equivalent as cal./cm.^{2}/min. of total radiation, and for converting the average to daily income of total radiation. In using the data, averages of measurements from four days were calculated to give the mean intensity during the periods which photosynthesis was measured. It is assumed that variations in the spectral composition of daylight are averaged out and that the average composition is constant enough that the limited spectral sensitivity of the exposure meter does not prevent adequate estimate of radiation.

Phytoplankton samples were taken at the surface and at 3- and 6-meter depths at station 1. A sample was placed in a tall cylindrical vessel and formalin added to bring the concentration of formaldehyde to 1 or 3 percent. Four days were allowed for the suspended material to settle. After that time the upper four-fifths of the liquid was drawn off and the residue placed in a vial. Subsequently, the reduced sample was centrifuged at 6,700 r. p. m. for 10 minutes in large tubes with a small calibrated projection at the bottom, permitting the volume of the packed plankton to be measured directly. This is a rather rough index of population size as the degree of packing is dependent somewhat on the character of the organisms.

In addition to the measurement provided by the packed volume, counts of cells were made using a standard method (Lackey 1938).

Net plankton was sampled by pouring measured quantities of water through a No. 20 net and by means of a Clarke-Bumpus sampler. It had been intended to use only the Clarke-Bumpus plankton sampler for zooplankton, and to employ a No. 20 net in order to catch small organisms. All the 1950 samples and those of 1951 through July 23 were taken with the No. 20 net. This fine-meshed net has been used successfully elsewhere (Edmondson 1955), but the dense phytoplankton population clogged the net in Bare Lake, and the watermeter did not work properly. The method was changed, and the rest of the 1951 samples were taken by pouring 80 liters of surface water through a No. 20 net. In 1952 both techniques were employed. A sample of the smaller zooplankton was taken by pouring 3-liter water samples collected at each meter depth from 0 to 6 meters through a No. 20 net. On each sample day two such composite samples were taken at adjacent locations in the lake giving two samples of 21 liters each. The Clarke-Bumpus apparatus was used with a No. 10 net in order to get a proper sample of the larger copepods. In use, the sampler was lowered close to the lake bottom while the boat was in motion and then raised slowly so that all depths were sampled. One revolution of the propeller represented 5.1 liters of water. The samples were counted in aliquots which were either about $\frac{1}{5}$ or in some cases $\frac{1}{25}$ of the whole volume.

When used under conditions in which the net clogs, the water measuring mechanism of the Clarke-Bumpus sampler does not operate properly in that the propellor turns more slowly than it should, and the quantity of water filtered is underestimated. At low rates of flow, the propeller may stop altogether. The critical level at which stoppage occurs, seems to vary among different instruments, possibly having to do with the balance of the propellor.

The effect of this on the results obtained with the sampler used in Bare Lake was studied by towing the net at different speeds and comparing the computed population density with that obtained from the samples in which measured quantities of water were poured through a net. It was found with our instrument that even at low rates of flow, fairly consistent results were obtained. In one series of 7 samples, the coefficient of variation for one of the rotifers was only 25 percent when the rate of turning of the meter varied from as low as 3 to 15 turns per minute, both values well below the range of linearity for most instruments. Ordinarily, it is considered desirable to have a rate of 30 to 40 turns per minute. (C. S. Yentsch, personal communication.) It was found that at the low rates, the results obtained with the sampler overestimated the population density of rotifers and nauplii, but the results were consistent enough to permit us to adjust the 1950 and 1951 data to give a rough measure of the population. The copepodid stages of the copepods seem able to evade the sampler when the rate of flow is slow, and a separate adjustment was made for them. Only samples were used which were well within the range of volume and rate studied, the others were discarded. The samples taken with a No. 10 net present no problems of adjustment. The early samples obtained with the No. 20 net varied from 42 to 339 liters in volume. The 1952 samples taken with the No. 10 net varied from 535 to 1,219 liters. The tows were made at an approximate speed of 2.2 miles (3.6 kilometers) per hour and were ordinarily of 5 minutes duration.

EXPERIMENTAL PROGNOSIS OF PROBABLE EFFECT OF FERTILIZER

Four trips were made to Bare Lake during July 30 to September 23, 1949. An examination of the water was made on the first trip to the lake on July 30. On that date the Secchi disc was visible to a depth of 5 meters. The water temperature was 13.6° C. at all depths, and the water was nearly saturated with oxygen at the surface and bottom. Further analyses showed 4.0 mgm./l. of SiO_2 to be present but no soluble phosphorus was detected. Subsequent trips into the lake were devoted to an examination of the fish fauna; however, it was observed that no visible change in the water transparency took place during the season.

Circumstances prevented extensive work at Bare Lake during 1949. In a preliminary experiment, 18 one-gallon jugs of surface water from Bare Lake were flown to Karluk Lake on August 10. The water was strained through bolting silk to

remove the large zooplankton. One group of jugs was held as a control and to the others were added varying amounts of a solution of KH_2PO_4 and $NaNO_3$ to realize definite concentrations (table 1).

TABLE 1.—*Results of 1949 Bare Lake jug experiment, showing initial concentration of phosphate phosphorus and nitrate nitrogen in each group, production of oxygen and phytoplankton for periods after fertilization and cost of fertilizer on an acre foot basis*

Group	Phosphorus mgm./l.	Nitrogen mgm./l.	Gross O_2 produced mgm./l./day Aug. 10–17.	Phytoplankton cells/ml. (mean for period)		Cost of fertilizer per acre-foot.[1]
				Aug. 11–19	Aug. 21–27	
Jug A	0.000	0.000	0.18	59	149	----------
Jug B	.025	.250	.21	140	----------	$0.16
Jug C	.050	.250	.39	287	1,924	.18
Jug D	.050	.500	.31	391	2,936	.32

[1] 1 acre foot=43,560 cu. ft. or 1,234 cu. meters.

After the addition of the fertilizer, the water was thoroughly mixed, the oxygen content measured, and the light and dark bottles were set out for measuring rates of photosynthesis in the groups. Unfortunately, several of the jugs were lost in a storm, so lack of water prevented photosynthesis determinations after August 17 and phytoplankton counts in group B jugs after August 19. In table 1 the gross rate of photosynthesis and the mean phytoplankton population are shown for each series of jugs during periods following fertilization. Also, the cost of the fertilizers per acre foot is given. Of the groups tested it appears that the greatest increase in phytoplankton per dollar resulted from the concentrations used in group C jugs.

FERTILIZATION OF BARE LAKE

One of the initial problems in fertilizing lakes is the determination of the amount and proportion of nutrient elements to introduce. In the carcasses of red salmon the ratio of nitrogen to phosphorus is 10.4 to 1 by weight, but the ratio in algae tends to be considerably lower (Ketchum and Redfield, 1949). The ratio in the fertilizations used was relatively low, about 5 parts of nitrogen to 1 of phosphorus. This ratio is within the range required by algae, and at the same time is relatively economical since nitrogen fertilizers are expensive. The amount of fertilizer to be added was based on the concentration used in jug C of the prognostic experiment. Knowing the volume of the lake, one could add fertilizer annually to increase the concentration of phosphate phosphorus and nitrate nitrogen by approximately 0.05 mgm./l. and 0.25 mgm./l., respectively. This amount is in excess of the concentration which might be obtained from the carcasses of red salmon in a year of a large escapement. However, it appeared advisable to use a larger amount as the success of the experiment depended upon getting a large population of plankton.

The first fertilization at Bare Lake took place on July 12, 1950, when 2,500 pounds of 19 percent super phosphate and 6,500 pounds of sodium nitrate were added to the lake. This amount of fertilizer was calculated to increase the nitrate concentration 0.244 mgm./l. and the phosphate concentration 0.047 mgm./l.

In 1951, the lake was fertilized on July 12 with the same amount of fertilizer as used the previous year. On September 14, 600 pounds of nitrate and 650 pounds of phosphate were divided into approximately equal lots. One lot was placed on a west side beach of the lake, the other lot on an east-side beach, to leach into the water during the fall and following spring.

In 1952, the lake was fertilized with approximately the same amount of nitrate and phosphate as used in the former July applications. However, half the amount was introduced on June 11 and the rest on July 16. Correspondingly, in 1953 very similar applications were made on June 10 and July 15. Table 2 shows when the various fertilizations were made and the expected concentration of nitrates and phosphates which should be realized in the water by the amount added. Also the lapse in time is given before the nutrients were reduced to prefertilization levels.

Two days after each fertilization a series of water samples was taken and the concentration of nitrate and phosphate measured. The mean values for each series indicated that the nitrate had dissolved and the concentration approximated the expected values. Concerning phosphate, less than 20 percent of the amount added could be measured in solution after fertilizations with 19 percent superphosphate in 1950 and 1951 and 47 percent phosphate in 1952. In 1951, a few measurements were made of total nitrogen and phosphorus. Maximum concentrations found were

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0.423 and 0.060 mgm./l. of *N* and *P*, respectively. The ammonium monohydrogen orthophosphate, $(NH_4)_2HPO_4$, used in 1953, although expensive, is more soluble, and approximately one-half of the amount added was accounted for in solution.

TABLE 2.—*Fertilizations of Bare Lake during 1950–53*

Fertilizer	Date applied	Pounds	Concentration expected mgm./l.		Approximate lapse in days before disappearance [1]
			Nitrogen	Phosphorus	
Sodium nitrate	July 13, 1950	6,500	0.244		17
Super phosphate, 19 percent	do	2,500		0.047	12
Sodium nitrate	July 12, 1951	6,500	0.244		13
Super phosphate, 19 percent	do	2,600		0.049	5
Sodium nitrate	Sept. 14, 1951	600	0.023		
Super phosphate, 19 percent	do	650		0.012	
Sodium nitrate	June 11, 1952	3,300	0.124		9
Super phosphate, 46 percent	do	540		0.025	9
Sodium nitrate	July 16, 1952	3,300	0.124		10
Super phosphate, 46 percent	do	540		0.025	11
Sodium nitrate	June 10, 1953	2,700	[2] 0.125		9
Ammonium orthophosphate	do	500		0.027	5
Do	July 14, 1953	500		0.027	6
Sodium nitrate	July 15, 1953	2,700	[2] 0.125		9

[1] This refers to the interval of time in days following fertilization when the amount of nitrogen or phosphorus added had decreased to the prefertilization level.

[2] The expected concentration includes nitrogen derived from both sodium nitrate and from ammonia in the 500 pounds of ammonium monohydrogen orthophosphate $(NH_4)_2HPO_4$.

The equipment and method used in the application consisted of a 6-man life raft decked over with 2″ x 12″ x 10′ planks on which the fertilizer was hauled. This was towed by a motor-propelled skiff in a zig-zag course over designated sections in the lake. Two men with brooms on the raft swept the mix into the water. Usually the mix was spread in the littoral zone; however, on two occasions it was distributed over the entire lake. Subsequent tests of the nitrate and phosphorus in the water showed no significant difference in the concentrations from the two methods of application.

RESULTS

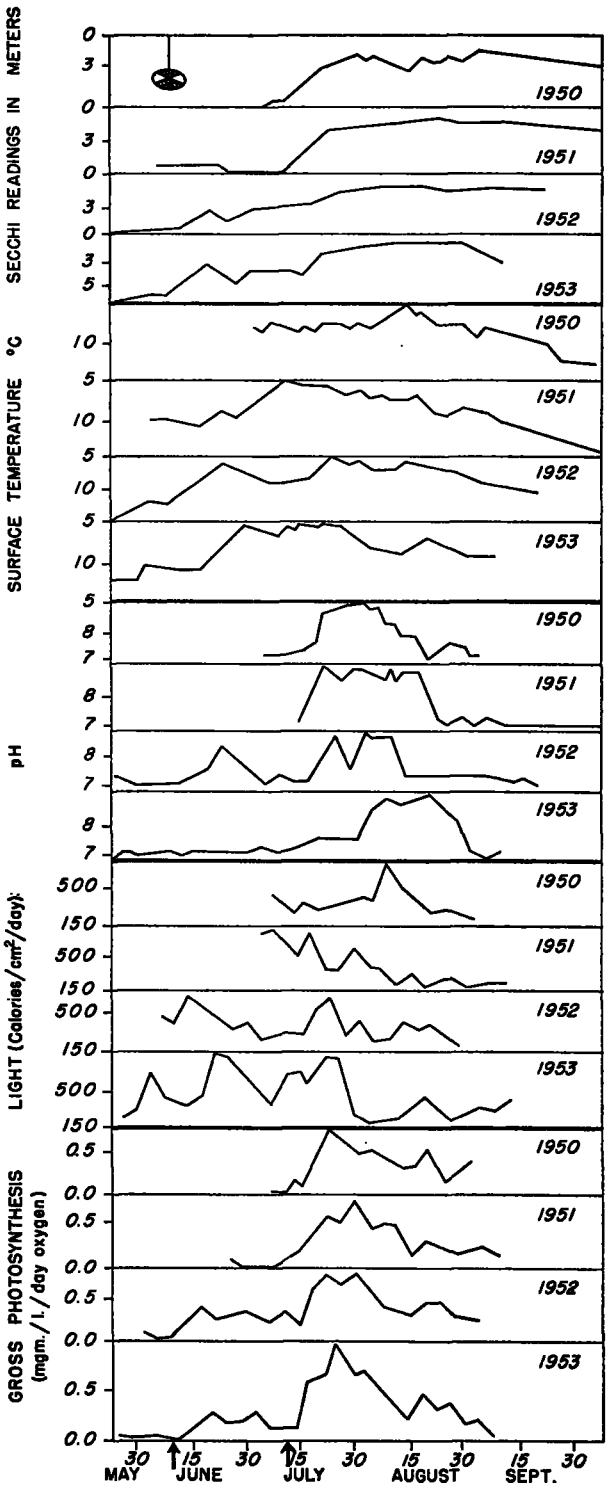
CHEMICAL CONSEQUENCES OF FERTILIZATION

Each year before and after fertilization chemical analyses were made of the lake water. No nitrate or phosphate was detectable prior to fertilization in the four years using the methods as outlined previously. The amount of these elements introduced at fertilization disappeared from the water rapidly. Although some of the material must have been lost to the bottom muds and some utilized by the rather sparse-rooted aquatic plants and moss, the amount taken-up by the phytoplankton created noteworthy changes in the chemistry of the lake.

Before the first fertilization each year the secchi disc reading ranged from 5.5 to 7.0 meters. Following the initial fertilizations the disc reading decreased at the average rate of 1 meter every 3 days for 9 days. About a month later in 1950 and 1951 the readings decreased another meter, whereas in 1952 and 1953 large decreases did not occur until after the second fertilization (fig. 2). Such a pattern in the latter years might be expected as the initial fertilizations were half as large as those of 1950 and 1951. Disc readings were lowest a month after the second fertilizations in 1952 and 1953. In all years the readings had increased by the end of September. Little variation in transparency during the periods of study can be attributed to runoff or meteorological conditions. It should be re-emphasized that such a striking decrease in transparency did not take place in 1949 when the lake was not fertilized.

Free carbon dioxide was present at all depths in the lake each year before fertilization in a concentration of from 0.5 to 2.0 mgm./l. As carbon dioxide was removed from the water by photosynthesis, the increased rate following fertilization reduced the amount of carbon dioxide in solution. From approximately the latter part of July to the latter part of August each year it was absent from the water. Removal of carbon dioxide by photosynthesis reduced the acidity of the water as indicated by the rise in pH values from 7.0 before fertilization to a maximum of 8.8 to 9.3 following fertilization (fig. 2).

Mineral analyses of Bare Lake surface waters were made during the years 1951–53 (table 3). The results show the lake is of the bicarbonate type. Included in the table is a comparison of the concentrations of the major constituents at Bare Lake with the normal concentration occurring in bicarbonate-type lakes having the same specific conductance (Rhode 1949). Bare Lake varies from the normal by having more chloride and sodium and less calcium and bicarbonate. The water is very soft and rather low in dissolved solids. Silica is rather abundant; however, the



amount present in the water has decreased during 1951–53. Following the July fertilizations of 1951 and 1952 large decreases occurred in the silica concentration which probably were caused by blooms of diatoms.

The oxygen concentration remained high at all depths during the seasons of experimentation. As the lake is shallow and often mixed by frequent winds, no stratification of consequence occurred. Measurements of the oxygen production or the rate of photosynthesis before and after fertilization will be considered in the following sections.

RATES OF PHOTOSYNTHESIS

Fertilization of the lake was followed by an immediate increase in photosynthesis, as measured in bottles. Later measurements successively increased for a time, then declined somewhat, appearing to fluctuate around a more or less steady level which was about the same for the 4 years (fig. 3). The second fertilizations in 1952 and 1953 occurred after this condition had been reached, and were followed by large increases in rate. In 1952, the maximum following the second fertilization was insignificantly higher than that which followed the single fertilization in 1951, but was distinctly higher than that of 1950. The highest rate yet observed in Bare Lake occurred after the second fertilization in 1953.

The magnitude of the increase is given numerically in table 4 where the average values are presented for 10-day periods before and after fertilization. The ratio of photosynthesis in the period immediately after the first fertilization to that just before is seen to vary from a minimum of 2.5 in 1953 to a maximum of 7 in 1950. The maximum 10-day rate after the second fertilization varied from 7 to 12 times the prefertilization period.

FIGURE 2.—Graphs of the secchi disc readings, surface water temperatures and pH, light, and gross photosynthesis for the years 1950 through 1953. Arrows denote approximate dates Bare Lake was fertilized (June application in 1952 and 1953, July application in all years).

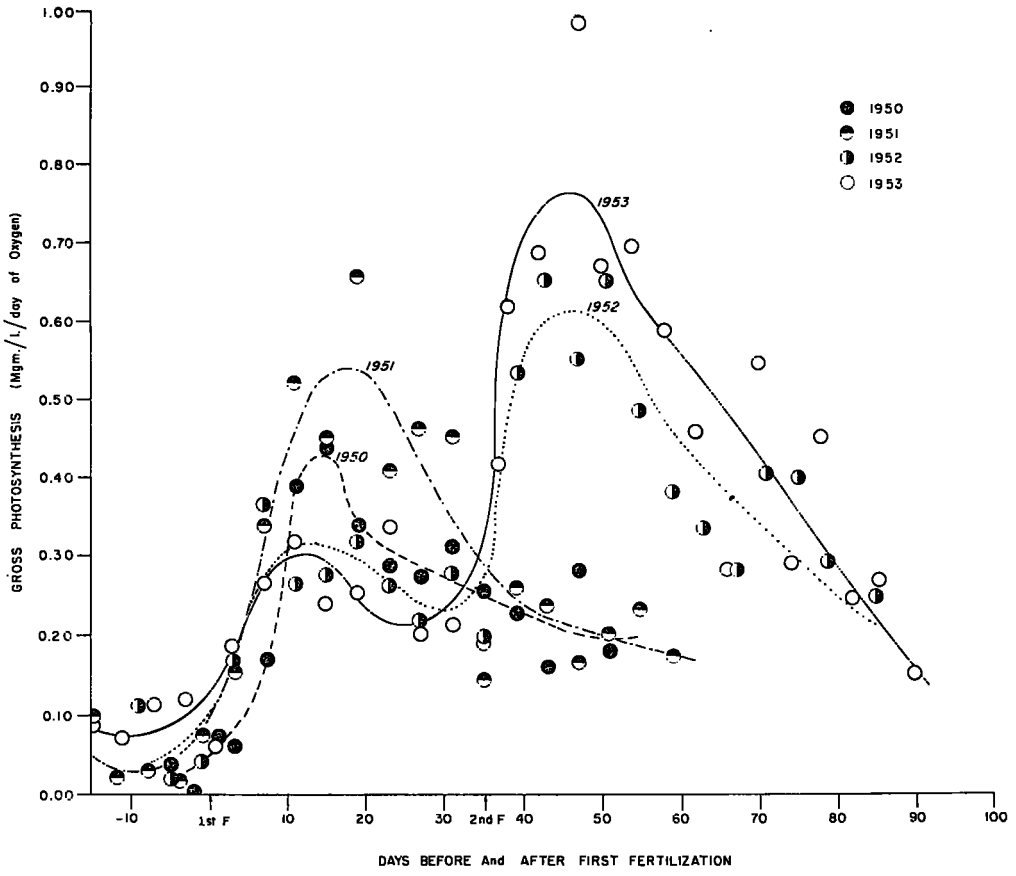


FIGURE 3.—Mean gross photosynthesis of Bare Lake as mgm././day of oxygen. Circular symbols represent mean value during 4-day exposure periods. Curves smoothed by eye show the trends.

TABLE 3.—*Mineral analyses of surface water samples collected at Station 1, Bare Lake, during 1951, 1952, and 1953*

Item	1951					1952						1953						Mean	Normal [1]
	June 9	June 22	July 10	July 15	Aug. 10	May 27	June 16	July 15	July 18	Aug. 19	Sept. 29	May 22	June 14	July 13	July 18	Aug. 24	Oct. 1		
Silica	5.9	6.5	6.0	4.6	7.0	3.7	5.1	5.5	3.4	4.3	4.1	4.2	3.3	3.0	3.0	2.6	2.3	4.4	------
Iron	0.01	0.01	0.01	0.01	0.03	0.01	0.01	0.03	0.01	0.03	0.02	0.02	0.02	0.02	0.02	0.05	0.03	0.02	------
Calcium	3.6	3.7	4.2	4.7	3.8	4.8	4.7	4.4	5.6	4.0	4.1	3.4	3.6	3.9	3.7	4.0	3.8	4.1	6.8
Magnesium	1.5	2.0	1.7	1.5	1.8	1.6	1.6	2.1	2.2	1.7	1.7	1.1	1.3	1.6	1.1	1.4	1.1	1.6	1.1
Sodium	5.6	3.4	4.4	3.0	5.6	5.1	5.0	6.0	4.3	7.2	5.9	5.1	5.1	5.1	5.6	5.0	5.5	5.2	1.9
Potassium												0.2	0.0	0.1	0.2	0.4	0.4	0.2	0.7
Carbonate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	------
Bicarbonate	16	14	14	13	12	16	16	22	17	20	18	14	16	18	18	17	16	16.3	24.2
Sulfate	3.3	3.0	4.0	3.3	4.4	4.4	3.3	3.5	5.8	5.0	4.1	3.7	3.7	2.3	3.7	2.2	2.2	3.6	4.0
Chloride	7.5	7.0	8.2	7.2	10.0	8.5	8.8	7.5	8.8	7.5	7.5	8.0	9.2	9.0	8.5	9.2	8.9	8.3	1.9
Fluoride	0.1	0.1	0.0	0.0	0.2	0.0	0.1	0.1	0.0	0.1	0.1	0.0	0.1	0.1	0.0	0.1	0.1	0.1	------
Dissolved solids	35	33	35	31	39	36	37	40	39	40	37	39	41	40	45	46	43	38.6	------
Total hardness as $CaCO_3$	15	17	18	18	17	19	18	20	23	17	17	13	14	16	14	16	14	16.8	------
Specific conductance (micromhos at 25° C.)	56.1	53.7	52.4	55.7	59.4	57.7	59.0	61.6	61.4	61.2	60.5	54.9	56.6	57.1	57.8	60.1	58.7	57.9	------
Ignition loss	------	------	------	------	------	------	------	------	------	------	------	9	11	10	13	14	13	12	------

[1] Values in this column are the standard composition of major constituents found in bicarbonate type lakes having a specific conductance of 52 micromhos at 20° C. (from table 2, p. 384, Rhode 1949). The specific conductance of 52 micromhos at 20° C. is equal to 58 micromhos at 25° C.

TABLE 4.—*Mean rate of gross photosynthesis during 10-day periods before and after fertilization*

[Upper part: Rates are given as mgm. oxygen per liter per day. Lower part: Rates are given as cal./cm.²/day to permit comparison with the input of solar energy in the same units]

Period	1950	1951	1952		1953	
			First	Second	First	Second
−17− −10		0.03			0.08	
−10−0	[1] 0.02	.04	0.05		.10	
0−10	.14	.28	.25	0.50	.25	0.68
10−20	.39	.52	.28	.59	.27	.74
20−30	.29	.45	.26	.38	.25	.48
30−40	.25	.26	[2] .37	.36	.20	.41
40−50	.22	.20		.31		.33
50−59		.19				.21
	Cal./cm.²/day [3]					
−17− −10		0.04			0.11	
−10−0	0.03	.06	0.07		.14	
0−10	.20	.40	.36	0.71	.36	0.97
10−20	.55	.74	.40	.84	.38	1.05
20−30	.41	.64	.37	.54	.36	.68
30−40	.37	.36	.53	.51	.28	.58
40−50	.31	.28		.44		.47
50−59		.27				.30

[1] Period 6 to 0.
[2] Period 30 to 35.
[3] To convert mgm. oxygen/l/day to cal./cm.²/day, multiply by 1.42. This is a composite factor; 1 mgm. oxygen is equivalent to 3.51 cal. The volume under 1 cm.² at mean depth of the lake is 0.405 liters. 3.51×0.405=1.42.

The results show that fertilization was followed by a large and prolonged increase in photosynthesis, and a second fertilization was followed by a swift rise in rate. It may be assumed that the most efficient way of using fertilizer would be to add it in several small doses rather than all at once, since, when several small doses are used, the first dose will develop a large phytoplankton population which can then absorb much of the second dose before it settles out or becomes adsorbed onto the bottom.

In the second fertilization in 1953, phosphate was added alone, followed by nitrate the second day. The nitrate had an additional effect in stimulating photosynthesis, but the magnitude of the effect is hard to evaluate exactly since there were differences in the mean light intensity to which the two sets of bottles were exposed.

The rate at which photosynthesis increased (acceleration) varied somewhat from year to year, but varied only between about 0.026 and 0.044 mgm./l./day/day. These values are approximations of the average rate of increase to the maximum, read from the graphs. The most rapid acceleration in photosynthesis was in 1952 and least in 1953, with 1950 and 1951 intermediate and about equal. The differences are probably a result of the combined effects of differences in light and initial population, but there seems to be no possibility of evaluating the effects separately here. There is no evident correlation with the temperature at time of fertilization.

During the course of each year, large changes occurred in the rate of photosynthesis (fig. 2); to some extent they can be attributed to changes in light, temperature, and population. The shading effect of the greatly increased phytoplankton bloom was probably important in regulating the photosynthesis in the lower water. Before the changes in time can be fully appreciated, a comparison must be made of the photosynthesis at different depths.

VERTICAL VARIATIONS IN PHOTOSYNTHESIS

The vertical pattern of rate of photosynthesis differed considerably from time to time during each year. Most often the maximum rate was at the surface and the minimum at 6 meters, although the distribution was usually not closely exponential. Various degrees of departure from this pattern existed; sometimes the surface and 3-meter rates were nearly alike with the bottom rate distinctly lower, and rarely were the three approximately the same. At other times, the surface rate was distinctly lower than that at 3 meters, and 2 classes of this condition could be recognized; in one the bottom rate was lower than that at 3 meters so that there was a definite maximum in photosynthesis at mid-depth. In the other, the maximum rate was at the bottom, the minimum at the surface.

It was necessary first to examine the distribution of plankton to see whether the differences in photosynthesis can be attributed to this factor. Since the lake was never even weakly stratified for long periods, it would not be expected that the phytoplankton would exhibit strong stratification. Two kinds of evidence are presently available; cell counts (1951 and 1952), and rate of respiration (all years). While both of these measures were nearly uniform in many of the series, there were some fairly large relative differences in vertical distribution. In these, the differences were larger than could be attributed to variation resulting from random sampling from a normal population. Nevertheless, none of the periods of strongly reduced surface photosynthesis coincided with an unusually low plankton content of surface water.

Therefore the low surface rates cannot be attributed to low population.

A further examination of the observations was made by cataloging the various patterns of vertical distribution of photosynthesis according to the relative degree of inhibition, and plotting against light intensity, taken as average daily income during the period of each measurement. There was a great scatter in the tabulation, but all 7 examples which had the maximum rate at surface and considerably larger than that at 3 meters occurred with weak light, below 200 cal./cm.^{2}/day of total illumination. The distributions which had surface photosynthesis about equal to or less than that at 3 meters tended to occur at higher intensities. When the data were selected so that only cases were considered in which there was considerable uniformity in the vertical distribution of respiration, the pattern was very much more distinct. Of the 26 selected dates, only 4 showed surface inhibition at relatively low light intensities, and these were all from 1953 at times when the lake was rather transparent.

The observations can easily be understood on the basis of existing data on the relationship between light intensity and rate of photosynthesis by planktonic algae (Manning, Juday, and Wolf, 1938), and the penetration of light into lakes (Birge and Juday, 1929). Since light saturation occurs at an intensity that is only a fraction of full sunlight, and the intensity of full sunlight is distinctly inhibitory, at least when carbon dioxide is present in low concentrations, it may be expected that on bright days photosynthesis will proceed at maximal rate only at some depth below the surface. Surface inhibition is well known from the work of a number of limnologists; the demonstrations by Schomer and Juday (1935) and Curtis and Juday (1937) were based on 3-hour runs in lake water, using uniform suspensions of algae which were kept in unialgal, though not bacteria-free cultures. Since the population in their work was the same at all depths, the lower rate at the surface must have been a physiological phenomenon. Surface inhibition has been demonstrated in longer exposures that include a night (Jenkin 1930 and 1937). Manning and Juday (1941) have presented calculations of photosynthetic rates at different depths in a rather transparent lake at various times of day. During most of the day the surface rate was less than at 1 meter, and at noon, the surface rate was 26 percent of the maximum, which was at 5 meters.

On this basis, it is not surprising that Riley (1940) and Anderson (1954) found very low correlations between light and photosynthesis of natural populations in surface waters, and obtained higher correlations only when considering the entire depth of the lake. Similar calculations for Bare Lake show that during most of a bright day, the maximum rate will probably occur at depths between 0 and 3 meters.

To verify these calculations two special runs were made in 1954, measuring photosynthesis at 1 and 2 meters in addition to the usual depths 0, 3, and 6 meters. The mean rate of photosynthesis for the two runs at each depth, taking the maximum as 100 percent, was as follows, starting at the surface: 89, 100, 87, 69, and 45 percent. The average light intensity was 382 cal./cm.^{2}/day of total radiation, and the results are in good agreement with what would be expected from the works cited in the discussion above.

It is evident that on bright days, our measurements of photosynthesis will somewhat underestimate the actual average rate of photosynthesis in the lake, since the maximum values occur between 0 and 3 meters. The actual amount of underestimation depends upon the actual intensity and the transparency of the lake, but will rarely be more than about 5 percent.

These considerations have led to a much more detailed examination of the vertical distribution of photosynthesis in lakes, but an account of the results would be out of place in the present paper. (See Edmondson 1956.)

VARIATIONS OF PHOTOSYNTHESIS IN TIME

It may be expected that variations in the rate of photosynthesis will be caused principally by changes in the population, in light intensity, in temperature and in nutrition, all of which were measured. Most attention will be given to light.

With respect to the factors causing variations in photosynthesis rates, it is worth mentioning a study by W. T. Edmondson of fertilized phytoplankton populations at the Woods Hole Oceanographic Institution (Edmondson 1955b). In this experiment, nutrients were added to sea

water in large shaded concrete tanks and daily measurements made of photosynthesis, solar radiation, chlorophyll, phytoplankton population, and phosphate. It was shown that almost half of the variation in photosynthesis during the period could be attributed to variations in chlorophyll and solar radiation. Temperature varied little during the period. Interestingly, although there were great changes in the taxonomic composition of the population, there seemed to be no concurrent change in the relationship of photosynthesis with light and chlorophyll; the quantity of chlorophyll was evidently more important in determining the rate of photosynthesis than was the taxonomic position of the cells containing the chlorophyll.

The quantity of chlorophyll showed a very low correlation with cell count, a better though still low relation with total volume of phytoplankton material. While it is unfortunate that conditions did not permit measurements of chlorophyll at Bare Lake, an analysis of the photosynthesis-chlorophyll relationship was not the main objective of the work.

Examination of the graphs of photosynthesis and light in Bare Lake (fig. 2) shows that while some of the major changes were simultaneous, the highest rates of photosynthesis did not coincide with the brightest days; this phenomenon is in agreement with the previous discussion of vertical variations in rate of photosynthesis.

EFFECT OF FERTILIZATION ON THE EFFICIENCY OF THE LAKE

As an initial step in analyzing the response of photosynthesis to fertilization, and to permit comparison with other lakes, a calculation was made of the gross efficiency of the lake, that is, the ratio of the energy used in gross photosynthesis to that available at the surface of the lake. The efficiencies are expressed as percentages of solar radiation and can be considered units of photosynthesis accomplished per calorie of energy. To conform with previous practice by other authors, the solar energy input is taken as the total radiation. As pointed out by Comita and Edmondson (1953) who made a summary of available data on lake efficiencies, it would be somewhat more realistic to use visible light as the basis of the calculation. On such a basis, the published efficiencies would be at least doubled since visible light is about one-half the total radiation (Kimball 1928).

The effectiveness of the fertilizer in raising the efficiency of the lake is strikingly demonstrated when the average efficiency for the entire period following fertilization is compared with that before (table 5), being larger by more than an order of magnitude in 1951 and 1952. It should be noted that the figures in the upper part of table 5 refer to an arithmetic average of the plotted individual efficiencies for each determination. This value will be different from the ratio of the average photosynthesis to average light during the longer periods; the latter is also given in the lower half of table 5, since it is comparable to most published values.

It is unfortunate that we are not able to present measurements of the efficiency for an entire summer without fertilization, for it must be expected that in prefertilization years Bare Lake probably developed a larger population than that found at the beginning of the seasons under discussion. Nevertheless observations of 1949 and pre-fertilization values in July of 1950 and 1951 compared to values in early July of 1952 and 1953 after fertilization, are sufficient to make it almost certain that the rates observed after fertilization are very much larger than anything likely to be found in the unfertilized lake.

TABLE 5.—*Gross efficiency before and after fertilization calculated in two ways*

[In percent]

Duration of time	1950	1951	1952	1953
Mean of individual efficiencies for each 4-day determination:				
Before fertilization	0.018	0.009	0.010	0.036
Entire period after first fertilization	.096	.149	.149	.169
Between the two fertilizations	-------	-------	.098	.059
After second fertilization	-------	-------	.192	.235
Ratio of mean photosynthesis to mean light during entire period:				
Before fertilization	.016	.008	.009	.033
Entire period after first fertilization	.092	.135	.128	.115
Between the two fertilizations	-------	-------	.085	.054
After second fertilization	-------	-------	.165	.186

The fact that light was usually at or above saturation level for photosynthesis is clearly demonstrated in figure 4 where efficiency is plotted against the mean daily light income during the 4-day period of the measurement. The highest efficiencies are at the lowest intensities. It happens that many of the low intensities and high

rates came at such a time after fertilization that the efficiency would be expected to be high. To give some idea of the effect, points representing times of high population (total cell count) are marked for 1951. The marked points have a distinct trend in that they occur in the upper half of the field of points as might be anticipated.

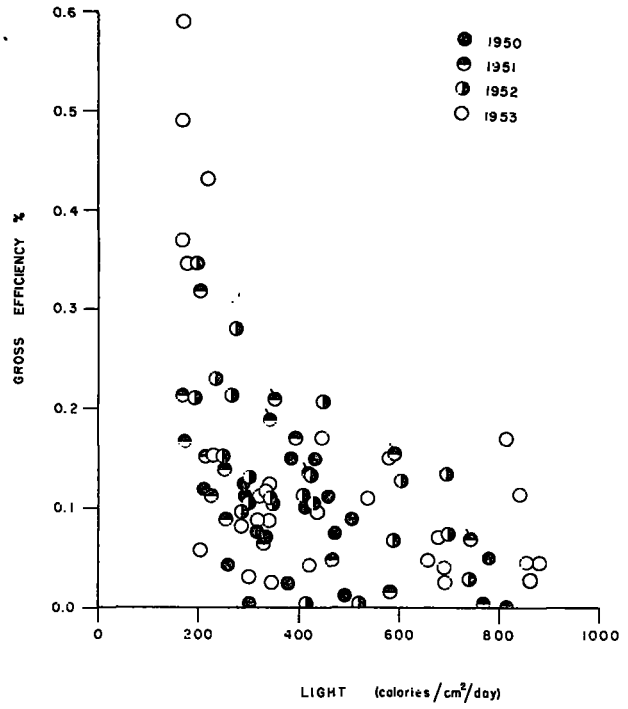


FIGURE 4.—Correlation diagram showing the relationship between total light and the gross efficiency in percentage. Circles represent the mean light and efficiency during 4-day exposure periods. Ticks extending from 1951 symbols denote times of high phytoplankton population (total cell count).

PHYTOPLANKTON

Data on phytoplankton population are available for 1951 and 1952. As would be expected from the large and immediate effect on photosynthesis, fertilization was followed by a rapid increase in the population of photosynthetic organisms (fig. 5). For purposes of the present paper, the population size is characterized by the total cell count. In addition, a few easily recog-

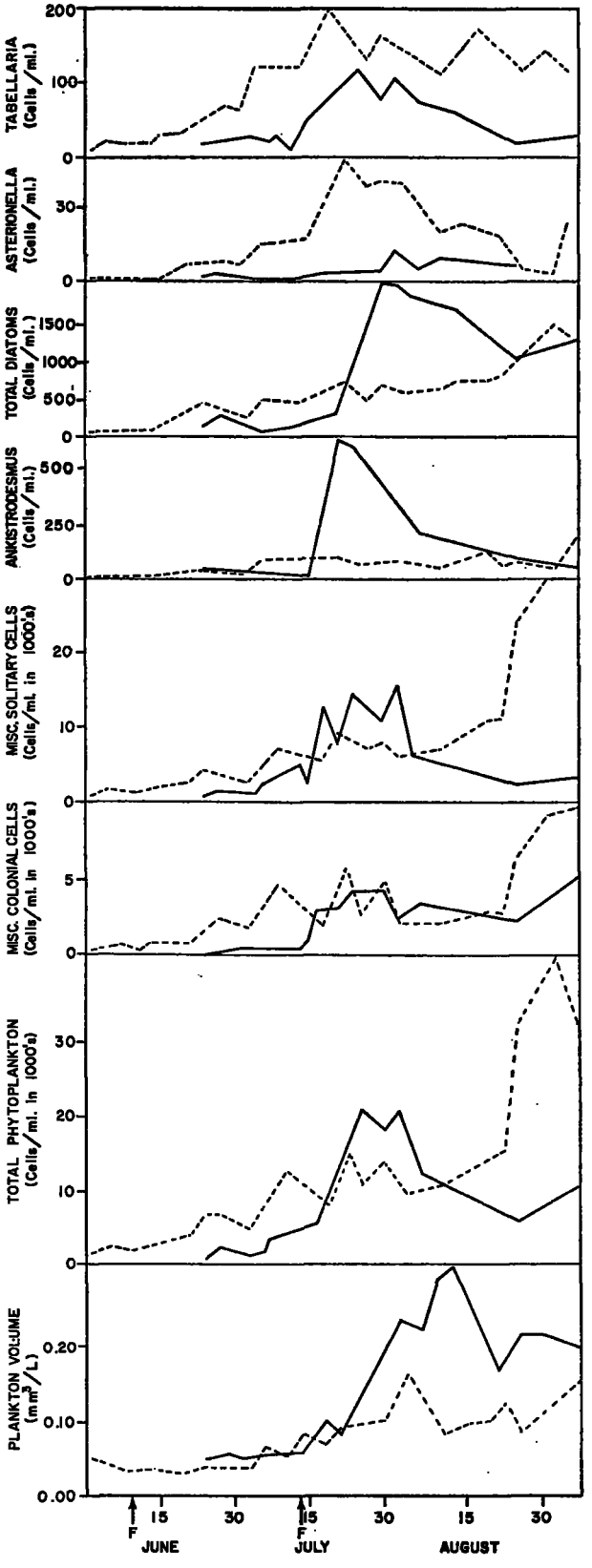


FIGURE 5.—Seasonal abundance of phytoplankton during 1951 (solid line) and 1952 (dotted line). Arrows denote fertilization dates during the two years (July 12, 1951, June 11 and July 16, 1952).

nized genera are listed, and the rest of the population cataloged as miscellaneous solitary cells and miscellaneous colonial cells. When authoritative identifications of our material have been made it will be possible to present a discussion of the specific changes in population composition, and to present data representing the mass of the total population and its components.

As an additional measure of distinct but limited usefulness, we have recorded the packed volume after centrifugation. Unfortunately, this measure varies with the strength of preservative when there are many filamentous algae present; apparently the filaments are stiffer and pack less closely when preserved with 3 percent rather than 1 percent formalin. The packed volume shows about the same trends in total cell count, except the total cell count in 1951 showed a considerable rise to a maximum density more than 10 times that of the prefertilization period, after which it declined. In 1952 the maximum population was somewhat lower but after the second fertilization eventually achieved a size about 20 times prefertilization level. The rate of rise was very different in the 2 years. While there were differences in temperature, they are insufficient to explain the difference in rate of rise, particularly in view of the data on photosynthesis. The curve for packed volume followed that for total cell volume rather well at first, but showed striking departures during the latter part of each year, indicating considerable changes in the makeup of the population.

The comportment of different organisms was strikingly different in the 2 years. In 1951, *Tabellaria* decreased after its maximum in the middle of the summer, while in 1952 the population reached a higher level for the rest of the summer. *Asterionella* was a very inconspicuous member of the population in 1951, and while in 1952 it never became abundant, it was in fact several times as abundant as during most of 1951. Conversely, *Ankistrodesmus* which showed a very sharp rise in 1951 maintained low numbers in 1952.

It would be improper to generalize from these data about the effect of fertilization in encouraging or discouraging particular forms. Carlin has shown (1943) that in unfertilized waters great changes in the relative dominance of different species of phytoplankton and zooplankton can occur from year to year during a 6-year period.

In terms of cell numbers, the average for the two years shows little difference except that produced by a great increase of several forms at the end of the season in 1952. Cell volume appeared to be somewhat higher in 1951 than in 1952. While the difference is in the same direction as that observed for photosynthesis (table 4), it seems somewhat out of proportion. A reduction in standing crop of algae could result from increased grazing activities by the zooplankton.

ZOOPLANKTON

In this study, the zooplankton organisms must be considered because of their importance as consumers and transformers of phytoplankton. The zooplankton organisms at Bare Lake are to a small extent of direct use as food of the very young fish, and some of them may be of indirect use to larger fish if they are eaten by larger benthic organisms such as Tentipedid larvae. The zooplankton organisms may be of significance in another way, as competitors with some species of the bottom fauna for phytoplankton food. Each adult zooplankter at the end of its life represents at least several times its own bulk in consumed food. As the zooplankton make up a very small portion of the food of the fish, these animals represent a diversion from the end product which is regarded as important. Even if the bottom fauna contains species capable of eating small zooplankton, there is still a loss of efficiency with each additional interposed trophic level.

While the return of salmon will be the empirical test of the hypothesis on which this project is based, any satisfactory explanation of the results must be based on consideration of the distribution of matter through the entire biota. Because of the nature of the food and reproduction of the zooplankton, a delay may be expected in the manifestation of the results of fertilization. Not only must the phytoplankton first increase to a degree that will increase the effective reproductive rate of the animals, but time for a number of generations must pass before a greatly enlarged population develops. Moreover, if there are predatory animals present whose feeding efforts match the increased rate of food production, little elevation in population-size may be found. Animals with a long generation time may show effects only after more than a year. With these considerations in

mind, some aspects of the zooplankton populations will be examined, but others will be more profitably considered after measurements from several more years have accumulated. An interesting discussion of production in an aquatic community has been given in detail by Harvey (1950).

Rotatoria

The rotifer populations consisted of a variety of species. Those forming the largest populations are equipped to feed on very small organisms or fine particles of detritus, namely, *Keratella cochlearis* Gosse; *Kellicottia longispina* (Kellicott), *Conochilus unicornis*[2] Rousselet. Others are predatory, capable of piercing small animals and sucking out the contents as *Ploesoma truncatum* Levander, *Ploesoma hudsoni* Imhof, and *Synchaeta pectinata* Ehrenberg, or swallowing small animals, as *Asplanchna priodonta* Gosse. Of the former group only *Ploesoma truncatum* appeared in relatively large numbers. *Ploesoma hudsoni* was consistently present, but formed less than 1 percent of the entire *Ploesoma* population. It is well known as a voracious rotifer, and may have been the cause of much zooplankton mortality. Other species found in small quanities were *Polyarthra vulgaris* Carlin[3] and *Gastropus stylifer* Imhof.

Two of the important rotifers, *Keratella cochlearis* and *Kellicottia longispina* carry eggs attached to the lorica. The eggs were counted as well as post-embryonic animals in the expectation that a sudden increase in food supply might be indicated by an abrupt increase in the ratio of eggs to female. A sudden increase in the production of eggs would be followed by a period in which many of the females would be immature, and the ratio would decrease even if the rate of egg production by the adults remained the same. The period of embryonic development and immaturity may amount to more than 4 days in some species, although data are not available for the present species under consideration at the temperatures prevailing in Bare Lake.

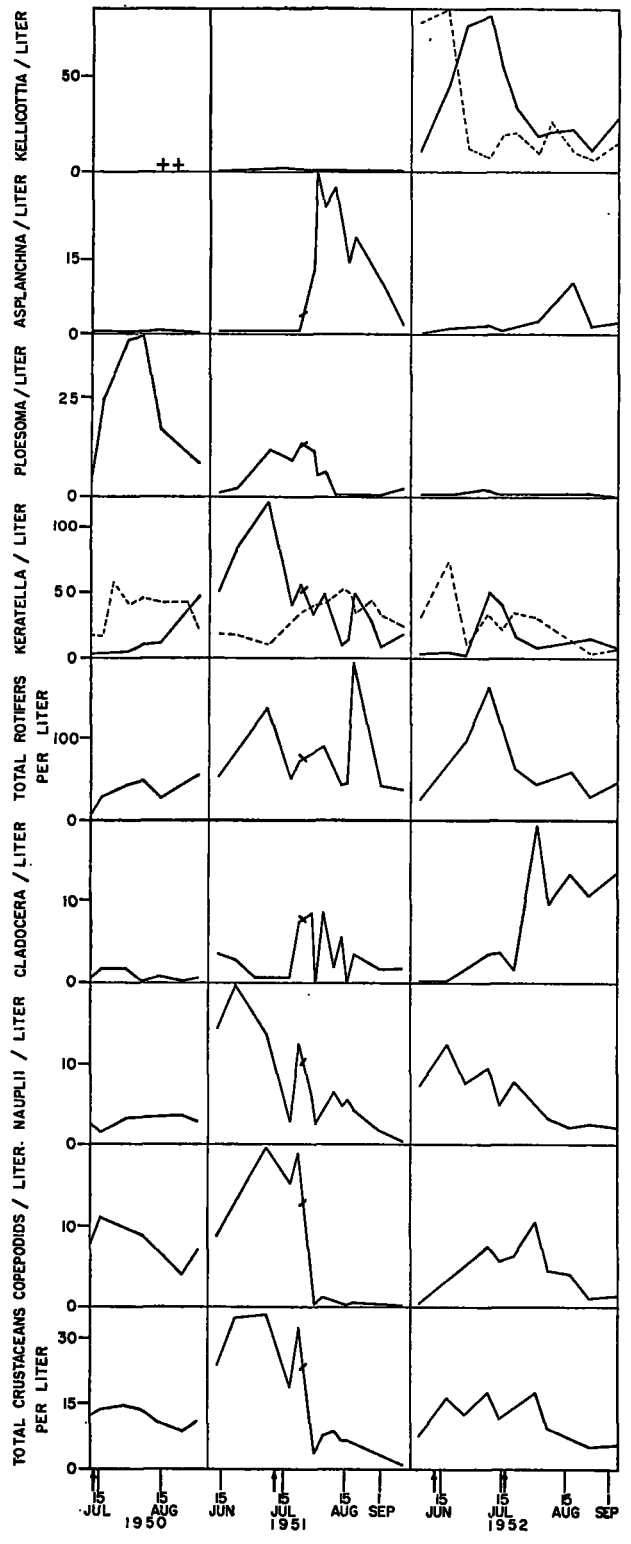
[2] The contracted specimens were named on the basis of one undivided coronal antenna. Since it may be that a number of species with one antenna have been grouped under the name *unicornis*, the identification should be regarded as provisional.

[3] This is the *P. trigla* of many authors. Carlin asserts that it is now impossible to assign the name *trigla*.

The seasonal changes in the more abundant species were considerable (fig. 6). The data plotted have been selected so that intercomparison is possible. All data plotted are based on collections with the No. 20 net, the No. 10 net samples being used only for larger organisms. Unfortunately, it was necessary to change the technique of collection during 1951, and the samples after July 23 refer only to the surface population. The apparent change in population size cannot be entirely attributed to the difference in technique, since as will be shown, the mortality of some species actually increased. In any case, the data of 1950 and 1952 should be comparable, and those of the first part of 1951 with 1950.

The graphs are self-explanatory, but some features deserve comment. *Keratella cochlearis* formed the largest population observed in the 3 years, but in 1952 it was surpassed by *Kellicottia longispina*. Both species might be expected to benefit by an increase of small algae or of bacteria, and can be regarded as competitors. About a week after fertilization in 1950, the egg ratio of *Keratella* had doubled, and remained high until the end of the season when it fell somewhat. In 1951 there was a similar change, but rather slower. In 1952, the greatest value of the ratio ever observed occurred 6 days after fertilization. *Kellicottia* was abundant enough to permit profitable calculation of the ratio only in 1952. The ratio, which was high in the first collection, was even higher in the collection 6 days after fertilization, and fell subsequently, showing fluctuations during the rest of the year.

Ploesoma truncatum is known to kill *Keratella cochlearis*, and in fact two of the collections contained a *Ploesoma* fixed in the act of pumping out the contents of a *Keratella*, having first grasped it by the corona. It is interesting therefore to see some suggestion of reciprocal relationships between the populations of the two species. In 1950, when the population of *Keratella* was small, *Ploesoma* was at its 3-year maximum. After the *Ploesoma* population had fallen drastically in 1950, *Keratella* increased. In the prefertilization period of 1951, the 3-year maximum population of *Keratella* developed and began to fall off in the presence of a smaller *Ploesoma* population. A very large population of *Asplanchna*, known to kill *Keratella*, developed late in July, and *Kera-*



tella fell to a low level. The quantitative details are obscure here because of the necessary change in sampling technique, but qualitatively there seems little doubt about the decline, especially in view of the fact that an unusually large number of empty *Keratella* loricae were observed in the sample of July 29 in company with an increasing number of *Asplanchna*.

The events in 1952 were rather different from those of the previous year in that some of the previously important species were especially scarce; i. e., *Ploesoma* and *Keratella* were represented by small populations. *Kellicottia* on the other hand was consistently present, and achieved its 3-year maximum. The largest *Kellicottia* population in 1952 occurred in the period before *Asplanchna* developed its maximum population.

Copepoda

The only copepod to occur in important numbers was *Epischura nevadensis* Liljeborg, kindly identified by Dr. G. W. Comita. Occasionally a small cyclopoid occurred in the samples. Although mature *Epischura* were found during much of the season, and females were collected bearing spermatophores, egg sacs occurred in only two collections. It appears that the egg sacs drop rapidly to the bottom.

Counts were made of nauplii and copepodids separately. The earliest collection of any year, June 3, 1952, contained nauplii and early copepodid stages only. Adults were not found until the middle of July. The first sample of 1951, June 13, contained no adults, the oldest copepodid collected probably was stage 4, judging by the appearance of the appendages, although a sample collected on June 14 contained a mature male. Mature specimens were present in numbers on

FIGURE 6.—Seasonal abundance of rotifers and crustaceans during 1950, 1951, and 1952. Arrows denote fertilization dates. On July 23, 1951, for the rest of that year the technique of collection was changed. Marks on the 1951 curves denote that date. Only selected rotifer species are shown separately. Time of occurrence of *Kellicottia* in 1950 is shown by plus signs as the numbers are too small to plot. The number of eggs per female is shown by dotted lines as percentage for *Keratella* and *Kellicottia*.

July 7. In 1950, mature specimens were present in all the collections.

In the first two years, the copepodids were most abundant in the first collections, and showed a general decline during the year. A possible explanation would refer to the predaceous rotifers which can attack nauplii and small copepodids. The population was reduced to a very low level at the end of 1951 which may account for the lower initial population in 1952 and the smaller average. Only the year 1952 shows the expected generally reciprocal relationship between abundance of nauplii and copepodids, the copepodids increasing as the nauplii decreased.

The copepods have such a long generation time that it is not to be expected that the quantity will increase immediately after an increase in phytoplankton. While the numbers may be expected to increase over the years, the fact that they do not increase greatly can be understood if they are effectively fed on by predators.

Other crustaceans

No crustaceans other than copepods were quantitatively important in the lake. There were a few Alonella, Chydorus, and other very small Cladocera. It is noteworthy that no Daphnia was ever seen. Some samples contained ostracods, but not in large quantities.

DISCUSSION

As far as we have ascertained, this is the first published account in which measurements of photosynthesis have been used to diagnose the productive condition of a fertilized lake, although the technique has been used in unfertilized lakes (e. g., Riley 1938) and in a fertilized salt-water bay (Edmondson and Edmondson, 1947). In most previous studies, reliance has been placed on changes in standing crop of phytoplankton, zooplankton or benthos, or growth of fish. In some, changes in phytoplankton density have been gauged by changes in secchi disc transparency (Ball and Tanner, 1951, Raymont 1947, Gross and others, 1947, 1950). In other cases, emphasis has been on following the added nutrient elements into the biota in different regions of the lake (Einsele 1941) or small bodies of water confined in tanks (Pratt 1950). Although the addition of radioactive phosphorus cannot be considered a fertilization, it gives useful information about the rates of uptake, exchange and distribution (Hutchinson and Bowen 1947, 1950, Coffin and others, 1949, Hayes and others, 1952).

While the standing crop of food organisms at any moment may be a measure of the availability of food to the predatory population at that moment, it may not be by itself a good measure of the rate of supply of food to the predators. The literature on fertilization of all kinds of waters indicates that ordinarily fertilization will be followed by an increase in the mass of many components of the biota. The work of Gauld (1950) is important in showing that the effect of fertilization on phytoplankton may not be apparent as an increase in the standing crop because of active grazing, which absorbs the increased production. Even when there is an increase in crop, it may not be in proportion to the increase in primary production. It is possible that the same effect may be found at other trophic levels; a copepod that has contributed to the growth of a fish will not be counted in a plankton sample.

The data presented in this paper show that certain limnological effects of fertilizing Bare Lake were immediate, prolonged, and great. Photosynthesis increased immediately, and was soon followed by a large increase in the quantity of phytoplankton. The reproductive activity of the rotifers was likely affected, but our data do not show a general increase in the abundance of zooplankton. Nevertheless, evidence is accumulating that the food supply of the fish has probably been increased. (U. S. Fish and Wildlife Service, unpublished records.) An analysis of the bottom fauna will be of interest when completed.

In conclusion, we should emphasize certain facts about the investigation. The main point of the work was to provide conditions by fertilization which would cause a great increase in the food supply of young red salmon, directly or indirectly. Thus, we were not making a study of fertilization as such, and we did not plan to make recommendations as to proper kinds and amounts of fertilizer. Such work can be more effectively done in more accessible lakes at lower latitudes where laboratory conditions permit elaborate analyses. It was not possible to establish a control in the form of an unfertilized lake, but this lack is not serious

in evaluating the immediate limnological effects, in view of the observations of 1949 and general limnological knowledge of the production of lakes. In the Bare Lake work, the initial quantity of fertilizer was chosen to fit certain requirements, and was repeated the second year without modification although it was obvious that less fertilizer would give satisfactory results. Since the second year, the fertilization program has been varied, the major concern being to obtain large effects. Thus, in 4 years we have a variety of additions of fertilizer, but in each case, the primary production of the lake has been greatly increased, and this is the essential requirement of testing the hypothesis on which we are operating.

The lack of a formal control may be important in connection with the survival and growth of the fish; however, some data of this nature are collected annually from the large lakes in the area, and these may offer a valuable comparison. It is planned to continue studies in Bare Lake for many years, alternating periods of fertilization with periods in which the lake is left unfertilized. This program may be expected to give more satisfactory results than one of short duration in which complete dependence is placed on a control lake.

For a complete understanding of the effects of fertilization, as full a set of measurements as possible must be made. The interpretation of measurements of photosynthesis in terms of possible growth rates requires further critical study, but photosynthesis seems to be the most direct measurement available, and one which permits very rapid diagnosis of the degree of effectiveness of a given fertilization. The technique of fertilizing jugs of water variously and observing the photosynthesis and standing crop for a period of time offers many possibilities for prognosis, and is capable of great development and refinement. A good many of the interpretations of populations depend on specific knowledge of algal physiology, much of which does not yet exist for important planktonic species, although a good beginning has been made (Chu 1943, Ketchum and Redfield 1949, Osterlind 1949, Rodhe 1948, Gerloff and others 1950, Vollenweider 1950, Burlew 1953).

The physiological condition of a population is so important in determining its productivity that it is doubtful that a list of species counts and a few simple chemical determinations will ever be sufficient to characterize a population for the purpose of assessing productivity or predicting the results of fertilization. The response of a population to changed conditions, as added nutrients or reduced grazers, will probably be found to be important information on which to base an assessment of productivity, or on which to base a program of fertilization. The development of improved techniques for such assessment is surely promising with increased knowledge of productivity.

It is possible that even with fertilization the return of salmon to a given lake will not be increased for reasons which have nothing to do with the success of fertilization. The data reported in this paper represent part of the information which will be used to evaluate the effect of fertilization and to interpret the final results of the experiment. If the fish population is successfully increased in Bare Lake but not in Karluk, we can relate the difference to a definite measure of basic productivity. If the return of fish is not increased, at least we will have information which may contribute to an explanation.

A discussion of the results of the fish investigation is not part of the present paper, but it is of interest to comment that each year since fertilization salmon leaving the lake have been distinctly longer and heavier than the year before (unpublished data).

SUMMARY

1. Bare Lake, a 120-acre unstratified lake on Kodiak Island, Alaska, was fertilized in 4 successive years with commercial inorganic phosphorus and nitrogen fertilizers.

2. The quantity of fertilizer was in part decided on the basis of prognostic experiments in which jugs of Bare Lake water were fertilized and the increase of photosynthesis and population measured.

3. The effect of fertilization on the rate of photosynthesis by the existing population in the lake was immediate and large. The rate in the 10-day period after fertilization was increased by a factor of 2.5 to 7 as compared to the 10-day period before fertilization.

4. The rate of photosynthesis progressively increased after fertilization, then fell to a rather

steady level well above the initial value. A second fertilization resulted in a rate greater than the first maximum.

5. Light was supraoptimal, photosynthesis at the surface frequently being about equal to, or less than at 3 meters. The highest efficiencies of utilization of sunlight occurred in periods of relatively low light. Efficiency was increased by fertilization.

6. Following each of the yearly fertilizations the phytoplankton population increased manyfold, the transparency decreased from about 6 to less than 2 meters and the pH increased from 7.0 to a high of 9.0. Phosphate and nitrate fell to an undetectable level in a few days.

7. Some rotifers seemed to show an effect of increased food supply in that egg production was apparently accelerated.

8. The planktonic crustaceans did not show a significant increase in population size from 1950 to 1952, possibly as a combined result of their long life cycle and effective predation.

9. Salmon leaving the lake have been longer and heavier in successive years, suggesting that they are responding to increased food supply.

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LIMNOLOGICAL STUDY OF THE LAKES IN CONVICT CREEK BASIN MONO COUNTY, CALIFORNIA

BY NORMAN REIMERS, JOHN A. MACIOLEK
AND EDWIN P. PISTER

FISHERY BULLETIN 103

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The 10 glacial lakes of Convict Creek Basin in eastern California lie within a drainage area of 16 square miles, yet have enough variety in altitude, size, and depth to be representative of many high-altitude trout lakes in the Sierra Nevada range. All are relatively poor in dissolved mineral substances, available heat, and aquatic vegetation. As a step toward finding a more precise measure of alpine lake productivity, this report presents analyses of physical, chemical, and biological data obtained in surveys conducted on these lakes between July 1950 and September 1951. The information has been treated separately in the following categories: physical influences, chemical influences, bottom fauna and plankton abundance, food habits of trout, and age composition and growth of trout populations. In each of these categories (except food habits) the 10 lakes have been ranked in high-to-low order of productive potential or production. The data have also been integrated to illustrate the degree of correspondence in ranking among physical, chemical, and biological divisions.

The lakes of the basin fall into groups and rough gradients for nearly all measurements, but the orders of lakes with respect to biological productivity are not in general agreement with the orders established on the basis of physical and chemical influences. Important causes of production differences were not definitely indicated, and no environmental factor or related group of factors can be named as a controlling influence on productivity as measured. The lack of biological agreement found among these lakes in terms of food availability and growth rates of trout suggests the need for a biological evaluation less biased than those now in use, possibly a measurement at the bacterial or "primary consumer" level.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

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LIMNOLOGICAL STUDY OF THE LAKES IN CONVICT CREEK BASIN, MONO COUNTY, CALIF.

By NORMAN REIMERS, JOHN A. MACIOLEK, and EDWIN P. PISTER, *Fishery Research Biologists*

In the Sierra Nevada of eastern California there are several thousand mountain lakes, most of which contain trout populations. Collectively these lakes support a recreational fishery that is unparalleled in the Western States, yet their environmental conditions and levels of fertility have been little studied. In 1934, United States Bureau of Fisheries surveys for the purpose of developing stocking policies on National Forest waters included the Sierra, Inyo, and Mono National Forests; a similar survey, concerned with stocking policy and flow-maintenance structures for lakes in the Sequoia National Forest, was made by the United States Forest Service in 1936.[1] The 1934 surveys briefly covered physical, chemical, and biological conditions, but were hampered in their scope of investigation by lack of time and the large number of waters considered; further research was urged. Curtis [2] studied the life history of golden trout in the Cottonwood Lakes. Needham and Vestal (1938), and Needham and Sumner (1941) published short papers dealing with growth and management of trout in high lakes. Moffett [3] reported on fishery problems of Kings Canyon and Sequoia National Parks, and made management recommendations consistent with observations somewhat more penetrating than those of the 1934 surveys. Calhoun (1944a, 1944b) reported on the food of trout in two Sierra lakes, and on the bottom fauna of one of these.

There has been very little detailed limnological work on other Sierra Nevada lakes, and the combined study of limnology and trout production has been neglected in the region. Like alpine waters in other regions, the Sierra lakes vary greatly in productive capacity due to many ecological factors, some of which are but partly understood in the analysis of their effects on trout. In consideration of the need for more basic information on the fertility of these waters, and with the ultimate purpose of establishing reliable indices of productivity [4] for oligotrophic mountain lakes, the United States Fish and Wildlife Service in 1950 began an investigation of alpine and montane lakes in Mono County, Calif. Convict Creek Basin was selected as a trial study area because its drainage is rather small and because the 10 lakes occupying it are typical of many in the region. These lakes present a range of conditions in altitude, substrate materials, area, depth, and general conformation.

The design throughout the course of this preliminary study has been to compare the lakes by as many criteria as feasible in order to determine whether the causes of biological productivity differences can be demonstrated specifically by means of presently used survey methods and, if possible, to determine whether any individual factors consistently control productivity in a group of alpine lakes. Certain physical, chemical, and biological data appear with the maps on pages 494–503, and facilitate gross evaluations of the lakes individually. In the sections which follow, however, the discussions are concerned mainly with the lakes as a group. With the emphasis thus on comparison among 10 lakes it has not been practicable to give detailed descriptions of the lakes individually in this report, which fulfills the following objectives:

1. Survey, map underwater topography, compute standard morphometric data, obtain summer temperature characteristics, measure transparency, and catalog shore and bottom types, trout spawning areas, and aquatic plants.

2. Analyze and compare physical characteristics of the lakes.

[1] The Inyo-Mono surveys were conducted by Drs. Osgood R. Smith and P. R. Needham, the Sierra survey by P. R. Needham and H. A. Hanson. The Sequoia survey was reported by Paul S. Bartholomew. All reports are unpublished manuscripts.

[2] The golden trout of Cottonwood Lakes, by Brian Curtis. Unpublished M. A. thesis, Department of Biology, Stanford University, 1934.

[3] A preliminary report on the fishery problems in Kings Canyon National Park (1941), and A survey of fishery management problems in some waters of Sequoia National Park (1942), by J. W. Moffett. Unpublished reports, U. S. Fish and Wildlife Service.

[4] Throughout this report the term "productivity" is used in the general sense which implies richness, rather than in the more restricted sense which implies rate of production or yield at a specified trophic level.

3. Analyze and compare chemical characteristics of the waters, and relate dissolved mineral compositions to geological sources.

4. Analyze and compare age compositions, rates of growth, and condition of trout populations.

5. Analyze and compare food production in terms of bottom and plankton samples, and associate these data with food habits of trout as determined from examination of stomach contents.

6. Determine whether any conspicuous relationships exist among the above factors and measures of production.

Field headquarters were at the United States Fish and Wildlife Service's Convict Creek Station, located 35 miles north of Bishop, Calif., near United States Highway 395. Convict Lake, in the lower part of the basin, is two-and-one-half miles upstream from the station and is easily reached by road during the summer. The upper basin is part of a United States Forest Service primitive area, and is without roads or other improvements. Riding and pack animals were required to transport personnel, equipment, and supplies to centrally located base camps from which daily work on the upper lakes was carried on. With the exception of the collection of data from several hundred spawning brown trout in Convict Lake (autumn, 1951 and 1952) the field work was done during the summer months of 1950 and 1951. To facilitate presentation, field and laboratory methods employed are discussed in the sections to which they pertain.

H. D. Kennedy, fishery research biologist, participated in the 1950 field work, drafted the maps and figures, and assisted with the calculation of morphometric data. B. D. Combs, fishery research biologist, assisted in the 1951 field work, morphometry calculations, and preparation of the manuscript. The California Department of Fish and Game furnished stocking records for the lakes in the study area.

Sincere thanks are due the following persons for their aid in identifying aquatic organisms: Dr. Willis W. Wirth of the United States Department of Agriculture, Chironomidae; Dr. G. Dallas Hanna of the California Academy of Sciences, Mollusca; Dr. Irwin M. Newell of the University of Hawaii, Hydrachnida; Jack Lattin of the University of California, Coleoptera and Hemiptera; Dr. James A. McNab of Vanport Extension Center, Oreg., Oligochaeta; Rufus W. Kiser of Centralia Junior College, Washington, Cladocera; Gabriel W. Comita of the University of Washington, Copepoda; and Dr. J. M. Proskauer of the University of California, Algae.

GEOGRAPHY, VEGETATION, AND CLIMATE

GEOGRAPHY

Convict Creek Drainage of the Owens River System is on the eastern slope of the Sierra Nevada near the upper end of Owens Valley, in Mono County, Calif. There are 10 lakes in the 16-square-mile area of the drainage, with elevations ranging from 7,583 to 10,950 feet above sea level (United States Geological Survey, 1934; Mount Morrison Quadrangle).

The nine lakes of the upper basin are located in more or less distinct groups (figs. 1 and 2). In one group are Lakes Constance, Witsanapah, Bighorn, and Dorothy; these lakes drain into Lake Mildred at the head of the main canyon of Convict Creek, and are separated from the group to the northwest by a sharp ridge which forms the west shore of Lake Dorothy. Lakes Cloverleaf, Edith, and Genevieve form the northwest group, which is drained by a stream that joins Convict Creek at a point about 1 mile below Lake Mildred. Bright Dot Lake is separated from the two main groups of lakes by Convict Creek canyon. This lake is situated at an elevation of 10,600 feet in a glaciated basin that overhangs Convict Creek canyon to the west, and its outlet joins the main creek near the junction of the outlet stream from Lake Genevieve. From Lake Mildred, Convict Creek drains into Convict Lake in the lower part of the basin, falling 2,317 feet in 3 miles. The creek runs northward until it leaves Convict Lake, then swings to the east and empties into Lake Crowley, a reservoir controlling the flow of Owens River.

The basin is bounded on the west by Laurel Mountain and Bloody Mountain, on the south and west by Mammoth Crest, and on the east by a massive ridge which forms Mount Morrison and Mount Baldwin (fig. 2). This ridge runs roughly north and south, and joins the main Mammoth Crest slightly to the east of Red Slate Mountain (elevation, 13,152 feet).

VEGETATION

A single lake of the upper basin, Lake Constance, is above the general timberline. The other eight are surrounded in varying degree by light growths of lodgepole pine, mountain willow,

FIGURE 1.—Convict Creek Basin.
(Aerial photograph courtesy of Symons Flying Service, Bishop, Calif.)

1. Mount Morrison
2. Mount Baldwin
3. Red Slate Mt.
4. Lake Constance
5. Lake Witsanapah
6. Bighorn Lake
7. Lake Dorothy
8. Cloverleaf Lake
9. Lake Edith
10. Lake Genevieve
11. Bright Dot Lake
12. Lake Mildred
13. Convict Creek Canyon
14. Convict Lake

and a small assortment of hardy shrubs. Limber pine, whitebark pine, and mountain hemlock occur rarely, and on a few favorable spots below 10,000 feet there are stands of aspen. Convict Lake is surrounded by sagebrush, Jeffrey pine, aspen and cottonwood, willow, and mountain mahogany. Beginning with the highest lake the study area grades from the Hudsonian life zone through the Canadian into the upper part of the Sierra transition.

Aquatic rooted plants are scarce in the upper basin, and only Lakes Genevieve, Edith, and Cloverleaf were observed to support them in notable quantities. A half-acre bed of *Ranunculus* is present in a shallow inlet bay of Lake Genevieve, and small patches of the same species were found in shallow, sandy areas at the inlet end of Lake Edith. Small rushes (*Juncus* sp.) grow in the shallows of Lakes Cloverleaf and Edith. Convict Lake supports moderate growths of *Ranunculus* and *Myriophyllum* in a few sandy-bottom areas. A filamentous green alga (*Rhizoclonium* sp.) is fairly abundant in Lakes Cloverleaf and Mildred, and is present sparsely in Lakes Edith, Bright Dot, and Convict.

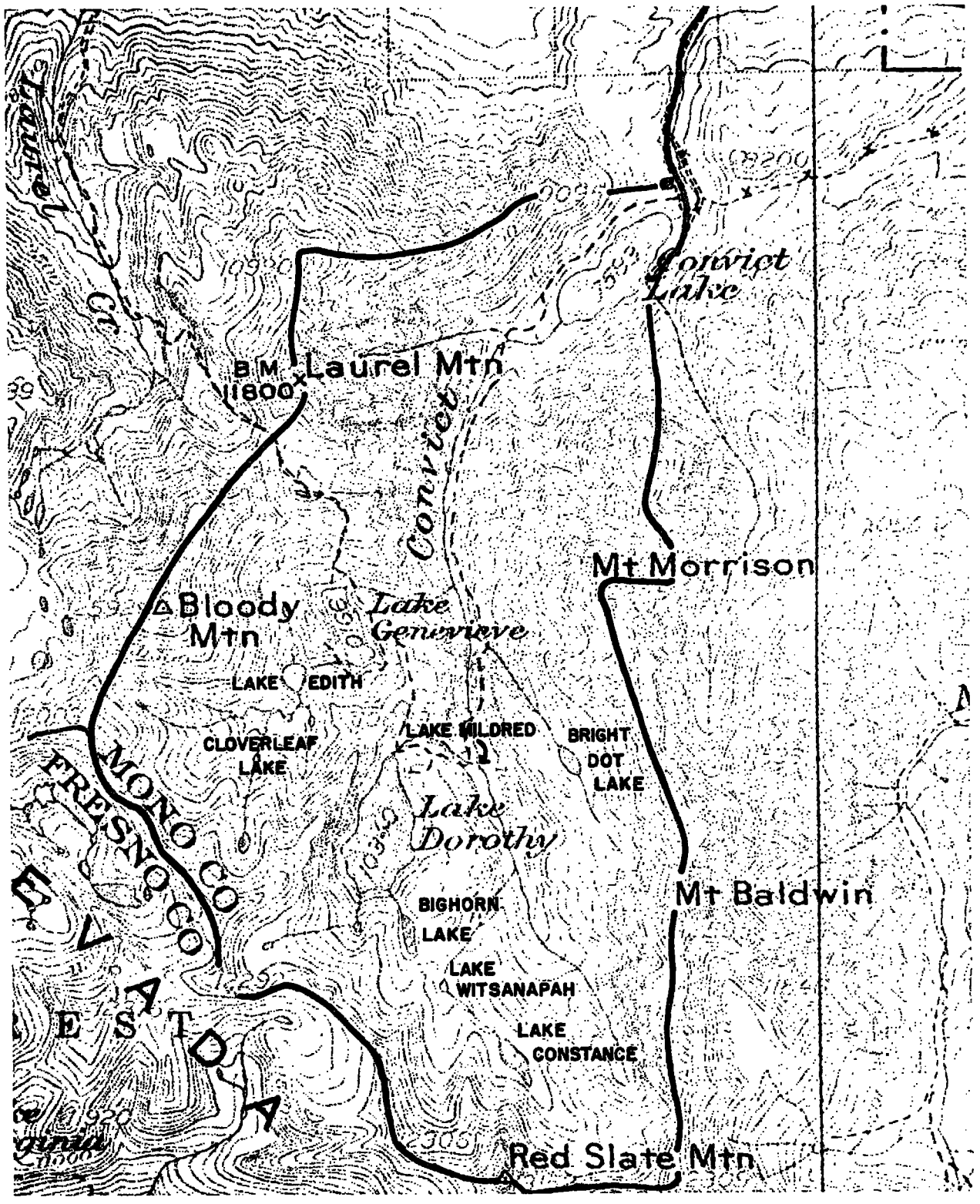

FIGURE 2.—Topography of Convict Creek Basin. (Drainage area enclosed by heavy black line. Section enlarged from Mount Morrison Quadrangle, United States Geological Survey, 1934.)

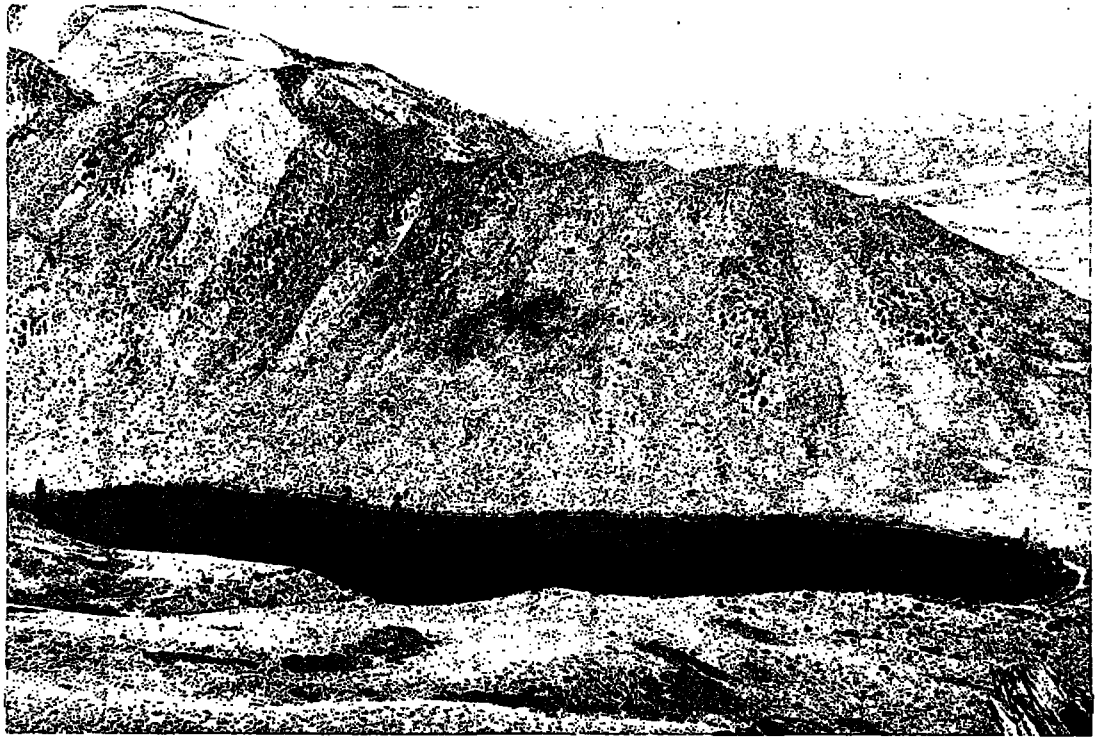

FIGURE 3.—Convict Lake, from glacial moraine to the east; main crest of Sierra Nevada in background.

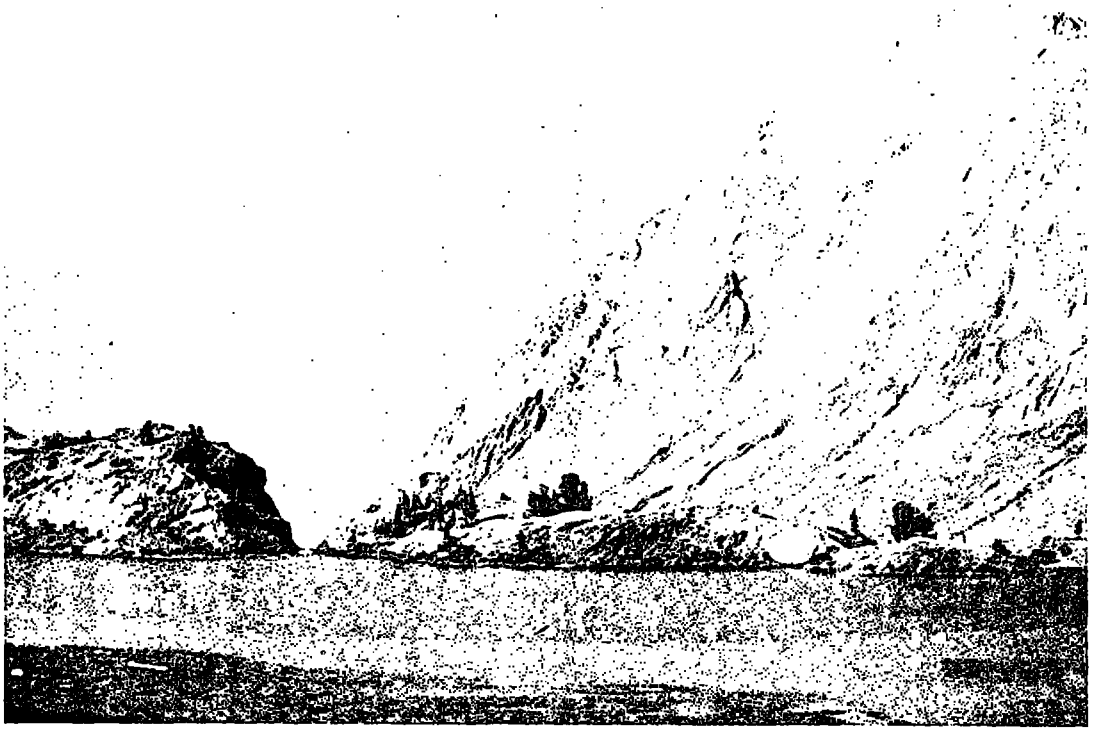

FIGURE 4.—Lake Mildred, from point on west shore; looking northeast toward outlet.

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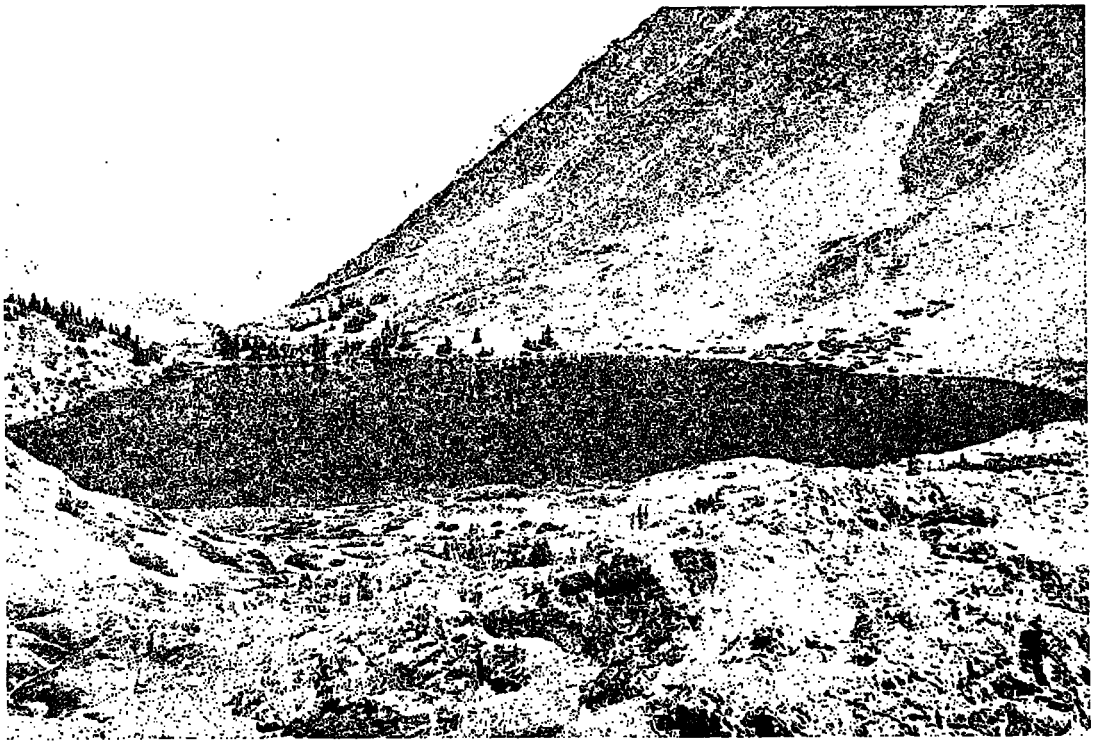

FIGURE 5.—Bright Dot Lake, from ridge above south shore; Convict Creek Canyon located below outlet at far end.

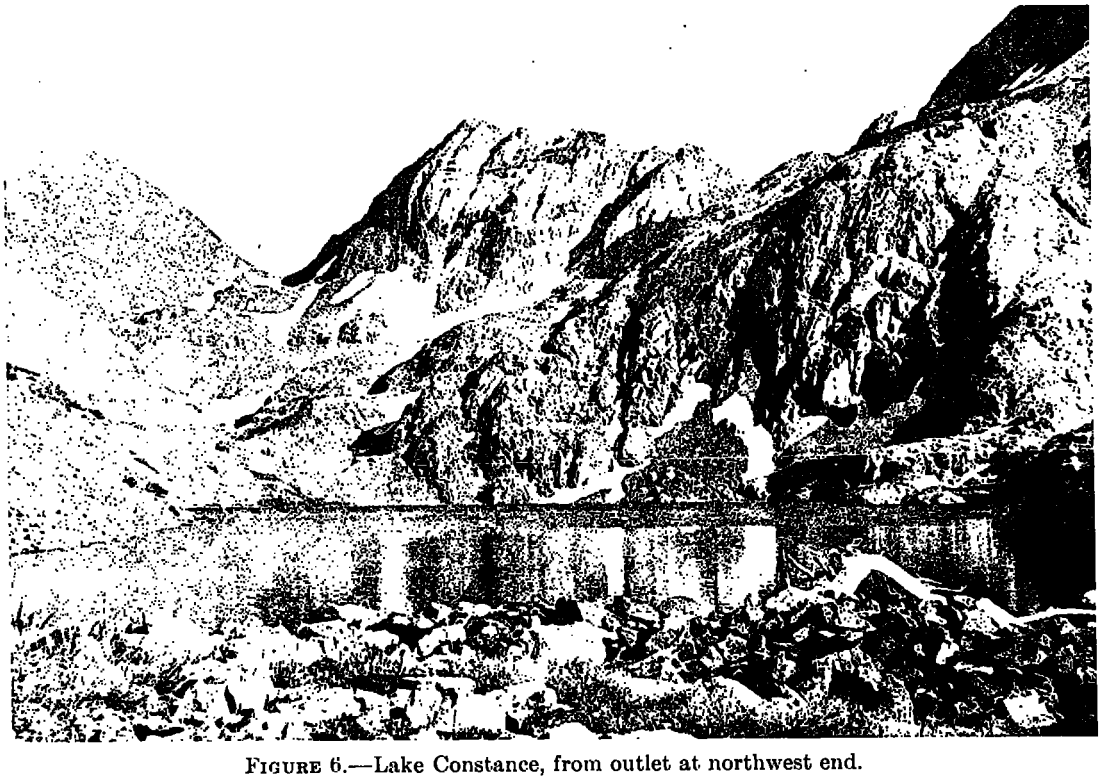

FIGURE 6.—Lake Constance, from outlet at northwest end.

FIGURE 7.—Lake Witsanapah, looking southeast toward Red Slate Mountain.

FIGURE 8.—Bighorn Lake, looking southeast toward Red Slate Mountain; outlet in foreground.

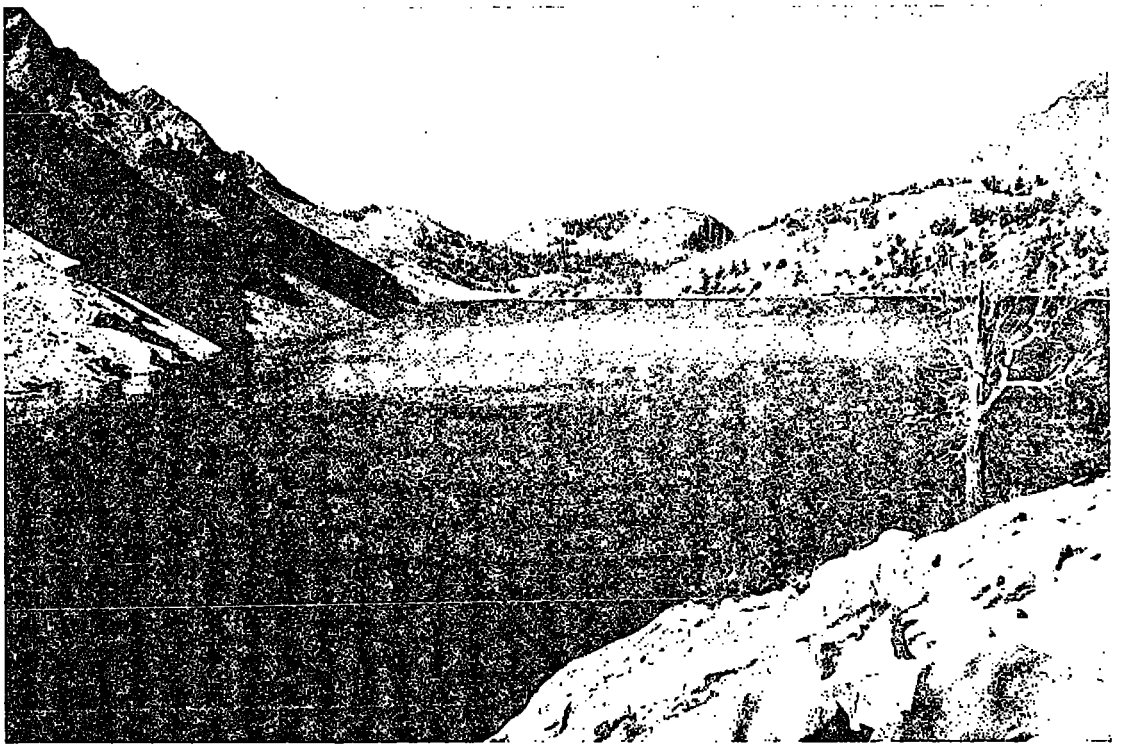

FIGURE 9.—Lake Dorothy, from point on south shore.

FIGURE 10.—Cloverleaf Lake, looking east toward Mt. Morrison; inlet in foreground.

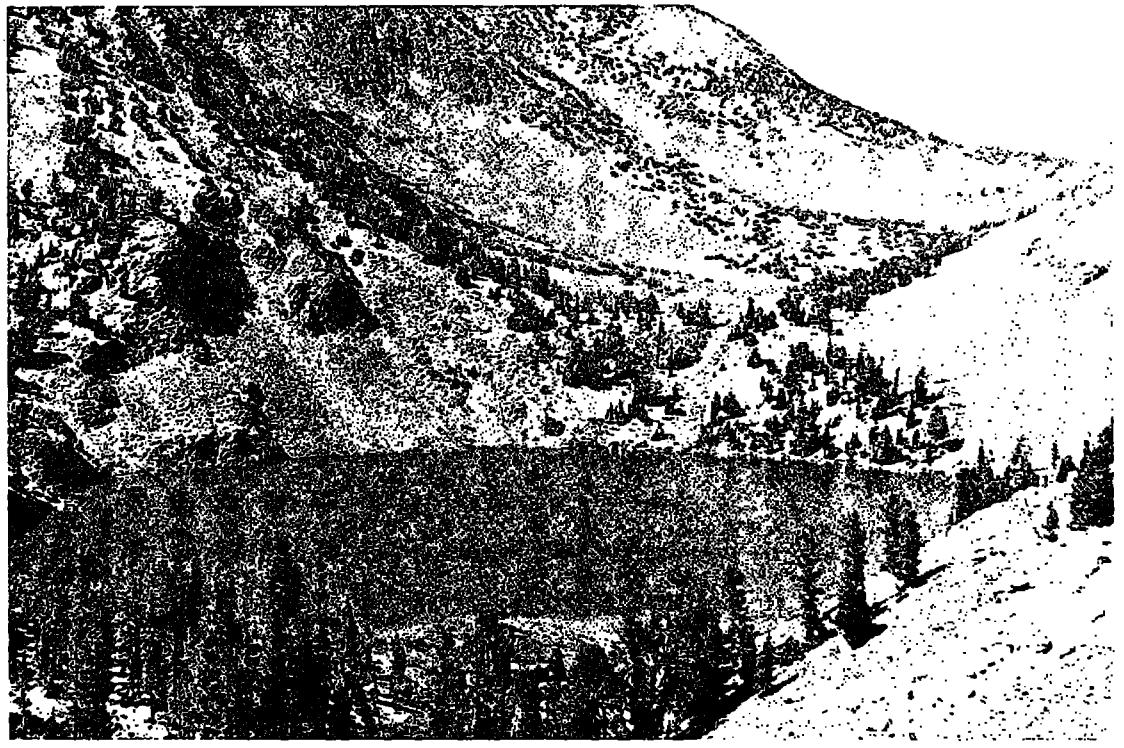

FIGURE 11.—Lake Edith from point above south shore; inlet shoals in foreground.

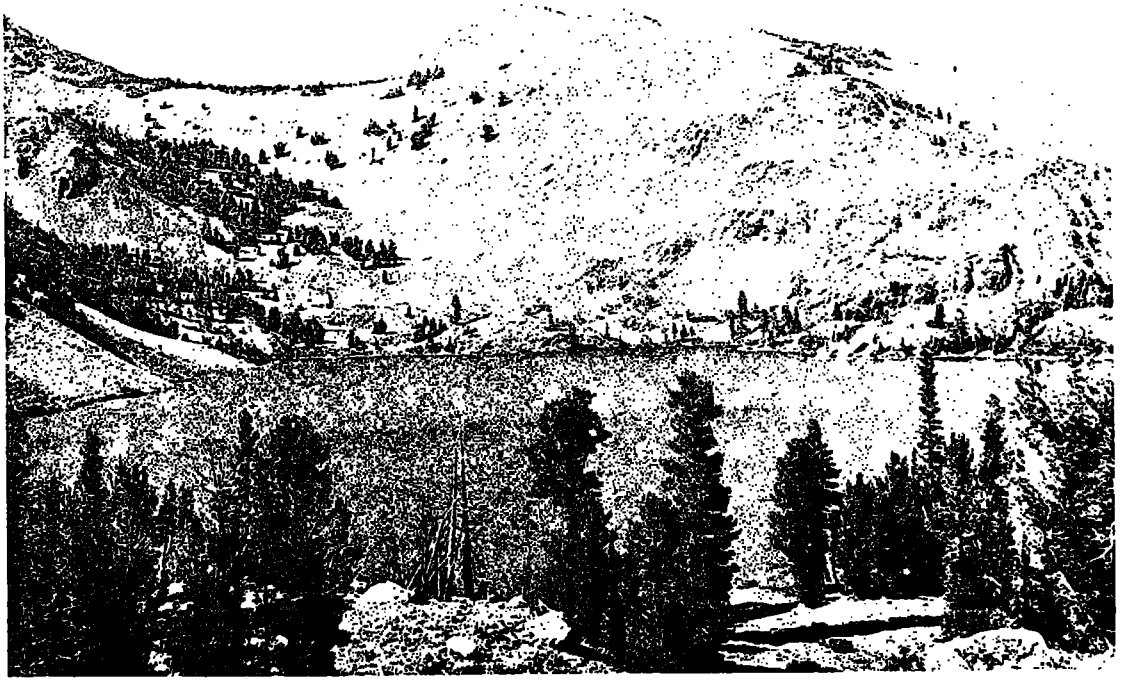

FIGURE 12.—Lake Genevieve, looking northward from point above south shore.

CLIMATE

The climate of the eastern slope of the Sierra Nevada is similar to that of other western mountain areas which lie to leeward of high ranges, with respect to prevailing westerly winds and Pacific storm systems. Summer rains fall on the western slopes, and the high country about Convict Creek Basin is dry from May to October except for scattered thunderstorms. Summer daytime temperatures in the basin reach 70° to 75° F., dropping into the thirties at night. Winters are characterized by heavy snows, severe windstorms, and frequent subzero temperatures. Winter winds are almost constant among the high peaks, and velocities to 80 miles per hour have been recorded at Convict Creek Station. The average duration of ice cover on the upper basin lakes is not known, but is estimated to be 2 or 3 months longer than on Convict Lake, which in 1951–52 was iced over from December 20 to May 1. In 1953, after a somewhat milder winter, the ice left the highest lake in the upper basin (Lake Constance) in mid-July.

GEOLOGY

The Sierra Nevada is approximately 430 miles long and occupies a large part of eastern California, extending from Tehachapi Pass in the south to the Feather River Basin in the north. It is from 40 to 80 miles wide and consists essentially of a single, tilted granitic block of the earth's crust, formed by uplift during the end of the Pliocene and the beginning of the Pleistocene epochs. The range is strongly asymmetrical in profile. The western side slopes gradually, and the eastern side is an abrupt fault escarpment with many peaks in excess of 13,000 feet. The main axis of the Sierra is north and south, but in the vicinity of Bishop, Calif., it bears westward bypassing an extensive volcanic area dominated by Mammoth Mountain. The Sierra Nevada is not a simple linear mountain range, but is broad enough to bear numerous smaller ranges; Mammoth Crest is a remnant of one of these, and a part of it forms the southwest boundary of Convict Creek Basin. Convict Creek is one of several streams that drain the north slope of this westerly bearing section of the main range.

Four glacial cycles occurred in the million-year duration of the Pleistocene epoch, and as a result of this tremendous glaciation several thousand lakes now exist throughout the range. These lakes are all young geologically, as none are older than the most recent glacial cycle. Some Sierra lakes are more recent, as evidenced by the existence of glaciers which are still in the process of recession. As the earth warmed and the last glacial cycle came to an end, lakes of two principal types were created: those occupying bedrock basins and those held by morainal deposits. Both types are found in Convict Creek Basin.

The upper basin is composed principally of hornfels and slaty hornfels, quartz monzonite, granodiorite, granite, crystalline limestone, and diorite (Mayo 1934). Metamorphic rock is the predominant substrate material in which the upper lakes lie (fig. 3) and Convict Creek Basin is perhaps somewhat unique in this respect, since the Sierra is largely granitic. The lower basin, which encloses Convict Lake, is composed of alluvium and morainal materials resulting from erosion and glaciation of the area above.

Valleys harboring the upper lakes were formed early in the Pleistocene epoch and were later undercut by vigorous canyon formation and consequently left hanging (Kesseli[5]). Lakes Genevieve and Bright Dot hang 500 and 1,000 feet, respectively, above Convict Creek canyon. Lake Dorothy's valley ends about 450 feet above Lake Mildred, and the valley from Lake Constance hangs by a similar amount.

With the exception of Lake Witsanapah, all of the upper lakes lie in bedrock. Lake Dorothy occupies a basin of hornfels and slaty hornfels, quartz monzonite and a variety of less prevalent materials, and is retained by a bedrock ridge. Lake Constance lies in diorite and metaquartzite, and is held by a small morainal ridge. Lake Bighorn lies in hornfels and slaty hornfels, and is retained by a block moraine of the same material. Two block moraines of hornfels from the Lake Constance valley glacier form the basin of Lake Witsanapah.

In the northwest group, Cloverleaf Lake lies in a basin of quartz monzonite, granodiorite, and other less prevalent rocks and is held by morainal materials. Lake Edith occupies a basin of hornfels and slaty hornfels and is retained by a small block moraine. Lake Genevieve lies in metaquartzite and hornfels and is separated from the main

[5] Pleistocene glaciation in the valleys between Lundy Canyon and Rock Creek, eastern slope of the Sierra Nevada, California, by J. E. Kesseli. Vol. 1, Part IV, Moraines of the Convict Creek Valley. Pp. 167–230. Unpublished Ph. D. thesis, University of California, 1938.

canyon of Convict Creek by a strike-oriented metamorphic ridge.

Bright Dot Lake lies in hornfels and slaty hornfels and is held by numerous low bedrock knolls, through which its outlet drops into Convict Creek, a thousand feet below. Lake Mildred, the lowest lake of the upper basin, also occupies a basin of hornfels and slaty hornfels. Immediately after cutting through the bedrock ridge which retains Lake Mildred, Convict Creek begins its abrupt drop down the main canyon to Convict Lake. Approximately a mile long and a half-mile wide, Convict Lake is the largest lake in the basin and receives the drainage of the nine upper lakes. It occupies a terminal glacial basin and is surrounded by vast morainal deposits, attesting to the heavy glaciation of the area above.

PHYSICAL CHARACTERISTICS OF THE LAKES

METHODS

Perimeter surveys of the lakes were made by triangulation and stadia, following a procedure similar to that given in the "plane table survey" outlined by Welch (1948). Shoreline positions were marked with large pieces of white sheeting to supplement the few prominent natural objects. Soundings were made with a portable, wire-line instrument (Reimers and Pister, 1953), and were located by cross bearings along transects between flagged points on shore; they averaged about one per acre, with a denser pattern on the smaller lakes. Hydrographic maps were prepared from these data and lengths of shorelines and areas at various contour levels were calculated from them. Standard formulas were employed to calculate volumes, volume developments, mean slopes, and shore developments. The composite maps, showing topography, selected morphometric features, graphic and other data, appear on pages 494–503. Lake elevations were obtained from the United States Geological Survey map of 1934 (Mount Morrison Quadrangle) and are indicated on the maps.

Air and water temperatures were measured with a Foxboro resistance thermometer graduated in half-degrees Fahrenheit (−20° to +130°). Temperature observations included vertical series over the deepest point in each lake, air temperatures, and surface temperatures at the points of inlet and outlet. Water transparency was measured in the middle of calm days with a white Secchi disk 10 centimeters in diameter and the mean of several disappearance and reappearance values, in feet, was used as the final estimate.

BOTTOM AND DRAINAGE CONDITIONS

Littoral bottom areas of the lakes are typically steep-sloped and rocky, although sandy or gravelly shoals are associated with the inlet streams and some of the outlets. In each lake basin, parts of the underwater slopes consist of talus or jumbles of large, broken rock, and the "productive shoal area" in these places is nonexistent. Seven of the lakes have high percentages of this bottom type (table 1). The other 3 lakes (Mildred, Cloverleaf, and Bighorn) are relatively shallow and are not directly flanked by ridges, so that the proportions of sandy shoal are larger. Although these sandy and gravelly areas presumably produce more trout food than rocky areas, they are relatively barren when compared with shoals of similar gradient in lowland lakes. Neither soil nor mud was found in the shallow areas of any of the lakes, and the scarcity of aquatic vegetation has been mentioned. Shoreline features are illustrated in photographs of the lakes (figs. 3–12).

Bottom materials were classified as bedrock, talus and broken rock, gravel, sand, mud, ooze, and detritus. Their distribution pattern varies somewhat among the 10 lakes, owing to differences in substrate, form of individual basins, and surrounding terrain; yet the character of the littoral and sublittoral is much the same throughout: rock shelves, boulders, submerged talus deposits, sand, and gravel shoals with protruding rock. As the profundal zone is approached in the deeper lakes, bottom materials grade into the mud, organic ooze, and fine detritus from which most bottom organisms were taken in samples. The gradation is gradual in a few areas, but interrupted by bedrock formations and blocks of rock in most. Variations of several feet in depth within a few horizontal feet were encountered while taking soundings below 150 feet in Lake Dorothy, and below 100 feet in Lake Constance. Because of slate chips and bedrock, several attempts were often required to obtain one productive Ekman dredge sample in some deep water areas.

Small but well-defined streams flow into and out of Lakes Constance, Witsanapah, Cloverleaf,

TABLE 1.—*Distribution of bottom materials in the littoral zones of the lakes of Convict Creek Basin*

[Visual estimation of bottom types from shoreline to a depth of 20 feet]

Lake	Percentage of bottom types			
	Bedrock	Talus and large broken rocks	Gravel	Sand
Constance	30	60	5	5
Witsanapah	20	60	5	15
Bighorn	20	30	10	40
Dorothy	15	70	5	10
Bright Dot	20	35	15	30
Mildred	5	10	15	70
Cloverleaf	15	5	10	70
Edith	30	50	5	15
Genevieve	10	65	5	20
Convict	20	50	10	20

Edith, and Genevieve. Lakes Mildred and Convict receive and discharge the main stem of Convict Creek, which provides a limited amount of good spawning area. Evidence of trout spawning was found in the inlets of six of these lakes; the inlet of the other (Lake Constance) is too small and steep for spawning. Lakes Bright Dot, Bighorn, and Dorothy have permanent outlets, but no principal inlets; they receive water from many small rills and from seepage. Water does not flow over appreciable distances of substrate before being discharged, even into the lower lakes, because of the compactness of the drainage. Melting snow and ice is the source of practically all water entering the lakes, and the rate of water exchange is considered to be low in all lakes except Mildred and Witsanapah. In these two lakes the volume of stream flow is comparatively high in relation to lake volume. Variations in lake levels have no effect on lake areas except in Lakes Mildred and Cloverleaf, where small amounts of shoal area are added during periods of peak runoff. In the higher lakes of the drainage the rate of deposition of bottom materials is extremely low. Although Lakes Genevieve, Mildred, and Convict undoubtedly receive more fine material from their larger inlets, all streams of the basin are clear and unsilted throughout the heaviest runoff.

MORPHOMETRY

Morphometric and other physical features of each lake are presented on maps (pp. 494–503) and summarized for all 10 lakes in tables 2 and 3. The lakes range in surface area from 4.4 to 168.0 acres, and three size groups may be noted. The two smallest and the two largest lakes are comparable as pairs; Lakes Witsanapah and Bighorn are 4.4 and 6.5 acres, respectively, whereas Lakes Dorothy and Convict are 151.8 and 168.0 acres. The remaining six lakes form an evenly distributed series between these extremes.

TABLE 2.—*General physical features of the lakes in Convict Creek Basin*

Lake	Elevation (feet)	Surface area (acres)	Volume (acre-feet)	Maximum depth (feet)	Maximum length (feet)	Maximum width (feet)	Length of shoreline		Direction of main axis
							Feet	Miles	
Convict	7,583	168.0	14,810	140	4,597	2,053	12,250	2.32	NE-SW
Bright Dot	10,650	27.5	1,092	80	1,522	1,158	4,515	.85	NW-SE
Mildred	9,900	10.7	290	60	1,126	572	3,300	.63	NW-SE
Bighorn	10,675	6.5	103	35	1,160	490	2,848	.54	NW-SE
Witsanapah	10,760	4.4	124	50	700	410	1,800	.34	N-S
Constance	10,950	33.6	2,600	170	2,490	1,035	6,896	1.30	NW-SE
Genevieve	9,910	42.3	2,570	120	2,500	1,040	6,800	1.29	NW-SE
Edith	10,100	18.0	1,070	110	1,216	986	3,690	.70	NW-SE
Cloverleaf	10,310	11.6	141	25	987	930	5,498	1.04	NW-SE
Dorothy	10,340	152.0	20,600	290	5,190	1,880	13,020	2.47	N-S

TABLE 3.—*Specific physical characteristics considered most influential on relative productivity levels of the lakes in Convict Creek Basin*

Lake	Mean slope (percentage)	Shoal area 0 to 20 feet (percentage)	Shore development	Mean depth (feet)	Transparency (feet)	Temperature (° F.)		Heat intake [1]	
						Bottom-surface range	Lake mean	Summer heat income	Annual heat budget
Convict	16.7	13.1	1.28	88	51	44.0–58.5	51.4	18,173	22,984
Bright Dot	17.7	28.8	1.16	39	55	47.0–58.0	55.0	10,424	12,556
Mildred	23.2	43.8	1.41	27	40	50.0–54.5	52.0	5,822	7,298
Bighorn	19.5	63.4	1.47	16	Bottom	39.5–57.5	52.7	4,130	5,005
Witsanapah	30.2	34.5	1.16	28	30	42.0–50.0	47.4	3,827	5,358
Constance	40.4	19.5	1.61	71	60	40.0–50.5	42.9	4,420	8,086
Genevieve	26.7	18.3	1.42	61	59	41.0–56.0	49.9	11,023	14,358
Edith	27.5	21.3	1.14	59	46	39.5–57.5	47.8	8,601	11,826
Cloverleaf	13.2	81.4	2.18	12	Bottom	50.5–52.5	51.6	2,514	3,170
Dorothy	33.9	9.0	1.44	136	67	40.0–58.5	47.0	17,967	25,402

[1] Expressed in gram calories per square centimeter of lake surface.

Seven of the lakes have simple basin forms with single and more or less centrally located depressions. Of these seven, all but Convict Lake are fairly uniform in slope from the margin to the greatest depth. Mean slope values for the 10 lakes range from 13.2 to 40.4 percent, with a mean for the drainage of 24.9 percent. Convict Lake has an extensive flattened bottom with the result that about one-half of the surface area is contained within the 120-foot contour. Lake Cloverleaf has four arms, each with a shallow depression. Lake Mildred has two distinct, cup-like depressions, and Lake Dorothy takes the form of a long, deep scar, with the deepest point midway in its length and secondary depressions toward each end.

The general steepness of lake margin slopes dictates rather low shore development values for nine of the lakes, the range of these being 1.14 to 1.61. Cloverleaf Lake, due to its peculiar shape, has a value of 2.18. The relative extent of shoal area to a depth of 20 feet was calculated for all lakes, and these values are listed with other physical features affecting productivity (table 3). Although the depth of 20 feet is arbitrary, a proportional measurement of shoal area is usually indicative of the potential for bottom-food production, and it should be noted that only in the shallowest of these lakes do the shoals amount to a considerable percentage of total surface area.

Maximum depths, mean depths, and total volumes of the lakes are given in tables 2 and 3, and are indicated on the maps. No serious effort was made to locate the points of absolute maximum depth. The depth at the lowermost contour is given as maximum for each lake, and the absolute maximum in all cases is within one contour interval of this figure.

Further examinations of dimensional features may be made by referring to the maps and photographs. For present purposes it is sufficient to state that enough variations in area, depth, and volume exist among the lakes to permit comparisons of chemical and biological features with physical dimensions and depth distributions.

TRANSPARENCY

Like most high-altitude glacial lakes, those in the study area are exceptionally clear. Pelagic algae were rare in the samples, and, although the variations in observed transparency are attributed to plankters, the zooplankton density in general was too light to interfere seriously with visibility (table 3). Lakes Bighorn and Cloverleaf are shallow, and are transparent to their bottoms. The Secchi disc was visible for distances of 40 to 67 feet in the lakes of greater depth; readings for each lake are given on the maps. Lake Witsanapah, 50 feet deep, was anomalous in being clear to only 30 feet. This relatively low transparency was considered due to a temporary silted condition brought about by agitation during the peak of snow-melt runoff, as Lake Witsanapah is the smallest lake of the group and has a relatively large inlet. No net plankton was found in this lake.

TEMPERATURE

The range of temperature from surface to bottom was measured once at the point of greatest depth for each lake, at intervals of 10 feet or less. Time did not permit continued observations for all lakes, and these measurements were sufficient to establish a probable summer maximum of 60° F. for the lakes of the upper basin, an average summer minimum of 43°, and to show that some stratification occurs in the deeper lakes. The highest water temperature measured in the upper basin was 58.5° F., at the surface of Lake Dorothy; other surface temperatures ranged from 50.0 to 58.0°. The deepest strata of Lakes Mildred, Bright Dot, and Cloverleaf indicated August and early September temperatures of 50.0, 47.0, and 50.5°, respectively. Convict Lake had a minimum summer temperature of 44.0°, and minimum temperatures of the other 6 lakes ranged from 39.5 to 42.0 degrees.

A graph of a summer vertical temperature series, with the date of observation, appears on each lake map on pages 494–503. All observations were made in July, August, and early September of 1950, and the series are summarized for all lakes in table 4. In the upper basin, Lakes Genevieve and Edith had weak thermoclines between 30 and 50 feet in August. Lakes Dorothy, Constance, and Bright Dot were stratified in August, but had no thermoclines. Lakes Mildred and Cloverleaf were nearly homothermous. The other two shallow lakes, Bighorn and Witsanapah, exhibited gradients of a few degrees but did not stratify. Convict Lake stratifies in summer and develops a weak thermocline.

Weekly temperature observations were maintained on Convict Lake from April 1951 to May

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1953 (Reimers and Combs,[6] and significant dates of autumn and spring circulation were established. Autumn overturns were recorded on closely corresponding dates in the two years, November 30, 1951, and December 4, 1952. The time of spring circulation is affected more by the nature of the preceding winter. The winter of 1951–52 was very severe, with ice cover on Convict Lake until the end of April, and the beginning of circulation was delayed to May 4. In the spring of 1953, following an average winter, differential heating of upper strata was evident the first week in April. No overturn data are available for the lakes of the upper basin and observations are limited to a few in mid-July 1953, 1 to 3 weeks after the ice had melted. Lake Constance was homothermous at 40° on July 18, and other lakes had weak gradients with deeper water approaching the temperature of maximum density. The foregoing indicates that the duration of ice cover in a normal year is 6 to 7 months on the upper lakes, and approximately 4 months on Convict Lake.

Heat intake, expressed as summer heat income and annual heat budget, has been grossly estimated and the results appear in table 3. A mean winter temperature of 36° F. (2.2° C.), based on 2 years of observations on Convict Lake, was arbitrarily used in the heat budget calculations for all lakes since no winter observations are possible on the upper lakes. An inspection of the table shows that heat intake values are controlled by the mean depths of the lakes rather than by temperature differences. For this reason heat budget values cannot be compared among the lakes, nor do they provide a reliable thermal index for association with other physical characteristics.

[6] A study of the thermal characteristics of Convict Lake, Mono County, Calif., with a proposed method for the evaluation of temperature in lakes, by Norman Reimers and B. D. Combs. Unpublished manuscript, U. S. Fish and Wildlife Service, 1954.

RANKING OF THE LAKES IN TERMS OF COMBINED PHYSICAL FACTORS

In physical evaluations, irregular shorelines, low declivity, shallowness, and high temperatures are considered to operate in favor of increased production. Climate is considered similar for all the lakes, although the growing season for Convict Lake is longer than the others and would move this lake up the scale if included. Increasing area is sometimes found to signify decreasing productive capacity (Rounsefell 1946), but such an influence is questionable in the present series and the inclusion of area would not change the physical ranking of lakes if growing season were also added. Only lake means have been used from the temperature data since ranges do not apply directly, and means of the shoal strata refer to only parts of lakes.

TABLE 4.—*Vertical distribution of temperature in the lakes of Convict Creek Basin*

[Temperatures in degrees Fahrenheit]

Stratum	Dorothy Aug. 8, 1950	Constance Aug. 2, 1950	Convict July 3, 1950	Genevieve Aug. 22, 1950	Edith Aug. 16, 1950	Bright Dot Aug. 25, 1950	Mildred Sept. 3, 1950	Witsanapah Aug. 3, 1950	Bighorn July 25, 1950	Cloverleaf Aug. 25, 1950
Surface	58.5	50.5	58.5	56.0	57.5	58.0	54.5	50.0	57.5	52.5
10 feet	58.0	50.0	56.5	55.5	55.0	57.0	52.5	48.5	55.5	51.5
20 feet	56.0	50.0	55.5	55.5	54.0	56.5	51.0	48.0	47.0	50.5
30 feet	51.0	48.5	55.0	55.0	51.5	56.5	50.5	46.5	39.5	
40 feet	48.5	46.0	53.5	54.0	46.0	55.5	50.5	42.5		
50 feet	47.5	44.5	52.0	47.5	43.0	51.0	50.0	42.0		
60 feet	46.5	43.0	52.0	44.0	41.0	48.0	50.0			
70 feet	45.0	42.5	50.5	42.5	40.0	47.5				
80 feet	44.0	42.5	48.0	41.5	40.0	47.0				
90 feet	44.0	42.0	46.0	41.5	40.0					
100 feet	44.0	41.5	45.0	41.0	40.0					
110 feet	44.0	41.5	44.0	41.0	39.5					
120 feet	43.5	41.0	44.0	41.0						
130 feet	43.0	41.0	44.0							
140 feet	43.0	40.5								
150 feet	42.5	40.5								
160 feet	42.5	40.0								
170 feet	42.5	40.0								
180 feet	42.5									
190 feet	42.5									
200 feet	42.5									
210 feet	42.5									
220 feet	42.0									
230 feet	42.0									
240 feet	42.0									
250 feet	42.0									
260 feet	41.5									
270 feet	41.5									
280 feet	40.5									
290 feet	40.0									

Heat budgets could not be used because of their inability to indicate heat independently of size and depth. Transparency was omitted because of nearly uniform clarity of the waters, and because the two shallowest lakes were transparent throughout.

In table 5 the 10 lakes have been arranged in high-to-low order on the basis of average values derived from shore development, mean slope, percentage of shoal area, mean depth, and mean temperature. In order to average these factors and establish a ranking order among the lakes, a ranking scale of 10 was adopted and the absolute range of each factor was reduced to a range of 10–0. For each factor, highest rank (10) was given to the lake with maximum value on the absolute scale and lowest rank (0) was given to the lake with minimum value.[7] The column of averages reported in table 5 thus gives equal weight to each physical factor considered, and represents a proportionate scale of productive capacity in terms of combined physical factors. In the combined ranking, shallow Lakes Cloverleaf and Bighorn are far above the average for the drainage, nearly all factors being favorable. Lake Witsanapah does not fall within the favored shallow group because of excessively steep slope, regular shore, and low temperature. Bright Dot Lake's position in the scale is raised considerably by higher water temperature, and Convict Lake ranks higher than its depth would indicate due to favorable slope and temperature conditions. Lakes Genevieve and Edith are slightly below average, and deep Lakes Constance and Dorothy are indicated as physically poor.

TABLE 5.—*Ranking of the lakes according to proportionate ratings of selected physical measurements*

Lake	Proportionate ratings					Average and proportionate rank
	Shore development	Percentage slope	Mean depth	Percentage shoal area	Mean summer temperature	
Cloverleaf	10.0	10.0	10.0	10.0	7.2	9.4
Bighorn	3.2	7.7	9.7	7.5	8.9	7.4
Bright Dot	1.9	8.4	7.8	2.7	10.0	6.2
Mildred	2.6	6.3	8.8	4.8	7.5	6.0
Convict	1.3	8.7	3.9	5.7	7.0	5.3
Witsanapah	1.9	3.7	8.8	3.5	3.7	4.3
Genevieve	2.7	5.0	6.0	1.3	5.8	4.2
Edith	0	4.7	6.2	1.7	4.0	3.3
Constance	4.5	0	5.2	1.4	0	2.2
Dorothy	2.9	2.4	0	0	3.4	1.7

SUMMARY OF PHYSICAL CHARACTERISTICS

Discussion and tabulations of physical features include distribution of littoral bottom types, nature of inlet and outlet streams, morphometry, water transparency, and summer temperature characteristics. Detailed hydrographic maps were prepared to aid interpretation of the data.

Steep slopes and rocky bottoms characterize seven of the lake basins, and three of the shallower lakes have a predominance of sandy bottom. The lakes showed no significant altitudinal grouping with respect to summer water temperature; mean temperatures ranged from 42.9° to 55.0° F. Weak thermal stratification in the deeper lakes was evident in July and August. Comparison of ice cover duration between upper and lower parts of the basin indicates a three-month handicap in length of growing season for the higher lakes.

In the scale of potential productive capacity derived from morphometry and mean temperatures, shallower lakes ranked high due to both depth and temperature factors. Two of the deepest lakes were indicated as the poorest potential producers.

[7] The method of determining proportionate ratings on a 10-0 scale was suggested by R. A. Fredin and R. Lander of the Pacific Salmon Investigations, Fish and Wildlife Service. The following relations may be considered for any factor in which an increase in value is associated with greater productive influence:

$$(1)\quad \frac{\text{Value for given lake} - \text{minimum value of all lakes}}{\text{Range of values for all lakes}} = \text{Proportionate distance that the value of the given lake lies between the minimum and maximum for all lakes.}$$

To place this lake in a 10–0 scale (range=10–0), consider

$$(2)\quad \frac{\text{Value for given lake} - \text{minimum value of all lakes}}{\text{Range of values for all lakes}} = \frac{\text{Rank for that lake}}{10}.$$

If rank for that lake = X, solve

$$(3)\quad X = \frac{(10)\ \text{value for given lake} - \text{minimum value of all lakes}}{\text{Range of values for all lakes}}.$$

For any factor related inversely to productivity, equation 3 should be revised to

$$(4)\quad X = \frac{(10)\ \text{maximum value for all lakes} - \text{value for given lake}}{\text{Range of values for all lakes}}.$$

This procedure puts all factors on a common scale and permits placing the intermediate ranking lakes in proportion to their absolute values throughout the range 10–0. Rank values for each lake may then be averaged for a group of factors (e. g. physical factors), and the final or average ranking for the group will not be weighted by discrepancies in absolute range among the factors.

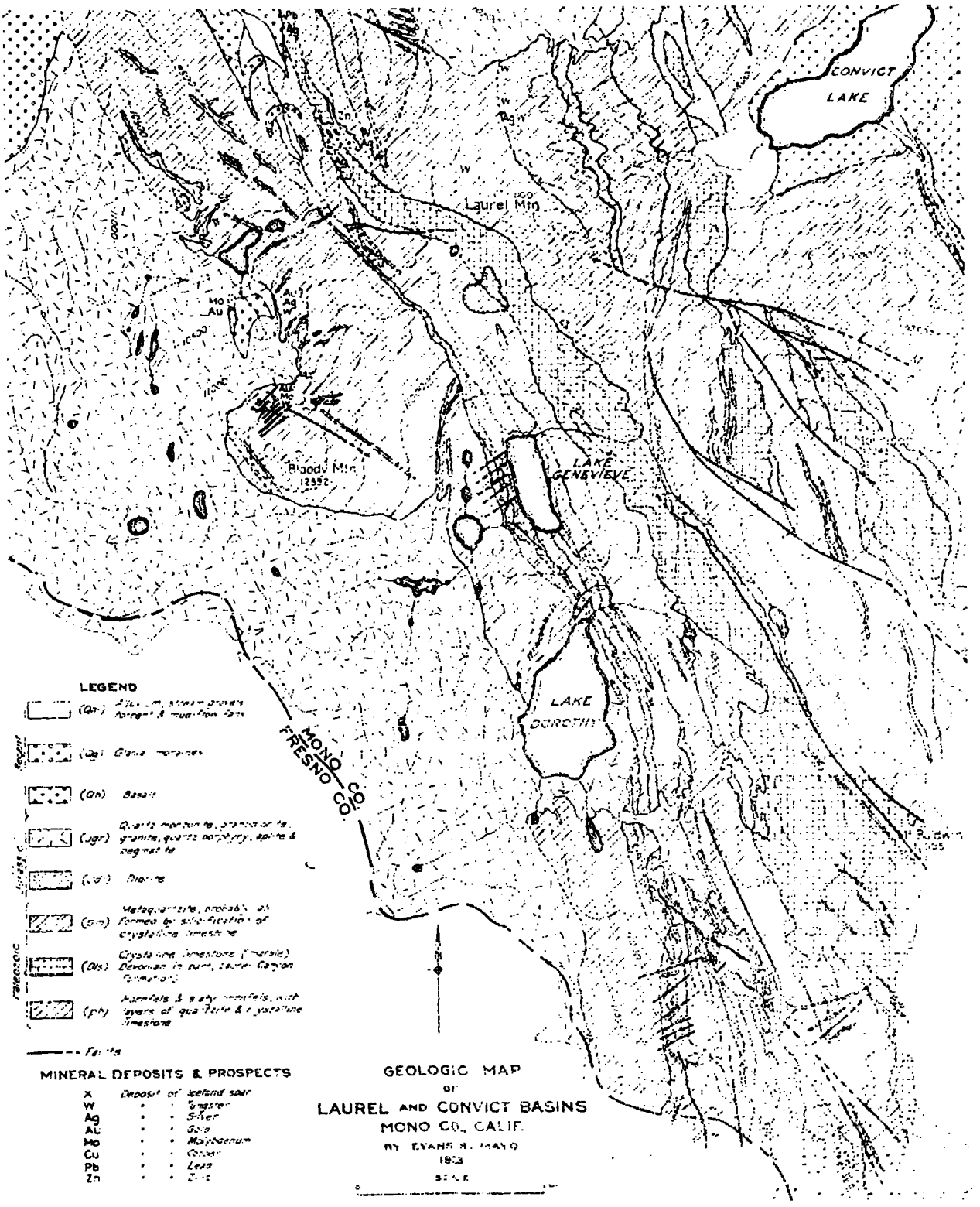

FIGURE 13.—Geologic map of Convict Creek Basin. (Enlarged from Mayo, 1934).

HYDROCHEMISTRY AND MINERAL SOURCES

Pearsall (1930) stated, "Any attempt to classify lakes on the basis of the dissolved substances is faced with the difficulty that a single series of analyses may not be representative owing to the possibility of abnormal conditions in one or more lakes of the series." Moreover, a complete description of any one lake should include the seasonal pattern of fluctuation. In this study it is assumed that chemical fluctuations are minimized because of the location of these lakes at the very origin of a compact drainage system, where the edaphic and biotic influences which cause abnormalities in chemical composition of the water are so slight as to preclude pronounced seasonal and other changes. Certain factors, such as pH and dissolved carbon dioxide, are subject to relatively rapid fluctuations and are limited in their usefulness; others, such as total dissolved solids and relative electrolyte composition, are considered more stable. In accordance with the objectives of lake description and comparison, emphasis is placed on those factors which appear least variable, since continued sampling of these lakes was not possible. Geochemistry is included in order to relate the mineral content of the water to the substrates of the drainage.

FIELD METHODS

Vertical series of water samples were taken at 10-foot depth intervals over the point of maximum depth in each lake, using a 1,200 cubic centimeter Kemmerer sampler. Hydrogen ion concentration was determined immediately with a Hellige comparator, and fixed oxygen samples were titrated at the base camp according to the Winkler method. A few water samples were titrated for methyl orange alkalinity.

Additional samples were collected at middepths in all lakes for detailed analysis, and at 10 feet below the surface and 10 feet above the bottom for partial analysis. Other samples for partial analysis were taken from inlet and outlet streams of all lakes having such streams. These samples were transferred to glass containers in special shipping crates and shipped to the United States Geological Survey, Quality of Water Branch, Salt Lake City, Utah, where the analytical work was performed.

Detailed analyses of the middepth water samples included total dissolved solids, loss on ignition, specific conductance, total and noncarbonate hardness and quantities of various ions. Partial analyses included specific conductance, hardness, and quantities of prominent ions.

COMPOSITION AND SOLUBILITY OF THE SUBSTRATE

The sources of dissolved inorganic matter may be both atmospheric and terrestrial. Probably the greatest proportion of mineral solutes in the waters of Convict Creek Basin results from the contact of drainage water with rock substrates. The rock types which occur in different parts of the area have been described previously and appear on the geologic map (fig. 13). The chemical compositions of these rock forms, as mineral sources, are interpreted from Clarke's (1924a) discussion of geochemistry, bearing in mind that similar rock formations from different geographic localities may vary somewhat in mineral constituent typology and chemical composition.

Igneous rocks are composed of numerous subtypes with feldspar, quartz, and micas predominating. Chemically, silica is the largest constituent, followed by alumina, alkaline metals, iron, and many trace elements. Quartz monzonite, quartz porphyry, and other granitoids (pegmatite, granite, aplite) resemble each other closely in having 70 to 80 percent SiO_2, 10 to 15 percent Al_2O_3, 1 to 8 percent alkaline metals (K_2O most abundant), 1 to 2 percent ferric and ferrous oxides, and less than 1 percent other minerals. Diorite and granodiorite differ slightly from this composition in having less than 60 percent silica and relatively more iron and phosphate.

Metamorphic rocks, with the exception of crystalline limestone, are similar in chemical composition to the igneous rocks described above. All have somewhat characteristic compositions. Quartzite and metaquartzite represent silicifications of sandstone and crystalline limestone, respectively. Hornfels are fine textured silicates produced by contact metamorphosis of shales. Quartzite has a high silica (80 percent) and ferrous iron content, but is lower than igneous rock in alumina, ferric iron, and alkaline metals. Hornfels contains nearly 60 percent SiO_2 and is noticeably different from igneous rock in that it has small but conspicuous amounts of SO_3 and copper. Meta-

quartzite and crystalline limestone are characterized by large percentages of calcium. The former rock contains about 50 percent silica, much alumina, and trace amounts of other elements. Crystalline limestone, basically $CaCO_3$, would be chemically simple were it not for varied impurities. Besides the prominent calcium and carbonate, it probably has significant quantities of MgO and SiO_2 plus other elements in trace amounts.

Clarke (1924a) also discussed the disintegration of rocks and attributes variation in decomposition rates largely to climatic (temperature and moisture) conditions. Solubility of rocks depends mainly upon the characteristics of the solvent. Oxygen, and especially CO_2, increase the solvent action of rainwater. Vegetation contributes further by adding organic acids to surface waters.[8] The electrolytic composition of water is also known to have a varied effect on the solubility of rocks. Certain general statements can be made as to the relative solubility of important minerals. Most of them are vulnerable to water containing carbonic acid. Silica (as a colloid), lime, magnesium, and alkali salts are readily dissolved, but compounds of aluminum and iron are nearly insoluble by comparison. Iron carbonate may be formed, but oxidizes rapidly to precipitate as ferric hydroxide.

CHEMICAL CHARACTERISTICS OF THE LAKES

Many limnologists have studied individual chemical elements as to distribution, fluctuation, and biological effect. Papers by Juday and others (1938), Rawson (1939), and Pearsall (1930) are a few examples of such treatment. However, because of the close, interrelated existence of dissolved gases, organic matter, and inorganic substances in natural water, it is not possible to separate the effects of individual substances entirely with regard to water composition and metabolism. Interaction of dissolved substances is evident in the carbon dioxide mechanism (discussed by Welch 1952, and Ruttner 1953) and in the electrolyte-specific conductance system (Rodhe 1949). Although relationships such as these are not completely understood it nevertheless seems desirable for a comparative study to begin with gross chemical conditions and to emphasize interrelationships of dissolved substances where possible.

Since data for this study are the result of analyses of samples taken in the months of July and August, the following presentation emphasizes the least variable factors and mineral relationships—an approach which better fulfills the objectives of description and comparison. Empirical values are given in parts per million which, according to Clarke (1924b), are the same as milligrams per liter for dilute solutions (nonsaline natural waters). Electrolytes have been calculated in milligram equivalents per liter of water, which represents their reactive weights, and percentages have been applied to show relative relationships.

Hydrogen Ion Concentration

Rawson (1939) considered pH an indicator of environmental conditions and described it as the result of many underlying chemical conditions. Basic factors which determine pH are difficult to elucidate and there is general agreement among limnologists that its true biological significance is rarely known. Most natural waters fall within the range 6.5 to 8.5 with highly productive waters on the alkaline side (pH around 8.0). Laboratory pH determinations for the Convict Creek Basin lakes were consistently higher than field measurements possibly due to the loss of free carbon dioxide from the samples. Values are omitted from tabular listing because of discrepancies between the two determinations, and because those taken in the field were too coarse to be used in comparing the lakes. In general, field determinations indicated that the basin's waters range close to neutrality (pH 7.0) with the Lake Genevieve group (Genevieve, Edith, and Cloverleaf Lakes) tending toward acidity and the remaining lakes ranging slightly above 7.0.

Dissolved Gases

Dissolved oxygen determinations (table 6) concern the top, middle, and bottom strata of each lake (middle strata in Bighorn and Cloverleaf Lakes omitted because of their shallowness). Intermediate levels are excluded since oxygen values were in agreement with the surface-bottom trend in all cases. The measured quantity of oxygen in the upper strata of the lakes ranged

[8] Bacterial action on alpine summits was reported by Clarke (1924a) to influence solubility. In drawing nourishment from snow and rain, these organisms convert ammonia to nitric acid which corrodes calcareous material. They further aid the solution of rock by decomposing sulfates and generating carbon dioxide from organic decomposition.

from 7.2 to 9.6 parts per million; that at middepth from 8.0 to 11.0 p. p. m.; and in the bottom strata, from 2.8 to 10.8 p. p. m. Only in the bottom strata of Lakes Edith and Genevieve did the dissolved oxygen content fall below 7.0 p. p. m.

Oxygen saturation values were corrected for altitude as described by Ricker (1934) and saturation percentages determined from a nomograph similar to that described by Welch (1948). The necessity for altitude compensation is demonstrated by uncorrected values (not shown) which are 3 to 4 parts per million higher than corrected values. All lakes were hypersaturated in the middle and upper strata. The bottom strata of Convict, Constance, Genevieve, and Edith Lakes were below saturation (table 6, column 14), but only the latter lake showed divergence of importance. Actual deficits in parts per million can be obtained by subtracting actual from saturation values. Absolute deficits exhibit little difference from actual deficits (less than 2 percent of saturation), since bottom waters are so near 4° Centigrade.

No analytical determinations were made for free carbon dioxide in any of the lakes because of the ease with which this gas escapes from water and because results are always uncertain due to difficulties in technique. However, greater accuracy can be obtained from pH and total alkalinity measurements by means of a stability diagram (Langlier 1946) and this method was used. In 5 lakes, the concentration of CO_2 ranged from 1 to 5 parts per million.

Dissolved Solids and Hardness

Total dissolved solids are the residue remaining after evaporation of a quantity of water and represent a measurement of both dissolved and colloidal matter (mineral and organic). Rawson (1951) stated that few lakes have less than 100 p. p. m. total residue, but Pennak (1945) reported a range of 13.0 to 55.4 p. p. m. for 8 alpine lakes in the Colorado Rocky Mountains. Table 7 indicates a range of 19.0 p. p. m. (Lake Dorothy) to 77.0 p. p. m. (Convict Lake), total dissolved solids for the lakes in Convict Creek Basin.

Loss on ignition, the difference in weight which results from firing the evaporated sample, represents the amount of organic matter, bound water, and volatile decomposition products of salts (Pennak 1945). If the latter is low, as in soft water, this determination is indicative of the dissolved organic content of the water. Pennak reported an average of 5.7 p. p. m. in 8 alpine lakes. Birge and Juday (1927) concluded that dissolved organic matter occurs in a reasonably definite quantity for each lake and does not show great variation with either depth or time. The average loss on ignition in the Convict Creek Basin lakes was 3.2 p. p. m. with a range of 2.0 to 5.4 p. p. m. (table 7). Expressed in relation to total dissolved solids, loss on ignition ranged from 3.9 percent in Convict Lake to 16.8 percent in Lake Dorothy.

The mineral content of the lake waters in Convict Creek Basin, as indicated by ash residues after firing, ranged from 15.8 to 74.0 p. p. m. with a basin average of 35.9 p. p. m. (table 7). These values are somewhat higher than the range of 9.7

TABLE 6.—*Dissolved oxygen present in the upper, middle, and lower depth strata of the lakes in Convict Creek Basin with saturation values corrected for altitude*

Lake	10 feet below surface				Middepth					Bottom				
	Temperature [1]	Oxygen (p. p. m.)		Percentage saturation	Depth (feet)	Temperature [1]	Oxygen (p. p. m.)		Percentage saturation	Depth (feet)	Temperature [1]	Oxygen (p. p. m.)		Percentage saturation
		Saturated	Actual				Saturated	Actual				Saturated	Actual	
Convict	13.6	7.9	7.7	98.0	73	10.0	8.5	9.1	108.0	130	6.6	9.3	8.8	94.0
Bright Dot	13.8	7.0	7.2	103.0	45	12.0	7.3	8.0	110.0	80	8.4	7.9	8.8	112.0
Mildred	11.3	7.6	8.5	111.0	30	10.3	7.8	8.9	114.0	60	10.2	7.8	9.0	116.0
Bighorn	13.2	7.1	9.3	>125.0						30	4.2	8.8	10.3	117.0
Witsanapah	9.1	7.7	8.6	111.0	30	8.2	7.9	8.7	111.0	50	5.4	8.5	10.8	>125.0
Constance	10.0	7.6	9.6	>125.0	85	5.6	8.4	8.4	100.0	170	4.5	8.6	7.6	89.0
Genevieve	13.1	7.3	7.9	108.0	65	6.2	8.6	11.0	>125.0	120	5.0	8.9	6.2	70.0
Edith	12.8	7.3	7.9	108.0	58	5.6	8.7	9.0	105.0	110	4.5	8.9	2.8	32.0
Cloverleaf	10.8	7.6	8.2	108.0						20	10.3	7.7	8.7	114.0
Dorothy	14.4	7.0	8.4	120.0	150	5.9	8.5	8.6	101.0	290	4.4	8.9	9.2	104.0

[1] Temperatures in degrees Centrigrade.

to 49.3 p. p. m. recorded by Pennak (1945) for a group of alpine lakes in Colorado.

The relationship of total dissolved solids, loss on ignition, and ash residue as found in the lakes is presented in figure 14. Each lake is represented by a circle whose area is proportional to total dissolved solids in parts per million and is divided into shaded and unshaded areas representing the respective components, loss on ignition and ash residue. The lakes are located diagrammatically as they occur in the drainage with respect to position and altitude. Outlets are depicted by straight lines with the direction of drainage from top to bottom of the page. A progressive increase in dissolved solids can be traced from Lake Constance to Convict Lake and from Cloverleaf Lake to Convict Lake.

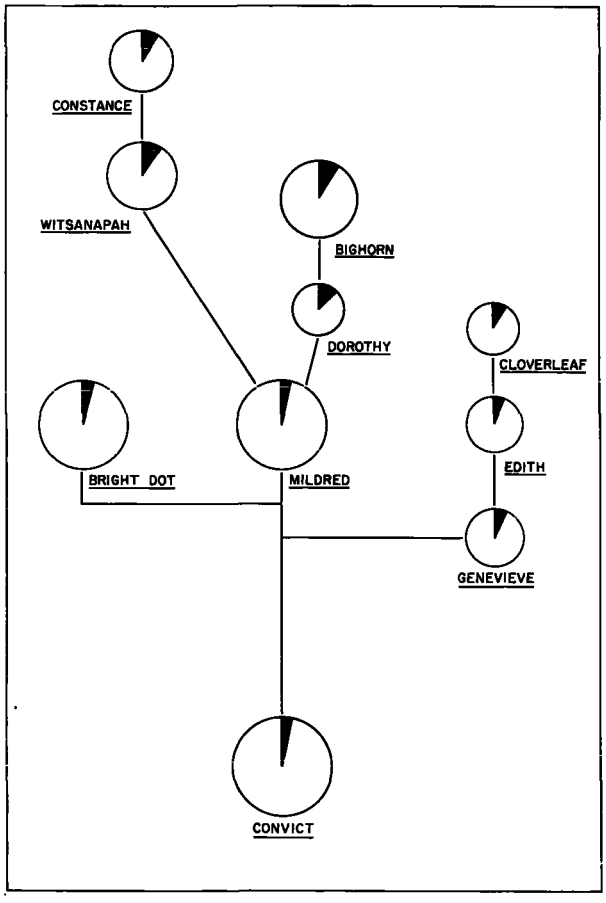

FIGURE 14.—Dissolved solids and mineral-organic components of water in the lakes of Convict Creek Basin arranged according to the drainage. (Absolute concentration of total dissolved solids represented by area of circle; shaded area=percentage loss on ignition; unshaded area=ash residue.)

Total hardness is a quantitative measurement of several dissolved chemical compounds reported as parts per million of $CaCo_3$. Calcium and magnesium carbonates are the chief factors in hardness, and often sulfate is the only other significant ion concerned (Theroux and others, 1943). Small amounts of aluminum and iron may also contribute to total hardness. Pennak (1945) noted the general contention that waters with a hardness below 50 p. p. m. are very soft and those with more than 100 p. p. m., hard. Total hardness in the lakes varied between 9 and 59 p. p. m. with a mean value of 26 p. p. m. Noncarbonate hardness was present in 5 lakes and ranged from 1 to 14 p. p. m. (table 7). It was most prominent in Bighorn Lake and formed nearly 50 percent of total hardness.

Electrolytes and Conductivity

Most of the ash residue described consists of mineral salts which, in fresh waters, exist in a high degree of dissociation. These electrolytes may be separated into anions and cations. Four of the anions (HCO_3^-, SO_4^{--}, Cl^-, and CO_3^{--}) and 4 of the cations (Ca^{++}, Mg^{++}, K^+, and Na^+) contribute practically all of the electrolytic composition to normal waters. Others (Cu^{++}, NO_3^-, etc.) are of relatively little significance. Electrical neutrality of the solution requires that total positive and negative charges balance each other. Clarke (1924b) therefore contended that the interpretation of water analyses must be founded on a study of equilibria.

Although dissociated, electrolytes are closely related. In treating water analyses from various parts of the world, Clarke (1924a) noted extreme ranges for the absolute concentration of electrolytes in fresh waters, but further observed similarities in ionic proportions regardless of the total amount present. He was able to distinguish two types of water on this relative basis: sulfate waters, that is, those in which SO_4 was represented as the major anion; and the prevalent bicarbonate type in which HCO_3 was the dominant anion. This concept has been further developed by Rodhe (1949), who emphasized the bicarbonate waters, contending that a general average of their ionic proportions are in a state of balance which most fresh waters seek to attain. Rodhe postulated a "standard composition" from which natural waters vary due to geochemical and climatic con-

TABLE 7.—*Chemical analysis of mid-depth water samples from the lakes in Convict Creek Basin exclusive of major electrolytes*

[Absolute values in parts per million]

Lake	Dissolved solids				Hardness		Silica		Nitrogen and total phosphate [1]				Minor elements				
	Total	Loss on ignition	Mineral residue	Percentage loss on ignition	Total	Non-carbonate	Amount	Percentage of mineral residue	PO_4	NO_3	NH_3 (N)	NO_2 (N)	Cu [1]	Fe [1]	B	Mn	F
Convict	77	3.0	74.0	3.9	59	8	11.0	14.9	0.06	0.12	0.017	0.003	0.12	0.01	0.01	<0.01	<0.10
Bright Dot	60	3.4	56.6	5.7	45	1	8.7	15.4	<.01	.06	.020	.001	.06	.01	.06	<.01	<.10
Mildred	58	2.8	55.2	4.8	43	5	8.0	14.5	<.01	.08	.052	.001	.08	.01	.04	<.01	<.10
Bighorn	47	5.4	41.6	11.5	30	14	7.6	18.2	<.01	.10	.020	.002	.10	.01	.01	<.01	<.10
Witsanapah	33	4.2	28.8	12.7	21	5	5.4	17.7	<.01	.04	.030	.001	.08	.02	<.01	<.01	<.10
Constance	28	3.2	24.8	11.4	19	0	4.7	19.0	.02	.10	.028	.001	.08	.01	<.01	<.01	.10
Genevieve	26	2.4	23.6	9.2	13	0	7.1	30.0	.07	.06	.024	.001	.08	.01	.01	<.01	<.10
Edith	23	2.0	21.0	8.7	10	0	7.0	33.3	<.01	.06	.024	.001	.12	.02	.01	<.01	<.10
Cloverleaf	20	2.4	17.6	12.0	9	0	5.5	31.2	.04	.19	.028	.001	.08	.02	<.01	<.01	<.10
Dorothy	19	3.2	15.8	16.8	11	0	3.6	22.8	<.01	.06	.016	.001	.10	.01	<.01	<.01	<.10

[1] From results of analysis of water samples taken summer of 1951. All others from samples analyzed summer of 1950.

ditions of the area. He represented this standard with Clarke's derived world average values, and attributed it to ionic exchanges between dissolved electrolytes and colloidal systems of the soils and lake muds. In regard to temporal variation, Juday and Birge (1933) noted that the quantity of electrolytes in surface waters of most northeastern Wisconsin lakes was nearly constant from year to year, with some seasonal variations due to biological activity and to changes in affluents.

Electrolytes in Convict Creek Basin waters are treated in table 8. Carbonate is omitted from the anion group because it is present in very small amounts, and its omission from the analysis has only a negligible effect on the resultant picture. Values of the electrolytes in parts per million are divided by the equivalent of respective ions to obtain the reacting weight, milligram equivalents per liter (me/l). The summation of milliequivalents of anions should equal that of cations for electrical neutrality in each lake. Small discrepancies which occur between total positive and negative ions are due to trace ions and analytical errors, but do not materially affect the validity of the data. Percentages of total anionic and cationic milliequivalents are listed for each ion in table 8.

Tabular data of electrolytes are difficult to interpret when more than two or three water samples are compared. To facilitate comprehension and comparison of these data, ion field diagrams have been plotted on figure 15 in the fashion described by Maucha (1932). Circular area represents total ions present; bisected vertically, each half-circle equals 100 percent, with anions on the left and cations on the right. Each half-circle is further divided into four sectors, one for each ion, the area of each sector corresponding to 25 percent of the total relative ion concentration. Actually, these diagrams are calculated on the basis of a 16-sided polygon, but are drawn as circles for convenience. The percentage of each ion (as given in table 8) is divided by a constant and plotted along a radius which passes through the center of each sector.[9] The shaded area, representing the percentage of total positive or negative milligram equivalents per liter for each ion, consists of two (if percentage is less than 25) or four triangles having a fixed value for one side. This places visual emphasis on extreme percentages and causes the circumference to be the "25 percent line" for each ion.

The lakes are placed in the pattern described for figure 14, and diagrams for basin and world averages have been included. It is obvious that nine of the lakes are bicarbonate and that Bighorn Lake represents the single sulfate type. Close scrutiny shows that three lakes (Convict, Mildred, and Bright Dot) are very strong in HCO_3 and Ca, but weak in all other ions except SO_4. Four lakes (Constance, Witsanapah, Bighorn, and Dorothy) have more than 25 percent sulfate and recognizable proportions of potassium and magnesium. The remaining lakes (Cloverleaf, Edith, and Genevieve) have less than 25 percent sulfate, discernible potassium and magnesium as did the above four, plus greater proportions of sodium than any of the other lakes. The diagram for Basin Average indicates the strong influence of Ca, HCO_3, and SO_4 in mean water composition.

[9] Scale used: 1 mm.^{2}=1 percent. Thus K=3.093 and distance is measured in millimeters along a radius of 8.082 mm.

TABLE 8.—*Major electrolytes and specific conductance in mid-depth samples with reactive weights of ions (milligram equivalents and their percentages) calculated from actual weights (parts per million)*

Lake and item	Anions				Cations					Specific conductance (micromhos at 25° C.)
	HCO_3	SO_4	Cl	Total milligram equivalents	Ca	Mg	K	Na	Total milligram equivalents	
Convict:										
Parts per million	62.0	9.1	0.1		22.0	1.0	1.7	1.1		121
Milligram equivalents	1.0161	.1895	.0028	1.2084	1.0978	.0822	.0435	.0478	1.2713	
Percentage of total	84.1	15.7	.2		86.3	6.5	3.4	3.8		
Bright Dot:										
Parts per million	54.0	5.2	.1		17.0	.7	1.0	.4		91
Milligram equivalents	.8850	.1083	.0028	.9961	.8483	.0576	.0256	.0174	.9489	
Percentage of total	88.9	10.9	.2		89.4	6.1	2.7	1.8		
Mildred:										
Parts per million	46.0	8.3	.2		16.0	.7	1.4	.7		91
Milligram equivalents	.7539	.1728	.0056	.9323	.7984	.0576	.0358	.0304	.9222	
Percentage of total	80.9	18.5	.6		86.6	6.2	3.9	3.3		
Bighorn:										
Parts per million	19.0	16.0	.4		11.0	.6	1.7	.4		68
Milligram equivalents	.3114	.3331	.0113	.6558	.5489	.0493	.0435	.0174	.6591	
Percentage of total	47.5	50.8	1.7		83.3	7.5	6.6	2.6		
Witsanapah:										
Parts per million	20.0	6.3	.7		7.6	.6	1.4	.7		47
Milligram equivalents	.3278	.1312	.0197	.4787	.3792	.0493	.0358	.0304	.4947	
Percentage of total	68.5	27.4	4.1		76.6	10.0	7.2	6.2		
Constance:										
Parts per million	17.0	5.4	.4		6.7	.5	1.4	.6		41
Milligram equivalents	.2786	.1124	.0113	.4023	.3343	.0411	.0358	.0261	.4373	
Percentage of total	69.3	29.7	2.8		76.4	9.4	8.2	6.0		
Genevieve:										
Parts per million	17.0	3.3	.3		4.4	.4	1.0	1.1		33
Milligram equivalents	.2786	.0687	.0085	.3558	.2196	.0329	.0256	.0478	.3259	
Percentage of total	78.3	19.3	2.4		67.4	10.1	7.8	14.7		
Edith:										
Parts per million	13.0	3.0	.4		3.3	.3	1.2	.9		26
Milligram equivalents	.2130	.0625	.0113	.2868	.1674	.0247	.0307	.0391	.2592	
Percentage of total	74.3	21.8	3.9		63.6	9.5	11.8	15.1		
Cloverleaf:										
Parts per million	14.0	1.8	.6		2.6	.5	1.1	1.3		23
Milligram equivalents	.2294	.0375	.0169	.2838	.1297	.0411	.0281	.0565	.2554	
Percentage of total	80.8	13.2	6.0		50.8	16.1	11.0	22.1		
Dorothy:										
Parts per million	11.0	3.8	.1		3.6	.4	1.7	.4		24
Milligram equivalents	.1803	.0791	.0028	.2622	.1796	.0411	.0435	.0174	.2816	
Percentage of total	68.7	30.2	1.1		63.8	14.6	15.4	6.2		

All lakes had less chlorine than the world average, and Cloverleaf Lake is the only one with a noticeable proportion.

Specific conductance values are also included in table 8 as micromhos (reciprocal megohms) at 25° C. Specific conductance is a reciprocal measurement of the resistance a water solution offers to current flow and, when expressed as micromhos, is proportional to total electrolytes. Rodhe (1949) prepared various concentrations of the major electrolytes in "standard composition" proportions, and measured the conductivity of these solutions. "Standard curves" have been plotted from his tabular data in figure 16. These are slightly curvilinear due to decreased ionization at increasing concentration. The heavy line is the standard curve of total electrolytes, and lighter lines are curves for the three most prominent ions. Other ions can be plotted in a similar manner. Horizontal lines represent specific conductance of the lake waters with points signifying absolute concentrations of total and major electrolytes. Comparison with standard curves in absolute values is easily accomplished by this method. The data for all lakes lie close to the curve for total electrolytes with Lakes Mildred and Constance falling directly upon it. In terms of the concentrations of SO_4, HCO_3, and Ca ions, most of the lakes (Bighorn Lake in particular) show divergence from "standard values." Least divergence is shown by Lake Genevieve.

Silica and Minor Elements

Table 7 lists quantities of chemical elements analyzed in addition to those previously discussed. Of this remainder, silica is the most abundant and independent of the influences of the other elements. Silicon is generally thought to occur as colloidal silica (SiO_2) or possibly in an ionic form (SiO_3), and is derived from the solution of feldspars and other rock-forming silicates (Clarke 1924a,b). Rawson (1939) stated that the silica content of lake waters is variable but usually less than 10 parts per million with stratification frequent. An

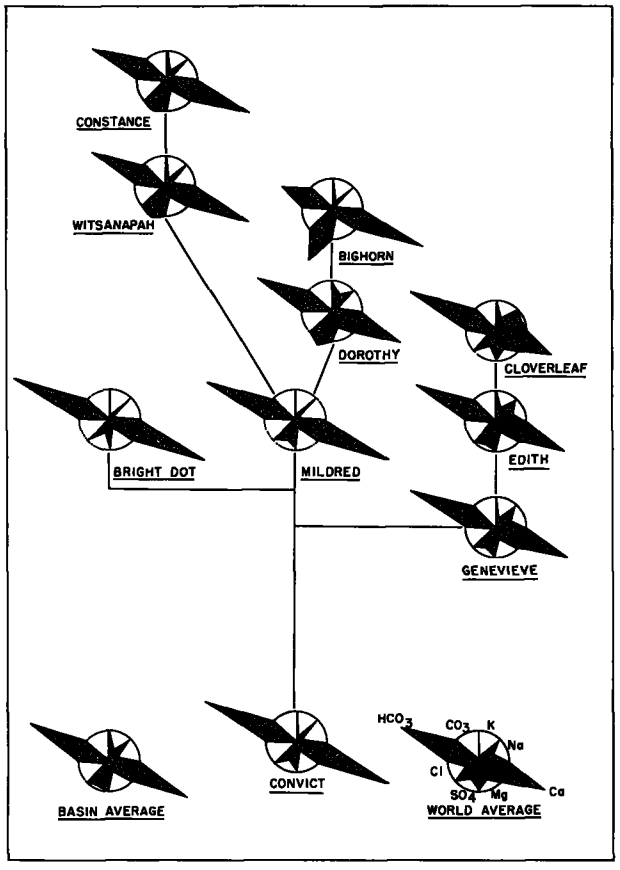

FIGURE 15.—Major electrolytes in the lakes of Convict Creek Basin compared on the basis of ion field diagrams with the lakes arranged according to their positions in the drainage systems.

inverse relation between silica content and diatom abundance in summer has been noted by Pearsall (1930), Meloche and others (1938). The silica content varied from 3.6 p. p. m. in Lake Dorothy to 11.0 p. p. m. in Convict Lake. The remaining 8 lakes form a compact group with 4.7 to 8.7 p. p. m. Silica is also expressed as a percentage of total mineral residue for comparative purposes. On this basis, two groups of lakes can be distinguished: Cloverleaf, Edith, and Genevieve with 30.0 to 33.3 percent, and the other 7 with 14.5 to 22.8 percent.

Phosphorus and nitrogen, as raw materials for protein synthesis, are often considered limiting to organic production. Dissolved phosphorus in uncontaminated waters is usually less than 0.05 p. p. m. (Rawson 1939) and often less than 0.001 p. p. m. in oligotrophic lakes (Ruttner 1953). Phosphate content is known to fluctuate widely with biological activity and, since organisms can utilize quantities of phosphorus beyond the limits of sensitive measurement, its minima are not known. Phosphate determinations in this study were not sensitive enough to show the nature of its distribution. In general, the dissolved phosphorus content of the lakes did not exceed 0.07 p. p. m., and 6 lakes contained trace amounts (less than 0.01 p. p. m.). Dissolved nitrogen is represented in table 7 by NH_3 and NO_2 nitrogen, and nitrate. Nitrate and ammonia are the forms of nitrogen readily available for plant metabolism. Osterlind (1949) was able to demonstrate selectivity in the utilization of these compounds by plants. Nitrate is usually less than 0.5 p. p. m. and ammonia is scarce in oxygenated waters (Rawson 1939). The former ranged from 0.6 to 1.9 p. p. m. and the latter from 0.016 to 0.052 p. p. m. in the lakes of Convict Creek Basin. Nitrite, intermediate between the above forms in the nitrogen cycle, was very low and ranged between 0.001 and 0.003 p. p. m. in the 10 lakes.

Copper was the most abundant of the trace elements analyzed in mid-depth samples and ranged from 0.06 to 0.12 p. p. m. Inorganic iron and manganese are highly insoluble in the presence of dissolved oxygen (Ruttner 1953) and consequently are at or below the sensitivity of measurement employed. The former element was found in a concentration of 0.02 p. p. m. in three of the lakes and 0.01 p. p. m. in the remaining seven. Manganese appeared in trace quantities in all lakes and fluorine occurred at less than 0.10 p. p. m. (except in Lake Constance where 0.10 p. p. m. was noted). Boron ranged from trace amounts to 0.06 p. p. m. in Bright Dot Lake.

VARIATIONS WITHIN LAKES

Partial analyses of water samples taken from lake surfaces, bottom strata, inlets, and outlets in August and early September, 1950, appear in table 9. Comparisons of surface and bottom waters indicate a tendency toward chemical stratification (an increase of mineral solutes at greater depths) in 5 of the lakes. Lakes Mildred and Cloverleaf did not show this tendency, and in Lake Dorothy it is questionable. Newcombe and Slater (1950) discussed two types of chemical stratification: biochemical, due to organic metabolic processes characterized by PO_4, SiO_2, total

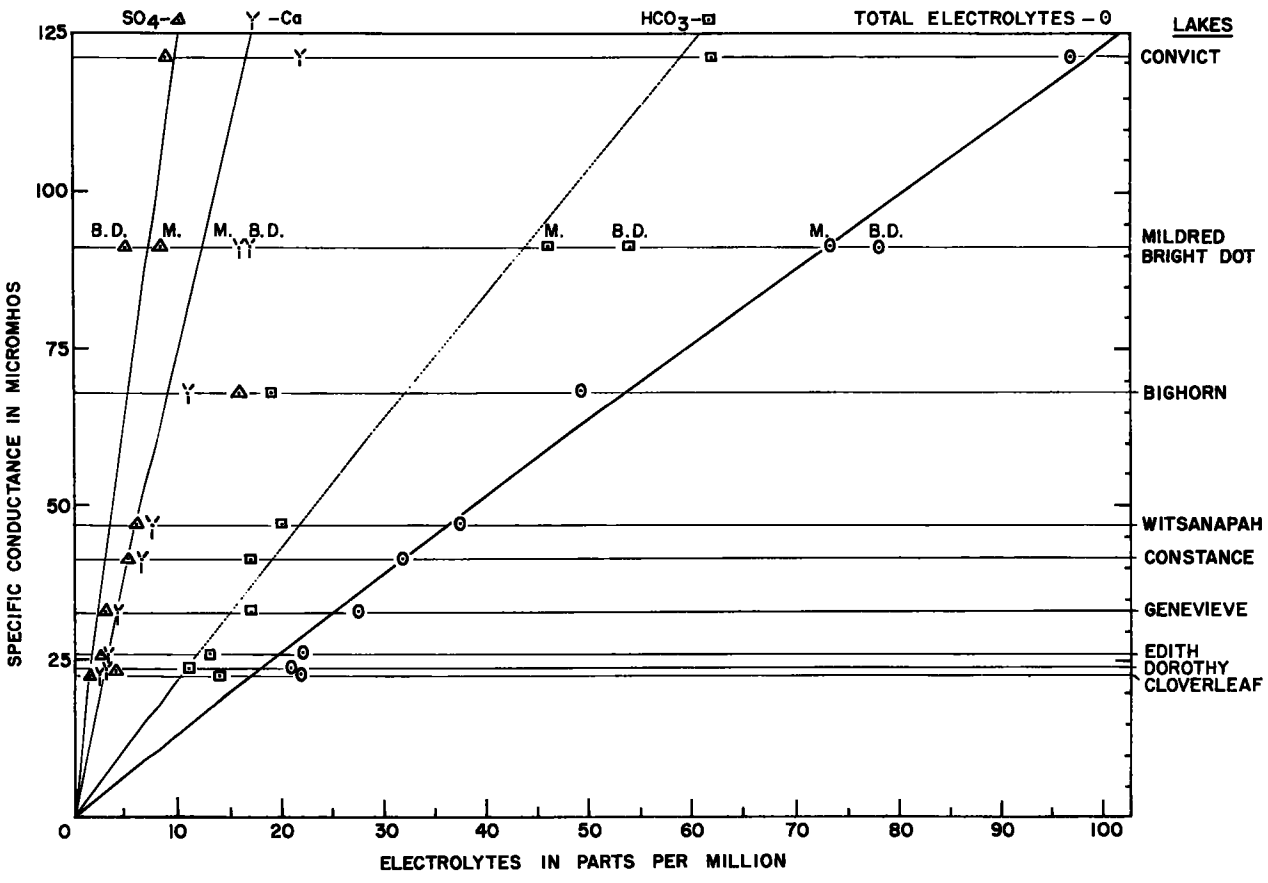

FIGURE 16.—Composition of water in the lakes of Convict Creek Basin in terms of specific conductance and absolute concentration of total electrolytes and important ions. (Composition of each lake [indicated by symbols] is compared to curves of standard composition.)

Fe, and Ca gradients; nonbiochemical, caused by subterranean water and generally having Cl, Na, and SO_4 stratified. Overall mineral increases with depth can be seen most easily by comparing conductance values. Sulfate did not accumulate with depth in any of the lakes whereas other substances did so slightly.

The tendency toward chemical stratification in some of the lakes is associated with both oxygen depletion and mineral accumulation at increasing depth, but it is not consistent with the aforementioned biochemical and nonbiochemical divisions. Chemical stratification was indicated in Lake Edith where abyssal oxygen deficits were found but was almost absent in the shallow lakes and in the remaining deeper lakes. Lake Dorothy had neither mineral accumulations nor oxygen deficiencies at 290 feet. Stratification apparently varies with the degree of mixing of the waters. Lake Dorothy is large and well-exposed to winds; mixing in Lake Mildred may be due to wind action and, possibly, to the effect of two relatively large inlet streams. Lake Edith is sheltered in a cup-like basin which allows greater opportunity for stratification to take place.

These analyses further demonstrate the occurrence of changes in the mineral content of the water within lake basins. Lake Mildred with two inlet streams is a good example. The west inlet was "soft" and weak in electrolytes (conductance) whereas the valley inlet was much "harder" and almost three times stronger in electrolytes. The single outlet stream closely approximated the valley inlet in most respects and the influence from the west inlet was slight. In instances where inlet and outlet values are given for the same lake (excepting Lake Mildred's valley inlet) outlet chemical concentrations were equal to or greater than inlet concentrations for all given determinations.

TABLE 9.—*Results of partial chemical analysis of water samples from various locations in eight lakes of Convict Creek Basin*

Lake and location of sample	Specific conductance (micromhos at 25° C.)	Parts per million					
		Hardness		HCO_3	SO_4	Na+K	Cl
		Total	Noncarbonate				
Convict:							
Surface [1]	115	58	8	61.0	11.0	2.0	0.6
Bottom (130)[2]	135	66	8	71.0	9.0	1.1	.6
Inlet	113	58	10	59.0	9.0	.4	.9
Outlet	118	60	10	61.0	12.0	1.7	.9
Bright Dot:							
Surface [1]	92	45	2	52.0	3.0	.6	.5
Bottom (80)[2]	97	47	1	56.0	3.0	1.2	.5
Outlet	92	49	6	53.0	7.0	1.1	.5
Mildred:							
Surface [1]	95	47	8	48.0	9.0	1.2	.7
Bottom (60)[2]	94	46	7	48.0	9.0	1.9	1.0
West inlet	38	16	1	18.0	7.0	3.0	.4
Valley inlet	100	49	9	49.0	9.0	.8	.8
Outlet	96	48	10	47.0	9.0	.7	1.2
Constance:							
Surface [1]	40	18	2	20.0	5.0	2.0	.6
Bottom (170)[2]	46	21	3	22.0	5.0	1.5	.7
Outlet	39	19	3	20.0	5.0	1.4	.4
Genevieve:							
Surface [1]	30	11	0	16.0	2.5	2.7	.8
Bottom (125)[2]	34	13	0	18.0	3.0	2.9	1.0
Inlet	22	9	0	12.0	1.6	1.6	.7
Outlet	30	11	0	16.0	2.6	2.7	.8
Edith:							
Surface [1]	24	8	0	13.0	3.0	3.0	.6
Bottom (105)[2]	32	12	0	16.0	3.0	2.5	.8
Cloverleaf:							
Surface [1]	24	8	0	14.0	1.3	2.7	.7
Bottom (20)[2]	25	9	0	14.0	1.6	2.2	.5
Outlet	26	8	0	14.0	3.0	3.7	1.0
Dorothy:							
Surface [1]	26	13	2	13.0	5.0	1.4	.1
Bottom (290)[2]	29	12	1	14.0	5.0	2.7	.8
Outlet	28	13	2	14.0	5.0	1.9	.4

[1] Surface values from samples taken 10 feet below the surface.
[2] Bottom values from samples taken within 10 feet of the bottom. Actual depths given in parentheses.

Mineral changes in interconnecting streams are exemplified by the composition of Lake Dorothy's outlet at its source and at its point of inflow to Lake Mildred (west inlet). The analyses indicate an increase at Lake Mildred of conductivity, HCO_3, SO_4, carbonate hardness, and Na+K. Chloride and noncarbonate hardness did not show gains. Outlet and surface determinations for each lake were similar.

GEOCHEMICAL INFLUENCE ON WATER QUALITY

Rainwater, according to Welch (1952), contains approximately 30 to 40 p. p. m. of total dissolved solids, but this estimate is far in excess of the total dissolved solids found in snow in the study area. Analyses of snow samples indicated a content of 5.6 p. p. m. of total dissolved solids. The proportions of dissolved matter in the lakes of Convict Creek Basin attributable to rock solution and precipitation cannot be stated in definite terms. However, the pristine nature of the drainage area and the low mineral content of precipitation suggest that the major source of mineral accumulation in the lakes must be due to the natural decomposition of rock.

Pennak (1945) found an increase of residues in water from higher to lower elevations and, in mountainous areas, attributed this directly to the "age" of water, that is, to the length of time that the water had been in contact with the substrate. A mineral gradient from uppermost to lowermost lakes of Convict Creek drainage is clearly evident in figure 14. Partial analyses of water samples (table 9) indicate that dissolved matter is contributed to flowing water by the substrate and to standing water in lakes by ionic exchanges within the lake basin with the former process exerting a greater influence. Lake Dorothy deviated from this pattern, but it can be explained by the geological nature of its drainage area. Six of the lakes (fig. 14) had a relatively high dissolved solids content whereas that of Lake Dorothy and of the Lake Genevieve group was low. Figure 13 shows that these mineral-poor lakes receive most of their drainage from igneous rock (although the actual basins of Lakes Edith and Genevieve lie

in metamorphic rock), which is less soluble than the metamorphic rocks forming most of the drainage areas of the six mineral-rich lakes.

Pearsall (1930) distinguished two types of drainages on the basis of water quality: rocky lakes of low pH and carbonate hardness, with high phosphate and silica; silted lakes with opposing features. Hardness, Pearsall found, was correlated directly with pH. The Convict Creek Basin lakes, in rocky drainages, agree in general with Pearsall's description and further, the pH-hardness relationship also appears to hold true.

Certain relationships between dissolved minerals and parent rock are evident. On this basis, it is possible to group the lakes according to rock types predominating in their drainages. Lakes Bright Dot, Mildred, and Convict (fig. 15) are strongly bicarbonate and calcium in composition. An obvious source of these ions is crystalline limestone. Figure 13 shows that these 3 lakes are the only ones with large proportions of crystalline limestone in their drainages. Lake Mildred receives most of its inflow from the valley inlet, which flows through alluvial material composed mainly of disintegrated crystalline limestone.

In a similar fashion, Lakes Genevieve, Edith, and Cloverleaf are distinguished by a high percentage of silica in their mineral residues (table 7). It has been established from Clarke (1924b) that silicate rocks (especially feldspars prevalent in igneous rock) are a prominent source of dissolved silicon. Clarke also indicated an accelerated dissolution of silica by organic acids. It seems significant that the major portion of this subdrainage is composed of igneous silicates (fig. 13) and that it is also the most densely vegetated part of the basin.

The 4 remaining lakes (Constance, Witsanapah, Bighorn, and Dorothy) are characterized in figure 15 by a high relative sulfate content. Sulfate, according to Clarke (1924b) is usually derived from deposits of pyrite. It has also been noted that the sulfate content of hornfels is higher than that of other types occurring in the basin. Either or both of these sources may be the cause of the high sulfate content found in these lakes. The sulfate content of Lake Dorothy is, however, a subject for speculation since neither of these sources occur in its immediate drainage area. Possibly the inflow from Bighorn Lake (small but exceptionally high in SO_4) or perhaps subterranean seepage rich in sulfate might both contribute.

COMPARATIVE RATINGS OF THE LAKES

The following ten chemical measurements form the basis of a chemical evaluation for each lake: total dissolved solids, mineral residue, specific conductance, total hardness, bicarbonate, calcium, magnesium, potassium, sodium, and silica. The selection of these measurements was governed primarily by the fundamental fact that aquatic life requires dissolved matter for sustenance and growth; especially in oligotrophic situations, quantity appears to be the most obvious limitation of chemical substance. Second consideration was given to the strength and validity of each chemical value in comparing the ten lacustrine environments. Total dissolved solids, mineral residue, conductance and, to a lesser extent, total hardness, are factors which somewhat duplicate each other. However, all are sound, relatively stable measurements indicative of the general mineral nature of the waters and their combination serves to smooth out irregularities in the individual analyses. Bicarbonate is important both as a buffer ion and as a carrier of CO_2 (half-bound). The remaining five ions function biologically as protoplasmic and skeletal constituents and occurred in readily measurable quantities.

Sulfate appeared in the analyses as one of the major anions but it has been excluded from the combined evaluation because definite knowledge concerning its local productive influence is lacking. It has been demonstrated (Moyle 1945) that certain organisms find optimum conditions in sulfate waters, but that others do so in bicarbonate waters. The biota of these alpine lakes seems best adapted to waters of the bicarbonate type but it cannot be stated that the amounts of sulfate involved have an inhibitive effect on productivity.

The lakes have been ranked in high-to-low order of productive influence in table 10. As with physical factors, each chemical measurement considered has been given a proportionate value for each lake. The richest lake in any given measurement has been assigned a rating of 10 and the remaining nine lakes have been rated through a 10–0 range in proportion to their actual measured values. (See footnote 7.) The composite chemical rank is based on the

average of all proportionate ratings for each lake. This procedure gives equal weight to each chemical component and obviously does not represent dissolved substances in accordance with their actual productive influences, but as the proper assignment of weight among these substances is only roughly known, it is best in the present gross comparisons to assume equal importance among them.

The grouping of lakes with respect to total dissolved solids, ash, conductance, and hardness indicates prominent gaps separating Convict Lake from Lakes Bright Dot and Mildred, the latter two lakes from Bighorn Lake, and Bighorn Lake from the remaining lakes. Similar gaps are apparent in the final chemical ranking (table 10). The lakes also follow the final ranking closely in bicarbonate, calcium, and magnesium ratings, with the same grouping and gaps except for low bicarbonate in Bighorn Lake. Final ranks of Lakes Genevieve, Cloverleaf, and Edith are raised slightly due to the influence of sodium and silica, but the overall chemical poverty of these three lakes may be discerned in the proportionate ratings for other individual determinations. Lakes Convict, Mildred, and Bright Dot rank highest in nearly all of the indivudual components. The composite chemical ranking is in accord with geological influences and altitudinal positions of the lakes as previously outlined.

SUMMARY OF CHEMICAL CHARACTERISTICS

Chemical determinations for the ten lakes indicate strongly oligotrophic conditions characterized by abundant dissolved oxygen, a paucity of mineral and organic solutes, and pH values near neutrality. Bicarbonate, silica, calcium, and magnesium were the principal constituents in total dissolved solids among the lakes. Amounts of nitrite nitrogen, copper, iron, potassium, and ignitible matter did not vary greatly. Phosphate, sulfate, chloride, sodium, noncarbonate hardness, nitrate, and ammonia nitrogen were distributed irregularly. Total dissolved solids increased in quantity in the waters of the basin in a downstream direction.

Ion field diagrams indicate that one lake is of the sulfate type, nine are bicarbonate, and that calcium, bicarbonate, and sulfate ions predominate in the chemical composition of the waters. Considerable variation in relative proportions of single ions existed among the lakes in terms of world-average or standard electrolyte compositions. However, absolute quantities of total electrolytes plotted against specific conductance showed close agreement with a standard curve derived from world-average or standard water composition values.

A tendency toward chemical stratification was indicated in a few lakes by oxygen deficiencies and mineral accumulations at increasing depth. The tendency appears to be caused by factors which prevent the mixing of the waters in those lakes.

The quality and quantity of mineral solutes in the waters of the basin appear to be associated with geologic formations. Low mineral residues and high silica content of water occurred in the more acid lakes that received most of their drainage from igneous rocks. Lakes that drained crystalline limestone areas were richer in calcium and bicarbonate and lakes in subdrainages of different metamorphic rock, notably hornfels and slaty hornfels, were relatively rich in sulfate.

TABLE 10.—*Ranking of lakes according to proportionate ratings of selected chemical measurements*

Lake	Proportionate ratings											Grand average and proportionate rank
	Gross determinations					Specific determinations						
	Total dissolved solids	Mineral residue	Specific conductance	Total hardness	Average rating	Bicarbonate	Calcium	Magnesium	Potassium	Sodium	Silica	Average rating
Convict	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	7.8	10.0	9.6	9.8
Mildred	6.7	6.8	6.9	6.8	6.8	6.9	6.9	5.7	5.7	3.3	5.9	5.7	6.2
Bright Dot	7.1	7.0	6.9	7.2	7.0	8.4	7.4	5.7	0	0	6.9	4.7	5.8
Bighorn	4.8	4.4	4.6	4.2	4.5	1.6	4.3	4.3	10.0	0	5.4	4.3	4.4
Witsanapah	2.4	2.2	2.4	2.4	2.4	1.8	2.6	4.3	5.7	3.3	2.4	3.4	2.9
Constance	1.5	1.5	1.8	1.8	1.6	1.2	1.6	2.8	5.7	2.2	1.5	2.5	2.0
Genevieve	1.2	1.3	1.0	.8	1.1	1.2	.9	1.4	0	7.8	4.7	2.7	1.9
Cloverleaf	.2	.3	0	0	.1	.6	0	2.8	1.4	10.0	2.6	2.9	1.5
Edith	.7	.9	.3	.2	.5	.4	.4	0	2.8	5.5	4.6	2.3	1.4
Dorothy	0	0	.1	.4	.1	0	.5	1.4	10.0	0	0	2.0	1.0

According to averages of selected quantitative values, Convict Lake ranked highest and Lake Dorothy lowest among the lakes.

FOOD AND FEEDING HABITS OF TROUT

The following aspects of the relationship between trout and their food supplies were studied: foods present and foods consumed; food habits of different trout species existing in the same bodies of water; food habits of rainbow trout from two lakes widely separated in elevation; and food habits of trout of various sizes. Foods available for consumption by trout were determined from bottom and plankton samples from each lake, and measures of invertebrate productivity were derived from analysis of these samples. The analyses of food habits are based on examination of stomach contents from 979 trout of three species, distributed as follows:

Lake	Species	Number of specimens
Dorothy	Brook trout	285
Genevieve	do	101
Edith	do	97
Cloverleaf	do	87
Bighorn	do	73
Witsanapah	do	70
Constance	do	65
Bright Dot	do	22
Mildred	Rainbow trout	70
Dorothy	do	25
Convict	do	23
Convict	Brown trout	61
Total		979

The high elevations of the lakes and consequent severity of winter conditions permit data collection only during the summer and early fall. As a result, the statements regarding productivity of food organisms and food habits of trout apply to the lakes only during ice-free months and do not necessarily hold true throughout the remainder of the year.

METHODS

Bottom samples were collected with an Ekman dredge of 6- by 6-inch opening. The samples were taken at regular intervals along several transects in each lake to obtain various bottom types. Samples were washed through a 30-mesh soil sieve and the residue was placed in white pans. Organisms were picked alive from the pans and preserved in a 5-percent solution of formalin. Volumes were later measured to the nearest 0.1 cubic centimeter according to the water displacement method described by Welch (1948). Following volumetric measurement the organisms were stored in 70 percent alcohol, from which the material was emptied into a specially constructed cell for examination and count under a dissecting microscope. The percentage of total volume constituted by each group of organisms was determined concurrently with each sample count. Gravimetric measurements to an accuracy of 0.01 gram were made with a torsion balance. Benthos production is expressed as grams per square foot of bottom area and as pounds per acre.[10]

Vertical plankton hauls were made from all levels to the surface over the deepest part of each lake. These collections were made with a Wisconsin type net of 11.6 centimeters opening, fitted with No. 20 silk bolting cloth in the straining cone and bucket. Plankton organisms were preserved in 5-percent formalin and allowed to settle for 24 hours in graduated centrifuge tubes. Volumes were determined in the field to the nearest 0.1 cubic centimeter. When organisms were visibly separated by appendages after settling, the samples were centrifuged until no separation was evident. The method used in counting zooplankton was the survey count described by Welch (1948). A Sedgwick-Rafter counting cell with a volume of one cubic centimeter was used, and counts were made under 27X magnification. Only crustaceans were counted, but the presence of other plankton organisms (rotifers, flagellates, and others) was noted. Final figures were expressed in numbers and volumes of plankters per cubic foot of water at various levels throughout the sampling zone.

Trout stomachs were removed with esophagus attached, sealed with wire, and placed in 10 percent formalin for storage. The stomach contents were transferred to 70 percent alcohol prior to ex-

[10] Because of the rocky character of the lake bottoms, Ekman dredge sampling in certain locations was not possible. These areas were considered to be unproductive of bottom fauna of the type occurring in bottom materials successfully sampled by the dredge. The analysis of data concerning the food and food habits of trout demonstrated beyond question that the successful dredge samples yielded organisms that were representative of the aquatic forms consumed by trout. Although the boulder and bedrock bottom types undoubtedly support some forms of aquatic life, this production cannot be regarded as significant in the direct fish-food interrelationship. Productivity figures are therefore based on successful dredge samples in terms of the percentage of total samples taken in each lake. Thus, if 50 successful samples were obtained out of 100 attempts, the lake considered would be assumed to have one-half of its bottom area capable of producing fauna important in the fish-food interrelationship. If the 50 successful samples indicated a mean value of 2 grams per square foot, the lake as a whole would be assessed a mean value of 1 gram per square foot of bottom area, or 50 percent productivity.

amination. Methods of enumeration and the determination of percentages of total volume were the same as those employed with the bottom samples.

FOODS PRESENT

The presence and abundance of trout foods in the lakes of Convict Creek Basin, as determined from bottom and plankton samples, are given in tables 11 to 15. Bottom organisms are listed according to taxonomic groups as they occur in the 10 lakes (tables 12, 13, and 14). All food organisms are considered in one of three categories: zooplankton, bottom fauna, or terrestrial insects. Lakes are also grouped according to relative productivities as indicated by quantitative analyses of bottom organisms (table 11). Table 16 contains identifications and distributions of aquatic fauna collected from all lakes.

TABLE 11.—*Analysis of standing crops of bottom fauna in the lakes of Convict Creek Basin, 1951*

[Numbers, volumes, and weights of organisms are based on the percentage of successful bottom samples]

Lake	Dates	Number of samples taken	Number of successful samples	Successful samples (percentage)	Average number of organisms per square foot	Average number of organisms per acre	Average volume [1] of organisms per square foot	Average volume [1] of organisms per acre	Average weight of organisms per square foot (grams)	Average weight of organisms per acre (pounds)
Dorothy	Aug. 20 to 23	102	60	58.9	83	3,627,676	0.40	17,424	0.20	19.20
Bighorn	Aug. 13 and 14	26	18	69.2	107	4,664,404	.68	29,620	.32	30.72
Convict	July 16, Sept. 10 to 13	105	49	46.6	111	4,830,043	.51	22,215	.36	34.57
Bright Dot	Aug. 27 to 31	32	23	71.9	175	7,645,651	.98	42,688	.52	49.93
Edith	July 25 to 27	28	26	92.8	212	9,234,720	1.75	76,230	1.16	111.39
Constance	Aug. 6 to 9	35	28	80.0	264	11,510,294	1.91	83,199	1.16	111.39
Genevieve	July 31, Aug. 1 and 2	31	31	100.0	306	13,355,496	2.06	89,733	1.32	126.76
Witsanapah	Aug. 10 to 13	16	14	87.5	241	10,508,414	2.31	100,623	1.40	134.44
Cloverleaf	Aug. 19, 20, 23	31	31	100.0	434	18,922,464	3.62	157,687	2.16	207.42
Mildred	Sept. 2 to 4	21	20	95.2	241	10,502,316	3.12	135,907	2.20	211.26

[1] Volume expressed in cubic centimeters.

TABLE 12.—*A comparison of the bottom fauna in the lakes of Convict Creek Basin*

[Figures are percentages of the total volume of organisms taken in bottom samples]

Organism	Constance	Witsanapah	Bighorn	Dorothy	Cloverleaf	Edith	Genevieve	Bright Dot	Mildred	Convict
Diptera:										
Larvae	58.25	71.23	32.93	59.12	58.16	51.92	60.93	69.15	22.60	61.09
Pupae	9.11	.98	9.07	2.03	.84	1.82	1.39	4.21	.21	
Trichoptera larvae		.29								.04
Coleoptera larvae									.08	
Megaloptera larvae		.39		.65		.89	.81			
Ephemerida naiads		.32								
Oligochaeta	21.16	4.67	55.44	31.39	15.61	35.95	19.79	4.76	12.52	30.42
Mollusca	10.71	22.12	2.20	3.50	25.30	9.42	16.70	21.65	15.02	1.06
Nematoda	.73		.36	3.28	.05		.38	.12	.26	.08
Crustacea: *Gammarus* sp									49.20	3.02
Turbellaria	.02									4.29
Hydracarina	.02			.03	.04			.11	.11	

TABLE 13.—*A comparison of the bottom fauna in the lakes of Convict Creek Basin*

[Figures are percentages of bottom samples containing the organism]

Organism	Constance	Witsanapah	Bighorn	Dorothy	Cloverleaf	Edith	Genevieve	Bright Dot	Mildred	Convict
Diptera:										
Larvae	100.0	100.0	100.0	95.0	100.0	92.3	100.0	100.0	95.0	98.0
Pupae	85.7	42.9	83.3	30.0	45.2	42.3	48.4	60.9	15.0	
Trichoptera larvae		7.1								2.0
Coleoptera larvae									5.0	
Megaloptera		7.1		5.0		7.7	6.5			
Ephemerida naiads		7.1								
Oligochaeta	96.4	.5	88.9	86.7	93.5	96.2	93.6	21.7	90.0	95.9
Mollusca	75.0	78.6	22.2	30.0	71.0	38.5	74.2	82.6	85.0	12.2
Nematoda	28.6		22.2	43.3	6.5		22.6	4.4	10.0	2.0
Crustacea: *Gammarus* sp									30.0	12.2
Turbellaria	3.6									4.1
Hydracarina	3.6			3.3	6.5			21.7	10.0	

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TABLE 14.—*A comparison of the bottom fauna in the lakes of Convict Creek Basin*

[Figures are percentages of the total number of organisms taken in bottom samples]

Organism	Constance	Witsanapah	Bighorn	Dorothy	Cloverleaf	Edith	Genevieve	Bright Dot	Mildred	Convict
Diptera:										
Larvae	47.3	67.2	34.6	68.2	51.7	52.9	59.2	73.0	27.0	65.3
Pupae	9.6	.7	9.8	1.3	.7	1.7	2.0	4.5	.2	
Trichoptera larvae		.1								.1
Coleoptera larvae									.1	
Megaloptera larvae		.1		.1		.3	.1			
Ephemerida nalads		.1								
Oligochaeta	20.5	5.4	52.0	23.3	18.7	34.7	21.0	3.1	24.2	30.8
Mollusca	20.5	26.4	2.9	3.5	28.7	10.4	16.6	19.1	17.9	.4
Nematoda	2.0		.7	3.5	.1		.5	.1	.7	.1
Crustacea: *Gammarus* sp									29.9	.8
Turbellaria										2.5
Hydracarina	.1			.1	.1		.6	.2		

TABLE 15.—*Vertical distribution of plankton crustacea in the lakes of Convict Creek Basin, 1951*

Lake	Date and hour of sampling	Depth range of sample (feet)	Average volume [1] of plankton per cubic foot of water	Average number of plankters per cubic foot of water	Average number of plankters per cubic foot of water		
					Cladocera	Copepoda	Nauplii
Constance	Aug. 6, 9:00 a. m.	0–20	0.00	0	0	0	0
		20–40	.02	4	0	4	0
		40–60	.04	33	0	33	0
		60–80	.00	0	0	0	0
		80–100	.04	78	6	72	0
		100–120	.06	22	0	22	0
		120–140	.02	19	0	19	0
		0–140	.02	22	1	21	0
Witsanapah	Aug. 10, 2:00 p. m.	0–49	.00	0	0	0	0
Bighorn	Aug. 13, 3:00 p. m.	0–5	.04	767	0	102	663
		5–10	.07	2,078	0	32	2,046
		10–15	.11	275	0	275	0
		15–20	.05	406	0	406	0
		20–25	.05	176	0	176	0
		25–29	.18	363	0	363	0
		0–29	.08	677	0	226	451
Dorothy	Aug. 20, 9:00 a. m.	0–270	.00	0	0	0	0
Cloverleaf	July 13, 10:00 a. m.	0–24	.00	0	0	0	0
Edith	July 25, 10:00 a. m.	0–15	.01	95	17	39	39
		15–30	.01	86	10	0	76
		30–45	.01	66	10	56	0
		45–60	.01	20	1	19	0
		60–75	.01	99	0	99	0
		75–90	.00	0	0	0	0
		0–90	.01	61	6	36	19
Genevieve	July 30, 4:00 p. m.	0–15	.09	49	49	0	0
		15–30	.06	115	45	32	38
		30–45	.06	291	60	143	88
		45–60	.06	50	50	0	0
		60–75	.03	237	0	79	158
		75–90	.00	0	0	0	0
		90–105	.03	283	0	194	89
		0–105	.05	146	29	64	53
Bright Dot	Aug. 31, 3:00 p. m.	0–10	.01	24	0	24	0
		10–20	.04	124	11	102	11
		20–30	.01	400	0	378	22
		30–40	.08	266	118	144	4
		40–50	.13	492	325	139	28
		50–60	.22	122	118	0	4
		60–70	.00	0	0	0	0
		0–70	.07	204	82	112	10
Mildred	Sept. 3, 10:00 a. m.	0–50	.03	24	2	19	3
Convict	Sept. 11, 2:00 p. m.	0–10	.03	172	0	92	80
		10–25	.03	257	0	209	48
		25–40	.06	142	0	126	16
		40–55	.03	89	38	51	0
		55–70	.03	198	21	177	0
		70–85	.12	187	187	0	0
		85–100	.03	121	56	0	65
		100–115	.00	0	0	0	0
		115–130	.00	0	0	0	0
		0–130	.03	130	34	73	23

[1] Volume expressed in cubic centimeters.

TABLE 16.—*Partial list of aquatic organisms present in the lakes of Convict Creek Basin determined by examination of trout stomach contents, lake bottom, and plankton samples*

Organism	Lake									
	Constance	Witsanapah	Bighorn	Dorothy	Cloverleaf	Edith	Genevieve	Mildred	Bright Dot	Convict
Diptera:										
Chironomidae:										
Tendipes	x	x	x	x	x	x	x	x	x	x
Pentapedilum	x	x	x	x	x	x	x	x	x	x
Calopsectra	x	x	x	x	x	x	x	x	x	x
Procladius	x	x	x	x	x	x	x	x	x	x
Spaniotoma	x	x	x	x	x	x	x	x	x	x
Rhagionidae:										
Atherix	----	x	----	----	----	----	----	----	----	----
Simuliidae:										
Simulium	----	x	----	----	----	----	----	----	----	x
Hemiptera:										
Cenocorixa	x	----	----	----	----	----	----	x	----	----
Trichoptera:										
Rhyacophilidae	x	x	----	x	x	x	x	----	----	x
Psychomyiidae	----	----	----	----	----	----	----	----	----	x
Ephemerida:										
Heptageniidae	----	----	----	----	----	----	----	----	----	x
Baetidae	x	x	x	x	x	----	----	----	----	x
Plecoptera:										
Nemouridae	x	x	----	x	x	----	----	x	----	x
Megaloptera:										
Sialis	x	x	x	x	x	x	x	x	x	x
Coleoptera:										
Stenelmis	----	----	----	----	----	----	x	----	----	----
Oreodytes	----	----	----	----	x	----	----	x	----	----
Bidessus	----	----	----	x	----	----	----	----	----	----
Hydracarina:										
Lebertia	x	x	x	x	x	x	x	x	x	x
Crustacea:										
Amphipoda:										
Gammarus	----	----	----	----	----	----	x	x	x	x
Cladocera [1]	x	----	----	----	x	x	x	x	x	x
Copepoda [2]	x	----	x	x	----	x	x	----	x	x
Mollusca:										
Pisidium	x	x	x	x	x	x	x	x	x	x
Planorbis	----	----	----	----	----	----	x	----	----	x
Limnaea	----	----	----	----	----	----	----	----	----	x
Nematoda:										
Mermithidae	x	x	x	x	x	----	x	x	x	x
Turbellaria:										
Dugesia	x	----	----	----	----	----	----	----	----	x
Oligochaeta:										
Limnodrilus	x	x	x	x	x	x	x	x	x	x
Tubifex	x	x	x	x	x	x	x	x	x	x

[1] *Daphnia pulex* and *D. longispina*; *Holopedium gibberum*.
[2] *Diaptomus signicauda*; *Cyclops vernalis*; *Eucyclops agilis*.

Bottom Fauna

Bottom fauna was limited to relatively few groups, but the abundance of organisms varied considerably among the lakes. Dipterans, represented almost entirely by chironomid larvae, were most abundant and occurred in more than 90 percent of all bottom samples taken. These organisms constituted the greatest percentage of total volume in each lake except Lake Mildred, where the amphipod *Gammarus* sp., was most abundant volumetrically and numerically, and in Bighorn Lake where oligochaetes were similarly dominant. In Lake Mildred, chironomid larvae were nearly equal to amphipods in number, but were less than half as abundant volumetrically. These amphipods were present but less plentiful in Lakes Genevieve, Bright Dot, and Convict.

Oligochaeta (*Limnodrilus* sp., and *Tubifex* sp.) and Pelecypoda (*Pisidium* sp.) were next in abundance and total volume, and these two groups alternated in the position of second importance in the remaining lakes. Chironomid pupae and various other immature aquatic insects and invertebrates composed the remainder of the bottom fauna sampled. These organisms were, for the most part, limited to no more than a fraction of a percent of the total number and volume of organisms present; among the more numerous were Hydracarina (*Lebertia* sp.), free-living Nematoda, and Megaloptera. Hydracarina were found in all 10 lakes, nematodes were collected in all of the lakes except Lake Edith, and megalopterans were taken in all lakes but Bright Dot Lake.

Chironomid larvae were abundant from sandy shore areas to black silt in the deeper parts of the lakes. Smaller-sized genera predominated in the sandy, shoal areas, and the larvae of *Tendipes* sp. (bloodworms) occurred in considerable numbers in deeper, silty bottom but were almost nonexistent in shoal areas. Amphipods were found only in algae and plant beds; oligochaetes were present chiefly in silty, deeper parts of lake bottoms; and pelecypods were taken only in sandy, littoral areas.

Zooplankton

The plankton Crustacea present in the lakes are species found commonly in oligotrophic situations. Lakes Witsanapah, Dorothy, and Cloverleaf did not yield macroscopic zooplankton, although numerous collection attempts were made in both 1950 and 1951. However, plankters were found in the stomachs of trout taken from Lakes Dorothy and Cloverleaf, which leaves only Lake Witsanapah unaccounted for. It seems unlikely that this lake should be completely devoid of plankton Crustacea, since Bighorn Lake, of similar size and depth and located only a quarter of a mile away, yielded an average plankton crop of 677 diaptomids per cubic foot of water. In addition, Lake Constance maintains a fair plankton crop and drains into Lake Witsanapah, only a short distance away. The inability to collect zooplankton from three lakes, when plankters were known to exist in two of them, is probably due to the inadequacy of sampling by ordinary methods.

Copepods (*Diaptomus* sp., *Cyclops* sp., and *Eucyclops* sp.) occurred in seven of the nine lakes containing plankton Crustacea and were the predominant plankton organisms. Cladocera (*Daphnia* spp., and *Holopedium gibberum*) were also present in seven of the lakes, but were less abundant than copepods. Nauplii were common in all samples from plankton-inhabited lakes except Lake Constance, and these immature forms constituted a large percentage of the measured plankton crop. Four lakes yielded large numbers of the rotifer *Notholca* sp. Bright Dot Lake contained considerable numbers of *Filinia* (*Triarthra*) sp. Lakes Edith and Convict contained the flagellate *Volvox* sp., and the latter lake revealed very large numbers of *Ceratium* sp.

Although plankton densities varied considerably among the lakes, their vertical distributions followed a more or less similar pattern throughout. Distributions were usually bimodal, with the peaks at the upper and lower limits of the "thermocline." Plankton in Lake Genevieve exhibited a trimodal distribution, with the third peak occurring between depths of 90 and 105 feet. This variation was possibly caused by an irregularity in horizontal distribution of the plankton organisms, thereby creating a false peak. In four of the lakes, one peak occurred above the lower limit of Secchi disc visibility and the other below it. In Bright Dot Lake both peaks were within the zone of transparency. In Bighorn Lake the zone of transparency extended to the lake bottom.

Terrestrial Insects

These forms consisted chiefly of ants, bark beetles, and leaf hoppers. Moths, butterflies, and grasshoppers occasionally appeared around the lake shores but were in a distinct minority when compared to the previously mentioned insects.

Comparative Productivity in Terms of Invertebrate Abundance

Productivity of bottom organisms differed considerably among the lakes, as shown in tables 11 and 12. Within the range of pounds per acre indicated in table 11, the 10 lakes fall into distinct groups. Comprising the most productive group are Lakes Mildred and Cloverleaf which yielded 211.3 and 207.4 pounds per acre, respectively. Next in order are Lakes Witsanapah, Genevieve, Constance, and Edith, producing roughly half the bottom fauna of the more productive lakes. Their values ranged from 134.4 to 111.4 pounds per acre. Calhoun (1944b) reported a similar yield of 134 pounds per acre for Upper Blue Lake, located at an elevation of 8,130 feet in Alpine County, Calif. In the third group are Lakes Bright Dot, Convict, and Bighorn, which produced 49.9, 34.6, and 30.7 pounds per acre, respectively. These standing crops were comparable to the wet weight of 49 pounds of bottom fauna per acre reported for Angora Lake (elevation 7,800 feet) by Needham and Sumner (1941), and slightly below the 57 pounds per acre reported by Needham and Hanson [11] from 23 lakes lying at higher elevations in the Sierra Nevada. Finally, Lake Dorothy with 19.2 pounds per acre had the lowest bottom fauna yield of the 10 lakes.

Brundin (1949), reporting on oligotrophic lakes in Sweden, stated that bottom fauna counts of 1,900 to 2,000 organisms per square meter are common. Rawson (1934) gave a figure of 1,363 organisms per square meter for Paul Lake in British Columbia, and Calhoun (1944b) listed 2,267 organisms per square meter for Blue Lake in the Sierra Nevada. These values are intermediate between the extremes represented by Lakes Dorothy and Cloverleaf which produced 896 and 4,674 organisms, respectively, per square meter of bottom area.

Zooplankton productivities ranged from 22 organisms per cubic foot of water in Lake Constance to 677 organisms per cubic foot in Bighorn Lake (column 5, table 15). The 10 lakes, compared in terms of mean plankton volumes (column 4, table 15), ranged from 0.00 to 0.08 cubic centimeters per cubic foot of water. Two lakes were thereby relatively rich in plankton (Bighorn and Bright Dot), one lake (Genevieve) mediocre, and four lakes (Mildred, Convict, Constance, Edith) relatively plankton-poor at the time of sampling. The apparent absence of zooplankton in the remaining three lakes has been noted.

In table 17 the 10 lakes are arranged in descending order of invertebrate productivity. For the purpose of comparisons in the final section of this report, the ranking of lakes with respect to food production has been reduced to a scale of proportionate parts of 10 since it is doubtful that quantitative standing crop differences among the lakes could be explained in terms of the physical and

[11] See footnote 1, p. 437.

chemical factors measured. The use of proportionate ratings for plankton alone was rejected because of negative samples from three lakes. It is evident in table 17 that plankton quantities were too small to affect the order of lakes except for Bighorn Lake, the heaviest producer of plankton. To include plankton in a summary ranking similar to those used with physical and chemical influences, the empirical values for bottom fauna and plankton were added together for each lake, and the proportionate ranking is derived from these sums. The final high-to-low order of lakes follows the order of bottom fauna abundance except for a minor reversal between lakes Bighorn and Convict.

TABLE 17.—*Ranking of the lakes according to proportionate ratings of abundance of invertebrate organisms*

Lake	Invertebrate organisms			Proportionate rating
	Bottom fauna (grams per square foot)	Plankton (cubic centimeters per cubic foot)	Total [1]	
Mildred	2.20	0.03	2.23	10.0
Cloverleaf	2.16	.00	2.16	9.7
Witsanapah	1.40	.00	1.40	5.9
Genevieve	1.32	.05	1.37	5.8
Constance	1.16	.02	1.18	4.8
Edith	1.16	.01	1.17	4.8
Bright Dot	.52	.07	.59	1.9
Bighorn	.32	.08	.40	1.0
Convict	.36	.03	.39	.9
Dorothy	.20	.00	.20	.0

[1] In these summations, it is assumed that cubic centimeters are equal to grams for the plankton measurements.

FOODS CONSUMED

General comparisons of the food habits of trout in the 10 lakes are presented in tables 18, 19, and 20. Food items are grouped taxonomically and, where practicable, according to life-history stages for each trout population. Values are given for unidentifiable material, but they are disregarded in the following discussion since this material is probably derived in entirety from food types listed.

The composition of trout diets, in percentages of total number of organisms consumed, is given in table 18. Zooplankton has been disregarded therein for obvious reasons, as were algae and unidentifiable material. A marked predominance of aquatic dipterans (chironomid pupae and larvae) is indicated for all trout populations. Except for terrestrial organisms in Lake Edith, hydracarines in Lakes Genevieve and Mildred, and amphipods in Convict Lake, other food items are numerically insignificant.

Table 19, showing percentage of stomachs containing each food type, expresses the relative number of fish in each lake consuming the various food items. Chironomid pupae again prevail as the most important food item, but relatively large numbers of trout utilize minor foods.

The relative importance of individual food items is probably best expressed as the percentage of total volume consumed (table 20). Bottom organisms were predominant among identifiable foods in all lakes except Mildred and Bright Dot; miscellaneous material [12] predominated in the stomachs of trout from these two lakes, and the aberrancy is explained by the heavier fishing from anglers using bait. All groups examined contained miscellaneous material which ranged from 7.59 percent in Convict Lake brown trout to 50.00 percent in Lake Mildred rainbow trout. If miscellaneous material is disregarded, immature chironomids accounted for more food volume than any other item in all populations except Convict Lake brown trout. Consumption of trout by large brown trout causes a disproportionate emphasis on a fish diet for this species in the general analysis. If larger brown trout (4 years and older) are excluded, it may be stated that immature chironomids constitute the most important single food item for all trout populations. Terrestrial organisms were next in importance, forming 32.86 percent of foods consumed by Lake Edith brook trout at one extreme, and 0.16 percent of the stomach contents of Bright Dot Lake brook trout at the other. Amphipods (*Gammarus* sp.) were important in Convict Lake, where they accounted for 23.37 and 16.59 percent of the diets of rainbow and brown trout; smaller percentages (1.74 to 4.10) occurred in stomachs of trout from Lakes Bright Dot, Genevieve, and Mildred. Zooplankton comprised 17.75 percent of the foods consumed by brook trout in Bright Dot Lake and was significant as food for all groups except rainbow trout in Lake Dorothy, brown trout in Convict Lake, and brook trout in Lake Witsanapah. Small trout were taken by rainbow

[12] Included are stones, wood, caddisfly cases, and commercial salmon eggs. The last two items were most abundant. Salmon eggs are important during the summer, when fishermen not only use them for bait but also throw large quantities into the water as chum to attract trout.

TABLE 18.—*Foods consumed by trout in the lakes of Convict Creek Basin*

[Figures are percentages of the total number of organisms consumed exclusive of algae and plankton]

Organism	Lake and species of trout											
	Constance, brook trout	Witsanapah, brook trout	Bighorn, brook trout	Cloverleaf, brook trout	Edith, brook trout	Genevieve, brook trout	Bright Dot, brook trout	Dorothy		Mildred, rainbow trout	Convict	
								Brook trout	Rainbow trout		Rainbow trout	Brown trout
Diptera:												
Larvae	1.17	8.70	2.48	39.05	5.40	2.42	1.89	20.01	8.36	23.94	12.22	38.02
Pupae	98.46	87.51	97.14	55.72	67.28	79.45	96.66	73.39	84.58	66.09	73.89	51.28
Adults		.01	.01	.10	.59	.68	.47	.45	.24	.06		
Hemiptera:												
Adults	.03									.64		
Trichoptera:												
Larvae	.07	.42		.12	.16	.43		.01	.07			
Adults					.11	.32		.07				
Ephemerida:												
Naiads	.02	1.20										
Adults			.01	.01				.01				
Plecoptera:												
Naiads	.01	.02						.03		.10	.09	.26
Adults				.01				.01				
Megaloptera:												
Larvae	.02	.06		.05	1.12	.05		.02		.22	.09	
Coleoptera:												
Larvae			.01	.03			.08	.02				
Adults								.16	.14			
Hydracarina	.06	.02	.20	3.62	2.99	10.03	.39	.78	.61	5.46	.28	
Crustacea:												
Gammarus						.58	.35			1.85	10.35	7.42
Mollusca	.13	.34	.01	.16	.12	3.76		.01		.39	.57	2.47
Oligochaeta										.03		.33
Nematoda	.01	.02						.01				
Fishes								.01		.06		.19
Terrestrial	.02	1.70	.14	1.13	22.23	2.28	.16	5.01	6.00	1.16	2.51	.03

TABLE 19.—*Foods consumed by trout in the lakes of Convict Creek Basin*

[Figures are percentages of stomachs containing the organism]

Organism	Lake and species of trout											
	Constance, brook trout	Witsanapah, brook trout	Bighorn, brook trout	Cloverleaf, brook trout	Edith, brook trout	Genevieve, brook trout	Bright Dot, brook trout	Dorothy		Mildred, rainbow trout	Convict	
								Brook trout	Rainbow trout		Rainbow trout	Brown trout
Diptera:												
Larvae	45.3	62.9	47.2	71.8	31.2	18.9	22.7	63.7	54.2	38.3	38.1	23.2
Pupae	100.0	95.7	98.6	98.9	87.1	97.9	90.9	95.0	87.5	78.3	42.7	30.2
Adults		1.4	1.4	14.2	5.4	4.2	22.7	6.5	8.3	1.7		
Hemiptera:												
Adults	3.1									16.7		
Trichoptera:												
Larvae	3.1	17.1		9.4	3.2	1.1		2.1	4.2			
Adults					8.6	15.8		5.8				
Ephemerida:												
Naiads	4.7	21.4										
Adults			2.8	1.2				1.1				
Plecoptera:												
Naiads	3.1	1.4						2.5		1.7	4.8	9.3
Adults				1.2				1.4				
Megaloptera:												
Larvae	7.8	4.3		5.9	14.0	4.2		1.8		10.0	4.8	
Coleoptera:												
Larvae			2.8	4.7			4.6	2.2				
Adults								5.3	8.3			
Hydracarina	6.3	8.6	23.6	32.9	14.0	55.8	4.6	20.1	12.5	6.7	4.8	
Crustacea:												
Plankton	25.0		13.9	22.4	34.4	12.6	40.9	5.0		16.7	9.5	
Gammarus						7.4	9.1			21.7	42.9	44.2
Mollusca	23.4	2.9	1.4	10.6	3.2	19.0		.4		8.3	14.3	14.0
Oligochaeta										1.7		2.3
Nematoda	1.6	1.4						.4				
Fishes								.4		3.3		11.6
Algae				1.2						16.7		
Terrestrial	6.3	32.7	23.6	31.8	47.3	19.0	4.6	65.2	37.5	20.0	19.0	2.3
Miscellaneous [1]	76.6	95.6	93.1	100.0	83.6	94.7	100.0	99.1	100.0	100.0	92.0	61.2

[1] Insect and other food fragments and unidentifiable material.

trout in Lake Mildred, brook trout in Lakes Dorothy and Constance, and brown trout in Convict Lake. Only in the latter lake was cannibalism important; 53.60 to 84.80 percent of the stomach contents of large brown trout was small fish. Some algae was found in stomachs of brook trout from Cloverleaf Lake, but this item was prominent only in Lake Mildred rainbow trout.

The abundance of immature chironomids (larvae and pupae) in stomach contents varied considerably among trout populations in different lakes, particularly with regard to volume. The range, in percentage of total volume of food consumed, was from 16.78 in Lake Mildred rainbow trout to 84.34 in Bighorn Lake brook trout. Numerically, chironomid consumption ranged from 89.30 percent of total in Convict Lake brown trout to 99.63 percent in Lake Constance brook trout. Percentages of stomachs containing chironomid pupae ranged from 30.20 for Convict Lake brown trout to 100 for Lake Constance brook trout. Between 90 and 100 percent of the stomachs of 7 trout groups contained chironomid pupae. In his discussion of the importance of chironomids as trout food, Johannsen (1937, pt. IV, p. 3) stated: "The ability of the chironomids to live on foodstuff that has a general distribution, their ability to build their own shelter and their consequent adaptability to a variety of conditions, their great reproductive capacity, and their brief life cycle, combine to make these insects so important a forage organism for fish."

Although oligochaetes and mollusks were generally the next most abundant foods present in the lakes, they were not utilized extensively. Mollusks were slightly more important than oligochaetes, and formed appreciable proportions (3.30 to 6.37 percent by volume) of the foods consumed in Lakes Convict and Genevieve. Oligochaetes were found only in stomachs of Convict Lake brown trout and Lake Mildred rainbow trout, where they formed 0.75 and 0.02 percent, respectively, of total volume consumed. The small degree to which oligochaetes were eaten is explainable by the fact that these organisms remain at least partially buried in bottom material in deeper parts of lakes and thus are not readily available as trout food.

TABLE 20.—*Foods consumed by trout in the lakes of Convict Creek Basin*

[Figures are percentages of the total volume of organisms consumed]

Organism	Lake and species of trout											
	Constance, brook trout	Witsanapah, brook trout	Bighorn, brook trout	Cloverleaf, brook trout	Edith, brook trout	Genevieve, brook trout	Bright Dot, brook trout	Dorothy		Mildred, rainbow trout	Convict	
								Brook trout	Rainbow trout		Rainbow trout	Brown trout
Diptera:												
Larvae	1.24	4.53	2.98	22.04	2.83	3.02	1.11	7.68	4.72	4.15	6.48	14.95
Pupae	64.75	46.60	81.36	48.50	29.25	53.41	32.42	50.12	44.43	12.63	22.29	13.90
Adults		.16	.01	.35	.39	.48	.13	.60	1.30	.05		
Hemiptera:												
Adults	.46									.63		
Trichoptera:												
Larvae	.49	2.43		.76	.30	1.07		.24	.57			
Adults					.52	3.59		.48				
Ephemerida:												
Naiads	.11	2.67										
Adults			.13	.01				.01				
Plecoptera:												
Naiads	.10	.40		.04				.23		.74	.09	.69
Adults								.46				
Megaloptera:												
Larvae	.28	.31		.46	2.79	.36		.10		.67	.24	
Coleoptera:												
Larvae			.11	.21			.03	.08				
Adults								.90	.68			
Hydracarina	.06	.01	1.32	1.90	.33	2.64	.03	.66	.30	.40	.47	
Crustacea:												
Plankton	5.02		.83	4.53	17.18	6.73	17.75	.12		11.87	4.24	
Gammarus						2.54	1.74			4.10	23.37	16.59
Mollusca	.52	.79	.01	.73	.19	6.37		.01		.51	3.30	4.25
Oligochaeta								.01		.02		.75
Nematoda	.01	.04						.01				
Fishes								.57		1.97		40.80
Algae				.10						10.28		
Terrestrial	.95	5.50	1.17	5.17	32.86	6.70	.16	22.73	23.85	1.98	18.89	.48
Miscellaneous [1]	26.01	36.56	12.08	15.20	13.36	13.09	46.63	14.99	24.15	50.00	20.63	7.59

[1] Insect and other food fragments and unidentifiable material.

FOOD HABITS IN RELATION TO SUPPLY

Considering all the lakes together, immature chironomids were easily the most abundant organisms, both in the environment and in the trout diet. The few exceptions which occurred in certain of the lakes have been stated. Chironomid pupae predominated in stomach contents, although the larvae were more abundant in bottom samples. This discrepancy can be explained in terms of availability, as the larvae of most chironomid species are bottom dwellers and are not readily available as trout food. Curtis (p. 437) reported an average of 155 pounds per acre of *Chironomus tentans* larvae in Cottonwood Lake (elevation 11,000 ft.), but failed to find one of these forms in trout stomachs. He attributed this lack at least partially to insufficient sampling during periods when the larvae were free-swimming. The larvae of some species of chironomids are known to be occasionally free-swimming (Malloch 1915), and the occurrence of such forms plus the trout's habit of nosing the bottom probably account for the consumption of larvae noted in the present study. Larvae occurred in about half of all stomachs examined (table 19) but the volume of consumption was small (table 20). Pupae are available during their ascent to the surface and also during the brief period of emergence. Both pupal and transitional forms were found in many trout stomachs.

Amphipods were consumed by trout in all lakes where they occurred, attesting to their availability as food, although the relative volumes consumed were not in proportion to the indicated supplies in the two lakes where these organisms were important. Lake Mildred rainbow trout ate 4.10 percent by volume of *Gammarus* where the organisms formed 49.20 percent of the bottom fauna, and Convict Lake brown and rainbow trout ate 16.59 and 23.37 percent where the amphipods constituted only 3.02 percent of the bottom foods in samples.

Mollusks (chiefly the pelecypod *Pisidium* sp.) were less abundant than oligochaetes but were utilized more as food, presumably because of greater availability. For the 10 trout groups in which mollusks occurred as food, importance of this item ranged from 0.01 percent of the total volumes consumed by Lake Dorothy and Bighorn Lake brook trout to 6.37 percent of the volume eaten by the same species in Lake Genevieve. There was no apparent relation between relative amounts available and amounts found in stomachs.

Hydracarina (*Lebertia* sp.) were present in littoral areas and were consumed by all trout groups except Convict Lake brown trout. Because of the minute size of these organisms, however, the percentages of total volume which they comprised were very small. A maximum of 2.64 percent was found in stomachs of Lake Genevieve brook trout.

Free-living nematodes were collected in small quantities from all lakes except Lake Edith but were consumed by brook trout only in Lakes Constance, Witsanapah, and Dorothy. As with the Hydracarina, very little of the total stomach volumes consisted of these organisms.

The remainder of the bottom food organisms were adult and immature insects (Hemiptera, Trichoptera, Ephemerida, Plecoptera, Megaloptera, and Coleoptera). These organisms originated in the littoral areas and were taken in varying small amounts (tables 18 to 20). Megaloptera larvae (*Sialis* sp.) were principal members of this group present in the bottom samples, and they appeared to a measurable extent in stomachs of trout from eight lakes. There was no apparent relationship between amounts of other aquatic insects present and those eaten, except for consumption of significant amounts of immature Trichoptera and Ephemerida in Lake Witsanapah, the only lake in which these forms were collected to any extent.

Zooplankters were utilized by 9 of the 11 trout groups to which they were available; only Convict Lake brown trout and Lake Dorothy rainbow trout stomachs were found without these organisms. Zooplankton consumed varied from 0.12 percent of total stomach volume in Lake Dorothy (brook trout) to 17.75 percent in Bright Dot Lake. There seemed to be no apparent relationship between amounts of plankton present in the environment and amounts eaten by trout.

Other foods consumed by trout were terrestrial insects, algae, fish, and miscellaneous material. They are listed in table 21 with the bottom fauna and plankton discussed above. These food groups were present in nearly all lakes and were assumed to be available to trout populations. However, terrestrial insects were taken in sizable amounts

TABLE 21.—*Foods present in the lakes of Convict Creek Basin compared with foods consumed by trout*

Lake and species of trout	Foods present		Foods consumed [1]					
	Fauna per square foot of bottom area (cubic centimeters)	Number of zooplankters per cubic foot of water	Bottom organisms	Zooplankton	Terrestrial organisms	Algae	Fishes	Miscellaneous [2]
Constance (brook trout)	1.91	22	68.0	5.0	0.9	0	0	26.1
Witsanapah (brook trout)	2.31	0	57.9	0	5.5	0	0	36.6
Bighorn (brook trout)	.68	677	85.9	.8	1.2	0	0	12.1
Cloverleaf (brook trout)	3.62	0	75.0	4.5	5.2	.1	0	15.2
Edith (brook trout)	1.75	61	36.6	17.2	32.9	0	0	13.3
Genevieve (brook trout)	2.06	146	73.5	6.7	6.7	0	0	13.1
Bright Dot (brook trout)	.98	204	35.5	17.7	.2	0	0	46.6
Dorothy (brook trout)	.40	0	60.5	.1	23.8	0	.6	15.0
Dorothy (rainbow trout)	.40	0	52.0	0	23.8	0	0	24.2
Mildred (rainbow trout)	3.12	24	23.9	11.9	2.0	10.2	2.0	50.0
Convict (rainbow trout)	.51	130	56.2	4.2	18.9	0	0	20.7
Convict (brown trout)	.51	130	51.1	0	.5	0	40.8	7.6

[1] Expressed in percentage of total volume of stomach contents.
[2] Includes unidentified material.

only by rainbow trout in Lakes Convict and Dorothy and by brook trout in Lakes Edith and Dorothy. The single noteworthy example of algae consumption occurred among Lake Mildred rainbow trout. Similarly, Convict Lake brown trout appeared to be the only piscivorous fish population.

COMPARISONS OF FOOD HABITS

Trout of Various Sizes

Analyses of stomach contents were made for each of several size groups of trout in each lake in order to determine changes in food habits. Percentage of total volume of foods eaten, percentage of total numbers, and percentage of stomachs containing an organism were calculated for each group. Tables 22 and 23 indicate the limits of size groups, and compare the feeding of rainbow and brown trout of different sizes in Convict Lake.[13]

The only radical change in food habits with increase in size was observed in the brown trout population of Convict Lake. These trout were found to subsist principally on amphipods and immature dipterans until they reached about 350 millimeters in total length, which corresponds roughly to the beginning of the fourth year of life. Above this size and age (table 23) small trout appeared in the diet and soon became the most prominent item, amounting to 84.8 percent of food volume for trout longer than 400 millimeters. Amphipods and chironomids continued to be significant as food for these large trout, however, as may be seen by the percentage of total number of organisms consumed (final column; table 23).

Convict Lake rainbow trout were also found to depend mainly on *Gammarus* and immature dipterans during the first three years of life. No larger rainbow trout were obtained from this lake, and no small trout were found in the rainbow trout stomachs examined.

Although the food habits of various size groups of brook and rainbow trout did not vary greatly, some interesting differences were noted. In general, the smaller brook trout consumed relatively large volumes of chironomid larvae, and the percentage eaten became increasingly smaller as the trout increased in size; this held true in all brook trout populations except those of Lakes Edith and Bright Dot. Conversely, the smaller brook trout consumed relatively fewer chironomid pupae, and this occurred without exception among all brook-trout groups.

Plankton was taken in smaller percentages by the smaller fish in all brook trout populations except that of Lake Genevieve. Large rainbow trout took a greater percentage of plankton than did smaller trout in Lake Mildred, but smaller rainbow trout consumed the greatest quantities of plankton in Lakes Dorothy and Convict.

Small trout also consumed greater percentages of terrestrial insects than did larger trout in all groups of brook trout except those in Lakes Edith and Witsanapah. Small rainbow trout consumed a greater percentage of drift foods than did large rainbow trout in Lakes Mildred and Convict, but

[13] Analysis identical to those presented in tables 22 and 23 were made for the remaining 10 trout populations, but tables have been omitted because of the lack of variation in food habits with size in the upper lakes.

TABLE 22.—*Food habits of different sizes of rainbow trout in Convict Lake, 1950*

Organism	Percentage of stomachs of size group [1] containing organism—length range (millimeters)					Percentage of the total number of organisms consumed by size group—length range (millimeters)					Percentage of the total volume of organisms consumed by size group—length range (millimeters)				
	<165	165–200	201–235	236–270	>270	<165	165–200	201–235	236–270	>270	<165	165–200	201–235	236–270	>270
Diptera:															
Larvae	-----	37.5	50.0	-----	50.0	-----	7.8	12.2	-----	45.4	-----	9.6	5.7	-----	10.6
Pupae	66.7	37.5	50.0	-----	-----	92.4	83.8	75.0	-----	-----	38.8	20.0	24.2	-----	-----
Plecoptera: naiads	-----	12.5	-----	-----	-----	-----	.6	-----	-----	-----	-----	.5	-----	-----	-----
Megaloptera: larvae	-----	-----	12.5	-----	-----	-----	-----	.2	-----	-----	-----	-----	.4	-----	-----
Hydracarina	-----	-----	12.5	-----	-----	-----	-----	.8	-----	-----	-----	-----	.7	-----	-----
Crustacea:															
Gammarus	33.3	37.5	50.0	-----	50.0	4.2	7.8	8.0	-----	50.0	36.3	18.5	18.9	-----	51.1
Plankton	33.3	12.5	-----	-----	-----	-----	-----	-----	-----	-----	7.1	21.2	-----	-----	-----
Mollusca	-----	-----	25.0	-----	50.0	-----	-----	.5	-----	4.6	-----	-----	4.1	-----	6.4
Terrestrial:															
Coleoptera: adults	33.3	-----	37.5	-----	-----	1.7	-----	1.0	-----	-----	1.8	-----	6.0	-----	-----
Hemiptera: adults	-----	-----	25.0	-----	-----	-----	-----	.7	-----	-----	-----	-----	.7	-----	-----
Hymenoptera: adults	33.3	-----	37.5	-----	-----	1.7	-----	1.2	-----	-----	1.1	-----	1.4	-----	-----
Orthoptera: adults	-----	-----	12.5	-----	-----	-----	-----	.4	-----	-----	-----	-----	22.2	-----	-----
Miscellaneous [2]	-----	37.5	50.0	-----	50.0	-----	-----	-----	-----	-----	-----	9.0	5.7	-----	21.3
Unidentified	66.7	75.0	67.5	-----	100.0	-----	-----	-----	-----	-----	14.9	21.2	10.0	-----	10.6

[1] 23 stomachs examined. [2] Rocks and Trichoptera cases.

TABLE 23.—*Food habits of different sizes of brown trout in Convict Lake, 1950*

Organism	Percentage of stomachs of size group [1] containing organism—length range (millimeters)					Percentage of the total number of organisms consumed by size group—length range (millimeters)					Percentage of the total volume of organisms consumed by size group—length range (millimeters)				
	<250	250–300	301–350	351–400	>400	<250	250–300	301–350	351–400	>400	<250	250–300	301–350	351–400	>400
Diptera:															
Larvae	11.1	-----	75.0	7.1	16.7	3.6	-----	77.1	1.5	50.0	0.9	-----	69.7	0.5	1.4
Pupae	-----	16.7	50.0	50.0	16.7	-----	90.1	20.8	83.2	6.7	-----	42.0	12.3	17.9	.4
Plecoptera: naiads	11.1	-----	-----	14.3	16.7	1.2	-----	-----	.9	1.6	.8	-----	-----	.3	2.0
Crustacea: *Gammarus*	88.9	66.7	12.5	35.7	16.7	83.3	9.9	1.9	3.2	35.0	86.3	48.1	9.3	6.6	7.1
Mollusca	-----	-----	25.0	28.6	-----	-----	-----	.2	10.8	-----	-----	-----	2.4	9.3	-----
Oligochaeta	11.1	-----	-----	-----	-----	11.9	-----	-----	-----	-----	11.5	-----	-----	-----	-----
Terrestrial:															
Lepidoptera: adults	-----	-----	-----	-----	16.7	-----	-----	-----	-----	1.7	-----	-----	-----	-----	2.0
Fishes	-----	-----	-----	14.3	50.0	-----	-----	-----	.4	5.0	-----	-----	-----	53.6	84.8
Miscellaneous [2]	-----	16.7	-----	7.1	-----	-----	-----	-----	-----	-----	-----	1.1	-----	.1	-----
Unidentified	11.1	33.3	50.0	85.7	16.7	-----	-----	-----	-----	-----	.5	8.8	6.3	11.7	2.2

[1] 61 stomachs examined. [2] Trichoptera cases.

large rainbow trout took more drift foods in Lake Dorothy.

Since small trout tended to consume greater volumes of chironomid larvae and terrestrial organisms, it appears likely that they feed more in the shoal area of lakes than large trout.

Two Species of Trout From the Same Lake

In order to detect differences in the food habits of two species of trout existing in the same body of water, table 24 was constructed to compare rainbow and brook trout in Lake Dorothy, and table 25 to compare rainbow and brown trout in Convict Lake.

The only striking difference between the Lake Dorothy trout was the much greater diversity of organisms consumed by brook trout. Brook trout ingested 19 different food items as compared to 9 taken by rainbow trout, although the percentages of major food items consumed by both species were similar. Brook-trout stomachs contained slightly greater percentages of chironomids than did those of rainbow trout. The relative amounts of terrestrial organisms taken by the two species were comparable, but the percentage of brook trout stomachs containing these organisms was almost twice as great as that for rainbow trout. This dissimilarity can probably be explained by the more pronounced shoal feeding habit of brook trout as compared to rainbow trout, which apparently feed more or less indiscriminately and do not limit their feeding to particular areas.

An examination of the data from Convict Lake (table 25) reveals similarity in the number of food groups fed upon by the two species of trout: 10 for rainbow trout and 9 for brown trout. The

TABLE 24.—*A comparison of the foods consumed by rainbow and brook trout in Lake Dorothy, 1950*

Organism	Rainbow trout [1]			Brook trout [2]		
	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents
Diptera:						
Larvae	54.16	8.36	4.72	63.67	20.01	7.68
Pupae	87.50	84.58	44.43	94.96	73.39	50.13
Adults	8.33	.24	1.30	6.47	.45	.60
Trichoptera:						
Larvae	4.16	.07	.57	2.15	.01	.24
Adults				5.75	.07	.48
Ephemerida: adults				1.08	.01	.01
Plecoptera:						
Naiads				2.52	.03	.23
Adults				1.44	.01	.46
Megaloptera: larvae				1.80	.02	.10
Coleoptera:						
Larvae				2.16	.02	.08
Adults	8.33	.14	.68	5.32	.16	.90
Hydracarina	12.50	.61	.30	20.14	.78	.66
Mollusca				.36	.01	.01
Nematoda				.36	.01	.01
Fishes				.36	.01	.57
Crustacea: plankton				5.04		.12
Terrestrial	37.50	6.00	23.85	65.18	5.01	22.73
Miscellaneous	100.00		24.15	99.00		14.99

[1] Size range 126 to 320 millimeters, 25 stomachs examined.
[2] Size range 131 to 345 millimeters, 285 stomachs examined.

percentage volumes of chironomids consumed by these two species were almost identical, although a higher percentage of rainbow trout than brown trout fed upon these organisms. Amphipods were consumed in greater quantity by rainbow trout but were fed upon by a higher percentage of brown trout. Comparisons of food volumes (table 25) are somewhat misleading, as the size range includes large and piscivorous brown trout but no large rainbow trout. A previous section has shown that brown trout in the same size range as the sample of rainbow trout consume similar relative volumes of dominant foods. Zooplankton was ingested by 9.5 percent of the rainbow trout and constituted 4.24 percent of the total volume of foods eaten, but none was found in brown-trout stomachs. Mollusks were consumed almost equally by both species, but the relative amount of terrestrial organisms eaten by rainbow trout was far greater than that eaten by brown trout. A divergence in foraging habits between these two species of trout is thus indicated by the relative amounts of zooplankton and terrestrial organisms consumed.

Rainbow Trout in Lakes Dorothy and Convict

The stomach contents of rainbow trout from Lakes Dorothy and Convict were compared in order to determine differences in food habits of a single trout species in a lake of the upper basin and in Convict Lake. These data are presented in table 26. Immature chironomids formed the largest percentage of volume of foods eaten in both lakes, but amphipods were important enough in Convict Lake to account for a greater percentage volume than chironomid pupae alone. Rainbow trout in Convict Lake contained plankton and mollusks, but those in Lake Dorothy did not. Terrestrial organisms were taken to a greater extent in Lake Dorothy than in Convict Lake. The trout in Convict Lake consumed a larger variety of food groups than did those in Lake Dorothy, but comparisons of stomach contents with bottom samples from these two lakes suggest that the observed differences in diet are due mostly to differences in availability of the various food organisms. Also, the small variety consumed by the Lake Dorothy fish may have resulted from feeding activities confined to emerging chironomid pupae with a consequent neglect of other foods.

Brook Trout in Lakes Constance and Witsanapah

In order to compare brook-trout food habits in two years, stomachs of this species were collected in both 1950 and 1951 from Lakes Constance and Witsanapah. The analyses are reported in tables 27 and 28, which demonstrate that the foods examined in 1951 were similar in both type and quantity to those taken in 1950.

TABLE 25.—*A comparison of the foods consumed by rainbow and brown trout in Convict Lake, 1950*

Organism	Rainbow trout [1]			Brown trout [2]		
	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents
Diptera:						
Larvae	38.10	12.22	6.48	23.25	38.02	14.95
Pupae	42.86	73.89	22.29	30.23	51.28	13.90
Plecoptera: naiads	4.76	.09	.09	9.30	.26	.69
Megaloptera: larvae	4.76	.09	.24			
Hydracarina	4.76	.28	.47			
Crustacea:						
Gammarus	42.86	10.35	23.37	44.18	7.42	16.59
Plankton	9.52		4.24			
Mollusca	14.29	.57	3.30	13.95	2.47	4.25
Oligochaeta				2.32	.33	.75
Fishes				11.63	.19	40.80
Terrestrial	19.05	2.51	18.89	2.32	.03	.48
Miscellaneous	9.85		20.63	61.16		7.59

[1] Size range 124 to 325 millimeters; 23 stomachs examined.
[2] Size range 164 to 772 mm.; 61 stomachs examined.

TABLE 26.—*A comparison of the foods consumed by rainbow trout in Dorothy and Convict Lakes, 1950*

Organism	Lake Dorothy [1]			Convict Lake [2]		
	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents
Diptera:						
Larvae	54.16	8.36	4.72	38.10	12.22	6.48
Pupae	87.50	84.58	44.43	42.86	73.89	22.29
Adults	8.33	.24	1.30			
Trichoptera: larvae	4.16	.07	.57			
Plecoptera: naiads				4.76	.09	.09
Megaloptera: larvae				4.76	.09	.24
Coleoptera: adults	8.33	.14	.68			
Hydracarina	12.50	.61	.30	4.76	.28	.47
Mollusca				14.29	.57	3.30
Crustacea:						
Gammarus				42.86	16.35	23.37
Plankton				9.52		4.24
Terrestrial	37.50	6.00	23.85	19.05	2.51	18.89
Miscellaneous	100.00		24.15	9.86		20.63

[1] Size range of trout 126 to 320 millimeters total length; 25 stomachs examined.
[2] Size range of trout 124 to 325 millimeters total length; 23 stomachs examined.

SUMMARY OF FOOD AND FEEDING HABITS

Bottom fauna production in the 10 lakes ranged from 19 to 211 pounds (wet weight) per acre, as determined from a transect system of bottom sampling. The variety of aquatic food organisms is limited, with immature chironomids most abundant in nearly all lakes. Amphipods (*Gammarus* sp.) are present in four lakes, and were important as food in Lakes Convict and Mildred. Plankton was sampled less fully but was shown to be useful as food in the seven lakes where it was present in samples. Plankton organisms also occurred in stomachs from two of the three lakes where no plankton was obtained in repeated hauls.

Food habits were determined by analyses of stomach contents from 979 summer-collected trout. Aquatic organisms other than plankton and fish formed the largest percentage volume of natural foods consumed; of these, immature chironomids (larvae and pupae) were taken in the greatest amounts by all populations. In Convict Lake, however, *Gammarus* accounted for greater relative volumes than chironomid pupae alone in both brown and rainbow trout diets. Convict Lake brown trout consumed more chironomid larvae than pupae, which was an exception to the general rule. Diptera (Chironomidae) formed 95.3 percent of the total number and 57.5 percent of the total volume of organisms consumed by trout in the nine upper lakes. Terrestrial insects were eaten by all trout groups and were secondary in importance as food (2.3 and 11.5 percent, respectively, of total numbers and volume). Other bottom organisms formed relatively small per-

TABLE 27.—*Food habits of Lake Constance brook trout compared for 2 years*

Organism	1950			1951		
	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents
Diptera:						
Larvae	37.5	2.61	1.76	45.3	1.17	1.24
Pupae	84.4	94.79	49.46	100.0	98.46	64.75
Adults	3.1	.08	.09			
Hemiptera: adults	15.6	.12	1.53	4.7	.03	.46
Trichoptera:						
Larvae	6.2	.03	.22	3.1	.07	.49
Adults	6.2	.20	2.34			
Ephemerida:						
Naiads	12.5	.32	3.24	4.7	.02	.11
Adults	15.6	.87	7.57			
Plecoptera: naiads				3.1	.01	.10
Megaloptera: larvae				7.8	.02	.28
Hydracarina	6.2	.52	.06	6.2	.06	.06
Crustacea: plankton	6.2		1.07	25.0		5.02
Mollusca	6.2	.02	.11	23.4	.13	.52
Nematoda				1.6	.01	.01
Terrestrial:						
Coleoptera: adults	25.0	.27	2.27	4.7	.01	.23
Hymenoptera: adults	15.6	.12	1.28	1.6	.01	.72
Lepidoptera: adults	3.1	.02	.16			
Fishes	9.4	.03	16.32			
Miscellaneous [1]	12.5		1.01	34.4		20.47
Unidentified	78.1		11.51	40.6		5.54

[1] Includes Trichoptera cases and salmon eggs used for bait.

TABLE 28.—*Food habits of Lake Witsanapah brook trout compared for 2 years*

Organism	1950			1951		
	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents	Stomachs containing organism (percentage)	Percentage of total number of organisms	Percentage of total stomach contents
Diptera:						
Larvae	76.7	25.78	16.10	62.9	8.70	4.53
Pupae	80.0	63.31	34.20	95.7	87.51	46.60
Adults	3.3	.19	.21	1.4	.01	.16
Trichoptera:						
Larvae				17.1	.42	2.43
Adults	6.7	.22	.71			
Ephemerida:						
Naiads	15.3	5.88	6.18	21.4	1.20	2.67
Adults	10.0	1.40	3.17			
Plecoptera: naiads	6.7	.59	.71	1.4	.02	.40
Megaloptera: larvae				4.2	.06	.31
Hydracarina	3.3	.07	.10	8.6	.02	.01
Mollusca	3.3	.19	.22	2.9	.34	.79
Nematoda				1.4	.02	.04
Terrestrial:						
Coleoptera: adults	23.3	.30	1.90	11.4	.13	.99
Hemiptera: adults	20.0	.37	1.18	18.6	.58	1.46
Hymenoptera: adults	33.3	1.70	6.00	8.6	.99	3.05
Miscellaneous [1]	23.3		13.32	27.1		20.37
Unidentified	90.0		16.00	65.7		16.19

[1] Includes salmon eggs and earthworms used for bait and Trichoptera cases.

centages; within this group, hydracarines and mollusks were taken most abundantly. Immature aquatic insects other than dipterans occurred in stomachs to a small extent, as did free-living nematodes and oligochaetes. Plankton was taken by nine trout groups, mainly by smaller fish. Large brown trout subsisted primarily on small trout.

Brook trout in Lake Dorothy consumed the greatest variety of food types, followed by Lake Mildred rainbow trout and Cloverleaf Lake brook trout. Rainbow trout in Lake Dorothy, brook trout in Bright Dot Lake, and brown trout in Convict Lake ate the fewest types of food.

On the whole, foods taken by trout in the Convict Creek Basin lakes were found to be similar in relative importance to the foods consumed by black spotted trout (*Salmo clarkii henshawi*) in Upper Blue Lake, Calif., as reported

by Calhoun (1944a), and several species of trout in Angora Lake, Calif. (Needham and Sumner, 1941).

Trout were placed in size groups to determine food changes with growth. The most notable change of this kind was the development of piscivory in Convict Lake brown trout, apparent in the analysis at the beginning of the fourth year of life. Smaller brook trout took greater percentages of chironomid larvae and terrestrial insects, and smaller percentages of chironomid pupae than did larger trout, suggesting a more pronounced shoal-feeding habit in small trout. Chironomid larvae were more important than pupae to all sizes of brook trout in Cloverleaf Lake, which is shallow throughout. The diets of two coexisting trout species were compared in Lake Dorothy (brook and rainbow trout) and in Convict Lake (rainbow and brown trout). Brook trout were found to feed over a greater range of organisms, and to a greater extent on terrestrial foods, than rainbow trout. In Convict Lake, two species had similar diets in the first 3 years of life except that plankton was utilized by rainbow trout and apparently not by brown trout.

AGE, GROWTH, AND CONDITION OF TROUT

STOCKING HISTORY AND PRESENT STATUS

Trout are not native to the Owens River System. Although the Owens River had native populations of suckers and minnows, its tributary system of high lakes and most streams was barren of fish prior to stocking. Golden trout (*Salmo aguabonita* Jordan) were introduced to lakes of the upper Convict Creek Basin in the 1930's, and some fish of the initial generation planted are said to have reached 3 or 4 pounds after several years. The species failed to maintain itself, however, and it may be reasoned that spawning conditions were not suitable. Local history and observations indicate that numbers of golden trout attempted downstream spawning migrations and were destroyed by falling over cascades, or stranded where water passed under rocks in talus deposits.

Previous work on trout in the upper basin is limited to notes on the growth of golden trout in two of the lakes. Advanced fry of that species were planted in Bright Dot Lake in 1935, and in Bighorn Lake in 1936. Growth of these introduced trout was later found to be very good, and significance was attached to the fact that the lakes had been barren of fish prior to planting (Needham and Vestal, 1938). Food organisms were said to be abundant, and the trout were described as being in excellent condition. The Bighorn Lake fish reached an average length of 5.01 inches in one-and-a-fraction growing seasons, and the Bright Dot Lake trout grew to an average length of 8.3 inches in two-and-a-fraction growing seasons.

With the failure of golden trout to reproduce successfully, the upper lakes were stocked with hatchery-reared brook trout, *Salvelinus fontinalis* (Mitchill), and rainbow trout, *Salmo gairdneri* Richardson, presently distributed as shown below:

Lake	*Trout species*
Mildred	rainbow.
Dorothy	brook, rainbow.
Genevieve	brook.
Edith	brook.
Cloverleaf	brook.
Bright Dot	brook.
Bighorn	brook.
Witsanapah	brook.
Constance	brook.

The earliest record that could be found showed the first brook trout planted in the basin in 1944. The stocks have been replenished periodically since 1946 and 1947, when large numbers of this species were planted in most of the nine upper lakes. Rainbow trout have been planted in Lake Mildred almost annually since 1945, and were probably introduced earlier. Recent plantings made in Lake Dorothy have been rainbow trout, but brook trout still predominate there.

Convict Lake, accessible by road at the lower end of the canyon, is subject to heavy fishing pressure and has been restocked annually for many years with rainbow trout. This lake also has a large natural population of brown trout (*Salmo trutta* Linnaeus) from stocks introduced 20 years ago or earlier.

COLLECTION OF DATA

All trout collected from the upper nine lakes were removed by angling, mostly with artificial flies. Convict Lake brown trout were gill netted (1950) and trapped (1951–52). Weights to the nearest tenth of a gram and lengths (total, standard, and fork) to the nearest millimeter were determined soon after capture Fish collected

from the upper lakes were sexed at the time of stomach removal, and trapped brown trout were sexed in connection with a study of spawning. Scale samples were taken from the side of the body, above the lateral line and below the origin of the dorsal fin.

The total field collection comprised 1,656 trout of the three species listed. All scales from 143 samples were discarded because of poor symmetry, disfiguration, regeneration, or resorption at the margin. In reading and measuring the scales, 474 additional sets were classed as unreadable due to resorption or poor definition of annuli. The data used were therefore from an effective total of 1,039 specimens distributed over the 10 lakes as follows:

Lake	Species	Number of fish
Constance	Brook trout	101
Witsanapah	do	33
Bighorn	do	95
Dorothy	do	100
Do	Rainbow trout	26
Bright Dot	Brook trout	16
Cloverleaf	do	98
Edith	do	86
Genevieve	do	78
Mildred	Rainbow trout	78
Convict	do	25
In 1950	Brown trout	68
In 1951–52	do	235

METHODS

Selected scales were soaked in water, cleaned under a dissecting microscope, and mounted dry on microscope slides. The dry-mounting technique was satisfactory for all scales and was particularly well-suited to brook trout scales, which are very small (fig. 17 and 18: photomicrographs of rainbow and brook trout scales, at roughly the same magnification). It was found that uniform adherence of the scales to the slides was made easier by cleaning only part of the mucus from the smooth side of each scale; when the upper surface of the scale is thoroughly clean, the small amount of mucus left does not interfere with clear projection.

Four selected scales from each fish were mounted, and in subsequent examinations the best of each four was used for measurement. The scales were examined and measured at magnifications of 85 to 295 diameters with the aid of a Rayoscope microprojector, mounted on a high stand and adapted to use in diffuse daylight by an enclosed screen arrangement. All vibration

FIGURE 17.—Scale from a Lake Mildred rainbow trout (magnification × 65). Numbers indicate annuli.

was eliminated from the system by cooling the built-in projector lamp with a small stream of compressed air rather than with the attached rotary blower.

Ages of trout were determined by counting scale annuli and rates of growth were assessed, with the aid of a nomograph, by calculating past lengths of fish at times of annulus formation. The calculations were made by the Dahl-Lea or direct-proportion method, in which it is assumed that the body-scale ratio does not vary with fish length. Although this method does not yield absolute accuracy, its use in comparing growth rates of trout among these 10 lakes produces the same magnitude of differences and the same order of results as would be found by methods which employ an empirical body-scale relationship. Series of past total lengths were calculated and averaged for each trout population, and measures of variability and probable accuracy (standard deviation and standard error of mean) were computed. Populations were then compared by average yearly growth increments and by lengths attained in three years. The Convict Lake brown trout col-

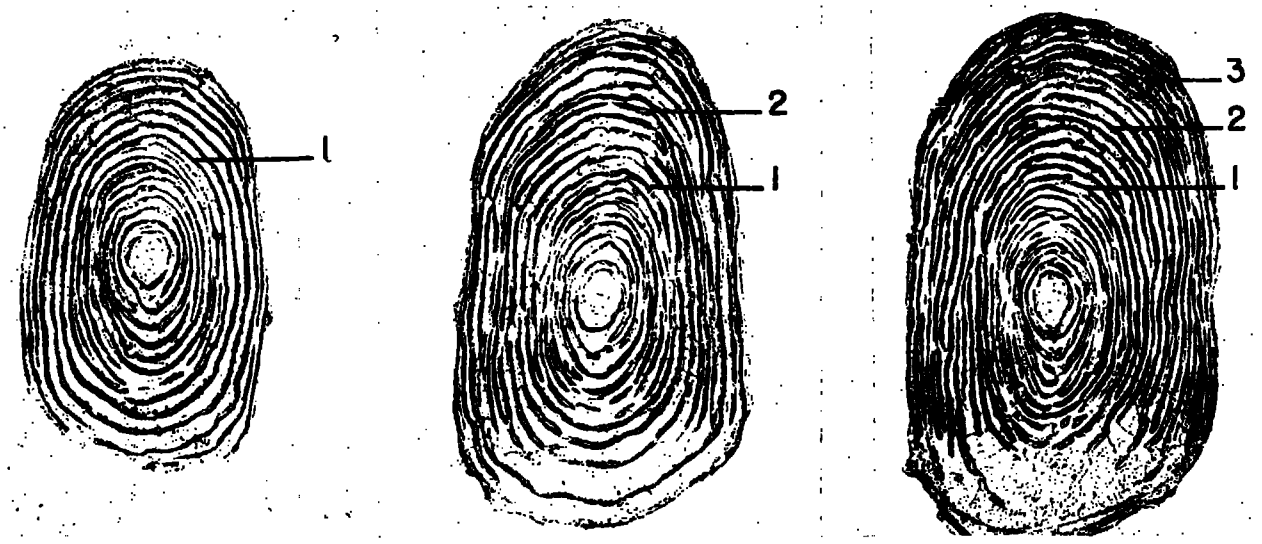

FIGURE 18.—Scales of brook trout from the upper lakes of Convict Creek Basin. Age groups I, II, and III have annuli indicated by numbers.

lections were made during the spawning period when the scales from most older fish were not reliable for measuring purposes and many were unfit to read. An additional evaluation of the growth characteristics of the spawning segment of this population was made by aging a series of 235 fish, and averaging the total lengths at capture for each age group.

AGE

The majority of the trout populations sampled were young and artificial in structure due to exploitation and continued restocking. Age composition figures are of little value in these circumstances, but present data on age give some indications of spawning success in the upper lakes.

Brook Trout

The collections of both 1950 and 1951 were composed of age groups I, II, and III. Older and larger fish were probably present, but the intensive sampling effort conducted in 1950 gave a strong indication that brook trout of age group IV and older were few in number. A few of the largest fish collected in 1951 exceeded the length range for age group III of the previous summer, but a careful examination of the scales revealed only three annuli.

Age group II predominated in the 1950 catch from five of the eight brook trout lakes (table 29). Since no brook trout were planted in 1948, these II's must represent natural reproduction and could only have resulted from successful spawning of trout planted in 1946 or earlier. Evidence that these trout do spawn during their second year in the lakes was found in Bright Dot Lake, where numbers of young-of-the-year were observed in the shallows in 1950. This lake was first stocked with brook trout in 1947, and was not restocked until 1951. Fish of the 1947 plant evidently spawned on suitable areas of the lake bottom in the fall of 1949, and the fry emerged in the spring of 1950. All Bright Dot Lake trout in the 1950 collections, and in creel checks of anglers, were from age group III. Their first offspring (age group I) predominated in the small 1951 collection. Naturally spawned brook-trout fry were observed frequently in Lakes Cloverleaf, Edith, and Genevieve, and were seen occasionally in Lake Constance.

Rainbow Trout

The samples from Lakes Dorothy and Convict were too small to give more than clues as to survival and possible reproduction. Several age groups (I, II, III, and IV) were collected from Lake Dorothy, which may indicate natural spawning in view of the fact that the records show a gap in the planting of rainbow trout there between 1945 and 1949. Fish of age groups I, II, and III were taken from Convict Lake; larger rainbow trout (1–5 lbs.) are reported during the angling season, but none were available for aging.

Sufficient length variations were found in rainbow trout of the Lake Mildred collection to permit

TABLE 29.—*Numbers and percentages of trout in the 1950 samples by age groups*

[Includes only those trout used in age and growth determinations. Numbers in parentheses are percentages]

Lake and species of trout	In age groups—							Total
	I		II		III			
nstance: Brook trout	None		11 (10.9)		90 (89.1)			101
horn: Brook trout	23 (24.2)		46 (48.4)		26 (27.4)			95
ght Dot: Brook trout	None		None		16 (100.0)			16
ith: Brook trout	18 (20.9)		59 (68.6)		9 (10.5)			86
nevieve: Brook trout	22 (28.2)		51 (65.4)		5 (6.4)			78
verleaf: Brook trout	16 (16.3)		62 (63.3)		20 (20.4)			98
tsanapah: Brook trout	20 (60.6)		4 (12.1)		9 (27.3)			33
rothy: Brook trout	2 (2.0)		76 (76.0)		22 (22.0)			100
	I	II	III	IV	V	VI	VII	
rothy: Rainbow trout	None	2 (7.7)	13 (50.0)	10 (38.5)	1 (3.8)			26
ldred: Rainbow trout	8 (10.2)	12 (15.4)	19 (24.4)	27 (34.6)	12 (15.4)	[2]		78
nviet: Rainbow trout	9 (36.0)	14 (56.0)	2 (8.0)					25
nviet: Brown trout	15 (22.1)	18 (26.5)	21 (30.9)	8 (11.8)	2 (2.9)	2 (2.9)	2 (2.9)	68

stinction of several year classes, both stocked id naturally spawned. The oldest fish caught in ake Mildred were in their sixth year of life, but me older individuals were probably present. oung-of-the-year rainbow trout were observed the shallows of this lake, and a fine inlet stream sures successful reproduction.

Brown Trout

The brown trout of Convict Lake show a size stribution which is suggestive of a well-maintained itural population. These trout are descended om hatchery-distributed fish, but the population ay be considered wild because the lake has not en restocked with the species for many years. pproximately 80 percent of the fish sampled in 50 were in age groups I to III. Of more than 500 spawning brown trout captured during the awning seasons of 1951 and 1952, 80 to 90 rcent were about equally divided between age oups II and III. Older fish (IV, V, and VI) ltered the trap readily but were taken in smaller mbers (3 to 17 percent). Still larger fish were served but not captured. The relative number large brown trout (5 to 15 pounds) could not e estimated; a few fish in this size range are ught by anglers each year.

RATES OF GROWTH

In the following discussion the factor of popula-on density has not received the consideration it eserves, since it could not be measured except by ugh estimates based on the quality of the gling. At present there is no reliable method of estimating the numbers of fish in these lakes, and comparisons can be made only on the basis of calculated differences in growth.

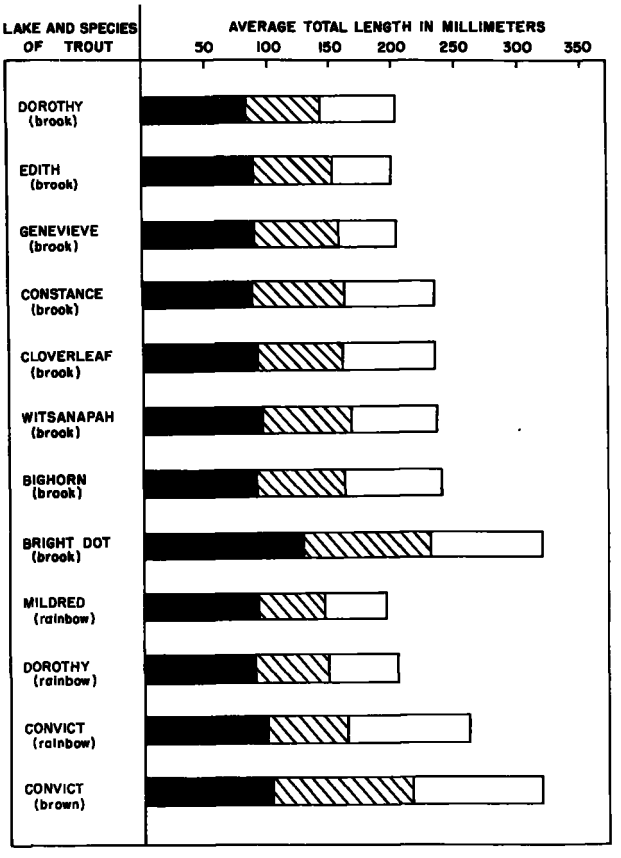

FIGURE 19.—Three-year growth summaries for all trout populations of Convict Creek Basin Lakes. (Full length of bars=length at annulus 3; vertical lines within bars=lengths at annuli 1 and 2.)

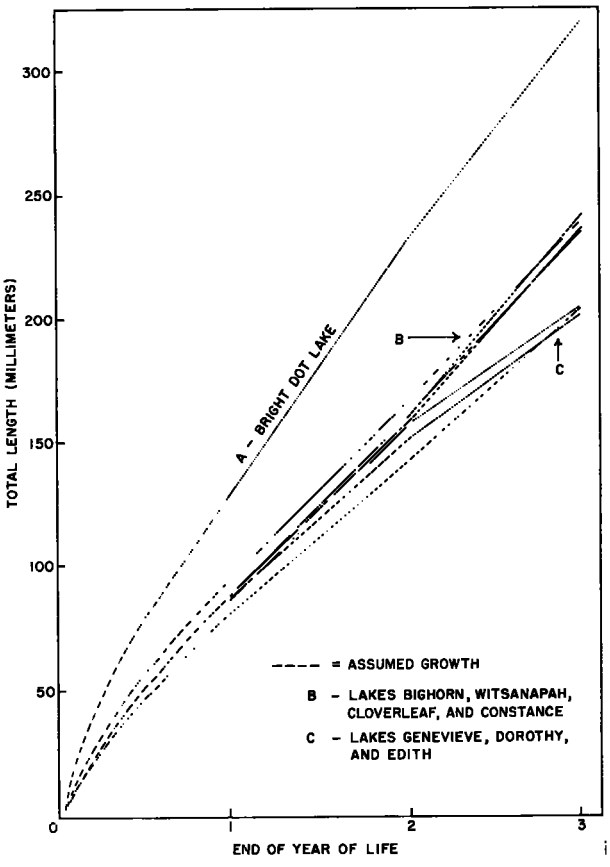

FIGURE 20.—The three patterns of brook trout growth in the upper lakes of Convict Creek Basin.

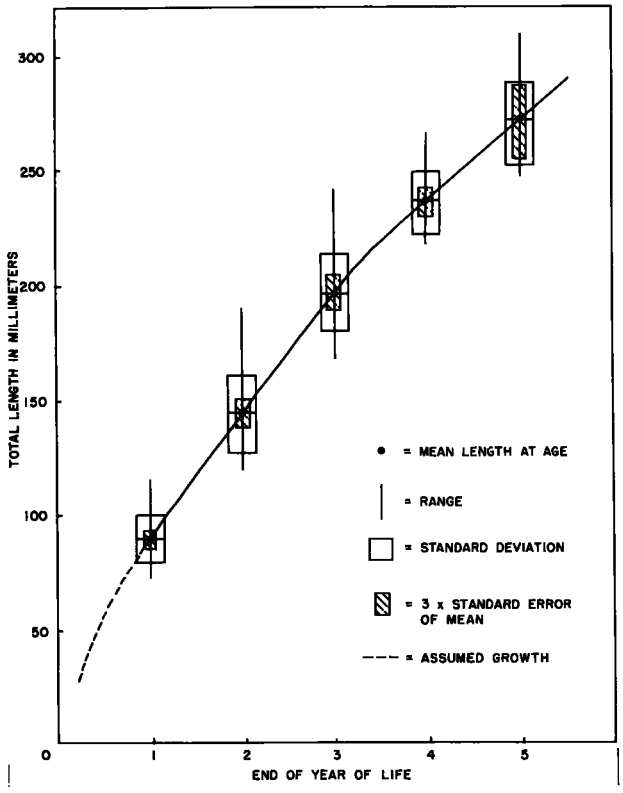

FIGURE 21.—Growth of Lake Mildred rainbow trout (1950) as indicated by mean and dispersed total lengths at each annulus (end of year of life).

Brook Trout

Based on the figures for 3 years' accumulated growth, the eight brook-trout lakes of Convict Creek Basin follow a gradient which falls into three classes. Based on the first 2 years' growth, only two classes are apparent. These patterns of growth are best described graphically, and can be distinguished in the chart of calculated lengths (fig. 19) and in the slopes of the growth curves (fig. 20). Significance of differences among mean calculated lengths at the third annulus was tested by analysis of variance, and the results are summarized in table 30. Since the variance ratios (F-values) of samples among lakes of each group are smaller than table values for 95-percent probability ($F.95$), growth through 3 years is not significantly different among populations of each group. Length differences between groups are highly significant, however, and three classes of growth are therefore distinct at the end of the third growing season.

The growth of present stocks of brook trout in four of the upper lakes (Bighorn, Constance, Witsanapah, and Cloverleaf) may be considered satisfactory or average when their position in the local gradient is compared with the large range of growth rates found in various brook-trout waters. Fish from these lakes grew at nearly identical rates for the first 3 years, reaching a grand average of 3.5 inches in 1 year, 6.3 inches in 2 years, and 9.3 inches in 3 years. Growth during the fourth year was somewhat slower, as indicated by the apparent difference in length between the end of the third year and the dates of capture.

Lakes Dorothy, Edith, and Genevieve showed no significant differences in growth among them, and are classed as poor with respect to the other lakes. Fish from these three lakes grew to an average total length of 3.3 inches in 1 year, 5.9 inches in 2 years, and 8.0 inches in 3 years. Growth during the first and second years in these lakes is approximately the same as that measured in the four lakes just discussed (table 31). It is in the third year that growth lags considerably.

TABLE 30.—*Results of analysis of variance in mean total length at third annulus in eight brook-trout populations.*

Groups[1] tested	Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*	*F* (.95)
A	Between lakes	38	2	19.0	0.21	3.30
	Within lakes	2,919	32	91.2		
	Total	2,957	34			
B	Between lakes	753	3	251.0	1.53	2.68
	Within lakes	21,661	132	164.1		
	Total	22,414	135			
A and B	Between groups	29,991	1	29,991	199.80	3.91
	Within groups	25,371	169	150.1		
	Total	55,362	170			
B and C	Between groups	63,276	1	63,276	310.80	3.91
	Within groups	29,321	144	203.6		
	Total	92,597	145			

[1] Group A: Lakes Dorothy, Edith, Genevieve.
Group B: Lakes Witsanapah, Constance, Bighorn, Cloverleaf.
Group C: Bright Dot Lake.

TABLE 31.—*Average calculated lengths of brook and rainbow trout at annuli*

Given in order under each year of life are: total length in millimeters, total length in inches, and numbers of fish (in parentheses) used in calculating averages]

Lake and species of trout	Year of life				
	1	2	3	4	5
Dorothy: Brook trout	81	142	203		
	3.2	5.6	8.0		
	(93)	(92)	(22)		
Edith: Brook trout	87	151	201		
	3.4	6.0	7.9		
	(84)	(67)	(9)		
Genevieve: Brook trout	86	157	204		
	3.4	6.2	8.0		
	(78)	(56)	(4)		
Constance: Brook trout	86	160	234		
	3.4	6.3	9.2		
	(100)	(98)	(84)		
Cloverleaf: Brook trout	88	158	235		
	3.5	6.2	9.3		
	(96)	(79)	(20)		
Witsanapah: Brook trout	94	166	238		
	3.7	6.5	9.4		
	(32)	(12)	(8)		
Bighorn: Brook trout	88	160	240		
	3.5	6.3	9.5		
	(93)	(64)	(24)		
Bright Dot: Brook trout	127	251	318		
	5.0	9.1	12.5		
	(18)	(15)	(10)		
Mildred: Rainbow trout	90	144	196	236	270
	3.6	5.7	7.7	9.3	10.6
	(70)	(69)	(57)	(36)	(12)
Dorothy: Rainbow trout	86	147	207	260	
	3.4	5.8	8.2	10.2	
	(22)	(26)	(24)	(10)	
Convict: Rainbow trout	97	162	282		
	3.8	6.4	11.1		
	(22)	(16)	(2)		

The growth of trout in Bright Dot Lake, although not phenomenal, far outclassed that of other brook-trout populations in the study area. Fingerlings planted in 1947 grew to 5.0 inches in the first year, to 9.1 inches in 2 years, and 12.5 inches in 3 years. These trout, taken in August and early September of their fourth year, reached 16 inches in total length and more than one pound in weight. Young-of-the-year collected in August (1950) were 2.5 to 3.0 inches long, and members of the same year class taken 1 year later averaged 7.3 inches in total length at capture, with the first annulus formed at 4.7 inches.

Rainbow Trout

It is apparent from the length data in tables 31 and 32 that rainbow trout in the upper lakes (Mildred and Dorothy) have not grown as rapidly as most of the brook trout. Ten- to twelve-inch rainbow trout were found to be in their fifth and sixth years of life, and brook trout of like size (Lakes Constance, Bighorn, Witsanapah, and Cloverleaf) were in their fourth year at corresponding dates of capture. The growth of these rainbow trout roughly parallels that of the brook trout in Lakes Edith, Genevieve, and Dorothy. The growth pattern of Lake Mildred rainbow trout is indicated in figures 17 and 21.

TABLE 32.—*Variability of calculated lengths of brook, rainbow, and brown trout at annuli*

Lake and species of trout	Annuli	Mean total length[1]	Range	Standard deviation	Standard error of mean
Dorothy: Brook trout	1	81	68–94	5.802	0.60
	2	142	118–163	9.695	1.01
	3	203	171–219	7.817	1.70
Edith: Brook trout	1	87	71–102	7.095	.77
	2	151	129–186	12.043	1.47
	3	201	193–212	6.656	2.22
Genevieve: Brook trout	1	86	70–97	8.828	.77
	2	157	134–176	9.556	1.28
	3	204	188–212	13.756	6.88
Constance: Brook trout	1	86	60–107	8.912	.89
	2	160	130–189	13.198	1.33
	3	234	204–258	12.590	1.40
Cloverleaf: Brook trout	1	88	73–106	7.435	.76
	2	158	138–176	9.410	1.06
	3	235	218–250	9.635	2.15
Witsanapah: Brook trout	1	94	76–104	8.785	1.55
	2	166	151–182	11.188	3.23
	3	238	227–258	14.452	5.11
Bighorn: Brook trout	1	88	70–105	8.570	.89
	2	160	136–188	10.970	1.36
	3	240	224–271	11.463	2.34
Bright Dot: Brook trout	1	127	112–150	10.803	2.55
	2	231	208–255	19.249	4.97
	3	318	278–349	29.206	9.24
Mildred: Rainbow trout	1	90	72–116	10.342	1.24
	2	144	119–189	16.967	2.04
	3	196	167–241	17.428	2.31
	4	236	217–266	14.015	2.27
	5	270	246–309	19.590	5.66
Dorothy: Rainbow trout	1	86	63–105	12.511	2.67
	2	147	124–174	14.125	2.82
	3	207	179–231	17.260	3.60
	4	260	228–291	19.099	6.37
Convict: Rainbow trout	1	97	66–120	13.362	2.85
	2	162	140–195	16.624	4.16
	3	282	270–295		
Convict: Brown trout	1	100	70–145	18.100	2.23
	2	215	142–314	35.010	4.90
	3	318	236–425	39.061	6.90
	4	407	330–492	56.607	15.13
	5	533	485–582		
	6	624	579–700		
	7	634	625–644		

[1] Expressed in millimeters.

The differences in growth rate found in populations of this species from Lakes Mildred and Dorothy seem paradoxical. Lake Mildred has a shallow basin and showed indications of plentiful food, both by general observations and by bottom samples. Deeper parts of the lake bottom had a heavy algal growth (*Rhizoclonium* sp.) and an introduced amphipod (*Gammarus* sp.) dominated the food supply. Its plankton, though small in comparison to those found in many more temperate lakes, was easily measurable. Furthermore it has an all-season inlet stream which drains a rather extensive meadow and should bring nutrient material into the lake in considerable amounts. Lake Dorothy, in contrast, has a deep, steep sided basin, is fed by seepage except for small rills, and is very poor in bottom organisms. Only traces of a plankton were obtained in hauls from all depths. These contrasting conditions indicate an advantage for the Lake Mildred rainbow trout which is not realized in the growth characteristics. An accurate knowledge of population densities would probably be informative in this instance; the fish growth in Lake Mildred, which has a surface area of only 10.7 acres, must be limited to some extent by the pressure of numbers, whereas Lake Dorothy has plenty of space but suffers from a basic food scarcity.

A comparison of rainbow trout growth rates in the upper and lower parts of the basin shows that growth in Convict Lake increases during the third year, when in Lakes Mildred and Dorothy it has begun to slow. Lake Dorothy rainbow trout at the end of the fourth year of life, and Lake Mildred rainbow trout at the end of the fifth year, have not reached the average length attained by Convict Lake rainbow trout in 3 years. These differences must be attributed to a combination of factors. In Lake Dorothy, slow growth is at least partly explainable by food scarcity; space is not a problem. In Lake Mildred, which is small and apparently well populated, food is very abundant but competition may be severe. Convict Lake ranks low in food abundance and, because of additions of 40,000 to 50,000 catchable-size rainbow trout each year, it is heavily populated. The lower lake, however, has a rapid growth season (based on temperature data and length of the ice-free period) which is estimated to be 2 to 3 months longer than the growing season in the upper basin, and it is logical to expect that this factor is sufficient to account for a large part of the growth advantage measured.

Brown Trout

The average length values calculated for age groups I through IV are considered sufficiently accurate for comparison with the data of the other populations. The first three years growth compares well with that found among brook trout in Bright Dot Lake (fig. 19), and the growth curves (figs. 22 and 23) provide an indication that the Convict Lake brown trout continue their rapid growth in the fourth and fifth years. In fact, scales from a few large specimens indicated clearly that some amazing growth had taken place in the sixth and seventh years, or later; figure 24 illustrates the wide bands of rapid scale growth in advanced years. The stomachs of large brown trout contained small trout in greater proportion than other foods and it is a fairly safe assumption that spurts in growth of the older trout are associated with a heavy toll among newly planted rainbow trout.

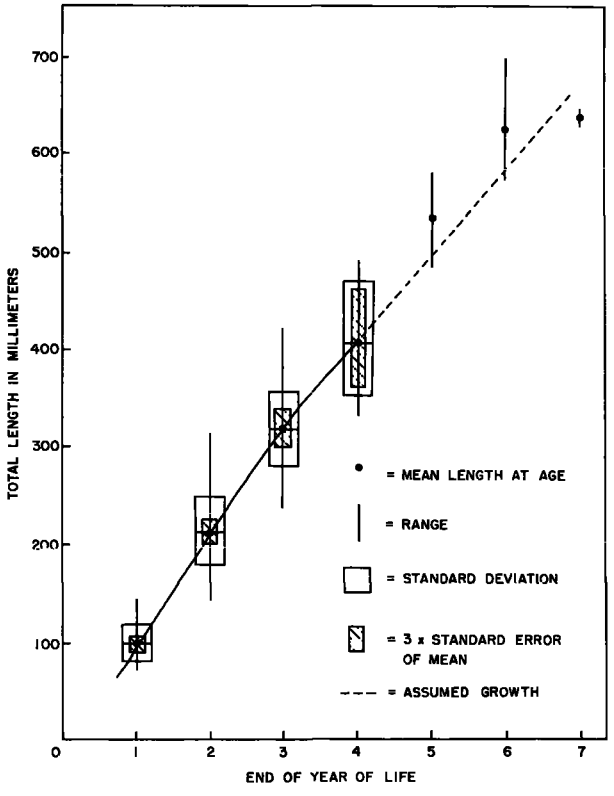

FIGURE 22.—Growth of Convict Lake brown trout (1950) as indicated by mean and dispersed total lengths at each annulus (end of year of life).

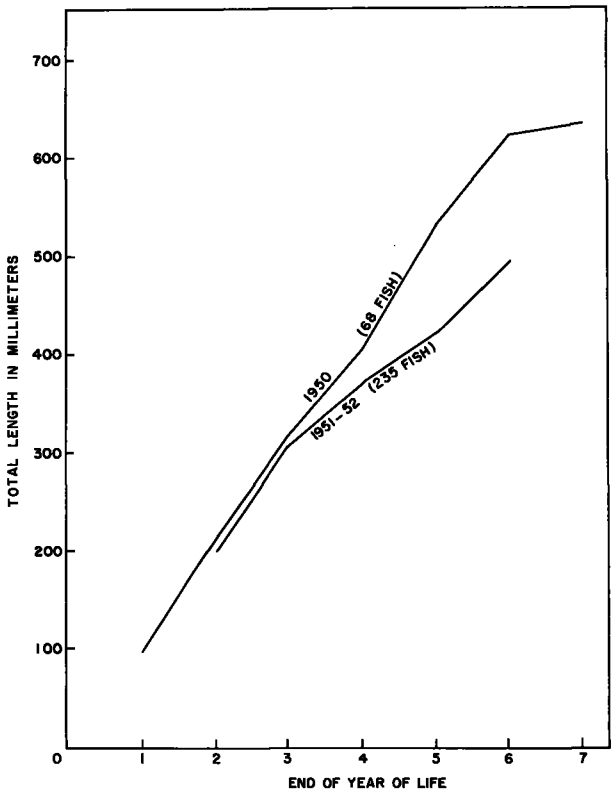

FIGURE 23.—Growth of Convict Lake brown trout (1950) as indicated by mean total lengths at annuli (end of year of life) and mean total lengths at age of capture (1951–52). Data from table 33.

Further comparisons of calculated lengths show that brown trout possess some type of advantage over rainbow trout in Convict Lake, although stomach examination records in the present report reveal that the two species feed upon the same food groups in similar proportions through the early years of rapid growth. Factors which could give the wild brown trout an advantage in growth are superior foraging ability, and occupancy of a wider depth range with improvement in food availability. An apparent, but false, growth advantage for brown trout can also be suggested if it is assumed that the faster growing members of each year class are more readily harvested than the slower growing members. Such a phenomenon has been observed in a number of fish populations, and its effect in Convict Lake would be to increase the apparent average lengths of brown trout over rainbow trout, since the harvest of brown trout is much smaller than that of rainbow trout.

FIGURE 24.—Scale of 26.5-inch Convict Lake brown trout Widely spaced circuli near the margin indicate abnormally rapid growth in the year immediately preceding capture.

Nearly all of the larger brown trout (age groups V–VII) were well into the breeding condition when taken, with thick skins and deeply embedded scales in males and extensive scale margin resorption in both sexes. The result of these effects was a large proportion of unreliable scales in the collection, and consequently the samples were too small and length variations too large to permit more than approximations of calculated length (table 33, 1950 fish). Scales and length data were taken from several hundred spawning brown trout in the late fall and early winter months of 1951 and 1952, and growth was also assessed on the basis of scale ages and lengths at capture of 235 such fish. All data for this check were obtained during the 2-month period of heavy spawning (October and November) when growth is assumed to be at a minimum. The average yearly growth determined by using this method parallels the 1950 data (past growth calculation) within a few millimeters for the second, third, and fourth years of life (table 33). There is much more divergence in the results of the two methods for the fifth and sixth years,

but considering the number of fish in the samples it is believed that the 1951–52 figures are more reliable. The accuracy of growth calculations based on scale measurements from larger members of the Convict Lake brown trout population, or from any fish which loses substantial portions of the scale margin in the breeding season (with the scales actually growing in retrograde) seems subject to doubt.

The Convict Lake brown trout apparently grow about 4 inches in the first year, 4 to 4½ inches in the second, 4 inches in the third, and 2½ to 3½ inches in the fourth year. Above this age the average yearly growth should be slightly less, but variation among individuals is high and acceptable averages of growth increment call for larger samples.

TABLE 33.—*Average lengths of Convict Lake brown trout at annuli (1950) compared with average lengths at age of capture (1951 and 1952)*

[Given in order under each year of life are: total length in millimeters, total length in inches, and numbers of fish (in parentheses) used in calculating averages]

Year of collection	End of year of life						
	1	2	3	4	5	6	7
1950	100 3.9 (66)	215 8.5 (51)	318 12.5 (33)	407 16.0 (14)	533 21.0 (6)	624 24.6 (4)	634 25.0 (2)
1951 and 1952	------ ------ ------	199 7.8 (17)	306 12.0 (111)	371 14.6 (82)	421 16.6 (22)	492 19.4 (5)	------

RANKING OF THE LAKES IN TERMS OF TROUT GROWTH

Considering all trout species together for the purpose of grossly comparing lake productivities, the 10 lakes may be placed in high-to-low order on the basis of total lengths reached in 3 years (table 34). In order that final comparisions may be made among all rankings, with each major factor given the same weight, the millimeters of growth representing each lake have been reduced to proportionate ratings comparable to those used in foregoing summary tables. Bright Dot Lake, in which growth was found to be most rapid, is assigned a value of 10, and the remaining lakes are rated on a scale of 10 in proportion to total lengths.

The arrangement in table 34 merely adds Lakes Convict and Mildred to the grouped order of lakes previously outlined for brook trout. Convict Lake ranks second to Bright Dot Lake in the outstanding group. Lakes Bighorn, Witsanapah, Cloverleaf, and Constance represent the average group. Lake Mildred is added to the below-average group of Lakes Genevieve, Dorothy, and Edith.

TABLE 34.—*Ranking of the lakes in terms of total lengths attained by trout in 3 years*

Lake	Species of trout	Total length (millimeters)	Proportionate rating
Bright Dot	Brook	318	10.0
Convict	Brown	[1] 306	9.0
Bighorn	Brook	240	3.6
Witsanapah	do	238	3.4
Cloverleaf	do	235	3.2
Constance	do	234	3.1
Genevieve	do	204	.7
Dorothy	do	203	.6
Edith	do	201	.4
Mildred	Rainbow	196	0

[1] Measured total length at 3 years; all others, total length calculated at third annulus.

COEFFICIENT OF CONDITION AND LENGTH-WEIGHT RELATIONSHIP

The condition factor K was calculated for 974 trout, the total number from which both lengths and weights were taken in 1950. This factor, which is in general use to indicate plumpness in relation to length, is calculated from the formula:

$$K=\frac{\text{Weight in grams} \times 100{,}000}{\text{Length in millimeters}^3}$$

The majority of specimens in the collections had slight to moderate gonad development, and males were not distinguishably different from females in condition. Sexually ripe or spent individuals, which would seem to raise or lower the average condition factor, amounted to 27 percent of all fish weighed and measured. Their average condition, however, did not depart significantly from the general average, and it is therefore felt that the general average of condition for both sexes in all stages of maturity has no serious bias.

Cooper [14] pointed out that comparisons of condition factors in brook trout may be made over a broad range of fish length without consequential error, since the exponent in the length-weight equation ($W=CL^n$) remains near a value of 3. The present data appeared by inspection to bear out this conclusion, and accordingly the condition factors for brook trout were averaged without reference to fish size. The samples of rainbow

[14] Age and growth of the brook trout in Michigan, by Edwin L. Cooper. Unpublished Ph.D. thesis, University of Michigan, Ann Arbor, 1949.

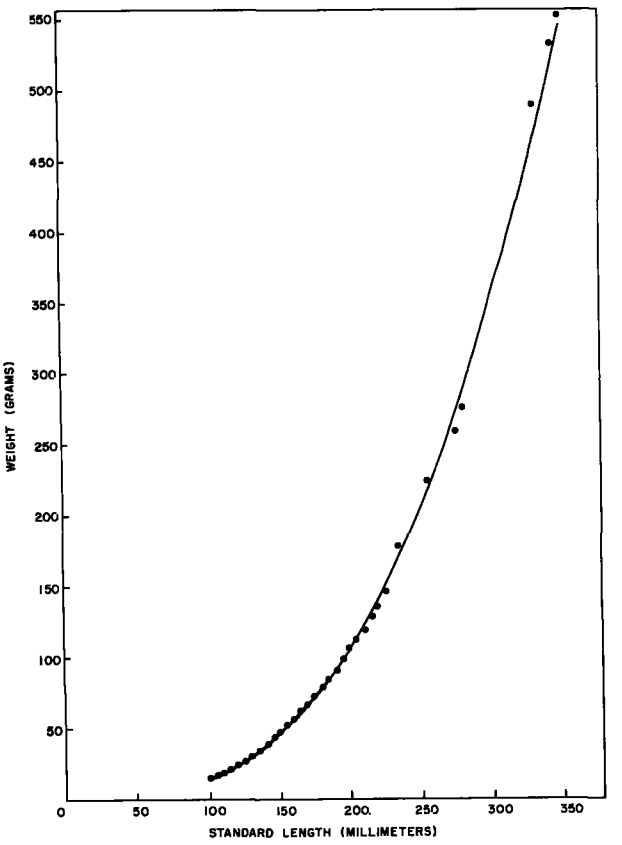

FIGURE 25.—Length-weight relationship of brook trout in the upper lakes of Convict Creek Basin. (Points are based on average lengths and actual weights, table 36.)

trout were not considered large enough to express accurately any differences due to fish length, and this species was handled in the same way as the brook trout. As there was a large spread in the size of brown trout, these fish were grouped in 50-millimeter classes.

The summarized data on condition factors appear in table 35. No large variations were found among the eight brook trout populations, and the values obtained compare favorably with those noted for more productive brook trout waters (Carlander 1950). Rainbow and brown trout of Convict Lake and rainbow trout from Lake Mildred were likewise in a condition which may be called average, in view of the large range described in the literature. The samples gave no indication that condition varies systematically with length in the Convict Lake brown trout. The Lake Dorothy rainbow trout are in competition with a larger population of brook trout, and their condition fell below average but was not low enough to permit classing these fish as poor.

Although the condition factor is not an expression of growth, it provides a rough indication of the state of nutrition and body maintenance. Poor condition may be indicative of high population density as well as of basic food scarcity, and normal condition among the trout populations of the basin is construed as evidence that population density differences did not seriously affect the growth rate differences which have been described.

The general agreement of condition factors for brook trout in the upper lakes, and the large number of this species weighed and measured, made possible the calculation of a length-weight relationship for the combined populations. According to the method described by Beckman (1948) the equation was determined to be:

$$W=2.087\times10^{-5}\times L^{2.9146}$$

or, $\log W=-4.6806+2.087 \log L$

where W=weight in grams

and L=standard length in millimeters.

The agreement of observed and calculated weights (fig. 25; table 36) indicates that weights of brook trout in these lakes can be computed with reasonable accuracy from measured lengths.

TABLE 35.—*Average coefficients of condition (K) for the trout of Convict Creek Basin lakes (July–September, 1950)*

Lake	Species of trout	Number of trout	Size range (total length milli-meters)	K Total length (milli-meters)	K Standard length (milli-meters)
Constance	Brook	31	180–337	0.953	1.322
Bighorn	do	72	112–290	.922	1.314
Bright Dot	do	6	317–403	.964	1.337
Edith	do	115	127–246	.992	1.337
Genevieve	do	103	120–258	.957	1.362
Cloverleaf	do	106	112–305	.935	1.347
Witsanapah	do	30	113–315	.931	1.321
Dorothy	do	198	131–245	.966	1.353
Dorothy	Rainbow	30	126–320	.881	1.266
Mildred	do	63	81–326	1.146	1.569
Convict	do	31	124–325	1.023	1.641
Convict	Brown [1]	75	150–800	1.051	1.587

[1] Weighted average of K calculated by 50-millimeter size groups.

SUMMARY OF AGE, GROWTH, AND CONDITION

Age and growth rate data were derived from scale and body length measurements of 607 brook trout, 129 rainbow trout, and 68 brown trout. Scale-ages and body-length measurements of 235 additional brown trout provided supplementary data for this species.

TABLE 36.—*Length-weight relationship of the brook trout in upper Convict Creek Basin lakes—observed and calculated weights*

Standard length in millimeters		Number of fish	Empirical weight (grams)	Calculated weight [1] (grams)
Range	Mean			
98–102	100.2	5	14.1	14.2
103–107	106.0	7	16.5	16.7
108–112	109.6	13	18.4	18.4
113–117	115.4	11	20.6	21.4
118–122	120.0	18	25.3	24.0
123–127	124.6	20	27.2	26.7
128–132	129.6	23	29.6	30.0
133–137	135.3	23	33.7	34.0
138–142	140.6	17	38.7	38.0
143–147	145.4	26	43.2	41.9
148–152	150.0	47	47.8	45.9
153–157	155.0	48	51.5	50.5
158–162	160.1	50	55.8	55.5
163–167	164.9	50	61.2	60.5
168–172	169.8	50	66.9	65.9
173–177	174.9	38	71.8	71.8
178–182	180.0	34	78.2	78.1
183–187	184.8	38	83.1	84.3
188–192	190.1	34	89.4	91.6
193–197	194.8	31	96.3	98.3
198–202	199.8	29	104.5	105.8
203–207	204.9	33	111.4	113.9
208–212	210.1	18	118.0	122.5
213–217	215.0	17	127.4	131.1
218–222	219.3	14	134.0	138.8
223–227	225.0	10	145.3	149.7
233–237	235.1	10	177.9	170.0
253–257	255.6	15	222.9	217.1
273–277	275.0	1	258.0	268.5
278–282	279.7	6	273.6	282.2
328–332	332.0	2	487.5	465.0
343–347	344.0	1	531.0	515.9
348–352	350.0	1	551.5	542.5

[1] Computed by the formula $W=2.087\times10^{-5}\ L^{2.9146}$.

At the time of study, age composition was largely artificial in the eight brook-trout populations. These trout were found to be 1 to 3 years old, and represented both plantings made since 1946 and natural reproduction of fish planted in 1946 or earlier. Young-of-the-year brook trout were present in 1950, indicating the occurrence of successful natural spawning without benefit of tributary streams. Rainbow trout collected comprised age groups I to V, and evidence of the natural spawning of this species was found in the inlet to Lake Mildred. The Convict Lake brown trout population is self-sustained and presumably includes all age groups within the natural life span; groups I to VII were collected.

Calculations of average total lengths at times of annulus formation were made for all trout populations in the 10 lakes. An analysis of differences in calculated lengths at the third annulus revealed three distinct classes of brook trout growth among eight lakes. Growth in Bright Dot Lake was clearly superior in each year of life, but the growth patterns in the other seven lakes containing brook trout were such that the above mentioned classes were not evident until the third year of life. Rainbow trout were found to grow more slowly than brook trout in the upper lakes, but the growth of rainbow trout in Convict Lake, lower in the drainage, was superior to that of the same species in two upper lakes. Ranking of all 10 lakes, in terms of trout growth, placed Bright Dot Lake slightly above Convict Lake (brown trout) in the outstanding group at the upper end of the scale. Lakes Bighorn, Witsanapah, Cloverleaf, and Constance ranged closely about the average for the basin in the order given, and Lakes Genevieve, Dorothy, Edith, and Mildred were below average with Lake Mildred indicated as the poorest.

Coefficients of condition (K) were calculated for 974 trout. Condition was normal in all populations except Lake Dorothy rainbow trout, in which it was somewhat low but not indicative of failure. The length-weight relationship of brook trout in the upper basin lakes was calculated from weights and standard lengths of 775 fish, and was found to be described by the equation

$$W=2.087\times10^{-5}\text{—}L^{2.9146}$$

INTERRELATIONSHIPS

Preceding sections have presented analyses of physical, chemical, and biological measurements which, in many limnological surveys, have been considered important criteria of lake productivity or valuable indicators of environmental conditions. The 10 lakes have been ranked as to potential productivity in terms of combined physical influences (table 5) and chemical influences (table 10). They have also been ranked in order of biological productivity as measured by invertebrate abundance and trout growth. Values of the individual measurements used in the physical and chemical rankings, and reasons for their selection, appear in the respective sections. It is recognized that some of the causative elements included in the present analyses exert a far stronger influence over productivity than others, but the relative degrees of influence of these individual factors are not ascertainable and all physicochemical determinations used were necessarily given equal weight. All lakes were given identical treatment, so that final comparisons are made among lakes by their grouped factors rather than by individual factors composing a group. Biological productivity rankings are based simply on quantities of invertebrates in samples, and on total lengths attained by trout in 3 years.

It may be assumed that dissolved substances influence productivity quantitatively in these lakes, and it is generally accepted that water temperature, depth, and those functions of depth which are associated with the development of littoral areas also have an important bearing on productive capacity. If the biological evaluations of the lakes are valid, they should at least coarsely follow the same rankings as the more stable environmental measurements. The following is an attempt to integrate the assumed causative factors (physical-chemical) and their effects (biological), and to demonstrate in simplest terms the degrees of association present among the various measurements.

In table 37 the various groupings of the lakes have been arranged in 10-to-0 order for comparisons. Physical, chemical, invertebrate abundance, and trout-growth ratings are from the final proportionate values in tables 5, 10, 17, and 34. The composite physical-chemical ratings are averages of the two components for each lake. Among these cause and effect categories, only rough and fragmentary associations can be made. Although there is no reason why the physical and chemical series should support one another, they appear partly to do so in that Lakes Bighorn, Mildred, and Bright Dot rank high in both, and Lake Dorothy is lowest in both. Ranking on the basis of combined physical and chemical series (col. 6, table 37) follows the chemical ranking rather closely, but the ranking based on invertebrate abundance (col. 8, table 37) is in almost total disagreement with either physical or chemical influences. Individually the biological measurements show little relation to each other, and the biological rankings of table 37 are at variance. Brook-trout populations varied widely in rates of growth, but the differences cannot be explained in terms of food abundance. Convict Lake is productive of relatively rapid trout growth, but ranks very low in bottom productivity. Bottom fauna weights form a definite pattern among the lakes but do not agree with zooplankton quantities. In fact, an inverse relationship is indicated wherein two lakes rich in plankton (Bright Dot, Bighorn) were benthos-poor, and two benthos-rich lakes (Cloverleaf, Witsanapah) were deficient in plankton at the time of sampling. Robertson (1947) found a similar lack of biological agreement in two alpine lakes in Wyoming: Upper No Name Lake had good trout growth, condition factors and benthos numbers, and Lower No Name Lake opposed these features but was far richer in plankton.

There is what appears to be a sound correspondence between rankings of brook-trout growth and quantities of dissolved substances, although the relationship is not clearly shown in table 37. The growth-rate differences based on calculated lengths of brook trout at the end of the third year of life (table 31) indicate superior growth of this species in Bright Dot Lake, which ranks first among the eight brook-trout lakes in the chemical series (table 10). Growth among the remaining brook-trout populations (except that of Cloverleaf Lake) also follows the sum of chemical influences closely as shown in the following summary from tables 7, 8, and 10:

Lake	Total length at 3 years (millimeters)	Sum of chemical values [1] used in table 10
Bright Dot	318	334.4
Bighorn	240	226.9
Witsanapah	238	165.5
Constance	234	143.7
Genevieve	204	126.6
Dorothy	203	90.5
Edith	201	105.7

[1] Sums given above are from empirical values which appear in tables 7 and 8. Table 10 lists only proportionate ratings for these selected measurements.

TABLE 37.—*Physical, chemical, and biological rankings of the lakes compared*

Physical		Chemical		Physical and Chemical		Invertebrate abundance		Trout growth	
Lake	Rating	Lake	Rating	Lake	Rating	Lake	Rating	Lake	Rating
Cloverleaf	9.4	Convict	9.8	Convict	7.6	Mildred	10.0	Bright Dot	10.0
Bighorn	7.4	Mildred	6.2	Mildred	6.1	Cloverleaf	9.7	Convict	9.0
Bright Dot	6.2	Bright Dot	5.7	Bright Dot	5.9	Witsanapah	5.9	Bighorn	3.6
Mildred	6.0	Bighorn	4.4	Bighorn	5.9	Genevieve	5.8	Witsanapah	3.4
Convict	5.3	Witsanapah	3.0	Cloverleaf	5.6	Constance	4.8	Cloverleaf	3.2
Witsanapah	4.3	Constance	2.2	Witsanapah	3.6	Edith	4.8	Constance	3.1
Genevieve	4.2	Genevieve	2.0	Genevieve	3.1	Bright Dot	1.9	Genevieve	.7
Edith	3.3	Cloverleaf	1.8	Edith	2.4	Bighorn	1.0	Dorothy	.6
Constance	2.2	Edith	1.6	Constance	2.2	Convict	.9	Edith	.4
Dorothy	1.7	Dorothy	1.2	Dorothy	1.4	Dorothy	0	Mildred	0

Cloverleaf Lake, the exception referred to, is apparently the one lake in which highly favorable physical conditions and resulting abundance of bottom foods had a marked effect on trout growth; its chemical favorability measured next to the lowest, whereas its trout growth approximated the average for the eight brook trout lakes. The association between trout growth and richness in dissolved substances is also apparent for brown trout and, to some extent, for rainbow trout. In Convict Lake, which ranked highest in the chemical appraisal, brown-trout growth paralleled that of the Bright Dot Lake brook trout. The growth of rainbow trout in Convict Lake was also markedly better than in Lakes Mildred and Dorothy.

The lack of association between trout growth and food supplies suggests either that food abundance is less critical than some other factor and is not directly associated with growth as measured, or that survey food sampling or trout growth assessment methods were not adequate to demonstrate the relationship. There was no evidence of any direct relationship between trout growth and the physical factors thought to bear on biological productivity.

Certain general statements may be made regarding the biological rankings. Lakes Mildred and Cloverleaf are strongly productive of bottom foods, relative to the other lakes, and this would appear to be the result of both physical and chemical conditions operating in their favor. High production of bottom foods and average trout growth in Cloverleaf Lake seem certainly due to the dominating influence of favorable physical conditions, since mineral solutes are so low. Superior trout growth in Lakes Bright Dot and Convict is clearly associated with chemical influence. Convict Lake's position is also advanced by its location at a lower elevation; nearly all of its chemical constituents are in greater concentration than in any of the upper lakes, and the benefits of its longer growing season have been mentioned. Lake Dorothy is consistently below average in all measurements, and low biological productivity is the probable result of combined adverse physical and chemical conditions.

The foregoing reasoning is supported by the measurements as well as the ranking values, but it includes only those associations which lend themselves to explanation. As if to confound such order, Lake Witsanapah ranks considerably higher in food abundance than would be expected from physical and chemical rankings; Bighorn Lake is well endowed physically and chemically, but is well below average in food abundance as measured. In view of its advantages, Convict Lake ranks inexplicably low in abundance of food organisms.

THE PROBLEM OF JUDGING PRODUCTIVITY OF ALPINE LAKES

As previously stated, the foregoing arrangements of lakes are an attempt to find consistency between common survey measurements of lake productivity and a number of environmental factors known to influence productivity. The major premises have been:

1. That various physical and chemical influences have net effects on biological productivity, and that by encoding their measurements in a common scale a group of related lakes may be ranked to indicate relative productive capacity in terms of the combined factors.
2. That an index founded on such a combination of causative factors is basic, and any other index measure should be conditional upon it.
3. That the relationship between any true index of biological richness and the index of combined environmental factors should be expressible as a ranking agreement.

Limitations on such an interpretation of the present data are thus considered to be imposed mainly by instability in the biological fraction, where measurements are subject to sampling errors and population vicissitudes. Benthos and plankton production were necessarily measured on a standing crop basis, and it has been noted (Ball and Hayne, 1952) that this measure is not directly related to the rate of production. Moyle (1949) concluded that quantitative plankton and bottom fauna measurements are unsatisfactory for ordinary surveys. The experience in the present work suggests that standing crop measurements of trout food organisms are not sufficiently representative for an accurate index feature of alpine lakes, although they may be suited to seasonal or sequential comparisons in a single water. The fact that fish growth can be linked with water fertility but not with the food supplies seems to constitute evidence that survey sampling of bottom fauna and plankton is inadequate. Although no evidence of overpopulation was found in the lakes,

it is also possible that the almost unknown variable of fish population density has affected, to some extent, the accuracy of conclusions on rate-of-growth differences.

Since these lakes have a relatively small range of chemical and physical suitability, and since all fall within the same category of low productivity and mineral scarcity, it might be suspected that productive differences could be attributed to variations in content of certain dissolved substances or to other single factors. However, the biological measurements show little relation to each other or to individual environmental conditions. Bottom fauna quantity is not associated with water temperature or content of various minerals, and is only indistinctly related to depth and slope conditions, possibly because of the type of fauna. Plankton quantity does not correspond to transparency or mineral content, nor to mean temperature of the upper stratum as suggested by Rawson (1942). Gross influence of physical and chemical groups on productivity as measured is somewhat more evident, and is in general agreement with the concept of mutual dependence among many environmental factors.

Although the cumulative effects of environmental factors form a pattern with which certain biological measurements may be reconciled, the prediction of alpine lake productivity by means of index measurements seems to be outside the range of ordinary survey methods. Key variables among physical and chemical factors, which would provide reliable and easily obtained environmental indices of productive capacity, do not exist in these lakes. There may be key biological variables which will be reliable indicators within certain classes of lakes, but they are not likely to be found in bottom fauna abundance, plankton abundance, or fish growth evaluations because of sampling limitations and the effects of unknown variations in population density.

Detailed surveys of environmental conditions in individual lakes are manifestly impractical, even though such surveys would provide a sound basis for evaluations of nutritive fertility and possibly for fish capacity guides.

In terms of the community biomasses of lakes which have practically no macrovegetation, the bacteria, phytoplankton, and periphyton constitute the primary converters of nutrients and are, next to the nutrients themselves, the basis of production. These forms, which are probably the least variable biological elements through a season, were not sampled in the present study but have since been under investigation as to the possibility of their use as trophic indicators. Through pilot studies it has been determined that the quantitative evaluation of living attachment material (periphyton) on submerged surfaces of known area can be made almost free of sampling errors. With suitable analytical procedures this measurement holds some promise as an index of general nutritive fertility of waters and as a possible substitute for extensive biological surveys, since the density and types of attachment organisms are in sensitive relation to controlling physicochemical influences.

Techniques of periphyton sampling and analysis were tested in 1952 (Nielson 1953) and preliminary sampling of all Convict Creek Basin lakes was completed in August 1953. Further general sampling, and selective sampling to determine the effects of certain physical factors (temperature, depth, and light) are being continued. The results of this phase of the investigation of alpine lake productivity will be reported at a later date.

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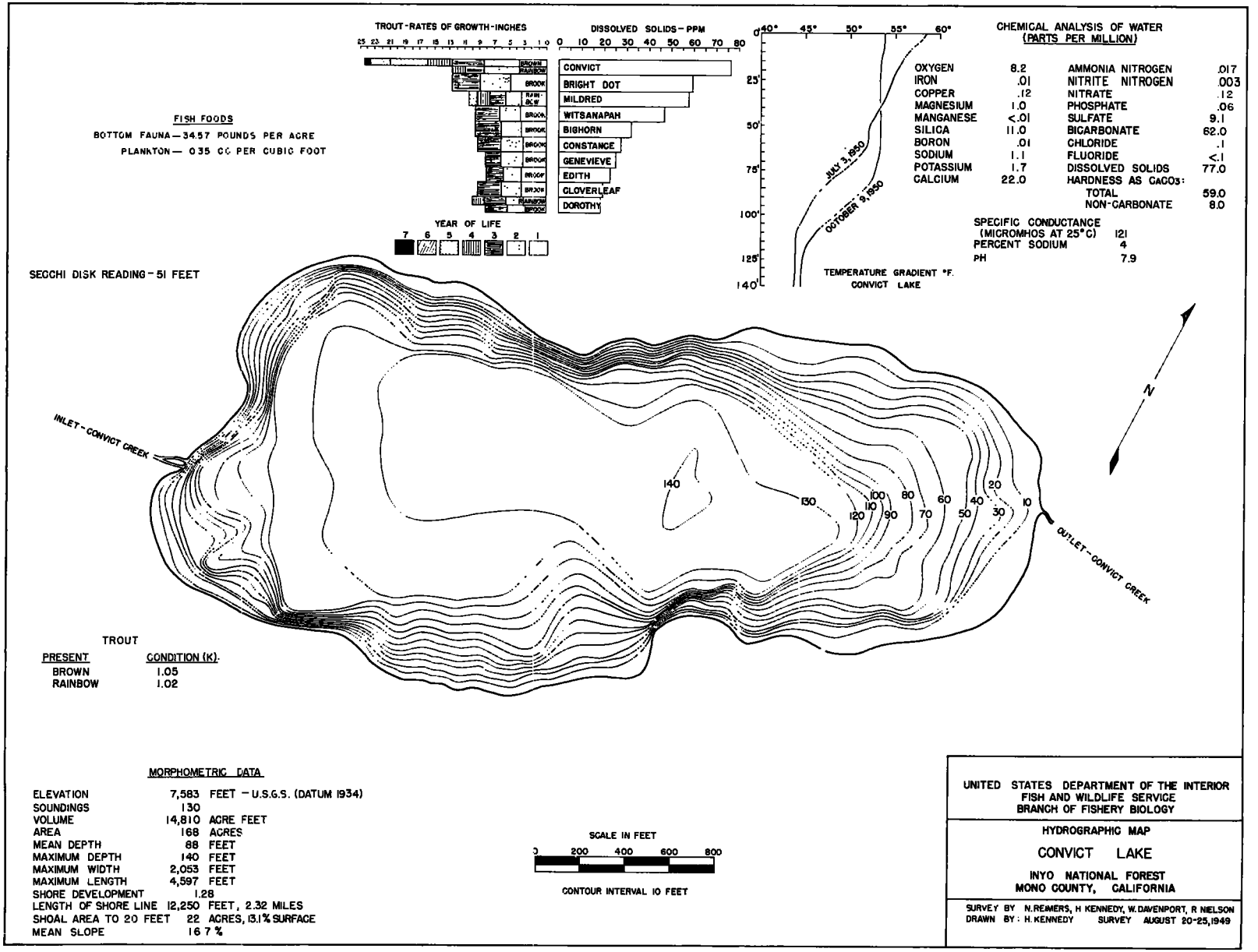
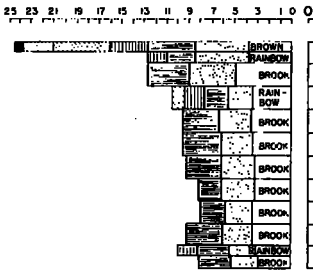
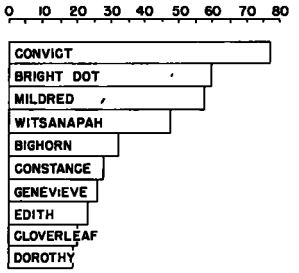

TROUT-RATES OF GROWTH-INCHES
DISSOLVED SOLIDS-PPM
CONVICT
BRIGHT DOT
MILDRED
WITSANAPAH
BIGHORN
CONSTANCE
GENEVIEVE
EDITH
CLOVERLEAF
DOROTHY
YEAR OF LIFE
FISH FOODS
BOTTOM FAUNA—34.57 POUNDS PER ACRE
PLANKTON— 0.35 CC PER CUBIC FOOT
SECCHI DISK READING - 51 FEET
JULY 3, 1950
OCTOBER 9, 1950
TEMPERATURE GRADIENT °F.
CONVICT LAKE
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)
OXYGEN 8.2
IRON .01
COPPER .12
MAGNESIUM 1.0
MANGANESE <.01
SILICA 11.0
BORON .01
SODIUM 1.1
POTASSIUM 1.7
CALCIUM 22.0
AMMONIA NITROGEN .017
NITRITE NITROGEN .003
NITRATE .12
PHOSPHATE .06
SULFATE 9.1
BICARBONATE 62.0
CHLORIDE .1
FLUORIDE <.1
DISSOLVED SOLIDS 77.0
HARDNESS AS CaCO3:
TOTAL 59.0
NON-CARBONATE 8.0
SPECIFIC CONDUCTANCE (MICROMHOS AT 25°C) 121
PERCENT SODIUM 4
PH 7.9
INLET - CONVICT CREEK
OUTLET - CONVICT CREEK
N
TROUT
PRESENT CONDITION (K)
BROWN 1.05
RAINBOW 1.02
MORPHOMETRIC DATA
ELEVATION 7,583 FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS 130
VOLUME 14,810 ACRE FEET
AREA 168 ACRES
MEAN DEPTH 88 FEET
MAXIMUM DEPTH 140 FEET
MAXIMUM WIDTH 2,053 FEET
MAXIMUM LENGTH 4,597 FEET
SHORE DEVELOPMENT 1.28
LENGTH OF SHORE LINE 12,250 FEET, 2.32 MILES
SHOAL AREA TO 20 FEET 22 ACRES, 13.1% SURFACE
MEAN SLOPE 16.7 %
SCALE IN FEET
0 200 400 600 800
CONTOUR INTERVAL 10 FEET
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY
HYDROGRAPHIC MAP
CONVICT LAKE
INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA
SURVEY BY N.REIMERS, H KENNEDY, W.DAVENPORT, R NIELSON
DRAWN BY: H.KENNEDY SURVEY AUGUST 20-25,1949

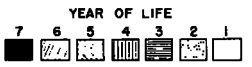
TROUT-RATES OF GROWTH-INCHES



DISSOLVED SOLIDS - PPM



YEAR OF LIFE



FISH FOODS

BOTTOM FAUNA — 211.26 POUNDS PER ACRE

PLANKTON — 0.03 CC. PER CUBIC FOOT

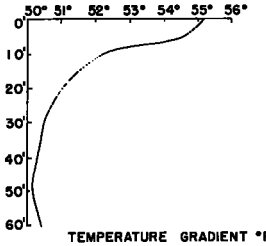
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	8.1	AMMONIA NITROGEN	.052
IRON	.01	NITRITE NITROGEN	.001
COPPER	.08	NITRATE	.08
MAGNESIUM	.7	PHOSPHATE	<.01
MANGANESE	<.01	SULFATE	8.3
SILICA	8.0	BICARBONATE	46.0
BORON	.04	CHLORIDE	.2
SODIUM	.7	FLUORIDE	<.1
POTASSIUM	1.4	DISSOLVED SOLIDS	58.0
CALCIUM	16.0	HARDNESS AS $CaCO_3$	
		TOTAL	43.0
		NON-CARBONATE	5.0

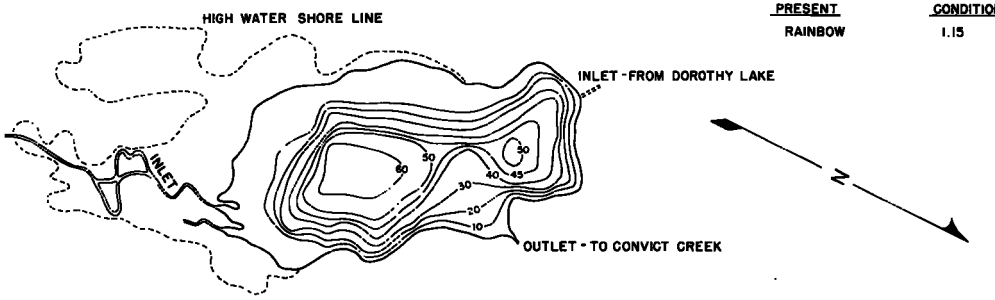
SPECIFIC CONDUCTANCE (MICROMHOS AT 25°C.)	91
PERCENT SODIUM	3
pH	8.0

TROUT

PRESENT	CONDITION (K)
RAINBOW	1.15



TEMPERATURE GRADIENT °F.
MILDRED LAKE - SEPT. 3, 1950

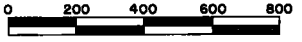


SECCHI DISK READING - 40 FEET

MORPHOMETRIC DATA

ELEVATION	9,900	FEET - U.S.G.S. (DATUM 1934)
SOUNDINGS	60	
VOLUME	290	ACRE FEET
AREA	10.7	ACRES, 18 ACRES-SPRING RUN-OFF
MEAN DEPTH	27	FEET
MAXIMUM DEPTH	60	FEET
MAXIMUM WIDTH	572	FEET
MAXIMUM LENGTH	1,126	FEET
SHORE DEVELOPMENT	1.41	
LENGTH OF SHORELINE	3,300	FEET, 0.63 MILES
SHOAL AREA TO 20 FEET	4.67	ACRES, 43.8 % SURFACE
MEAN SLOPE	23.1 %	

SCALE IN FEET



CONTOUR INTERVAL 10 FEET

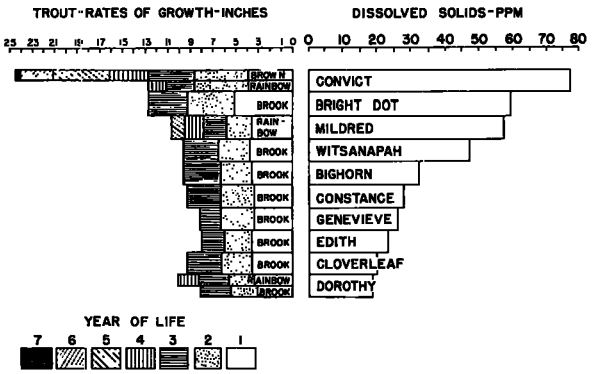
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

MILDRED LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY: N.REIMERS, J.MACIOLEK, E.PISTER, H.KENNEDY
DRAWN BY: H.KENNEDY SURVEY SEPTEMBER 1-4, 1950



FISH FOODS

BOTTOM FAUNA—49.93 POUNDS PER ACRE

PLANKTON— 0.56 CC. PER CUBIC FOOT

CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	8.0	AMMONIA NITROGEN	.02
IRON	.01	NITRITE NITROGEN	.001
COPPER	.06	NITRATE	.06
MAGNESIUM	.7	PHOSPHATE	<.01
MANGANESE	<.01	SULFATE	5.2
SILICA	8.7	BICARBONATE	54.0
BORON	.06	CHLORIDE	.1
SODIUM	.4	FLUORIDE	<.1
POTASSIUM	1.0	DISSOLVED SOLIDS	60.0
CALCIUM	17.0	HARDNESS AS $CaCO_3$:	
		TOTAL	45.0
		NON-CARBONATE	1.0

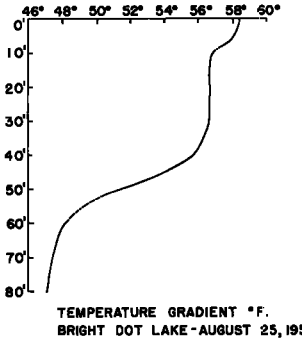
SPECIFIC CONDUCTANCE (MICROMHOS AT 25° C.) 91

PERCENT SODIUM 2

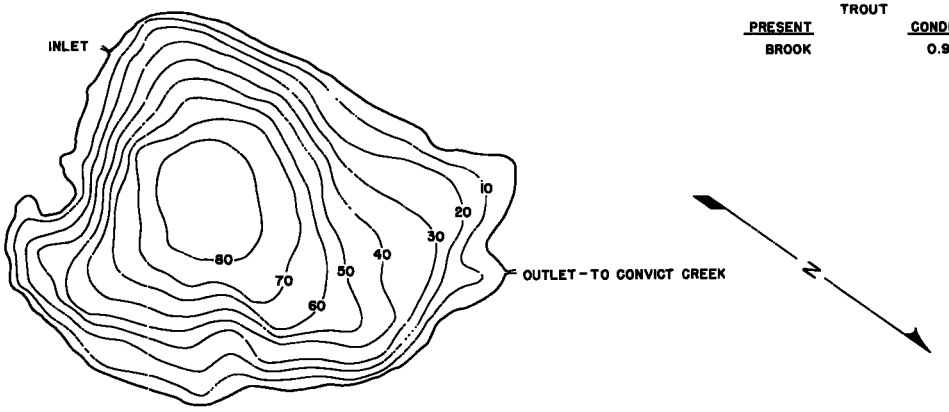
pH 7.9

TROUT

PRESENT	CONDITION (K)
BROOK	0.96



TEMPERATURE GRADIENT °F.
BRIGHT DOT LAKE-AUGUST 25, 1950



SECCHI DISK READING - 55 FEET

MORPHOMETRIC DATA

ELEVATION	10,650	FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	68	
VOLUME	1,092	ACRE FEET
AREA	27.5	ACRES
MEAN DEPTH	39	FEET
MAXIMUM DEPTH	80	FEET
MAXIMUM WIDTH	1,158	FEET
MAXIMUM LENGTH	1,522	FEET
SHORE DEVELOPMENT	1.16	
LENGTH OF SHORELINE	4,515	FEET, 0.85 MILES
SHOAL AREA TO 20 FEET	7.92	ACRES, 28.8 % SURFACE
MEAN SLOPE	17.7 %	

SCALE IN FEET

0 200 400 600 800

CONTOUR INTERVAL 10 FEET

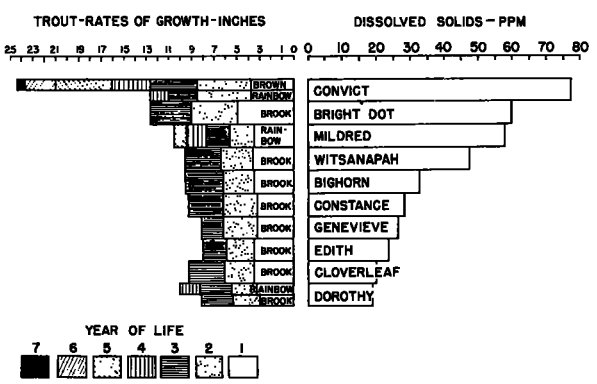
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

BRIGHT DOT LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY: N. REIMERS, J. MACIOLEK, E. PISTER
DRAWN BY: H. KENNEDY SURVEY AUGUST 25-29, 1950



FISH FOODS

BOTTOM FAUNA — 111.40 POUNDS PER ACRE

PLANKTON — 0.20 CC. PER CUBIC FOOT

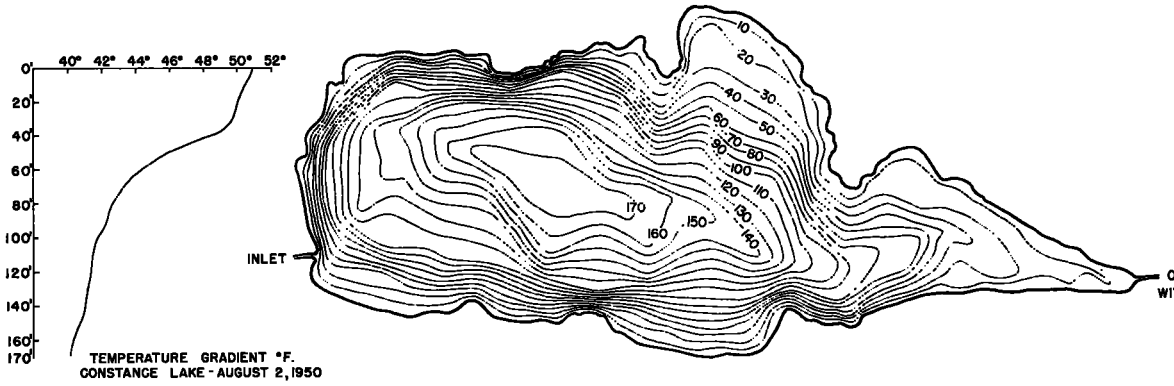
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	8.38	AMMONIA NITROGEN	.028
IRON	.02	NITRITE NITROGEN	.001
COPPER	.08	NITRATE	.1
MAGNESIUM	.5	PHOSPHATE	.02
MANGANESE	<.01	SULFATE	5.4
SILICA	4.7	BICARBONATE	17.0
BORON	<.01	CHLORIDE	.4
SODIUM	.6	FLUORIDE	.1
POTASSIUM	1.4	DISSOLVED SOLIDS	28.0
CALCIUM	6.7	HARDNESS AS $CaCO_3$:	
		TOTAL	19.0
		NON-CARBONATE	.0

SPECIFIC CONDUCTANCE (MICROMHOS AT 25°C.) 41

PERCENT SODIUM 6

pH 7.2



TEMPERATURE GRADIENT °F.
CONSTANCE LAKE - AUGUST 2, 1950

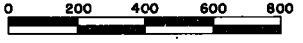
TROUT

PRESENT	CONDITION (K)
BROOK	0.95

SECCHI DISK READING - 60 FEET

MORPHOMETRIC DATA

ELEVATION	10,950	FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	122	
VOLUME	2,600	ACRE FEET
AREA	33.6	ACRES
MEAN DEPTH	71	FEET
MAXIMUM DEPTH	170	FEET
MAXIMUM WIDTH	1,035	FEET
MAXIMUM LENGTH	2,490	FEET
SHORE DEVELOPMENT	1.61	
LENGTH OF SHORE LINE	6,896	FEET, 1.3 MILES
SHOAL AREA TO 20 FEET	6.56	ACRES, 19.5% SURFACE
MEAN SLOPE	40.4%	



CONTOUR INTERVAL 10 FEET

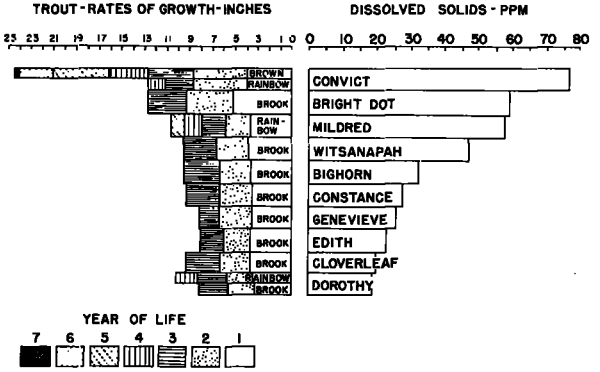
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

CONSTANCE LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY : J. MACIOLEK, E. PISTER, H. KENNEDY
DRAWN BY : H. KENNEDY SURVEY JULY 31 - AUG. 4, 1950



FISH FOODS

BOTTOM FAUNA — 134.44 POUNDS PER ACRE

PLANKTON — NONE

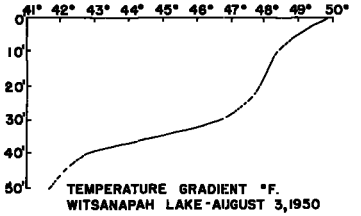
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	8.68	AMMONIA NITROGEN	.03
IRON	.02	NITRITE NITROGEN	.001
COPPER	.08	NITRATE	.04
MAGNESIUM	.6	PHOSPHATE	<.01
MANGANESE	<.01	SULFATE	6.3
SILICA	5.4	BICARBONATE	20.0
BORON	<.01	CHLORIDE	.7
SODIUM	.7	FLUORIDE	<.1
POTASSIUM	1.4	DISSOLVED SOLIDS	33.0
CALCIUM	7.6	HARDNESS AS CaCO3:	
		TOTAL	21.0
		NON-CARBONATE	5.0

SPECIFIC CONDUCTANCE (MICROMHOS AT 25° C.) 47

PERCENT SODIUM 6

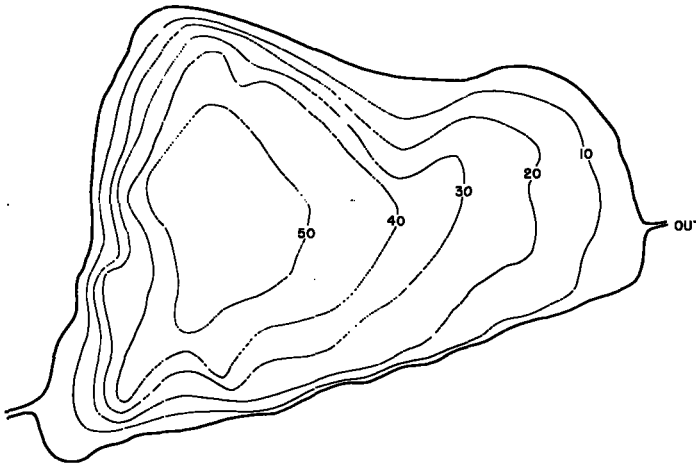
pH 7.3



TEMPERATURE GRADIENT °F.
WITSANAPAH LAKE - AUGUST 3, 1950

TROUT

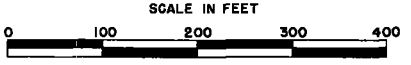
PRESENT	CONDITION (K)
BROOK	0.93



SECCHI DISK READING - 30 FEET

MORPHOMETRIC DATA

ELEVATION	10,760 FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	66
VOLUME	124 ACRE FEET
AREA	4.4 ACRES
MEAN DEPTH	28 FEET
MAXIMUM DEPTH	50 FEET
MAXIMUM WIDTH	410 FEET
MAXIMUM LENGTH	700 FEET
SHORE DEVELOPMENT	1.16
LENGTH OF SHORELINE	1,800 FEET, 0.34 MILES
SHOAL AREA TO 20 FEET	1.51 ACRES, 34.5% SURFACE
MEAN SLOPE	30.2%



CONTOUR INTERVAL 10 FEET

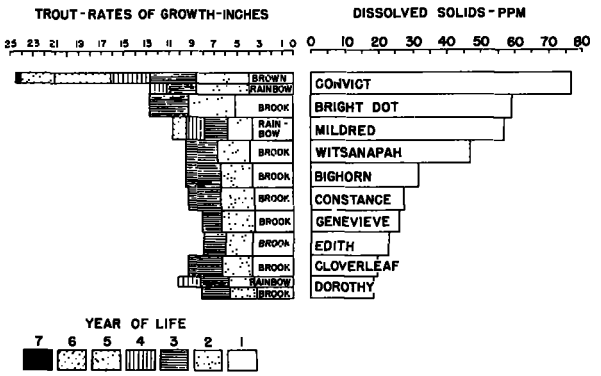
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

WITSANAPAH LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY: N.REIMERS, J.MACIOLEK, E.PISTER, H.KENNEDY
DRAWN BY: H.KENNEDY SURVEY JULY 24-27, 1950



FISH FOODS

BOTTOM FAUNA — 30.72 POUNDS PER ACRE

PLANKTON — 0.58 CC. PER CUBIC FOOT

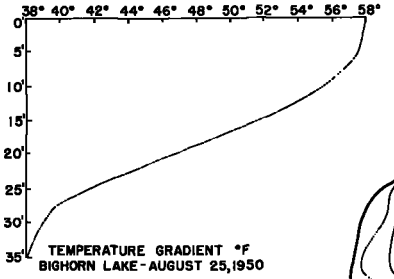
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	11.72	AMMONIA NITROGEN	.020
IRON	.01	NITRITE NITROGEN	.002
COPPER	.10	NITRATE	.1
MAGNESIUM	.6	PHOSPHATE	<.01
MANGANESE	<.01	SULFATE	16.0
SILICA	7.6	BICARBONATE	19.0
BORON	01	CHLORIDE	.4
SODIUM	.4	FLUORIDE	<.1
POTASSIUM	1.7	DISSOLVED SOLIDS	47.0
CALCIUM	11.0	HARDNESS AS $CaCO_3$:	
		TOTAL	30.0
		NON-CARBONATE	14.0

SPECIFIC CONDUCTANCE (MICROMHOS AT 25°C.) 68

PERCENT SODIUM 3

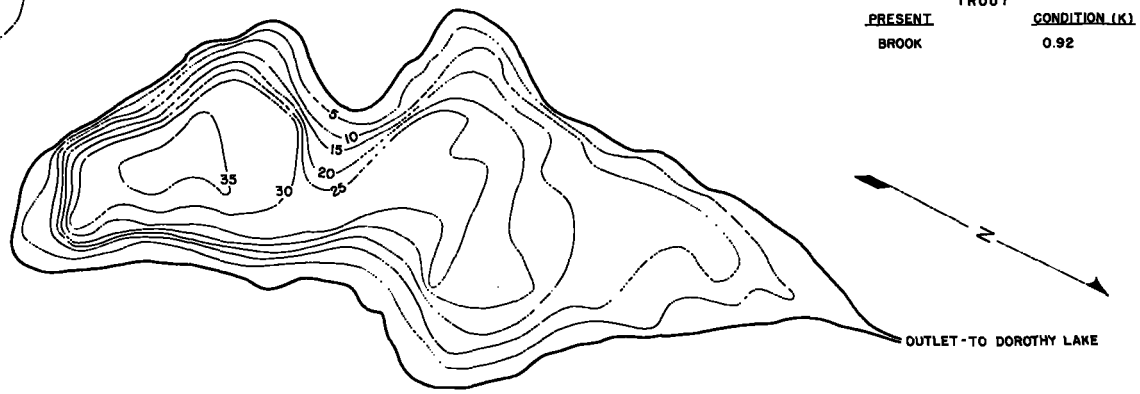
pH 7.3



TEMPERATURE GRADIENT °F
BIGHORN LAKE - AUGUST 25, 1950

TROUT

PRESENT	CONDITION (K)
BROOK	0.92



SECCHI DISK READING - 35 FEET (BOTTOM)

MORPHOMETRIC DATA

ELEVATION	10,675	FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	124	
VOLUME	103	ACRE FEET
AREA	6.5	ACRES
MEAN DEPTH	16	FEET
MAXIMUM DEPTH	35	FEET
MAXIMUM WIDTH	490	FEET
MAXIMUM LENGTH	1,160	FEET
SHORE DEVELOPMENT	1.47	
LENGTH OF SHORELINE	2,848	FEET, 0.54 MILES
SHOAL AREA TO 20 FEET	4.14	ACRES, 63.4 % OF SURFACE
MEAN SLOPE	19.5%	

SCALE IN FEET

0 100 200 300 400

CONTOUR INTERVAL 5 FEET

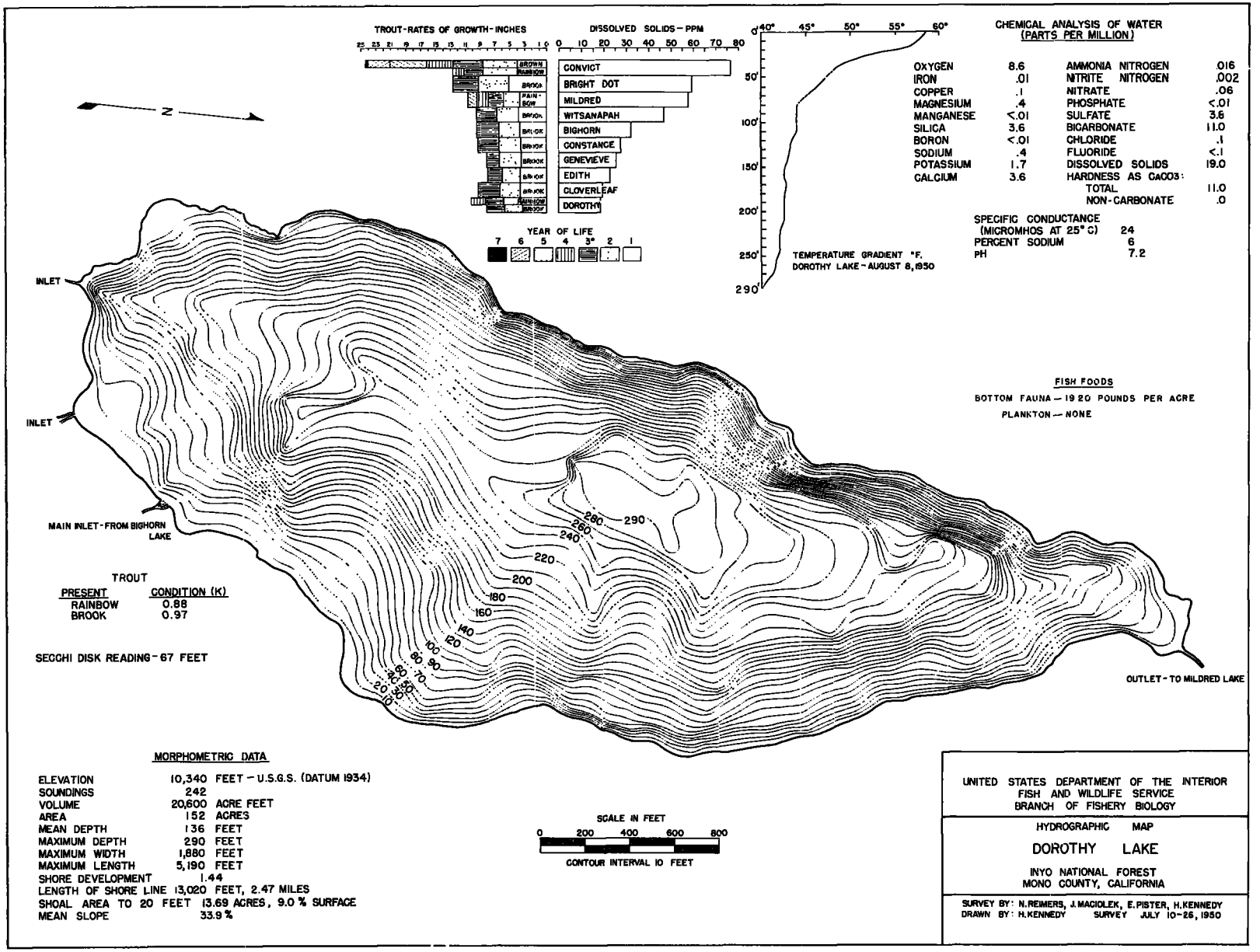
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

BIGHORN LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

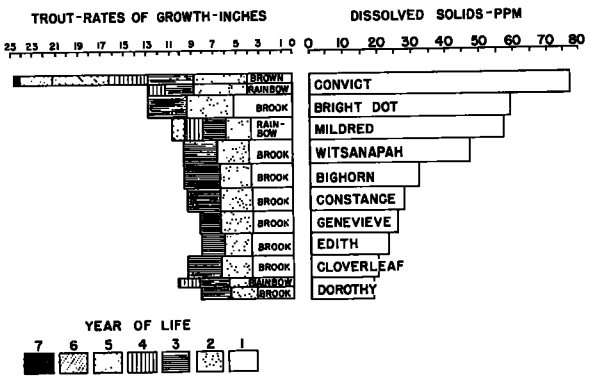
SURVEY BY : N. REIMERS, J. MACIOLEK, E. PISTER, H. KENNEDY
DRAWN BY : H. KENNEDY SURVEY JULY 21-28, 1950


TROUT-RATES OF GROWTH-INCHES
DISSOLVED SOLIDS – PPM
CONVICT
BRIGHT DOT
MILDRED
WITSANAPAH
BIGHORN
CONSTANCE
GENEVIEVE
EDITH
CLOVERLEAF
DOROTHY
YEAR OF LIFE
TEMPERATURE GRADIENT °F.
DOROTHY LAKE - AUGUST 8, 1950
CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)
OXYGEN 8.6
IRON .01
COPPER .1
MAGNESIUM .4
MANGANESE <.01
SILICA 3.6
BORON <.01
SODIUM .4
POTASSIUM 1.7
CALCIUM 3.6
AMMONIA NITROGEN .016
NITRITE NITROGEN .002
NITRATE .06
PHOSPHATE <.01
SULFATE 3.6
BICARBONATE 11.0
CHLORIDE .1
FLUORIDE <.1
DISSOLVED SOLIDS 19.0
HARDNESS AS CaCO3:
TOTAL 11.0
NON-CARBONATE .0
SPECIFIC CONDUCTANCE
(MICROMHOS AT 25° C) 24
PERCENT SODIUM 6
PH 7.2
N
INLET
INLET
MAIN INLET - FROM BIGHORN LAKE
OUTLET - TO MILDRED LAKE
FISH FOODS
BOTTOM FAUNA – 19.20 POUNDS PER ACRE
PLANKTON – NONE
TROUT
PRESENT CONDITION (K)
RAINBOW 0.88
BROOK 0.97
SECCHI DISK READING - 67 FEET
MORPHOMETRIC DATA
ELEVATION 10,340 FEET – U.S.G.S. (DATUM 1934)
SOUNDINGS 242
VOLUME 20,600 ACRE FEET
AREA 152 ACRES
MEAN DEPTH 136 FEET
MAXIMUM DEPTH 290 FEET
MAXIMUM WIDTH 1,880 FEET
MAXIMUM LENGTH 5,190 FEET
SHORE DEVELOPMENT 1.44
LENGTH OF SHORE LINE 13,020 FEET, 2.47 MILES
SHOAL AREA TO 20 FEET 13.69 ACRES, 9.0 % SURFACE
MEAN SLOPE 33.9 %
SCALE IN FEET
CONTOUR INTERVAL 10 FEET
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY
HYDROGRAPHIC MAP
DOROTHY LAKE
INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA
SURVEY BY: N.REIMERS, J.MACIOLEK, E.PISTER, H.KENNEDY
DRAWN BY: H.KENNEDY SURVEY JULY 10-26, 1950

FISH FOODS

BOTTOM FAUNA — 207.42 POUNDS PER ACRE

PLANKTON — NONE



CHEMICAL ANALYSIS OF WATER (PARTS PER MILLION)

OXYGEN	8.9	AMMONIA NITROGEN	.028
IRON	.02	NITRITE NITROGEN	.001
COPPER	.08	NITRATE	.19
MAGNESIUM	.5	PHOSPHATE	.04
MANGANESE	<.01	SULFATE	1.8
SILICA	5.5	BICARBONATE	14.0
BORON	<.01	CHLORIDE	.6
SODIUM	1.3	FLUORIDE	<.1
POTASSIUM	1.1	DISSOLVED SOLIDS	20.0
CALCIUM	2.6	HARDNESS AS $CaCO_3$:	
		TOTAL	9.0
		NON-CARBONATE	.0

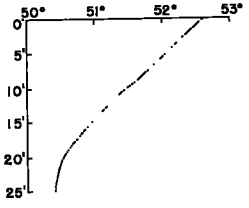
SPECIFIC CONDUCTANCE (MICROMHOS AT 25° C.) 23

PERCENT SODIUM 22

pH 7.1

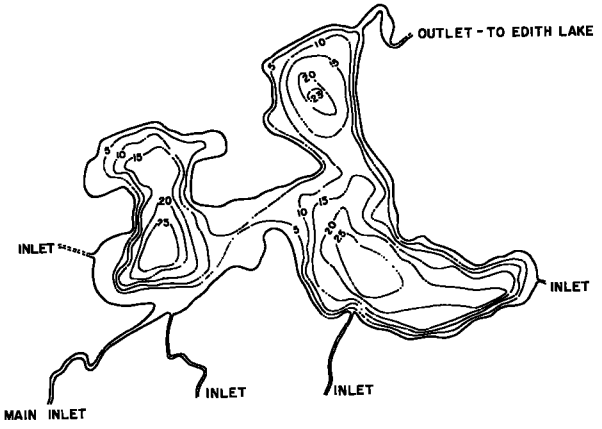
TROUT

PRESENT	CONDITION (K)
BROOK	0.94



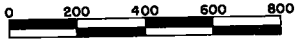
TEMPERATURE GRADIENT °F.
CLOVERLEAF LAKE - AUGUST 14, 1950

SECCHI DISK READING - 25 FEET (BOTTOM)



MORPHOMETRIC DATA

ELEVATION	10,310	FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	112	
VOLUME	141	ACRE FEET
AREA	11.6	ACRES
MEAN DEPTH	12	FEET
MAXIMUM DEPTH	25	FEET
MAXIMUM WIDTH	930	FEET
MAXIMUM LENGTH	987	FEET
SHORE DEVELOPMENT	2.18	
LENGTH OF SHORELINE	5,498	FEET, 1.04 MILES
SHOAL AREA TO 20 FEET	9.45	ACRES, 81.4 % SURFACE
MEAN SLOPE	13.2%	



CONTOUR INTERVAL 5 FEET

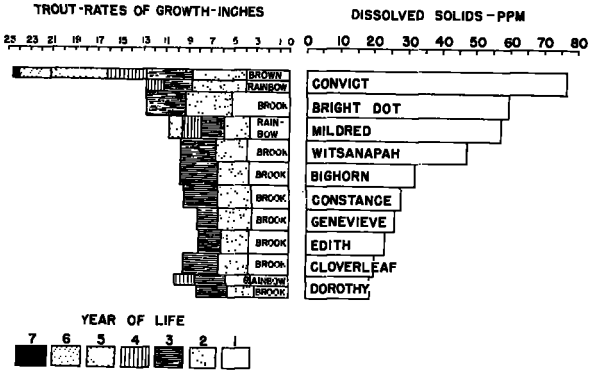
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

CLOVERLEAF LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY: N. REIMERS, J. MACIOLEK, H. KENNEDY
DRAWN BY: H. KENNEDY SURVEY AUGUST 14-16, 1950



FISH FOODS

BOTTOM FAUNA — 111.40 POUNDS PER ACRE

PLANKTON — 0.06 CC. PER CUBIC FOOT

CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	9.0	AMMONIA NITROGEN	.024
IRON	.02	NITRITE NITROGEN	.001
COPPER	.12	NITRATE	.06
MAGNESIUM	.3	PHOSPHATE	<.01
MANGANESE	<.01	SULFATE	3.0
SILICA	7.0	BICARBONATE	13.0
BORON	.01	CHLORIDE	.4
SODIUM	.9	FLUORIDE	<.1
POTASSIUM	1.2	DISSOLVED SOLIDS	23.0
CALCIUM	3.3	HARDNESS AS $CaCO_3$:	
		TOTAL	10.0
		NON-CARBONATE	.0

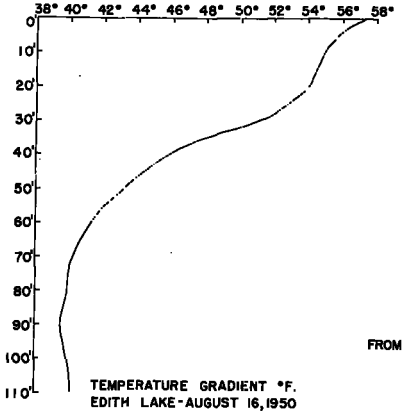
SPECIFIC CONDUCTANCE (MICROMHOS AT 25° C.) 26

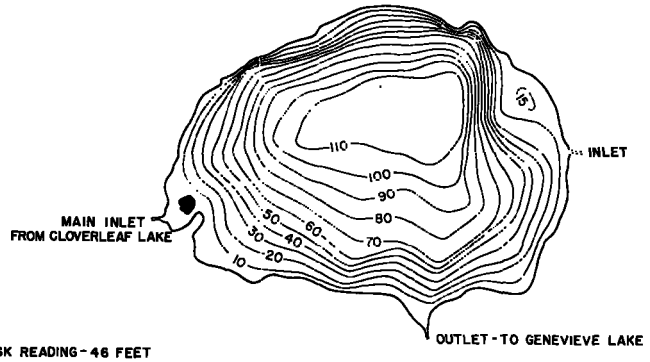
PERCENT SODIUM 15

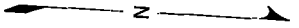
pH 7.0

TROUT

PRESENT	CONDITION (K)
BROOK	0.99



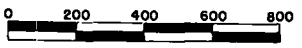




SECCHI DISK READING-46 FEET

MORPHOMETRIC DATA

ELEVATION	10,100 FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	59
VOLUME	1,070 ACRE FEET
AREA	18.0 ACRES
MEAN DEPTH	59 FEET
MAXIMUM DEPTH	110 FEET
MAXIMUM WIDTH	986 FEET
MAXIMUM LENGTH	1,216 FEET
SHORE DEVELOPMENT	1.14
LENGTH OF SHORELINE	3,690 FEET, 0.70 MILES
SHOAL AREA TO 20 FEET	3.85 ACRES, 21.3 % SURFACE
MEAN SLOPE	27.5 %



CONTOUR INTERVAL 10 FEET

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

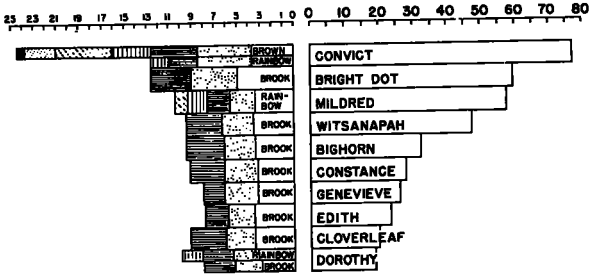
EDITH LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY: N. REIMERS, J. MACIOLEK, H. KENNEDY
DRAWN BY: H. KENNEDY SURVEY AUGUST 16-18, 1950

TROUT-RATES OF GROWTH-INCHES

DISSOLVED SOLIDS-PPM



YEAR OF LIFE

FISH FOODS

BOTTOM FAUNA—126.76 POUNDS PER ACRE

PLANKTON— 0.38 CC. PER CUBIC FOOT

CHEMICAL ANALYSIS OF WATER
(PARTS PER MILLION)

OXYGEN	11.2	AMMONIA NITROGEN	.024
IRON	.01	NITRITE NITROGEN	.001
COPPER	.08	NITRATE	.06
MAGNESIUM	.4	PHOSPHATE	.07
MANGANESE	<.01	SULFATE	3.3
SILICA	7.1	BICARBONATE	17.0
BORON	.01	CHLORIDE	.3
SODIUM	1.1	FLUORIDE	<.1
POTASSIUM	1.0	DISSOLVED SOLIDS	26.0
CALCIUM	4.4	HARDNESS AS CaCO3:	
		TOTAL	13.0
		NON-CARBONATE	.0

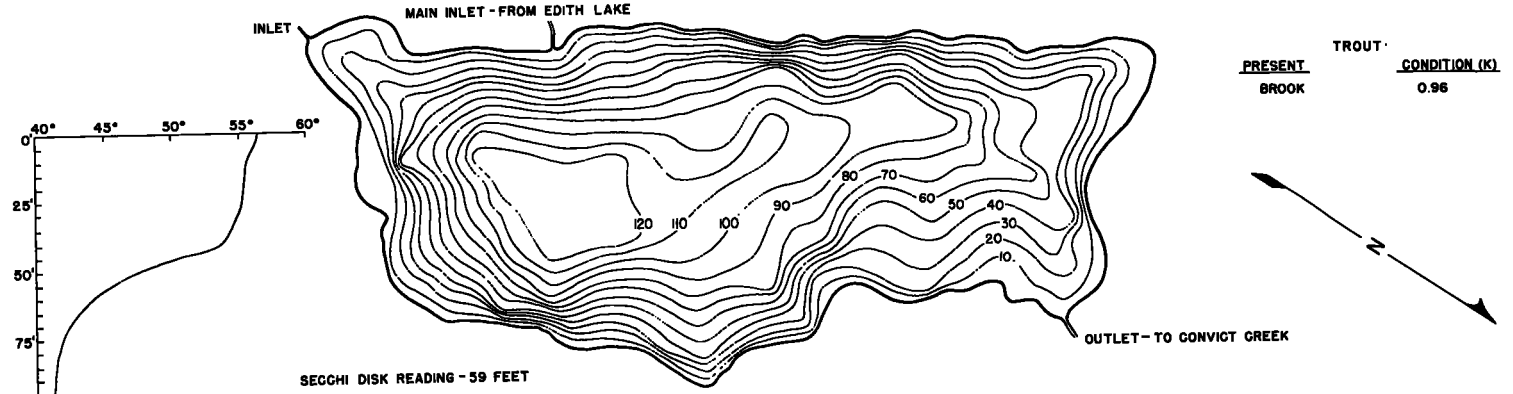
SPECIFIC CONDUCTANCE (MICROMHOS AT 25° C.) 33

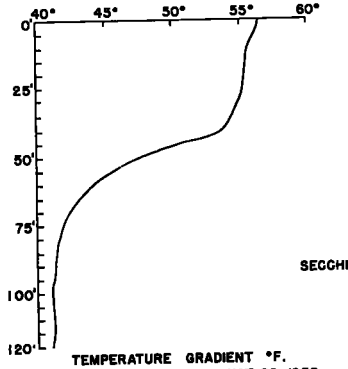
PERCENT SODIUM 15

pH 7.2

TROUT

PRESENT	CONDITION (K)
BROOK	0.96





SECCHI DISK READING - 59 FEET

TEMPERATURE GRADIENT °F.
GENEVIEVE LAKE - AUGUST 22, 1950

MORPHOMETRIC DATA

ELEVATION	9,910 FEET — U.S.G.S. (DATUM 1934)
SOUNDINGS	86
VOLUME	2,570 ACRE FEET
AREA	42.3 ACRES
MEAN DEPTH	61 FEET
MAXIMUM DEPTH	120 FEET
MAXIMUM WIDTH	1,040 FEET
MAXIMUM LENGTH	2,500 FEET
SHORE DEVELOPMENT	1.42
LENGTH OF SHORE LINE	6,800 FEET, 1.29 MILES
SHOAL AREA TO 20 FEET	7.77 ACRES, 18.3% SURFACE
MEAN SLOPE	26.7%

SCALE IN FEET

CONTOUR INTERVAL 10 FEET

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BRANCH OF FISHERY BIOLOGY

HYDROGRAPHIC MAP

GENEVIEVE LAKE

INYO NATIONAL FOREST
MONO COUNTY, CALIFORNIA

SURVEY BY : N. REIMERS, J. MACIOLEK, E. PISTER, H. KENNEDY
DRAWN BY : H. KENNEDY SURVEY AUGUST 19-21, 1950

U. S. GOVERNMENT PRINTING OFFICE : 1956—O-346212

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THE GAS BLADDER AND ITS RELATION TO THE INNER EAR IN *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX*

BY CHARLES P. O'CONNELL

FISHERY BULLETIN 104

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

In anticipation of physiological and behavior studies of the Pacific sardine (*Sardinops caerulea*) and the northern anchovy (*Engraulis mordax*), an anatomical study of the gas bladder has been made in both species. As in all clupeoid fishes, the gas bladders of these species have a close anatomical relation with the inner ears. A general description of this mechanism is presented, and some differences in cranial structure in the sardine and anchovy are noted.

The form and orientation of the gas bladder, which differ in the two species, are described. In the sardine, the pneumatic duct arises from the end of the blindsac of the stomach, and the gas bladder has only one chamber with a postanal opening to the exterior. In the anchovy, the pneumatic duct arises from the dorsal wall of the cardiac stomach, and the bladder is composed of two chambers with only a short blind caecum at its posterior end.

Histological descriptions are given of the pneumatic duct and bladder wall in both species, and of the postanal opening in the sardine and the posterior caecum in the anchovy. The structure of the pneumatic ducts strongly suggests a valvelike mechanism that prevents the passage of solid matter toward the gas bladder. The gas-bladder wall exhibits no secretory specialization in either species, but specialization of the muscle layer in the anchovy is indicative of a pumping mechanism between the two chambers of the bladder. In the sardine, the postanal opening of the bladder, which is not controlled by a muscular sphincter, probably opens and closes as a result of differences in gas pressure in the bladder and hydrostatic pressure in the external environment. In the anchovy, the posterior caecum of the bladder is a small and fairly complex structure, but its function cannot be surmised without further investigation.

The probable functions of the ear–gas bladder mechanism and the gas bladder proper, as well as the functional relation between them, are discussed. Definite conclusions will not be possible without experimental investigation. Because the structural differences in the gas bladders of these two species suggest the possibility of associated behavior differences, both species should be subjected to experimental investigation.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

THE GAS BLADDER AND ITS RELATION TO THE INNER EAR IN *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX*

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FISHERY BULLETIN 104
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THE GAS BLADDER AND ITS RELATION TO THE INNER EAR IN *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX*

By CHARLES P. O'CONNELL, *Fishery Research Biologist*

The California Cooperative Oceanic Fisheries Investigations[1] is primarily concerned with determining the causes of fluctuations in the abundance and availability of commercially important pelagic marine fishes. The extent to which a fish population is available to a fishery is a result of the interaction between the fish and the physical, chemical, and biological features of the environment. Changes in the environment result in changes in availability. Although many environmental features are being measured, very little is known about their effect on the behavior of fishes.

One approach to an understanding of availability is the investigation of behavior in the laboratory and in the field. Prior knowledge of the anatomy and physiology of the animal, particularly in regard to its sensory systems, is a prerequisite to such studies.

The Pacific sardine, *Sardinops caerulea*, and the northern anchovy, *Engraulis mordax*, are both commercially important species on the west coast of North America and are being studied by the California Cooperative Oceanic Fisheries Investigations. (These species will be referred to as sardine and anchovy in the text of this paper.) Since the behavior of both species will be studied in the near future, an anatomical study of each species has already been initiated.

The first organ system of these species to be examined was the gas bladder.[2] It became apparent, during the course of this work, that published descriptions of the gas bladder in other clupeoid fishes cannot, in all respects, be applied to the sardine and anchovy. For this reason, and also because the gas bladders of the sardine and anchovy exemplify certain marked anatomical contrasts that occur among clupeoids, the organ of each species is described in this paper.

The gas bladder in clupeoids is a retroperitoneal, tubular vesicle extending the whole length of the body cavity. It is connected to the alimentary canal by a pneumatic duct which arises from various positions along the dorsal wall of the cardiac stomach. In some species, the bladder opens to the exterior behind the anus; in others, it ends above the anus. In all clupeoid species, two capillary tubes, one on each side of the vertebral column, extend from the anterior end of the bladder into the cranium, where they expand into terminal vesicles encapsuled in bone. The two pairs of bony capsules are termed the prootic and pterotic bullae, in reference to skeletal elements involved. The anterior pair of bullae is closely associated with the inner ear. This relation, first described by Weber (1820) in *Clupea harengus*, involves the least understood, but most extensively investigated, feature of the bladder.

Apparently such gas-filled bony bullae are characteristic of all clupeoids, since Svetovidov (1950) was able to ascertain their presence in more than 50 species. As early as 1891, Ridewood described differences in the shape of these bullae, or capsules, in 6 species, and De Beaufort (1909) added to this information by describing such differences in more than 20 species, representing 10 genera. Despite differences in shape and proportion, the relation between these chambers and the ear is basically the same in all species. Tracy (1920 a) described the relation between the gas vesicles and the ear in *Pomolobus pseudoharengus*, with observations on a few other American species, and in another paper (1920 b) he gave a detailed

[1] A program sponsored by the Marine Research Committee and carried out cooperatively by the Scripps Institution of Oceanography of the University of California, the Bureau of Marine Fisheries of the California Department of Fish and Game, the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences.

[2] The author is in agreement with Woodland (1911) in regard to the terminology applied to this organ. Woodland states that "The terms swimbladder and airbladder are inappropriate, since fishes do not use the apparatus for swimming and it does not contain air." The term, "gas bladder," on the other hand, properly describes the organ without these implications.

description of each cranial bone involved. Wohlfahrt (1936), using *Clupea pilchardus*, has given by far the most detailed description of the whole mechanism.

I wish to express my gratitude to Dr. Rolf L. Bolin, Stanford University, for reviewing this paper, and for the many valuable suggestions he made. I would also like to thank George M. Mattson for his excellent drawings of the sardine and anchovy skulls.

RELATION BETWEEN THE GAS BLADDER AND EAR

GENERAL DESCRIPTION

In view of Wohlfahrt's work, only a general description of the relation between the ear and gas bladder in the sardine and anchovy will be presented here. Examination of sectioned cranii of the sardine and the anchovy showed the relation in these two species to be basically the same as it is in *Clupea pilchardus*. There are, of course, differences in the form of the cranial bones, but these probably do not modify the function of the ear–gas bladder mechanism. To study such differences in the sardine and the anchovy, skeletons of adult specimens were prepared according to the method described by Bolin (1935). Examination of articulated and disarticulated cranii was supplemented by dissections of formalin-preserved specimens.

Figure 1 shows, schematically, a dorsal view and lateral view of the ear–gas bladder relation on the left side of the cranium. The plane of the lateral view is indicated on the dorsal view; however, the dorsal view cannot be oriented in this way, because it shows structures at slightly different levels.

In most species the capillary extension of the bladder, immediately after it enters the exoccipital, expands slightly to form a small fusiform chamber in that bone. Anterior to this, the gas tubule bifurcates to produce a spheroid vesicle in the pterotic and a cylindrical vesicle in the prootic. The vesicles are enclosed in the hard, bony bullae already mentioned. The anterior, or prootic, bulla is divided into an upper and a lower chamber by a heavy, elastic, transverse membrane. The gas vesicle occupies the lower chamber, and in the wall of the upper chamber there is a transverse slit called the prootic fenestra. Through this slit the upper, perilymph-filled chamber is continuous with the large perilymphatic space under the floor of the recessus utriculus. The latter is strongly attached to the prootic bulla along the anterior lip of the fenestra. Between the posterior lip of the fenestra and the floor of the recessus, which are slightly separated, there is a thin sheet of loose connective tissue. The sparse and widely separated fibers of this tissue do not interrupt the continuity between the perilymph in the bulla and in the space beneath the recessus.

The pterotic bulla is located within the loop of the horizontal semicircular canal, which is not shown in the figure. The gas vesicle is completely enclosed by the bulla, and closely applied to its inner surface.

The nervus acousticus (VIII) innervates seven sensory areas of the membranous labyrinth, as in most fishes. So far as is known, the clupeoids are the only group in which the ramulus utriculus (one of the seven branches) is divided into three parts. These branches extend laterally under the floor of the recessus utriculus: the anterior branch along the anterior lip of the prootic fenestra, the medial branch approximately above its posterior lip, and the posterior branch over the large perilymphatic space. In figure 1 these nerve branches are indicated though not labeled. Each branch innervates an overlying macula in the recessus. The lapillus is seated on the medial and posterior maculae and attached to the anterior macula by a horizontal membrane that is triangular in cross section.

Wohlfahrt found the axis cylinders of the ramulus utriculus anterior in *C. pilchardus* to be smaller in diameter than any others in the ramus anterior VIII, but the same as those in the ramus posterior VIII. This condition has also been observed in the sardine and anchovy.

The membranous labyrinth of clupeoids is unique in being differentially thickened, and in having definite perilymphatic ducts running through some of the thickened portions. One of the most noticeable thickenings of the wall underlies the macula utriculus media, and the thinnest region is between it and the macula utriculus anterior, or directly above the prootic fenestra. The perilymphatic systems surrounding the two membranous labyrinths are, furthermore, continuous

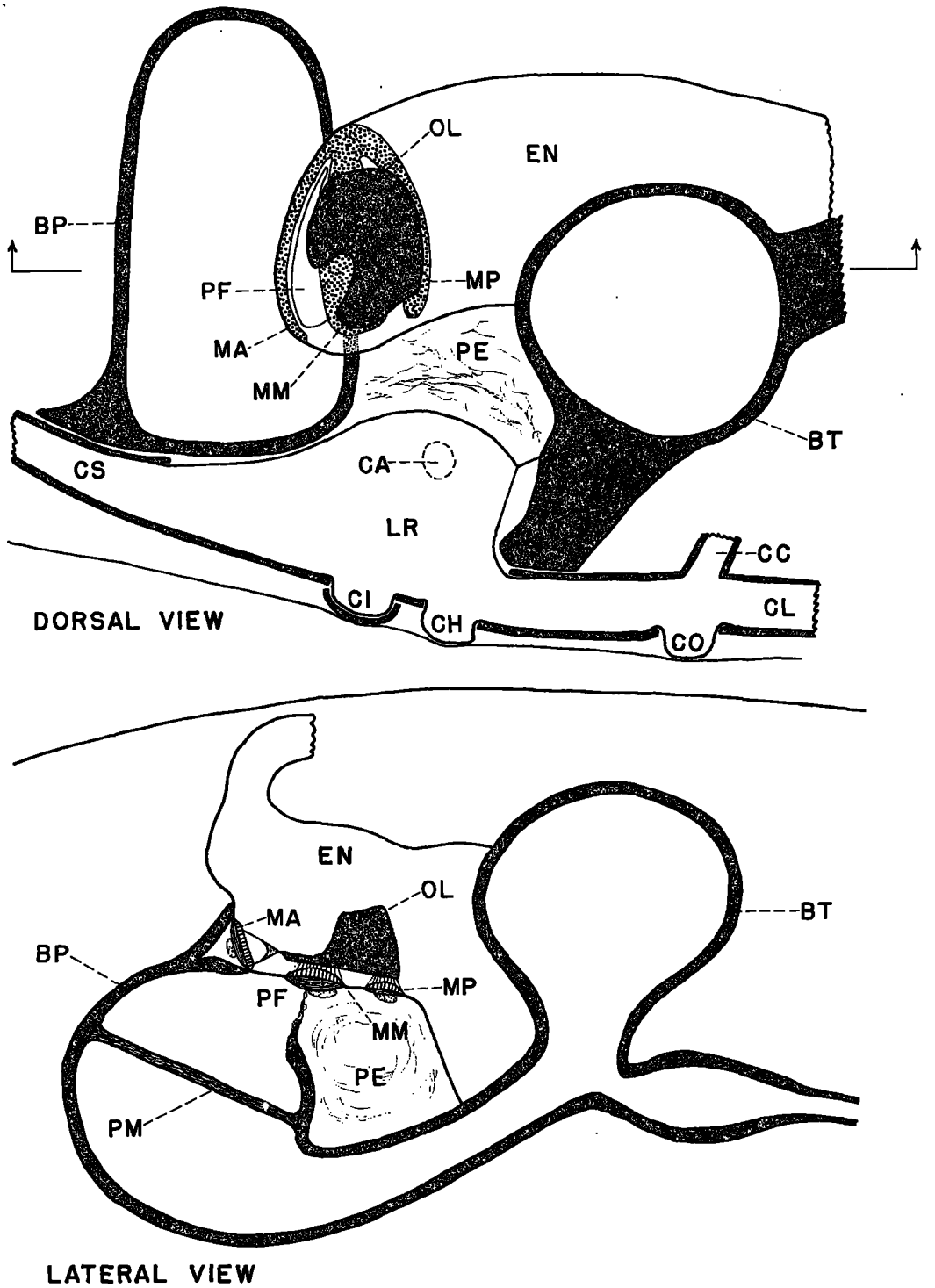


FIGURE 1.—Schematic drawing of relation between membranous labyrinth and gas vesicles on the left side of the clupeoid cranium. The plane of the lateral view is marked on the dorsal view. The solid black areas represent bone. *BP*, prootic bulla; *BT*, pterotic bulla; *CA*, accessory temporal sensory canal; *CC*, occipital sensory canal; *CH*, preopercular sensory canal; *CI*, infraorbital sensory canal; *CL*, lateral sensory canal; *CO*, opercular sensory canal; *CS*, supraorbital sensory canal; *EN*, endolymphatic space; *LR*, lateral recess; *MA*, macula utriculus anterior; *MM*, macula utriculus media; *MP*, macula utriculus posterior; *OL*, otolith (lapillus); *PE*, perilymphatic space; *PF*, prootic fenestra; *PM*, prootic membrane.

with each other below the brain anteriorly and above the brain posteriorly.

Laterally, the perilymphatic space under the floor of the recessus is separated from a large sinus of the lateral-sensory system by a very thin elastic membrane. From this sinus, located in the lateral recess of the cranium, five of the six primary lateral-sensory canals emanate. The proximal ends of four of these are obvious in figure 1, while the opening of the fifth, the accessory temporal canal, which passes through the roof of the lateral recess, is indicated by a dashed circle. The first sensory organs of the supraorbital, infraorbital, and preopercular canals, though not shown in figure 1, lie within the recess close to the mouths of their respective canals.

The supratemporal canal system, which extends over the surface of the parietal and the posterior wing of the frontal bone, arises from an expanded sinus that occupies the temporal foramen of the cranium. Mesially, this sinus projects through the temporal foramen and is separated from the ectomeninx by a thin hyaline membrane. It is, apparently, an isolated segment of the lateral-sensory system and does not show in figure 1. Laterally, it is covered only by the integument. The lateral recess and temporal foramen lie close to each other, a little behind, and approximately level with the top of the eye.

The auditory fenestra, an oval window lateral to the sacculus, is closed by a thin hyaline plate. In the living animal, the sacculus rests against the inner surface of the plate, while its outer surface is covered by the mucous membrane of the branchial chamber.

CRANIAL MODIFICATIONS IN *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX*

The sardine and anchovy differ from each other, and from many other clupeoids, in the size and shape of the bullae and in the bone construction of the lateral recess. In all probability, these differences are secondary, resulting from greater differences in the cranial bones involved in their formation. The terminology applied to the skull of *Sardinops caerulea* is taken from Phillips (1942), and since there is no published osteological description of *Engraulis mordax*, the same terminology has been followed as far as it was applicable to the anchovy.

It is apparent from the literature that, although there are differences in shape, the prootic bullae are almost always transversely elongate, and meet in the median plane to form a subcerebral ridge. Because the axes of the bullae are not quite horizontal, there is a slight dihedral in the ridge formed by them.

In figure 2, the bullae of the sardine and anchovy are sketched in dorsal view. Most noticeable is their difference in size, but since the anchovy is smaller than the sardine, the proportional size of their bullae is approximately the same. Figure 3 shows the relative size of the cranii.

The prootic bullae of the two species differ appreciably in shape. In the sardine, a slight constriction divides the bulla into a larger, lateral and a smaller, medial portion. The crescentic fenestra, about 0.3 the length of the bulla, is located on the dorsoposterior surface of the larger segment. Its margin is flush with the surface of the bulla. In the anchovy, the constriction in the prootic bulla is much more pronounced, and the larger lateral segment has a spherical shape. The fenestra, located in the same position as in the sardine, differs slightly in its construction. It has the same crescentic form, but its margin projects upward to form a ridge. Furthermore, at the narrowed end, the adjacent portions of the marginal ridge join to form a V-shaped groove, occluding the actual opening of the fenestra to about two-thirds that of the actual space encompassed by the ridge. The peripheral ridge is not an additional structure in this species. It results from differences in excavation of the surrounding surface of the bulla, and serves to retain, in the anchovy, the same relative distance between the fenestra and the overlying floor of the recessus that exists in the sardine.

Ridewood (1891) and De Beaufort (1909) have shown that the pterotic bulla varies considerably among clupeoid species, and that it is absent in some. Wohlfahrt (1936) suggested that its formation in the same position as the subtemporal cavity of cyprinoids indicates that it represents nothing more than the expansion of a portion of the gas-filled chamber into an available space in the cranium.

The pterotic bulla is well developed in both the sardine and anchovy. In each, it is separated by a slight constriction into a smaller lower chamber

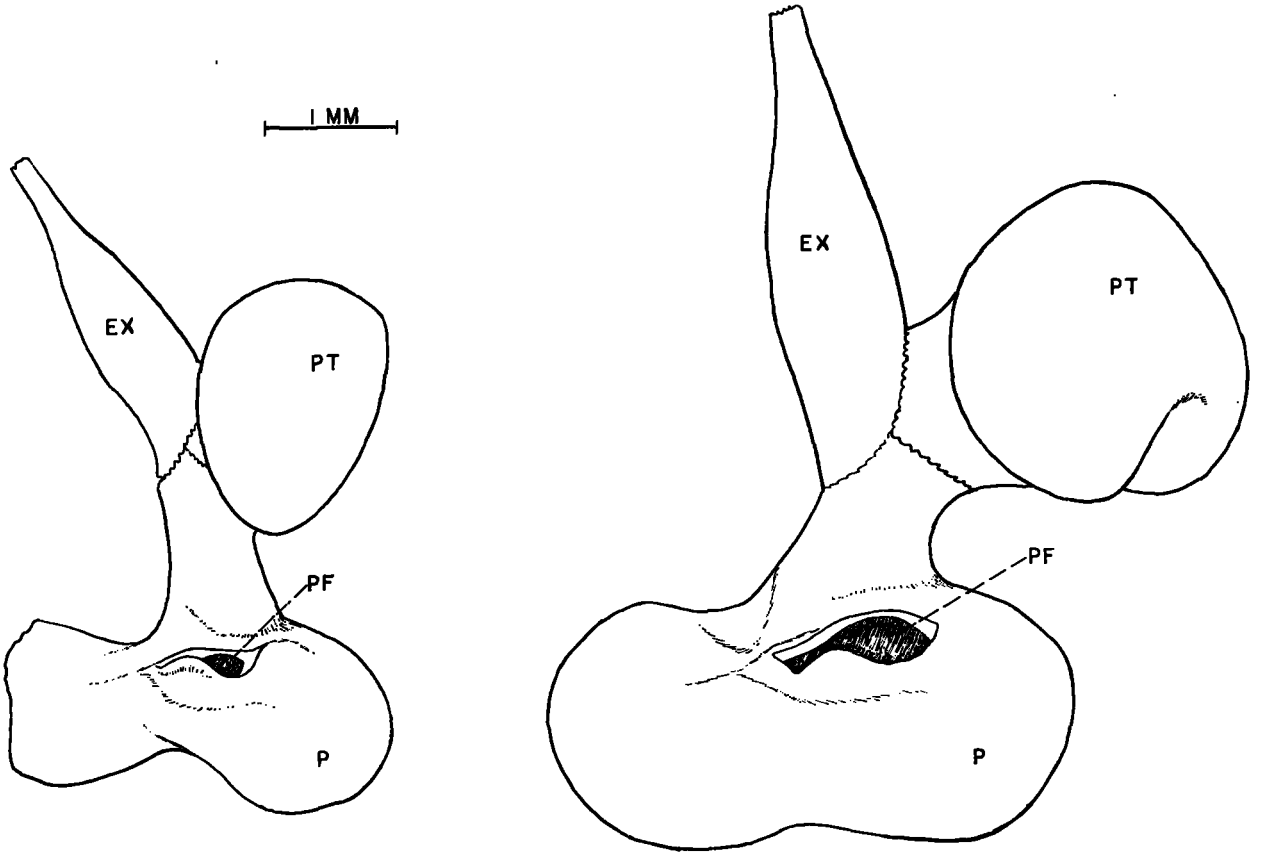


FIGURE 2.—Dorsal view of bony bullae removed from the left side of the cranii of *Sardinops caerulea*, 220 mm. standard length (right), and *Engraulis mordax*, 150 mm. stan dard length (left). *EX*, exoccipital; *P*, prootic; *PF*, prootic fenestra; *PT*, pterotic.

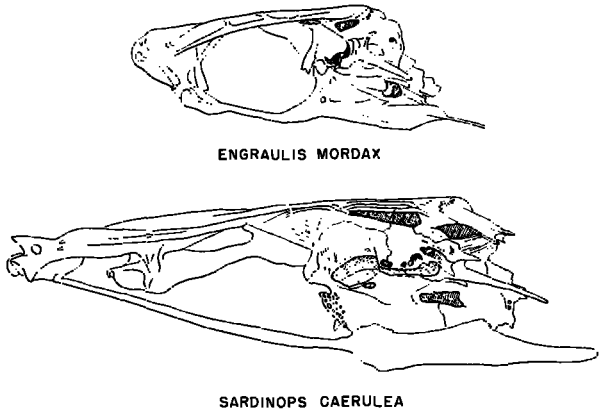


FIGURE 3.—View of left side of cranii of *Sardinops caerulea*, 264 mm. standard length (below), and *Engraulis mordax*, 147 mm. standard length (above), to show relative difference in size between adults.

and a larger, spheroid upper chamber. The upper chamber projects somewhat anteromesially, but in the sardine the anterior projection is more noticeable, while in the anchovy the mesial projection is more emphasized. The constriction between the two chambers is traversed by the horizontal semicircular canal in both species.

The extent to which the pterotic bulla is exposed on the outer surface of the cranium also differs from species to species. Tracy (1920 b) found that the capsule protruded slightly into the pre-epiotic fossa in *Pomolobus pseudoharengus*, was only slightly visible in *P. mediocris*, was covered except for a microscopic area in *Brevoortia tyrannis*, and was completely covered in *Alosa sapidissima*. These differences result from the extent to which the bulla is covered by the expansion of the pterotic bone. In both

sardine and anchovy, the whole upper surface of the bulla projects into the temporal groove between the temporal foramen and the pre-epiotic fossa (fig. 4). It is entirely covered by muscle, which in turn is partially covered by the thin, triradiate supratemporal bone. In the anchovy, the supratemporal completely overlies the surface of the bulla, while in the sardine part of the bulla is exposed in the temporal groove anterior to the leading edge of the supratemporal.

In the anchovy, the bones forming the lateral recess are thin and the lateral-sensory-canal foramina are relatively large, whereas in the sardine the bones are thick and the foramina relatively small. In the anchovy, the recess is bounded by the sphenotic, prootic, pterotic, and the lateral wing of the frontal. In the sardine, the lateral wing of the frontal does not form part of the wall; however, the pterotic forms a greater part than in the anchovy. *Pomolobus pseudoharengus* and *Clupea pilchardus* show the same differences as the anchovy and sardine. Tracy found that the posterior face of the sphenotic was deeply excavated to accommodate the recess in *P. pseudoharengus*. Wohlfahrt found the recess mainly located in the pterotic bone in *C. pilchardus*, and said that the lateral wing of the frontal did not form part of the recess wall, as in *P. pseudoharengus*.

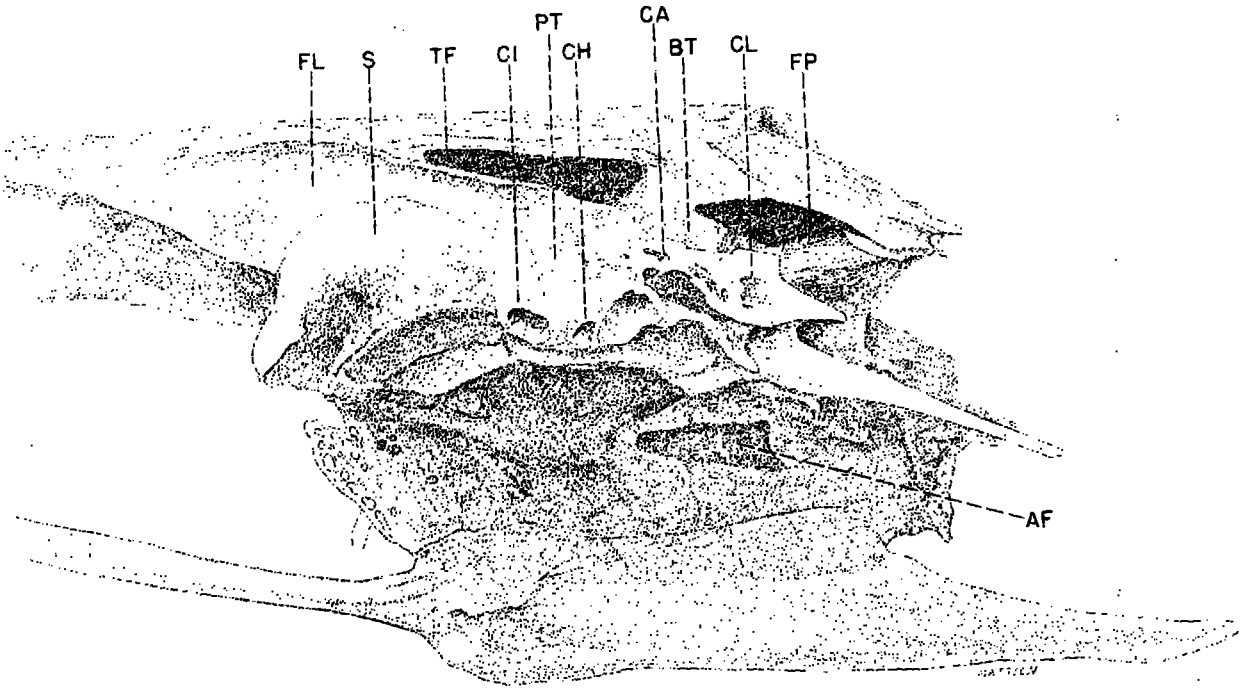
Except for the mesial communication with the auditory recess, which is interrupted by a thin elastic membrane, the only openings in the lateral recess are those of the lateral-sensory canals. The supraorbital canal runs anteromesially in the bony tube formed by the lateral wing of the frontal. The lateral canal passes posteriorly through the pterotic bone from the lateral recess. As it emerges, the opercular and exoccipital canals branch from it, and then it continues downward external to the pectoral girdle. The supraorbital and lateral canals give the impression of being one continuous tube, expanded as a sinus in the region of the lateral recess. The infraorbital, preopercular, and accessory-temporal canals open from the sinus at approximately right angles to the axis of this tube. The first two canals open laterally, one behind the other, while the third opens dorsally. Although identical lateral-sensory-canal foramina occur in both species, their sizes and locations in respect to the bones of the recess are not the same.

In figure 4, it can be seen that, in the anchovy, the lateral wing of the frontal is a broad, flat plate which forms most of the lateral wall and roof of the recess. Anteriorly, it overlies the sphenotic, and its curving ventroposterior margin parallels contiguous edges of the sphenotic and pterotic bones. It recurves dorsally to its junction with the temporal ridge of the frontal bone. The infraorbital, preopercular, and accessory-temporal canals emanate from the slit thus formed between these bones. The anterior half of the infraorbital foramen is formed by the excavated posterior face of the sphenotic, while its posterior margin is formed by a bony stay that projects obliquely up from the pterotic bone to the undersurface of the frontal wing. Dorsally, the foramen is closed by the lateral wing of the frontal. The preopercular foramen, incomplete dorsally, is formed by the wall of the pterotic and its oblique stay. Above the preopercular foramen, the gap between the frontal wing and pterotic is spanned by a sheet of tough connective tissue, leaving only the small opening of the accessory-temporal canal at the upper end of the gap. This sheet of connective tissue disappeared in the skeletonizing process.

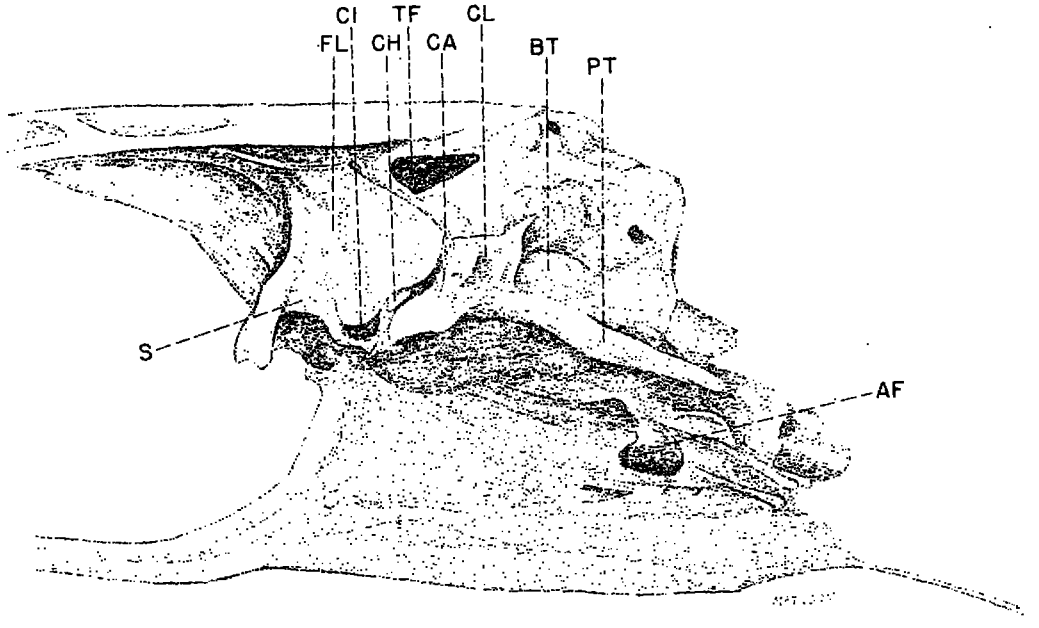
The lateral canal passes posteriorly from the lateral recess through a loop of bone projecting from the pterotic. The lateral segment is a narrow stay, but the mesial segment is produced posteriorly as a broad wall with a flared margin. At this point, the opercular canal branches ventrally and the occipital canal branches dorsally to pass into the supratemporal bone.

In figure 5, the supratemporal bone is in position and the lateral wing of the frontal has been removed. The triradiate supratemporal, bridging the temporal groove from the pterotic to the occipital, is well in advance of the exposed portion of the pterotic bulla. Removal of the frontal wing exposes an elongate, triangular plate produced from the end of the oblique stay of the pterotic. When this is removed, the end of the prootic bulla and (part of) the small fenestra into the auditory recess can be seen. The frontal wing and pterotic projection, of course, can be removed together.

In the anchovy, the greatest lateral projection of the cranium is the wing of the pterotic that re-



SARDINOPS CAERULEA



ENGRAULIS MORDAX

FIGURE 4.—View of left side of postorbital region of cranii of *Sardinops caerulea* (264 mm. standard length) and *Engraulis mordax* (147 mm. standard length). *AF*, auditory fenestra; *BT*, pterotic bulla; *CA*, accessory temporal sensory canal; *CH*, preopercular sensory canal; *CI*, infraorbital sensory canal; *CL*, lateral sensory canal; *FL*, lateral wing of frontal; *FP*, pre-epiotic fossa; *PT*, pterotic; *S*, sphenotic; *TF*, temporal foramen.

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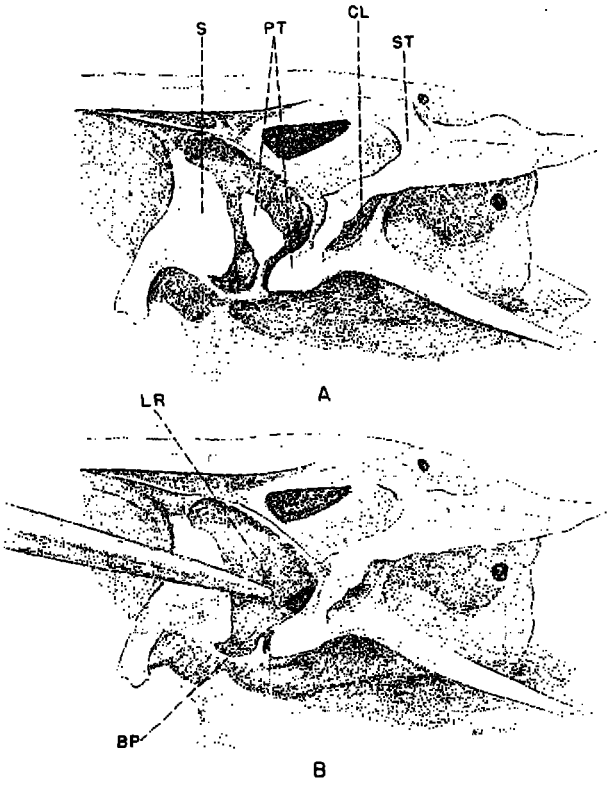

FIGURE 5.—Lateral view of cranium of *Engraulis mordax*. A. Lateral wing of the frontal removed. B. Pterotic extension removed. The dissecting needle points to the fenestra between the lateral recess and auditory recess. *BP*, prootic bulla; *CL*, lateral sensory canal; *LR*, lateral recess; *PT*, pterotic; *S*, sphenotic; *ST*, supratemporal.

ceives the second articular surface of the hyomandibular. This portion of the pterotic, furthermore, protrudes as a very small but distinct nob on the surface of the fish.

As already mentioned, the bones forming the outer wall of the lateral recess are much thicker in the sardine than in the anchovy. The lateral wing of the frontal, in the sardine, does not extend over the recess (fig. 4). It forms no more than the outer wall of the supraorbital tube, and the sphenotic and pterotic bones meet below it to form the lateral wall of the recess. A short distance below the junction of all three bones the foramen of the infraorbital canal intervenes between the sphenotic and pterotic. The other two foramina are located in the pterotic bone itself. The preopercular foramen is a small, circular opening a little distance behind the infraorbital foramen, and the accessory-temporal foramen is an even smaller opening dorsal and slightly posterior to the latter. There are several blind recesses of the pterotic in the vicinity of these prominent openings. This whole portion of the pterotic is thickened, and, consequently, the foramina are in the form of tubular passages through the bone.

The lateral canal passes from the recess through a long bony tube that emerges posteriorly from the surface of the pterotic. The terminus of this tube is expanded as a flat, triangular surface to accommodate a portion of the supratemporal bone.

Wohlfahrt described one dorsal and two lateral openings in the lateral recess of *Clupea pilchardus*. These, of course, are the infraorbital, preopercular, and accessory-temporal foramina, and are located exactly as in the sardine.

Owing to differences in cranial construction, the anchovy would probably be more amenable to surgical techniques than would the sardine. The lateral-sensory canals, opercular bones, and other structures in or beneath the integument are not visible externally in the living animal, but the projection of the pterotic on the outer body wall is a point of orientation. The thin bones and relatively large foramina should permit easier access to structures in the lateral recess and around the recessus utriculus. The only advantages offered by the sardine are the somewhat greater size of the fish and the easier accessibility of the pterotic bulla in the temporal groove.

THE GAS BLADDER

METHODS OF PREPARATION

The form and orientation of the gas bladder were determined by dissection of adult specimens. Eight such dissections were made of the anchovy, and 14 of the sardine. The smallest anchovy used was 145 mm. standard length, and the smallest sardine was 170 mm. standard length. All but one specimen of each had been preserved in formalin for periods ranging from several months to a few years. Although the one fresh example of each species facilitated distinction between the visceral organs, the thin-walled gas bladder retained its form much better during dissection in the preserved specimens.

Dissections were made in the following manner: The left wall of the body cavity was removed from the pectoral girdle to a point just short of the anus. The opercle and branchial arches on the left side

were also removed. The ribs and enough of the lateral muscle tissue were removed to expose the vertebral column. After excision of the left gonad, fat bodies, and the intestine, the stomach was moved down slightly to permit a better view of the gas bladder. Certain features of the bladder and stomach were then oriented in respect to the vertebral column, the dorsal and anal fins, and the anus. After this the gas bladder was removed and placed in a dish of 10-percent formalin for further examination and measurement. Bladders from preserved specimens were punctured in a few places so that liquid could enter the lumen and expand them fully.

Serial sections were made of some of the specimens, fixed in 10-percent formalin, to study the histology of the bladder wall. All preparations were dehydrated in normal butyl alcohol and embedded in 54° to 56° rubber paraffin *in toto*. The blocks were then cut into four or five portions, each of which was sectioned separately. Sections were cut at 10 or 12 microns, and attached to slides with Haupt's gelatin adhesive. A 0.5-percent aqueous solution of potassium dichromate was used to expand the sections on the slides.

All preparations were stained with a modification of Van Gieson's trichrome stain. Mayer's hemalum was used in place of Weigert's iron hematoxylin as a nuclear stain. Curtis' substitute (Leach 1946) was used in place of the acid fuchsin–picric acid counterstain employed by Van Gieson. It consists of 2-percent aqueous ponceau S, 5 cc.; saturated aqueous solution of picric acid, 95 cc.; 2-percent acetic acid, 2 cc.

Mayer's hemalum, although it does not resist destaining by the counterstain as well as Weigert's hematoxylin, was employed because it is relatively simple to apply and retains its strength for a much longer time. The advantages of Curtis' modified counterstain are that it stains reticular as well as collagen fibers and does not fade. As with Van Gieson's stain, Curtis' modification stains nuclei blue, muscle tissue yellow, and connective tissue red and various shades of brown. In practice it was found that the muscle tissue sometimes had a spotty overtone of orange, but this condition was almost entirely overcome by doubling the proportion of picric acid given by Leach.

The preparation represented in figures 12 and 13 differs from the others in that it was dissected from a freshly killed specimen and fixed in Zenker's fluid, then decalcified in a 2-percent solution of nitric acid in 70-percent ethyl alcohol.

ORIENTATION AND FORM

In figure 6, the gas bladder and part of the digestive tract of the sardine and the anchovy are outlined. The standard lengths of the two specimens are equilibrated so that differences are proportionate. The body cavity, and consequently the gas bladder, is relatively shorter in the anchovy. In the sardine, the pneumatic duct originates from the posterior end of the blindsac, or fundus of the stomach, the bladder has only one chamber and has a postanal opening to the exterior. In the anchovy, the pneumatic duct originates from the dorsal wall of the cardiac stomach, the bladder is composed of two chambers and lacks the postanal opening. Although these two species differ in the foregoing characters, the two combinations do not constitute alternative patterns within the clupeoids. De Beaufort (1909) has already shown that these anatomical features occur in various combinations.

The anterior capillary extension of the bladder also differs in the two species, but the bifurcated anterior portion of the single median tube in the anchovy is homologous with the pair of capillaries arising directly from the anterior end of the bladder in the sardine. The proximal end of the paired capillaries is located under the fourth vertebra in each species, and in each it embraces the ascending dorsal aorta. Thus, it is possible to compare the bladders proportionately by taking their lengths from bifurcation to posterior tip as 100 percent.

In figure 7, there are four drawings of bladders from the sardine and three of bladders from the anchovy. Numbers 1 and 5 depict the most typical form for each species; the others illustrate variations. Comparing the typical forms, the most striking difference is in the location of the greatest expansion; in the sardine it occurs in the anterior half of the bladder, in advance of the insertion of the pneumatic duct, while in the anchovy it occurs in the posterior half, behind the insertion of the pneumatic duct. The portion behind the duct in the sardine attenuates as it approaches the postanal opening. At the posterior end of the bladder

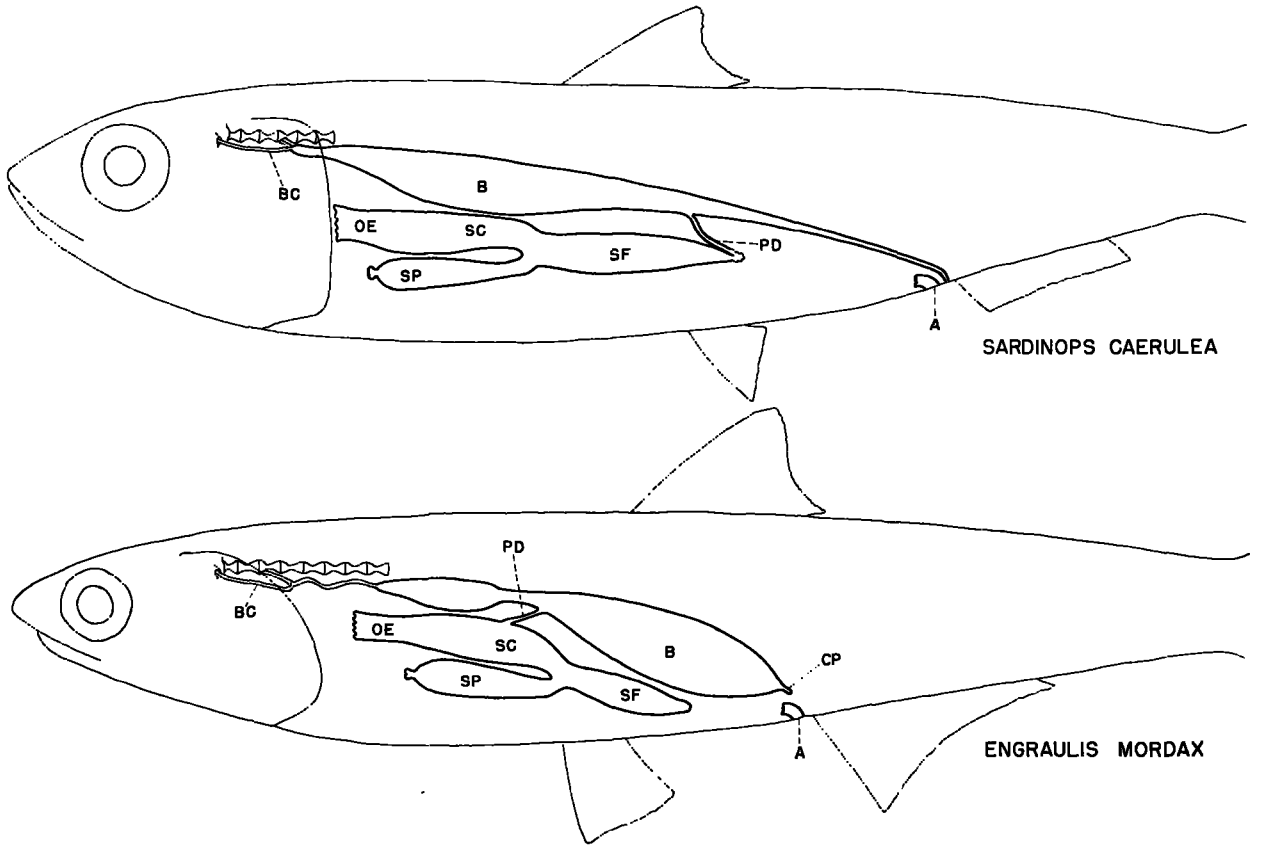

FIGURE 6.—Form and orientation of gas bladder and digestive tract in *Sardinops caerulea* (200 mm. standard length) and *Engraulis mordax* (145 mm. standard length). The standard lengths are equilibrated so that comparisons are proportionate. *A*, anus; *B*, gas bladder; *BC*, precoelomic capillary of gas bladder; *CP*, posterior caecum; *OE*, esophagus; *PD*, pneumatic duct; *SC*, cardiac stomach; *SF*, fundus of stomach; *SP*, pyloric stomach.

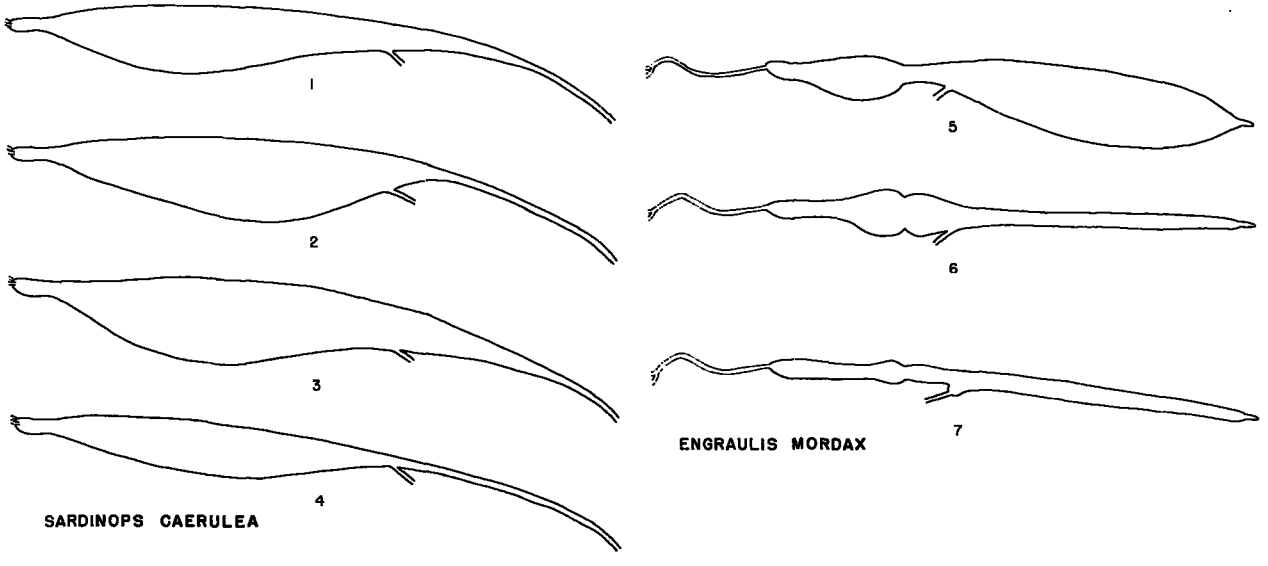

FIGURE 7.—Proportionate comparison of forms of the gas bladder in *Sardinops caerulea* and *Engraulis mordax*. Numbers 1 and 5 represent the typical form for each species, respectively; the others represent variations noted in dissection of preserved specimens.

in the anchovy, there is a short blind caecum. In the sardine, the only anterior differentiation is a very short, constricted portion of the bladder intervening between the expanded chamber and the bifurcation. In the anchovy, on the other hand, the portion anterior to the duct is composed of three distinct segments: a relatively short, constricted portion, an expanded but small anterior chamber, and a relatively long median-capillary tube that extends to the bifurcation. This median capillary, as well as the paired ones extending forward from it, is sheathed in cartilage, as are the paired capillaries in the sardine.

Variation in the shape of the bladder among the specimens examined was most marked in the anchovy, in which at times the large posterior chamber is contracted to tubular proportions, or the middle constricted segment is expanded to five or six times its usual diameter. No matter what the condition, the position of the transverse septum (see p. 519) is marked by a noticeable constriction, and the distance between the septum and the insertion of the pneumatic duct is proportionately the same.

Variation of form in the sardine is most noticeable in the expanded portion forward of the pneumatic duct, although I have not found it contracted to the degree that the posterior chamber may be in the anchovy. The portion behind the duct varies from a tapering, or triangular, form to a contracted, tubular one. When the anterior half is well expanded, the posterior half may be either tubular or tapering (numbers 2 and 3), but whenever the anterior half is contracted to any noticeable degree, the posterior half appears always to be tubular (number 4).

It is impossible to state here that these variations in the form of the bladder exemplify natural physiological conditions; however, they do illustrate the capacity of the bladder to expand and contract differentially. They are not attended by any evidence of rupture or folding.

THE PNEUMATIC DUCT

Some earlier workers have described the pneumatic duct of certain clupeoids as having a small lumen running tortuously through the tissue of the duct. Later investigators described a bulbous structure at the lower end of the duct in cases where the duct arises from the end of the blindsac of the stomach. Maier and Scheuring (1923), however, were the first to give a detailed description of this "bulb" in the herring, *Clupea harengus*. They described the duct as arising ventrally from the posterior end of the blindsac, the separation being effected by a horizontal partition arising from laterally opposed, longitudinal folds of the stomach mucosa. In the duct itself, they counted 15 to 17 overlapping septa. There is no similarly detailed description of the pneumatic duct in cases where it arises from other parts of the cardiac stomach, such as it does in the anchovy.

Sardinops caerulea

Throughout its length, the pneumatic duct of the sardine is approximately 0.6 mm. in diameter and the wall is between 35 and 60 microns thick in a 200-mm. specimen. When viewed in sagittal section, it can be seen that the lower end of the duct is divided into a series of pockets by incomplete transverse septa, radially arranged in conformity with the sharp curvature of the duct at this point (fig. 8). These septa are attached only to the lateral and lower, or posterior, walls of the tube, forming a series of blind pockets facing forward toward the stomach. The continuous passage between the successive pockets follows the lesser curvature of the bend closely, and is slightly irregular, so that the openings through the septa are not perfectly alined. This irregularity varies considerably among individuals, and probably changes with the activity of the duct. Where the duct begins to straighten, the openings through the septa gradually assume a more central position. In one specimen, 12 septa were counted in the lower half of the duct. There are no septa in the upper half of the duct, and the difference between the two parts is apparent to the naked eye in some of the formalin-preserved specimens.

The upper and lower halves of the pneumatic duct differ in histological detail as well as in gross morphology. The epithelium in the lower half of the duct is a simple layer of tall, columnar cells, which closely resemble but are not the same as those of the stomach. The cells in the stomach have fusiform basal nuclei, while those in the duct have round basal nuclei. The cytoplasm also stains differently. The epithelium of the duct is elevated into longitudinal folds which extend over the septa to give the inner surface of the duct a reticulate appearance. Although the epi-

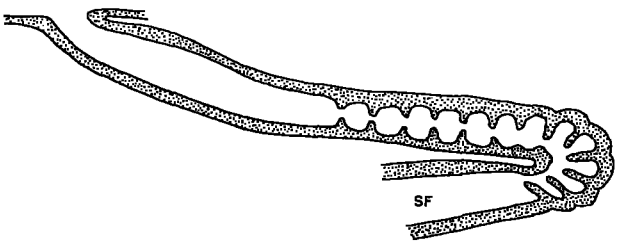

FIGURE 8.—Diagrammatic sketch of the pneumatic duct of *Sardinops caerulea*. *BL*, lumen of gas bladder; *SF*, fundus of stomach.

thelium and some of the folds are continuous between stomach and duct, the character of the cells changes abruptly at the first septal opening.

The submucosa in the stomach is a thick layer of dense connective tissue into which the gastric glands invaginate. It ends abruptly at the first septal opening, and apparently has no counterpart in the pneumatic duct. A thin layer of less-dense connective tissue, undoubtedly a part of the mucosa, is interposed between the epithelium and submucosa of the stomach, and is continuous with a similar layer in the pneumatic duct. The muscularis in both structures is composed of an inner layer of transverse smooth-muscle cells and a thinner, outer layer of longitudinal cells. Though the muscle coats of both structures have the same alinement, there is an oblique line of demarcation between them. The fibers are smaller in the duct than in the stomach, and stain a slightly different color. Furthermore, the outer, longitudinal layer is thinner in the duct.

From the arrangement of the tissue layers at the transition between the stomach and the duct, it may be tentatively concluded that the pneumatic duct is primarily an outgrowth of the mucosa of the digestive tract; and that the submucosa and muscularis of the stomach either end at the junction of the stomach and duct, or continue in the duct as incipient tissue layers, while the muscularis mucosa becomes prominent in the duct.

Although there are no transverse septa in the upper half of the pneumatic duct, a few of the longitudinal epithelial folds extend its entire length. The epithelial cells become cuboidal in the upper half of the duct, and the transverse muscle layer becomes much thinner, while the longitudinal layer is composed of more or less isolated loose bundles running longitudinally and obliquely in a thick layer of dense connective tissue. This connective tissue is continuous with that noted in the lower part of the duct. A section of this portion of the wall is shown in figure 10 at a magnification of × 680. Maier and Scheuring (1923) found a few very large, isolated fibers in the duct wall of *Clupea harengus*. Nothing fitting this description was found in the few specimens of the sardine examined, but it appears that the isolated longitudinal fibers were somewhat larger than the transverse fibers.

The lumen of the duct opens broadly into the bladder, and here the transverse muscle layer gradually becomes thickened. Aside from this, there is no specialized sphincter mechanism. Also at this point the longitudinal muscle fibers appear to invade the transverse muscle layer. The two types of fibers are intermingled in the adjacent region of the bladder wall, but, as described on page 519, one becomes dominant anteriorly and the other posteriorly.

Engraulis mordax

Externally, there is no evidence of a bulb in the pneumatic duct of the anchovy (fig. 9). Dissection and histological examination, however, show the duct to be septate over most of its length. For a short distance at each end, the epithelium forms high, longitudinal folds which traverse the septa, giving the inner surface of the duct a slightly reticulate appearance. The folds at each end of the duct occupy a considerable portion of the lumen. As it penetrates the dorsal wall of the stomach, the duct bends ventrally, and the septa are obliquely alined to the axis of the lumen. The openings through the septa are along the ventral wall, or lesser curvature, of the duct. Thus, although they arise from the opposite wall of the duct, the first few septa form blind pockets facing the stomach, as in the sardine. The diameter of the lumen is a little greater in the region of the bend

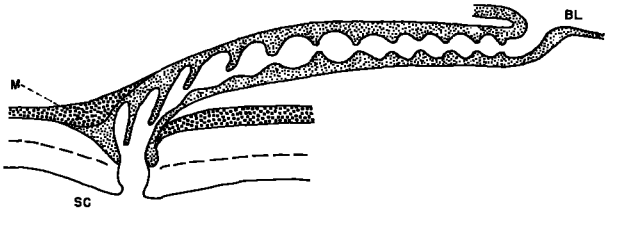

FIGURE 9.—Diagrammatic sketch of the pneumatic duct of *Engraulis mordax*. *BL*, lumen of gas bladder; *M*, striated muscle; *SC*, cardiac stomach.

than in the rest of the duct, where it is 0.8 mm., or slightly less, in a 145-mm. specimen.

The epithelial cells are cuboidal throughout the length of the duct. At the lower end, there is a sharp line of demarcation between epithelial cells of the stomach and of the duct, and at the upper end the cells change gradually to the squamous condition as the epithelium passes into the bladder.

The muscularis of the duct is composed of an inner layer of transverse smooth-muscle fibers and a very thin, outer layer of longitudinal fibers. At the lower end of the duct, adjacent to the region of longitudinal folds, the muscularis forms a slightly thickened ring. It was not possible to determine whether longitudinal as well as transverse fibers occurred here. This ring lies beneath the striated muscle coat and on a level with the submucosa of the stomach. The arrangement of the tissues at this junction again suggests, as in the sardine, that the pneumatic duct is primarily derived from the mucosa of the digestive tract. The transverse muscle layer of the duct wall projects into all the septa, and at the junction of the duct with the bladder it is considerably thickened.

Functions of the pneumatic duct

It is clear that the pneumatic ducts of the sardine and the anchovy are comparable in structure, and it is highly probable that the duct performs the same functions in both species. It may act as a valve or trap to permit gas but not food to pass towards the bladder. It may pump gas from the digestive tract to the bladder, or it may provide a passage for the escape of gas from the bladder. It could perform all three functions, which are not mutually exclusive.

Maier and Scheuring (1923) interpreted the structure of the "pneumatic bulb" in *Clupea harengus* as that of a valve which prohibits the entrance of food particles (and parasites) into the pneumatic duct. They hypothesized that the food mass, if compressed into the posterior part of the blindsac, would close the free edge of the first septum against the stomach wall opposite the septum; and that any particles passing the first septum would in the same way be stopped by succeeding septa. They did not consider the manner in which such particles would be eliminated from the duct once lodged there, remarking only that no portion of the duct is specialized as a sphincter.

Evans and Damant (1928) considered the pneumatic bulb of roach, tench, bream, carp, and minnows to be adapted to pumping air into the gas bladder. Jones and Marshall (1953) remarked that this is probably one of its functions in view of Plattner's work (1941). When Plattner cut the vagus branch running to the sphincter, air taken at the surface accumulated in the intestine and did not pass into the bladder. However, nothing in the ducts of the sardine and anchovy resembles the strong sphincter containing numerous striated muscle fibers described by Evans and Damant. On the other hand, certain authors have observed, in some of the clupeoids in which the duct arises from the end of the blindsac, that the duct has a "beady" appearance. A few also noted that this seemed to be variable. I have observed this condition in the lower half of the duct in the sardine, but not in the anchovy. These observations suggest that the duct carries on a sort of peristaltic action, at least in the sardine. Owing to the orientation of the lower septa in the sardine, muscular contraction of the wall would tend to expel foreign matter into the stomach, and a peristaltic action could possibly move gas away from the solid matter and pump it toward the bladder.

It is hardly necessary to comment on the function of the duct as a passage for the escape of gas. Expansion of gas in the bladder and relaxation of the muscularis of the duct would suffice to accomplish this.

THE GAS-BLADDER WALL

Fänge (1953) discussed at some length the differences in the terminologies that have been applied to the tissue layers of the gas bladder in fishes. He points out the need for a uniform and well-defined terminology, and suggests that the terms commonly used to designate the different tissue layers of the vertebrate digestive tube be applied to the gas bladder.

The four tissue coats of the digestive tract are mucosa, submucosa, muscularis externa, and serosa. The mucosa is further subdivided into epithelium, lamina propria, and muscularis mucosa. In applying this terminology to the gas bladder of euphysoclists, Fänge concluded that the muscle layer present can best be characterized as muscularis mucosa, and that there is, in place of the muscularis externa, a thick layer of connective

tissue. For the latter, he considered the term "tunica externa" more appropriate than "muscularis externa."

From his own observations on *Clupea harengus*, as well as those of Maier and Scheuring (1923), Fänge concluded that in clupeids the bladder is composed of an epithelium, an inner compact connective tissue layer, probably containing muscles, and an outer, voluminous connective-tissue layer. He further concluded that in physostomes, as in euphysoclists, the smooth muscles of the bladder wall may be characterized as muscularis mucosa.

Using Fänge's terminology, the tissue layers in the gas bladder of the sardine and anchovy were readily defined as epithelium, muscularis mucosa, tunica externa, and serosa. In both species, the epithelium is simple squamous, and, at certain points, elevated in longitudinal folds. The well-developed muscularis mucosa shows different specializations in the two species. Since both transverse and longitudinal elements are present, the terms "transverse smooth muscle" and "longitudinal smooth muscle" were applied to the accompanying illustrations. The tunica externa, a loose fibroelastic connective tissue, covers the whole bladder. It varies somewhat in thickness, but formalin fixation produced too much shrinkage and distortion to permit an accurate description. It can be stated, however, that no muscle fibers are present, and that the layer is but sparsely penetrated by blood vessels. The blood vessels supply a thin bed of capillaries, which vascularizes the mucosa, located between the muscularis mucosa and tunica externa. The serosa overlays the tunica externa, except on the dorsal side of the bladder. No submucosa could be distinguished in either species.

The detailed descriptions of the bladder wall that follow are based on sections made through various parts of the bladder in the sardine and anchovy. The tunica externa and serosa are not discussed.

Sardinops caerulea

In figure 10, drawings of four cross sections of the gas-bladder wall of the sardine are shown. All are enlarged × 680. The plane of each section is indicated on the drawing of the bladder. Sections D and E, through the pneumatic duct, are placed here for easier comparison with the bladder wall.

Sections A, B, and C are taken, respectively, through the anterior constricted portion, the region of greatest expansion, and the posterior tubular portion. Noticeable in all sections is the connective-tissue matrix in which the individual muscle cells are embedded. This tissue has the same composition as, and is continuous with, the lamina propria beneath the epithelium and the thickening between the muscle and vascular layers. Fänge, describing the bladder wall in euphysoclists, observed that there were sheets of connective tissue running through the muscle layer. He suggested, since these were probably continuous with the dense connective tissue on either side of the muscle layer, that the term "lamina propria" could be applied to all of the mucosa except the epithelium. The mucosa ranges in thickness from 15 or 20 microns in section B to 45 or 50 microns in section C.

In section A, the transverse muscularis is relatively thin, but the wall is considerably thickened by the connective tissue of the mucosa and by the vascular layer. The epithelium is raised in longitudinal folds about 20 or 30 microns high. The bladder lumen here, incidentally, is 160 or 170 microns in diameter. This is the only part of the bladder in which capillaries were definitely present in the thick connective tissue of the mucosa as well as in the vascular layer outside of it. Some of them are adjacent to and even appear to penetrate the muscular layer; however, none were detected in the connective tissue between the muscle coat and the epithelium.

The form of the epithelial cells of the longitudinal folds is difficult to ascertain. Some authors have described the cells as being low columnar in clupeoids they have examined. In my preparations, they varied in shape from squamous to columnar. Cells in the depressions between folds tended to be cuboidal, while those at the apex of the folds tended to be columnar. Along the sides of the folds they seemed to be squamous, but it is here that the greatest variation occurs, since these surfaces are complicated by some folding and branching. It is my impression that the cells are actually squamous over this whole region, as they are in the rest of the bladder; that they are compressed in the depressions and projected on end at the narrow peaks. This opinion applies to all regions exhibiting epithelial

folds in the gas bladders of the sardine and anchovy.

In section B, typifying the expanded portion of the bladder, the epithelium is a simple pavement of squamous cells, and the muscle coat is composed of transverse fibers.

A little anterior to the insertion of the pneumatic duct, occasional longitudinal muscle fibers appear within the transverse muscle layer. These increase in number posteriorly to become dominant a short distance behind the pneumatic duct (section C). There are, however, occasional groups of fibers having an oblique alinement. These merge gradually into the adjacent longitudinal cells, indicating perhaps that the fibers are "woven" to some extent. As the diameter of the bladder decreases towards its posterior end, the muscle cells become thinner, and the epithelium is again raised in longitudinal folds. Also, thin, tranverse muscle fibers appear among the longitudinal fibers.

Maier and Scheuring (1923) described the dense layer of tissue beneath the epithelium in *Clupea harengus* as a lamellar connective tissue composed of longitudinal fibers. They suspected the presence of muscle fibers, at least in the posterior part of the bladder, but could not make a conclusive statement, explaining that their specimens had been improperly fixed.

The terminal portion of the bladder, and its opening to the exterior, will be described in detail on page 523.

Engraulis mordax

The gas bladder of the anchovy differs from that of the sardine in having a well-developed transverse septum which divides it into a small anterior and a large posterior chamber, and in having, instead of an opening to the exterior, a very small caecum at its posterior tip.

Figure 11 is a series of sections of the bladder wall reproduced at different magnifications and in different planes. The tissue layers in the anchovy are basically the same as in the sardine. The most noticeable difference is that transverse muscle fibers predominate throughout. Also, the tunica externa is somewhat thicker and more dense around the middle, constricted portion of the bladder.

Section A, at a magnification of × 150, illustrates the cartilage-encased capillary that extends to the cranium. The outer diameter of the cartilaginous sheath is about 200 microns and the diameter of the capillary lumen is about 20 microns. It is probable that the capillary, composed of epithelium, a very thin muscularis, and a thin connective tissue layer, has contracted away from the inner wall of the cartilaginous tube, and that the lumen of the capillary, therefore, has a greater diameter in the living animal. Of course, section A is also typical of the more anterior, bifurcated portion of the capillary and its cartilaginous sheath. The only differences noted were slight variations in diameter. Except for a slight difference in size, the structure of the paired anterior capillaries is the same in the sardine though no description was given.

The anterior end of the bladder (not illustrated) has epithelial folds and a slightly thickened vascular layer, as in the sardine.

The mucosa of the bladder wall varies in thickness from 12 microns to about 50 or 60 microns. Both the anterior and posterior chambers are thin-walled with transverse muscle fibers and squamous epithelium. This is illustrated only for the posterior chamber (section D). In the constricted portion of the bladder, between the duct insertion and the septum, the mucosa is about five times as thick as elsewhere. This is illustrated in section C, a longitudinal section at the same magnification as section D. The increase in thickness is due in part to a marked thickening of the transverse muscle layer and in part to the addition of a layer of longitudinal muscle fibers between the transverse muscle layer and the tunica externa.

Section B is a longitudinal view of the septum at a magnification of × 45. The main component of the septum is a bundle of closely packed smooth-muscle fibers encircling its centrally located opening. In the preparation sketched, the septum is about 300 microns thick. Beneath the septal ring, there are muscle and connective-tissue fibers running in several directions, but it is clear that many of the muscle fibers of the longitudinal layer described above turn inward to the base of the septal ring itself. The dark sheets penetrating the ring vertically represent definite thickenings of connective tissue. Although no muscle fibers were detected within them, these dark sheets are in some instances clearly continuous with bundles of longitudinal muscle fibers, and are

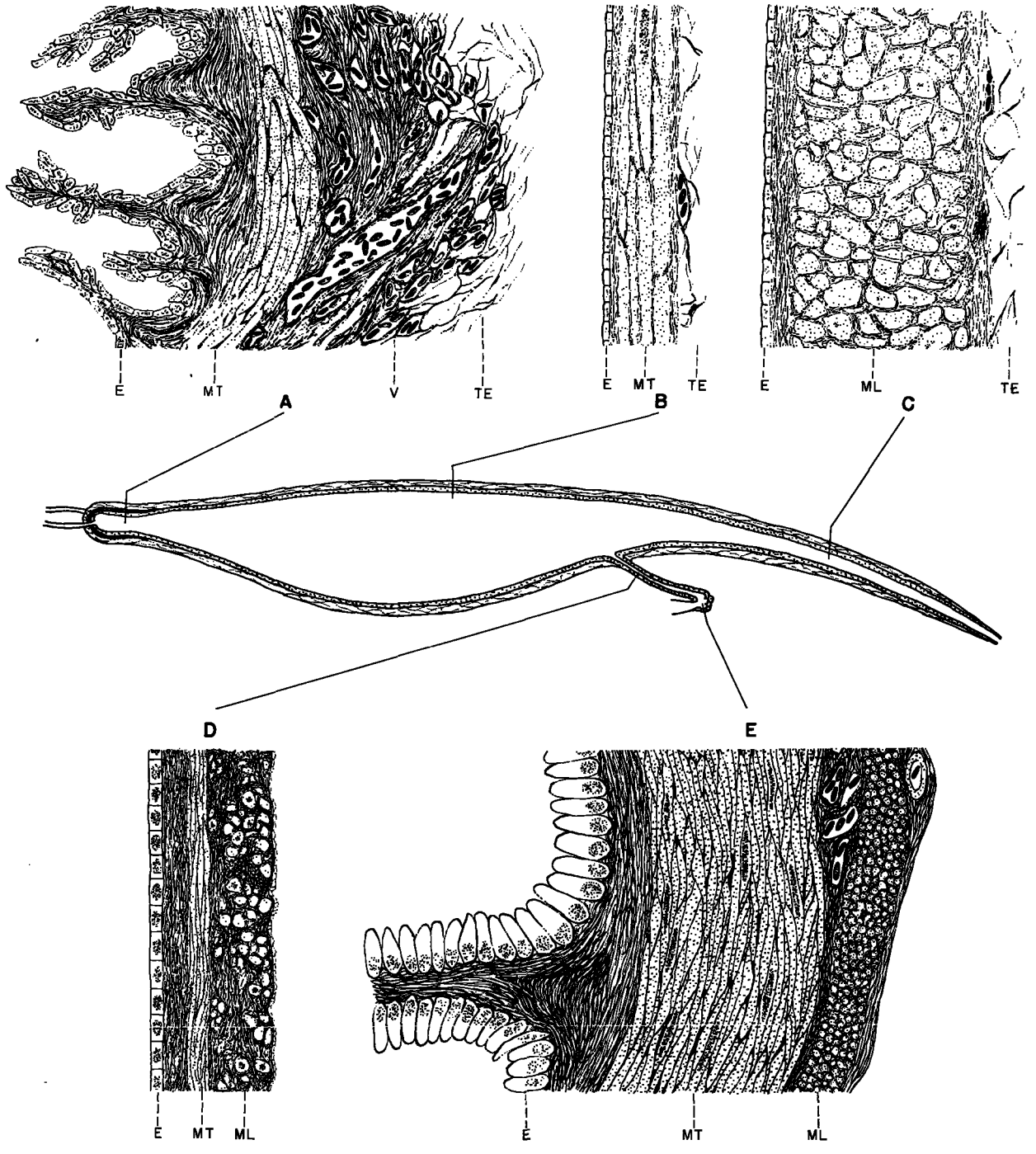

FIGURE 10.—Selected cross sections of the gas-bladder wall of *Sardinops caerulea* (195 mm. standard length). A. Anterior tubular portion. B. Expanded portion. C. Posterior tubular portion. D. Wall of the upper part of the pneumatic duct. E. Wall of the lower part of the pneumatic duct. Magnification × 680. *E*, epithelium; *ML*, longitudinal smooth muscle; *MT*, transverse smooth muscle; *TE*, tunica externa; *V*, vascularis.

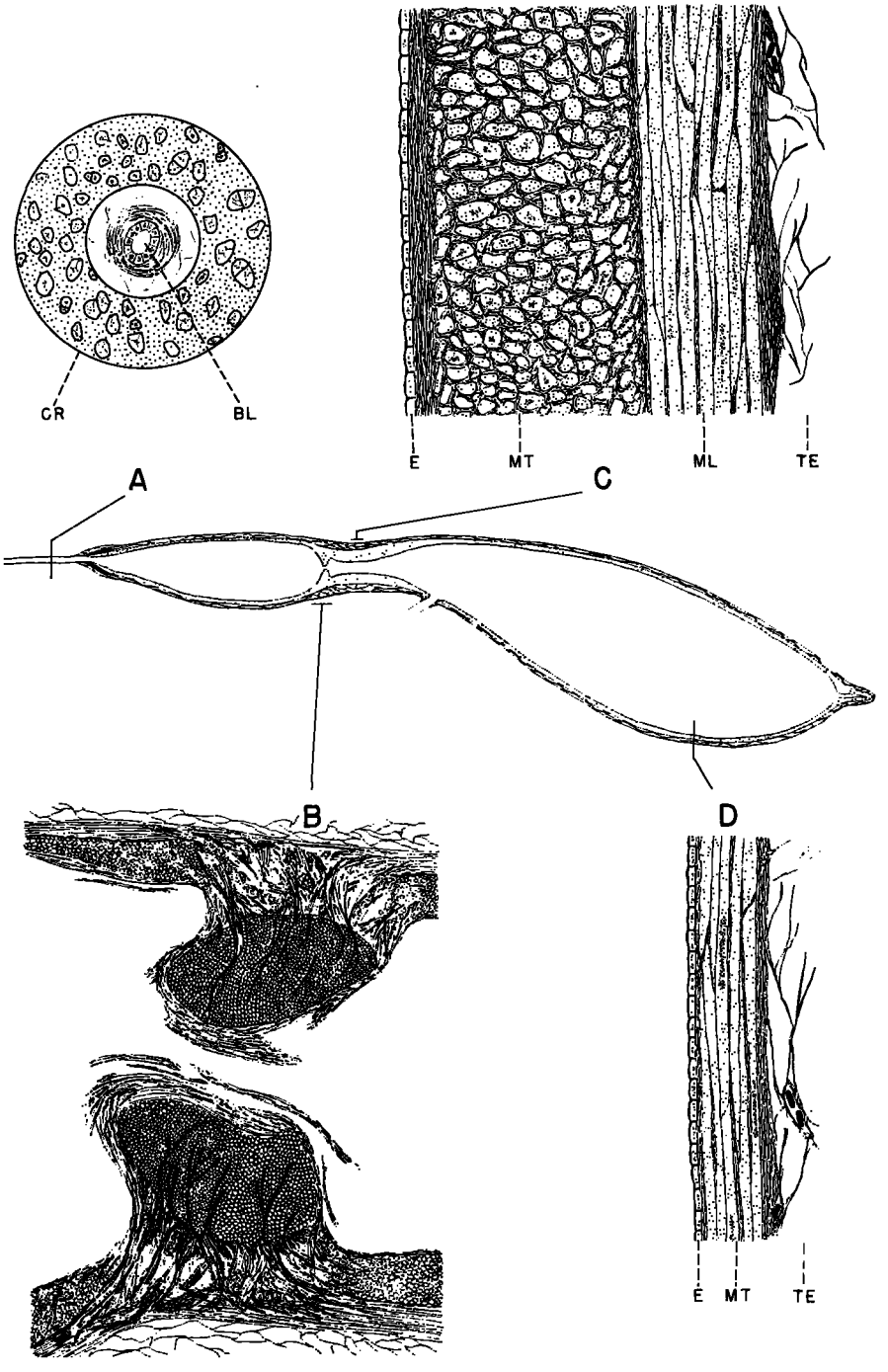

FIGURE 11.—Selected sections of gar-bladder wall of *Engraulis mordax* (145 mm. standard length). A. Cross section of the median capillary (× 150). B. Longitudinal section of septum (× 45). C. Longitudinal section from the middle, tubular portion (× 680). D. Cross section from the posterior chamber (× 680). *BL*, lumen of gas bladder; *CR*, cartilage; *E*, epithelium; *ML*, longitudinal smooth muscle; *MT*, transverse smooth muscle; *TE*, tunica externa.

probably tendons. The squamous epithelium is raised in longitudinal folds over both faces of the septum and along the thickened part of the bladder wall behind it. This accounts for the apparent irregularity in the thickness of the connective tissue over the inner surface of the muscle layer in section B.

Functions of the gas-bladder wall

In the sardine and the anchovy, the epithelium is primitive throughout, but the muscularis mucosa shows some degree of specialization. It is possible but not very probable that the epithelial folds in the bladders of these two species constitute gas-secreting organs. The epithelial folds differ in four essential ways from the well-developed gas glands to be found in physoclistous fishes, as follows:

1. The epithelial cells in the folded regions are squamous as in the rest of the bladder. In well-developed gas glands the epithelial cells are highly specialized, usually columnar, and larger than elsewhere in the bladder.

2. The epithelial folds are not complex. Although there may be irregularities in a given fold, there is no evidence of fusion between major folds. In well-developed gas glands there is usually greater complexity, ranging from scant fusion between folds of simple epithelium to fusion in stratified epithelium so complex that numerous glandular pits are formed.

3. There are no vascular specializations adjacent to the epithelial folds. The concentration of capillaries at the anterior end of the bladder in the sardine and the anchovy evidently represents a convergence of capillaries from extensive areas of the bladder wall to larger vessels of the venous system. The muscularis mucosa intervenes between the capillary layer and the epithelium. In physoclists, blood vessels extend directly to the glandular epithelium from the rete mirabile.

4. The folds are present only in constricted regions of the bladder, i. e., the most anterior portion in both species, the posterior, tapered portion in the sardine, and the middle, constricted portion in the anchovy. Among the physoclists, gas glands tend to occur in the anterior part of the bladder, but usually are not located in constricted regions.

Considering all four points, it seems quite possible that the folds in the sardine and anchovy represent nothing more than crowding of the epithelium in regions that are usually constricted, but capable of considerable expansion, as is the case in the teleostean digestive tract. Bridge (1904, pp. 262–263), in discussing the digestive tract of fishes, noted that "the simple longitudinal folds which are sometimes found in the oesophagus, stomach, and rectum, often disappear on distension, and probably merely provide for the enlargement of these cavities. . . ." Even in the absence of specialized glands, however, secretion by the epithelium at a very low rate is quite possible. Evans and Damant (1928) have demonstrated this in certain cyprinoids that do not have gas glands.

The muscularis mucosa is well developed in both species, but highly specialized only in the middle, constricted portion of the bladder in the anchovy. Fänge (1953) demonstrated that its function is primarily concerned with secretion and absorption of gas in the euphysoclist bladder. The opening of the oval sphincter is accompanied by the relaxation of the muscularis mucosa over the whole resorptive portion of the bladder, and its contraction over the whole secreting portion. Conversely, activation of the gas gland is accompanied by relaxation over the entire secreting portion and contraction over the entire resorptive portion. Evans and Damant (1928) and Franz (1937), on the other hand, have shown that the gas-bladder pressure in the Ostariophysi is slightly greater than atmospheric pressure. Jones and Marshall (1953) remarked that this pressure, which is supposed to keep the wall at a suitable tension for the functioning of the Weberian mechanism, is probably maintained by the tonic contraction of the bladder. Thus, the muscular coat of the bladder may perform different functions in different groups. There is nothing in the structure of the clupeoid bladder, however, that indicates the need for either of the above functions. Without further investigation, it can only be supposed that the tonus of the muscularis changes to maintain the wall at a constant tension against changes in volume.

The heavy development of the muscularis in the constricted portion of the bladder in the anchovy is indicative of some functional specialization. The ring of transverse muscles in the septum undoubtedly serves to close the central opening of that structure, and the longitudinal muscle fibers attached to it probably serve to expand the open-

ing. Along with this, the presence of both transverse and longitudinal muscle coats, particularly between the septum and pneumatic-duct orifice, suggests a peristaltic pumping mechanism capable of shifting gas from one chamber to the other.

THE POSTANAL OPENING IN *SARDINOPS CAERULEA*

Although the relative positions of the three openings behind the anus have been repeatedly noted for clupeoid species having a postanal opening of the gas bladder, there does not seem to be a detailed histological description of this region. Invariably the genital duct opens directly behind the anus, and the urinary duct directly behind the genital duct with the gas bladder opening to the left of the genital and urinary pores. Ridewood (1891) noted slight individual variation in the relative position of these openings in one species, but the bladder opening was always to the left of the others.

Tracy (1920 a), conjecturing on the functional relation between the gas bladder and its cranial vesicles, conditioned his hypothesis on whether the postanal opening of the bladder was controlled by a sphincter. Later Maier and Scheuring (1923), after examining this region histologically in *Clupea harengus*, concluded that the muscularis of the bladder wall near the opening could not function as a sphincter because it is composed almost entirely of longitudinal fibers. They attributed the function of closing the gas-bladder pore to a compact mass of striated muscle fibers, which they described as forming a ring around the whole anal field, i. e., enclosing all four openings. The sphincter, thus labeled in their drawing, corresponds in size and position to the protractor analii (or retractor ischii) of the sardine. According to Whittaker,[3] this is a pair of cylindrical muscles which arises from the pelvic girdle, extends along each side of the mid-ventral body line, and passes on either side of the anal opening to insertions on the first haemal spine. This pair of muscles, by virtue of its known function in protracting the anal fin and retracting the pelvic fins, could not serve efficiently to close the ducts opening in the anal region. Furthermore, it does not seem logical that these four openings, each serving a different organ system, would be controlled as a unit.

Figure 12 is a ventral view of the duct openings of a sardine 240 mm. standard length that was reconstructed from a serial section through this region. All four ducts terminate in a depression, or subcutaneous pit, located just anterior to the first haemal spine. The mouth of the pit is diamond shaped, 3 or 4 mm. long and 1.5 or 2 mm. wide. Anteriorly, the anus and the surrounding mucous membrane of the pit are flush with the body wall along the midventral line. Posteriorly, the pit deepens to the first haemal spine. Extending back from the rectal portion of the intestine is a median ridge that bears the genital and urinary openings. The former is a longitudinal slit, and the latter a small, round pore. This pore actually opens from the urinary bladder located within the ridge. The posterior margin of this ridge, or urogenital papilla, is formed by the recurved urinary duct descending into the primitive urinary bladder. The papilla, which protrudes almost to the level of the mouth of the pit, is a muscular structure serving as a sphincter for the genital and urinary openings.

The margin of the pit is lined with overlapping scales, which produce, along with the underlying mucous membrane, a narrow horizontal lip, or shelf. From this shelf, the walls on each side converge dorsally to their junction with the base of the urogenital papilla. The gas-bladder terminus appears as a small folded patch, or papilla, on the sloping left wall.

Figure 13 is a series of selected cross sections through the subcutaneous pit. The plane of each section, labeled by its number in the series, is indicated in figure 12. In each section, a small portion of the lip forming the margin of the pit is visible. The gas bladder, urinary duct, genital duct, and subcutaneous pit are labeled. The relative position of structures refers, of course, to their orientation in the fish.

Section 1, just behind the anus, shows the subcutaneous pit beginning to deepen, most of the space being occupied by the broad urogenital papilla. The genital duct is centered in the papilla. The urinary duct, running somewhat obliquely, is immediately above it, and the gas bladder is a discrete tubule to the left of the

[3] Whittaker, W. R., 1932. Anatomy of the North American pilchard and its bearing on the genetic relationships and nomenclature. Unpublished—submitted as M. A. thesis at University of British Columbia.

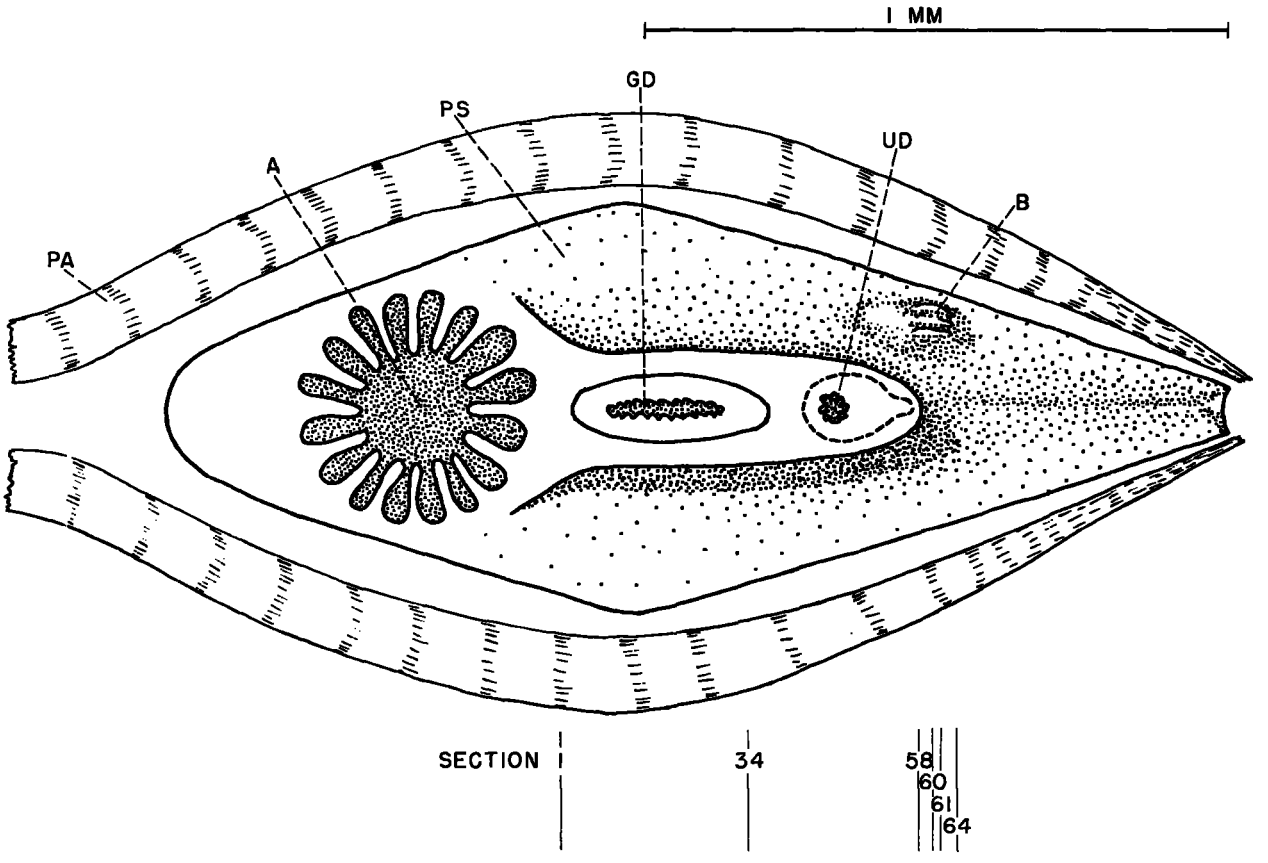

FIGURE 12.—Ventral view of postanal region of *Sardinops caerulea* (240 mm. standard length). The lines below the drawing mark the verticals of the sections shown in the next figure. *A*, anus; *B*, gas bladder; *GD*, genital duct; *PA*, protractor analii; *PS*, subcutaneous pit; *UD*, urinary duct.

urinary duct. The irregularity of the bladder lumen is apparent. The wall of the tube is composed of very small muscle fibers, mostly transverse. The darkly stained region just under the epithelium is dense connective tissue, constituting the lamina propria. Vascular elements were not present here. The epithelium is a simple layer of small cuboidal cells, quite different from the lining in other parts of the bladder. In fact, the epithelium changed abruptly less than a millimeter anterior to this section.

The urogenital papilla is actually a massive sphincter. It is composed of dense connective tissue permeated by numerous capillaries and small, striated muscle fibers running in various directions, and is covered externally by the mucous lining of the pit.

In section 34, the genital duct has already opened to the exterior, and the urogenital papilla now projects freely into the subcutaneous pit. The urinary duct is entering the muscular papilla, and the nerve from the right side of the papilla runs dorsad, eventually penetrating the region of the body muscles. The gas-bladder tubule is descending obliquely into the lining of the subcutaneous pit. The lamina propria is dwindling, and disappears suddenly a few sections later. At the same time the muscular wall ends, and the lumen of the tubule, bounded by the cuboidal epithelium, enters the mucous lining of the pit, becoming highly irregular.

In section 58, the gas-bladder lumen is visible as several small tubules in folds of a prominent papilla on the left wall of the subcutaneous pit. The nerve from the left side of the urogenital papilla passes dorsad close to the folds of the gas-bladder papilla. The terminal portion of the urogenital papilla projects freely into the pit.

Sections 60, 61, and 64, further illustrate the structure of the gas-bladder papilla. In this

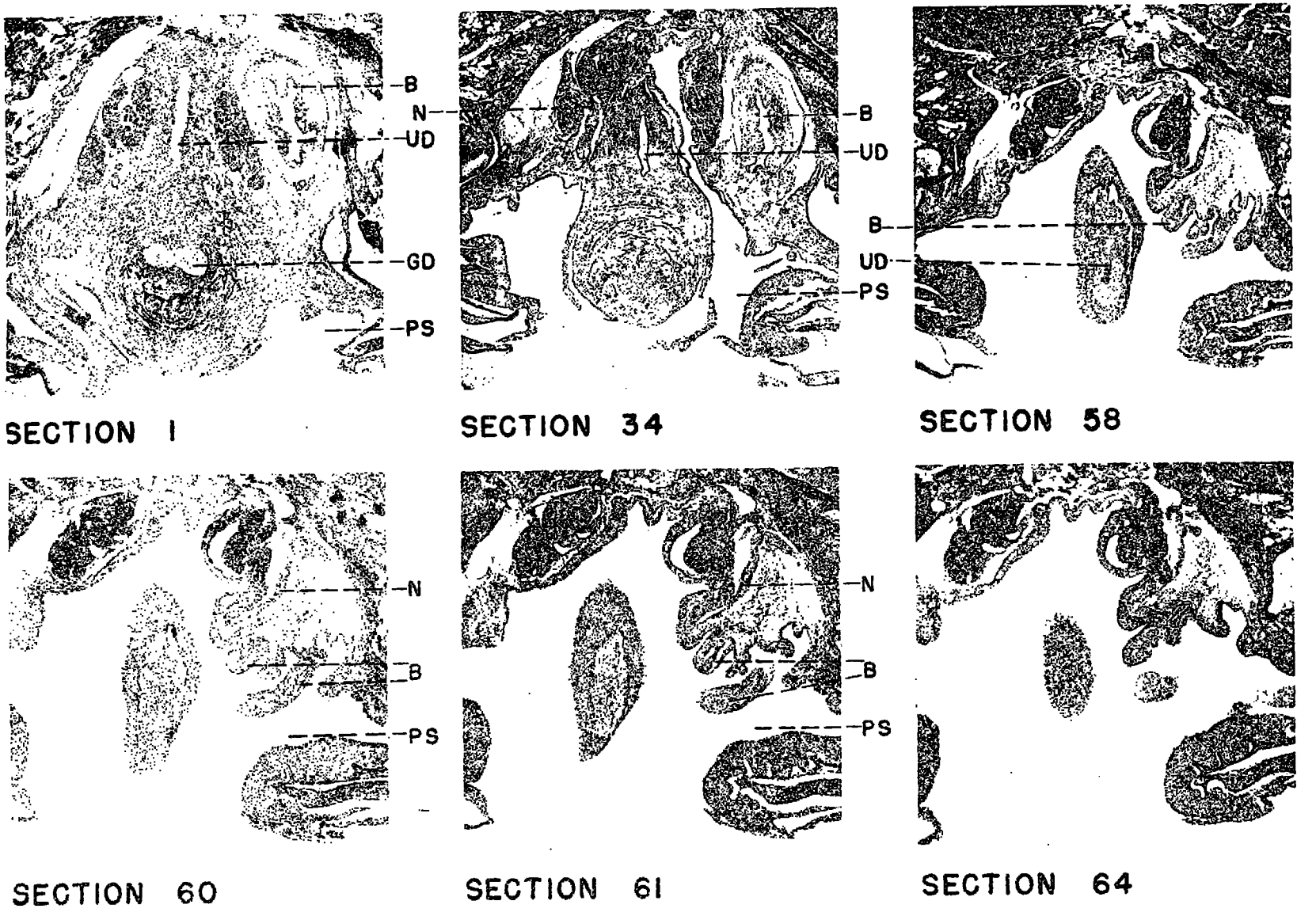

FIGURE 13.—Photographs of selected cross sections through the postanal region of *Sardinops caerulea* (240 mm. standard length). Each section is labeled by its number in the series, and the plane of section is indicated in figure 12. Magnification is × 40. *B*, gas bladder; *GD*, genital duct; *N*, nerve of urogenital sphincter; *PS*, subcutaneous pit; *UD*, urinary duct.

specimen, the papilla bears three short longitudinal folds, or lappets. The lateral and medial of these lappets contain a number of very small but distinct tubules lined by cuboidal epithelial cells. When traced, the spaces in each lappet were found to be discontinuous segments of one lumen. The lumen in the medial lappet, readily established as a continuation of the gas bladder, is a narrow and tortuous tubule. Three very small but definite, and apparently isolated, openings to the exterior were discerned. Continuity with the gas bladder could not similarly be established for the tortuous tubule in the lateral lappet; nor could openings to the exterior be detected. I surmise, however, that this tubule is also continuous with the gas bladder, the connection being fortuitously obscured by folding of the highly flexible papilla.

It is apparent from this series of sections that the intestine, genital and urinary ducts, and gas bladder tubule remain separate to their terminal openings. The genital and urinary openings are controlled by one massive sphincter, but no specialized sphincter occurs at the gas-bladder opening. As Maier and Scheuring remark, it is doubtful whether the scanty muscularis in the last few millimeters of the bladder wall constitutes an effective sphincter.

The structure of the gas-bladder papilla and its location in the mucous lining of the subcutaneous pit suggest that the papilla functions mechanically as a kind of check valve. Expansion of the gas in the bladder would distend the lappets and dilate the openings to the exterior, permitting gas to escape, whereas compression by the water outside would cause the papilla, its lappets, and included lumina to collapse upon themselves and effectively seal the openings to the exterior. A mechanism of this sort would be more sensitive and efficient and less complicated than a muscular sphincter in maintaining a relative pressure equality. When gas pressure exceeds water pressure, distension of the papilla permits gas to escape. When water pressure exceeds gas pressure, collapse of the papilla prevents water from entering the bladder. Of course, if the water pressure becomes too much greater than the gas pressure, it is possible that the papilla would rupture. Presumably, the fish possesses a reflex mechanism that would curtail movements causing too great a differential in this direction.

THE POSTERIOR CAECUM IN *ENGRAULIS MORDAX*

The posterior caecum of the bladder in the anchovy is about 2 mm. in length and 1 mm. in diameter, and its posterior tip turns slightly upward. The whole structure is covered by a relatively thick tunica externa. Figure 14 is a drawing of the caecum reconstructed from a series of cross sections, and figure 15 shows six selected sections from this series. The plane of each section, labeled by its number in the series, is indicated in figure 14. The last three photographs in figure 15 are at greater magnification than the first three.

Section 1 shows the mouth of the caecum at the upper end of the bladder. Shortly anterior to this, the muscularis of the bladder wall begins to thicken, and the epithelium begins to develop folds. The bladder lumen ends a few sections beyond.

Section 46 shows the typical form of the caecum. The tunica externa and muscularis are each about 150 microns thick. Although the muscularis is predominantly transverse, there are scattered longitudinal fibers. The lumen of the caecum, about 600 microns in diameter, is filled by very tall, branched epithelial folds. The latter appear in dissection as close-packed radial lamellae.

Posteriorly, the caecum and its lumen diminish in diameter until the lumen turns sharply upward and opens into a small, thin-walled chamber situated in the tunica externa (section 234). This chamber, which may be called the membranous chamber of the posterior caecum, is about 300 microns in both diameter and length, and is unequally bilobed. The caecal lumen opens into the larger segment, on the left in the fish. The two segments are about the same length and communicate by a small, transverse opening.

The size of the caecum makes a detailed study of the structure by dissection impossible. Microscopic examination of several specimens indicated that the membranous chamber has some range of expansion. In some, the chamber appeared to be 400 or 500 microns long.

Sections 237, 243, and 245 illustrate the detailed structure of the membranous chamber. The longitudinal folds of the caecum extend freely into the larger (left) segment to form a rosette occupying most of the available space. These folds, or lamellae, do not extend into the smaller (right)

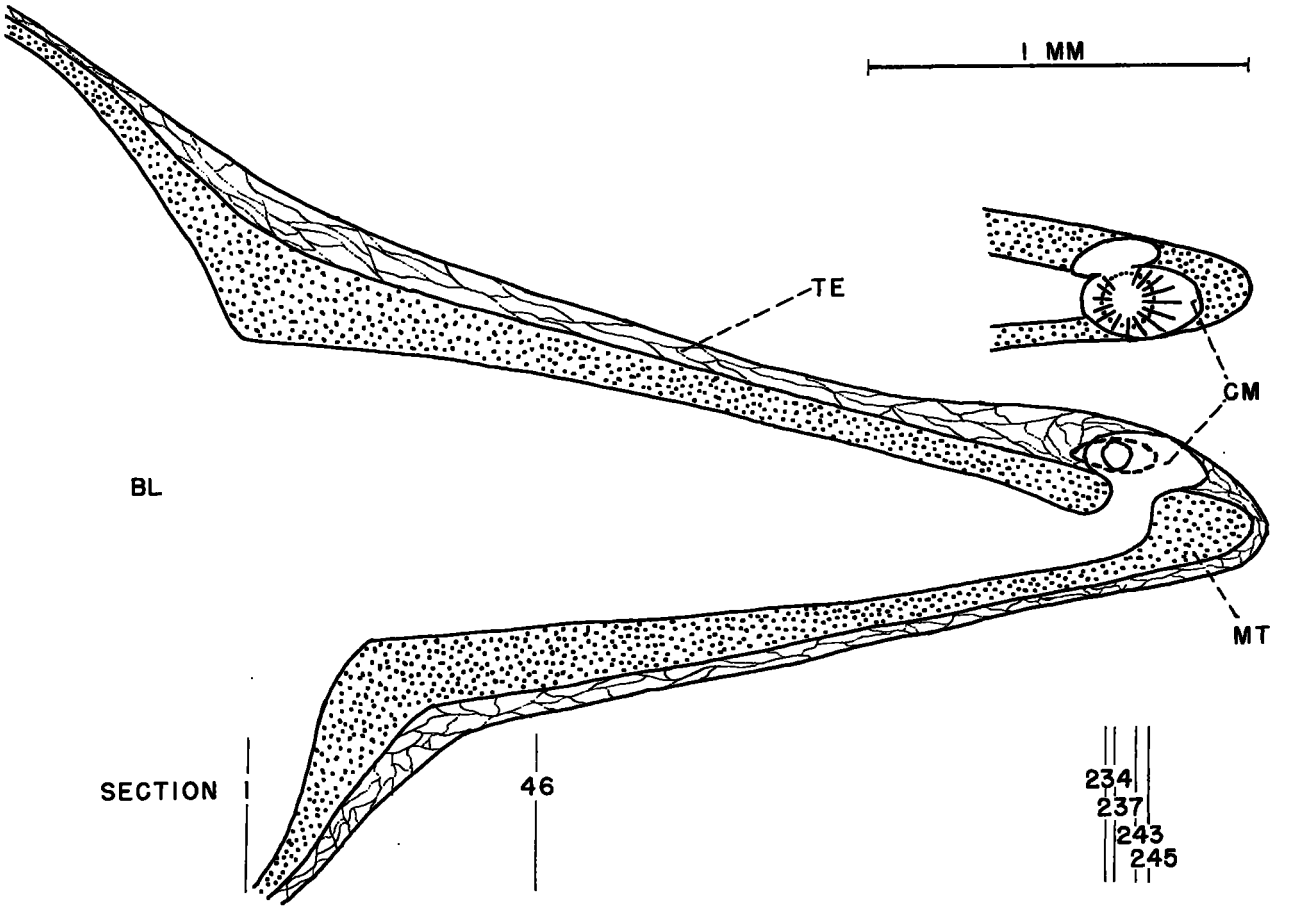

FIGURE 14.—Reconstruction of the posterior caecum of the gas bladder in *Engraulis mordax* (145 mm. standard length). The posterior tip is shown in dorsal as well as lateral view. The vertical lines below the drawing mark the verticals of the sections shown in figure 15. *BL*, lumen of gas bladder; *CM*, membranous chamber of posterior caecum; *MT*, transverse smooth muscle; *TE*, tunica externa.

segment, nor are they very prominent in the anterior part of the larger segment.

The wall of the chamber, about 6 microns thick, contains three tissue layers: epithelium, connective tissue of the mucosa, and fibrous connective tissue of the tunica externa. In other words, the muscularis is absent.

The epithelium in the caecum and in its membranous chamber is histologically the same as in other parts of the bladder; that is, the cells appear to be squamous, although they are distorted by the folding of the lining. The folds here, incidentally, are higher and more definite in form than are those described for other parts of the bladder. They are branched to some degree, but are not fused. Capillaries could not be found in the connective tissue of the folds; however, a heavy concentration of vascular elements passes through the tunica externa and enters the muscularis around the base of the membranous chamber. This is best shown in section 234. It does not constitute a capillary mass, or rete mirabile.

It is difficult to assess the function of the posterior caecum without further information. The extremely well-developed folds which extend from the caecum into the membranous chamber suggest, because of the increased surface thus developed, either a secretory or an absorptive function; however, the epithelial cells display no secretory specialization. Furthermore, there is no evidence of the vascular specializations that normally accompany well-developed secretory or absorptive structures. The absence of the muscularis, as well as the position of the organ on the dorsoposterior part of the bladder wall, are reminiscent of the oval present in many physoclistous fishes. The

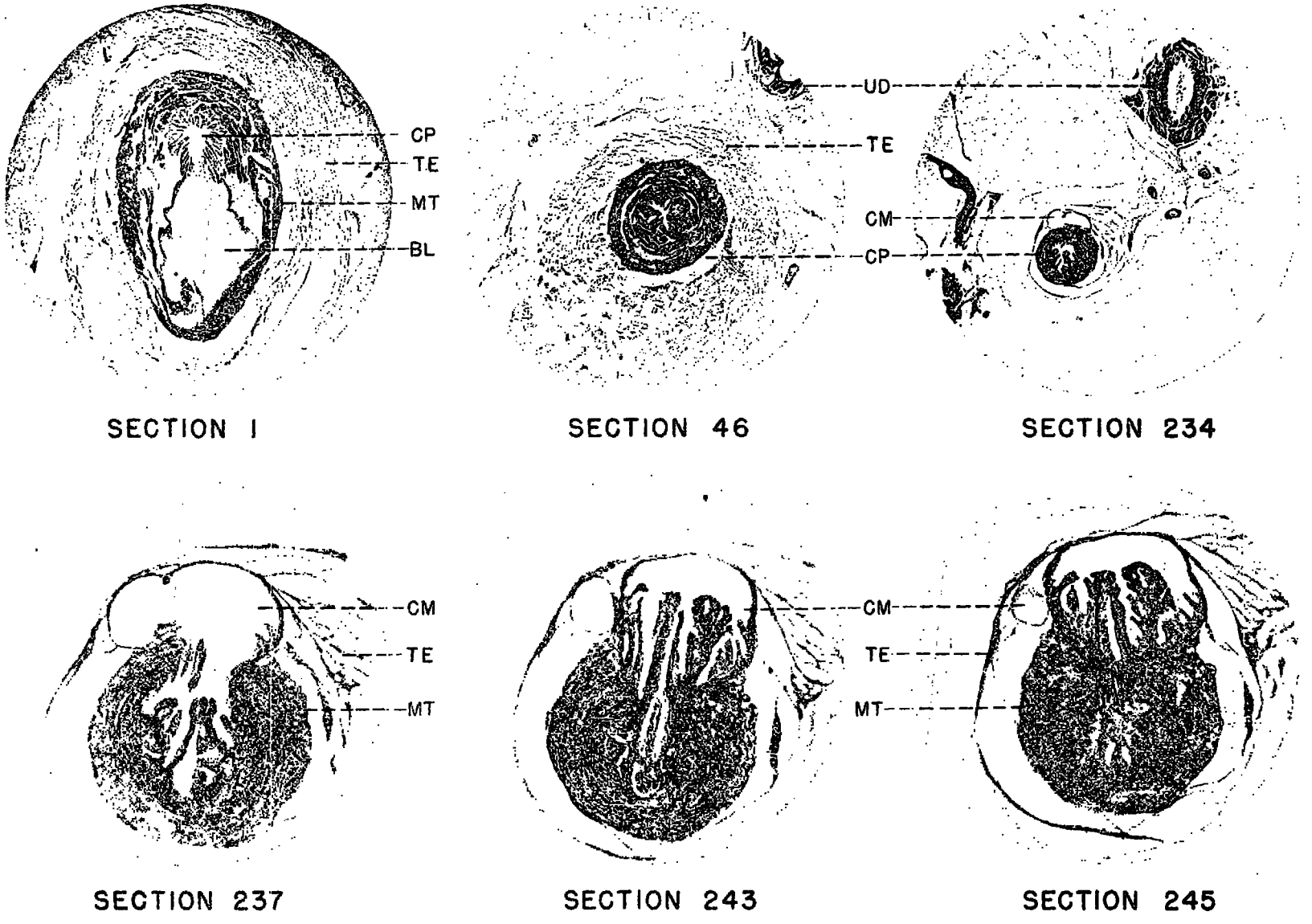

FIGURE 15.—Photographs of selected cross sections of posterior caecum of gas bladder in *Engraulis mordax* (145 mm. standard length). Each section is labeled by its number in the series, and the planes of section are marked in figure 14. Magnification is × 30, for sections 1, 46, and 234, and × 135 for sections 237, 243, and 245. *BL*, lumen of gas bladder; *CM*, membranous chamber of posterior caecum; *CP*, posterior caecum; *MT*, transverse smooth muscle; *TE*, tunica externa; *UD*, urinary duct.

muscular caecum in the anchovy could be analogous to the sphincter that opens and closes the oval. Should the structure actually be a diffusion membrane, it is a strikingly minute and atypical one.

A third possibility is that the caecum, or more specifically, its membranous chamber, functions as some sort of a sensory receptor in a reflex mechanism that controls volume changes in the bladder. However, no specialized sensory elements were found.

DISCUSSION

The relation between the gas bladder and the pars superior of the ear in clupeoids has provoked considerable conjecture. Among 19th and early 20th century investigators, the controversy was largely over structure, but now that the anatomical details are well defined, it has shifted entirely to function.

Association of the gas vesicles with the pars superior rather than the pars inferior of the ear caused some skepticism in assigning an auditory function to the mechanism. In all other groups of fishes, and for that matter in all other vertebrates, the pars inferior is the seat of auditory perception, while the pars superior is the seat of the sense of equilibrium. As Wohlfahrt (1936) pointed out, this difference is also reflected in the nerve tracts of the auditory nerve in all vertebrates. The axis cylinders of the ramus vestibularis (ramus anterior VIII) are always a little thicker than those of the ramus cochlearis (ramus posterior VIII). He found this to be the case in *Clupea pilchardus*, with the exception that the axis cylinders of the ramulus utriculus anterior have the same diameter as those of the ramus posterior VIII. For this and other anatomical reasons, he believed the macula utriculus anterior to be an auditory receptor.

Wohlfahrt, after considering at great length the functional theories developed by Evans (1932, 1935) and Tracy (1920 a), stated that the former investigator based his ideas on erroneous histological interpretations, while Tracy considered an auditory function unreasonable for both physical and biological reasons. Suffice it to say here that, in one paper, Evans designated the pars inferior as the seat of auditory perception, and considered the gas-bladder connection to the pars superior and the specializations of the recessus utriculus as part of a hydrostatic reflex mechanism to maintain an optimum tension within the membranous labyrinth (actually pressure exerted by the sacculus against the thin plate covering the auditory fenestra). Later Evans proposed the pars superior as the auditory receptor, but in both instances he described an improbable path of conduction for the transmission of sound waves. He also described the sensory elements of the recessus utriculus incorrectly. Tracy proposed a hydrostatic function for the mechanism, believing that bone and liquid in the cranium would be more efficient sound conductors than gas in the cranial vesicles.

Wohlfahrt assigned a double function to the pars superior. He presents convincing evidence of auditory reception in the macula utriculus anterior, but surmises that the lapillus still performs equilibrium functions. He considers the bony gas-filled bullae to be resonators that vibrate uniformly to sound waves, activating the prootic membrane.

This hypothesis can, perhaps, be carried one step further. Quite possibly the gas-filled bony chamber has a natural period of vibration and responds to a given acoustic frequency or range of acoustic frequencies in the environment. In this case, the pars superior would perform only an accessory auditory function, with the pars inferior functioning as in most other fishes.

The mechanism unquestionably perceives the same kind of stimuli in all clupeoid species, since in all so far investigated the lapillus, maculae utriculi, prootic fenestra, and prootic membrane have the same structural relation. The bony bullae that contain the gas vesicles, however, differ in size and shape in the sardine, anchovy, and other species. It is possible that such differences indicate specifically different ranges or degrees of perception, but this can only be determined by laboratory experiments. The presence or absence of pterotic bullae, for example, would not alter perception in kind, but might well alter it in degree.

What role this sensory mechanism has in the behavior of the fish is unknown. As an accessory auditory receptor it would probably increase the frequency range, and perhaps the sensitivity of hearing. The Ostariophysi and Mormyridae, which have other types of ear-gas bladder connections, perceive higher frequencies than fishes that

lack such connections (Griffin 1950). If the differences in the size and shape of the bullae produce different ranges and degrees of perception, some species are better equipped than others. On the other hand, it is possible that the mechanism plays some role in recognition among individuals of a species.

Very little is known of the functions of the gas bladder in clupeoids. Since it is present, the bladder must, of course, function as a hydrostatic organ; however, to what extent it serves to put the fish in hydrostatic equilibrium with its environment is not known. Magnan (1929) measured the density of *Clupea harengus*, but Jones and Marshall (1953) considered his figure surprisingly high for a pelagic fish with a well-developed gas bladder. From Magnan's data they calculated a sinking factor in the range of demersal fishes, and suggested that the determinations need repeating. They further noted that the herring (quoting Reay et al. 1943; Stansby and Lemon, 1941) shows considerable seasonal variation in fat content, and that more must be known about the tissue density of this fish before correlations between the size of the gas bladder and the fat present in the tissues are attempted. Since the density of fat is less than that of sea water, large accumulations of fat at certain seasons would reduce the bladder volume required to put the fish in hydrostatic equilibrium. Of course, concurrent changes in other organs, such as the gonads, may present a further complication.

The presence of well-defined layers of smooth muscle in the gas bladders of the sardine and anchovy and the different states of contraction noted in preserved specimens are indicative of an ability to alter the form and volume of the organ. Such differences, if necessitated by density changes in various tissues, could be sustained by changes in the muscle tonus of the bladder wall.

If buoyancy is maintained at a constant level during vertical movements, the gas-bladder volume must be kept constant. This can only be accomplished by adding gas during descent and discharging it during ascent. No matter what role the bladder plays in the behavior of the fish, its volume must be maintained within some limits to avoid extreme distortion and consequent loss of control by the fish of its vertical movements. It has been shown for some other species (Jones 1952), that there is, undoubtedly, a vertical range within which the fish can move comfortably without changing the gas content of the bladder. Beyond this range, the rate of vertical movement would be determined by the rate at which gas could be added or expelled.

In the sardine and anchovy, the only possible sources of gas are the pneumatic duct and the epithelium. Air swallowed at the surface could be transmitted to the bladder through the duct, but, as Jones and Marshall point out, glands are the only possible source of gas when the fish is at a distance from the surface. In these two species, the construction of the pneumatic duct would facilitate the movement of gas toward the bladder while excluding solids, and the epithelium, lacking gas glands, may be capable of secreting gas, but at a very low rate. This combination poses certain questions in regard to the behavior of the sardine and anchovy. For example, rapid addition of gas would be most useful during or immediately following descents to appreciable depths. Possibly these fish possess an unknown secreting mechanism, entirely different from that typical of physoclists. Alternatively, they do not descend to appreciable depths, or they do not have to maintain constant buoyancy in the process.

Whatever the hydrostatic functions of the bladder, relative pressure changes due to vertical movements would distort the prootic membrane. This membrane, if its primary function is oscillation, would require equal pressure on both sides for optimal performance. On this assumption, Evans' description of the precoelomic capillary extension of the bladder as a sort of Eustachian tube is reasonable. Hydrostatic-pressure changes transmitted through the lateral-sensory canal system and perilymphatic space would be balanced across the prootic membrane by gas-pressure changes transmitted through the precoelomic capillaries from the gas bladder. Of course, the length and, more particularly, the diameter of the gas-bladder capillaries would influence the rate at which equilibrium would be reestablished after a vertical movement.

In the sardine, there are no specializations for maintaining constant volume in the bladder during descents, but it is nevertheless possible that a constant relative pressure can be maintained. Air could not be added through the pneumatic duct

to maintain both volume and pressure against increasing external pressure unless the fish had gulped an excess of it at the surface before starting to descend, and such a behavior pattern is unlikely. If, however, the relative pressure is maintained at the expense of volume by contraction of the bladder wall, the fish would become heavier. This would maintain the prootic membrane in equilibrium, and the depths to which the fish could descend would be limited by the degree of negative buoyancy it could sustain dynamically.

During rapid ascents, where the situation is reversed, relative pressure could be kept reasonably constant by relaxation of the bladder muscularis and the escape of gas through the postanal opening of the bladder. The pneumatic duct also affords a passage for the escape of gas, but because of its muscular structure, and the fact that it opens into the digestive tract, this tube could not be as sensitive to relative pressure changes as is the postanal duct.

The presence of the septum, and what is perhaps a pumping mechanism in the gas bladder of the anchovy, suggests that this species, which also presumably maintains a pressure equilibrium across the prootic membrane, has a somewhat different pattern of behavior than does the sardine. If, for example, gas is pumped from the posterior to the anterior chamber of the bladder during descent, the vertical range over which the fish could maintain the prootic membrane in equilibrium would be extended. Conversely, pumping gas out of the anterior chamber during rapid ascent would facilitate the reduction of pressure at the prootic membrane. A considerable pressure could probably be tolerated in the posterior chamber until sufficient gas escapes through the pneumatic duct.

Experimental investigation of the functions of the gas bladder, its cranial vesicles, and the ear will yield considerable information on the behavior of clupeoid fishes. Either the sardine or the anchovy would suffice for determination of the kind of function performed by the ear–gas bladder mechanism, but it would be yet more informative to determine whether the two species show differences of degree. Because of structural differences in the bladders of the two species, the hydrostatic functions and the functional relation between the bladder and cranial gas vesicles should be investigated in both species.

SUMMARY

As one approach to understanding availability of the Pacific sardine, *Sardinops caerulea*, and the northern anchovy, *Engraulis mordax*, behavior studies of these species are planned. Since it is essential to know the anatomy of the animals before embarking on such work, the anatomy of both species is now being investigated. In this paper, the gas bladder and its relation to the inner ear are described.

1. The basic relation between the cranial extensions of the gas bladder and the inner ear is the same in the Pacific sardine and the northern anchovy as in other clupeoids that have been investigated.

2. The form of the gas bladder differs in the sardine and anchovy. In the sardine, the pneumatic duct arises from the posterior end of the stomach blindsac, the bladder is single-chambered and has a postanal opening to the exterior. In the anchovy, the pneumatic duct arises from the cardiac stomach, the bladder is two-chambered and does not have a postanal opening to the exterior.

3. In the sardine, the upper and lower halves of the pneumatic duct differ in structure. The muscularis and the arrangement of septa in the lower half constitute a valve. The muscularis is thinner and septa are lacking in the upper half of the duct. In the anchovy, the duct is shorter and uniform in structure. The muscularis and arrangement of septa constitute a valve, as in the sardine.

4. The pneumatic duct in both species probably permits gas but not solids to pass from the stomach to the gas bladder. It would also permit the passage of gas from the gas bladder to the stomach.

5. The wall of the gas bladder in the sardine is composed of mucosa and tunica externa. The mucosa consists of simple squamous epithelium and muscularis mucosa. The muscularis mucosa is well developed; its fibers are transversely alined anterior to the insertion of the pneumatic duct and longitudinally alined posterior to the insertion. The tunica externa is a layer of loose fibroelastic connective tissue that varies in thickness.

6. The wall of the gas bladder in the anchovy is composed of mucosa and tunica externa. The mucosa consists of simple squamous epithelium

and muscularis mucosa. The muscularis mucosa is transverse in both the anterior and posterior chambers. Between the two chambers there is a thick, transverse septum followed by a thick-walled, constricted region. There is a well-developed, longitudinal muscle layer surrounding the thick, transverse muscle layer in this region.

7. The muscularis of the bladder wall in these two species probably maintains the form of the bladder during changes in volume at constant relative pressure. The septum and middle, constricted portion in the anchovy strongly suggests a peristaltic pumping mechanism capable of moving gas from one chamber to the other.

8. The genital and urinary openings are controlled by a massive sphincter, but the postanal opening of the gas bladder in the sardine is not controlled by a sphincter mechanism.

9. The posterior caecum of the gas bladder of the anchovy consists of a muscular tube which terminates in a very small, membranous chamber that is filled by epithelial lamellae. Its function cannot be ascertained without further study.

10. The function of the ear–gas bladder mechanism is discussed for both species. The hydrostatic functions of the gas bladder and the functional relation between the gas bladder proper and the ear-gas bladder mechanism are considered for each species.

11. Because of differences in cranial construction, the anchovy would probably be more amenable to surgery involving the inner ear-gas bladder mechanism than would the sardine.

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METHOD OF EVALUATING TEMPERATURE IN LAKES WITH DESCRIPTION OF THERMAL CHARACTERISTICS OF CONVICT LAKE, CALIFORNIA

BY NORMAN REIMERS AND BOBBY D. COMBS

FISHERY BULLETIN 105

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

Two years of temperature observations at Convict Lake, a 168-acre alpine lake in eastern California, are used as the basis for a description of thermal characteristics including annual temperature cycle, distribution of temperature, and thermal stratification in relation to morphometry and weather. The heat-budget method of assessing heat in lakes has inherent limitations on lake size, depth, and geographical location that restrict its usefulness to general comparisons among large bodies of water. The method of measuring sustained heat intensity (temperature summation) presented here is free of these limitations. Data developed from temperatures of Convict Lake and other lakes of the same drainage basin support the conclusion that such a method can be serviceable for comparing lakes of various sizes and situations over selected periods of time, or for evaluating temperature in relation to other measures of lake productivity. A summation procedure is suggested in which the base temperature is 32° F. and the summation units are day-degrees in excess of the base.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
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METHOD OF EVALUATING TEMPERATURE IN LAKES WITH DESCRIPTION OF THERMAL CHARACTERISTICS OF CONVICT LAKE, CALIFORNIA

By NORMAN REIMERS and BOBBY D. COMBS, *Fishery Research Biologists*

One phase of productivity studies on the alpine lakes of Convict Creek Basin, Mono County, Calif., concerns the relation between aquatic productivity and available heat. The investigation of this relationship requires temperature data in a form that will permit thermal comparisons among lakes of various sizes and depths over selected periods of time, and that is also adaptable to problems of association between temperature and measurable production. A method of thermal comparison for alpine lakes should permit annual comparisons among lakes that can be observed the year round and short-term comparisons among lakes whose seasonal accessibility is limited.

This report presents an analysis of 2 years of temperature observations on Convict Lake, the lowermost lake in the Convict Creek Basin and the only one accessible throughout the year. Its purposes are to initiate a record of temperature cycles in alpine Sierra Nevada lakes of moderate size and to introduce a method of temperature summation that fulfills the above requirements and that may be useful for thermal comparisons involving other lakes of various sizes and locations.

The work was conducted from the United States Fish and Wildlife Service Convict Creek Station, located 2½ miles downstream and 5 miles by road from the lake. During the open season, transportation was by light truck and small boat. In winter, the lake was reached by ski or snowshoes, and temperatures were measured through the ice. The period of regular observations extended from May 1951 to May 1953, with a weekly schedule maintained when possible. Weather and ice conditions during the first winter resulted in a 2-month gap in the data, and the interval between observations was lengthened several other times because of storms. In all, 85 vertical temperature series were recorded during the study.

THE LAKE AND ITS WATER SUPPLY

Convict Lake is slightly less than a mile long, is 2,053 feet wide (maximum), and has a surface area of 168 acres and a volume of 14,810 acre-feet. More than half the surface area falls within the 100-foot contour, and a large central section approaches the maximum depth of 137 feet. Additional morphometric data are tabulated on the hydrographic map (fig. 1). In general, slope and bottom conditions are similar to those of many other glacial lakes of comparable size in the eastern Sierra Nevada. Prominent physical features of such lakes are low shore development, simple basins, abrupt shores, and a small percentage of shoal area. Convict Lake is situated at the foot of a steep, rocky canyon and is flanked by bedrock ridges and extensive glacial moraines. Although it appears to be sheltered on nearly all sides by steep slopes, the lake is fully exposed to frequent strong winds which funnel down the canyon from above. Its elevation (7,583 feet) subtracted from that of the nearest tributary lake (Mildred: 9,900 feet) gives a fall in the drainage of 2,317 feet in a little less than 3 miles (U. S. Geological Survey, datum 1934; Mount Morrison Quadrangle). Additional geographical and geological details may be obtained from the general report on the lakes of the basin (Reimers, Maciolek, and Pister, 1955).

The water supply consists almost entirely of melted snow from higher parts of the drainage. Convict Creek, the only tributary stream, enters the lake at its south end and continues from the north end to join an impoundment of the Owens River. Mean monthly discharges from Convict Lake varied from 8.3 to 50 cubic feet per second in 1951, and from 10.7 to 97.9 cubic feet per second in 1952. Records are from a gaging station located 1 mile below the lake and maintained by the

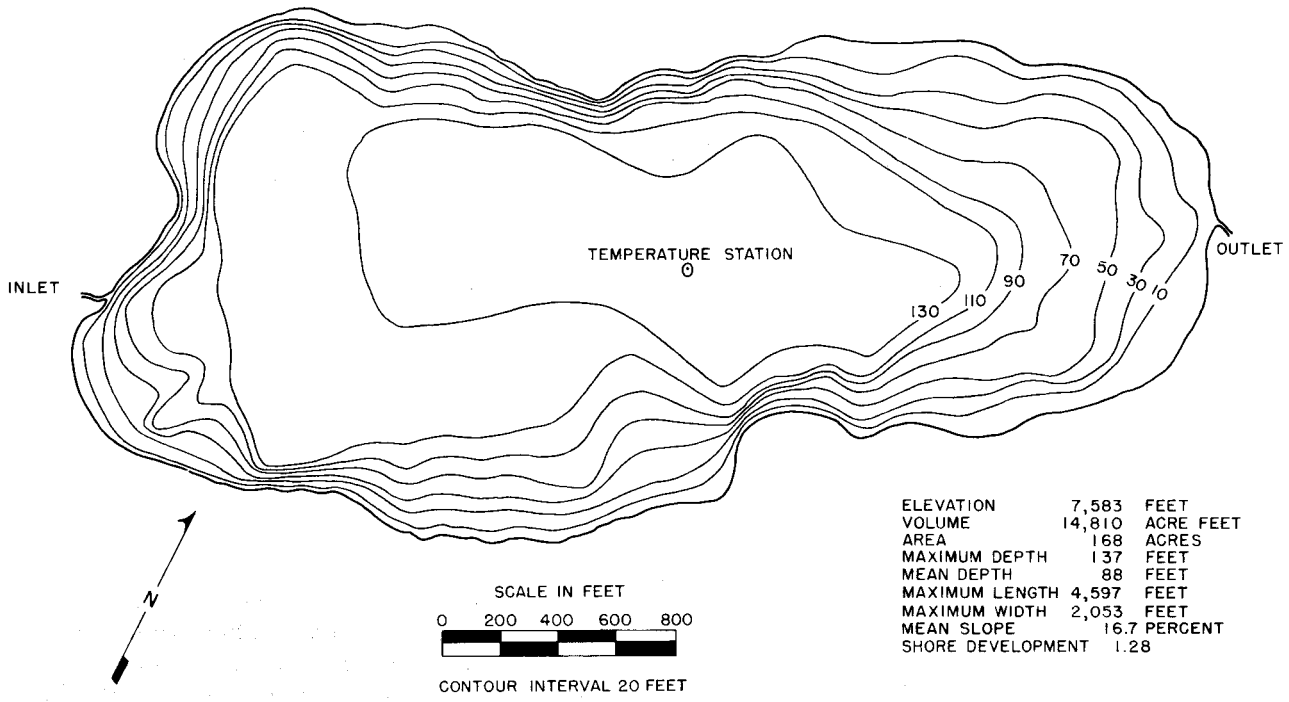

FIGURE 1.—Hydrographic map of Convict Lake, Calif.

City of Los Angeles Department of Water and Power. Seepage and springs account for a small fraction of the water entering the lake. Computations based on discharge records for several years indicate that average flows would produce a volume of water sufficient for a complete exchange of the lake water once in each 9 months.

NATURE OF THE OBSERVATIONS

Observations were made at a single station over the deepest part of the lake that coincided approximately with the center of oscillation. Because of the single, extended depression and slight shore development (fig. 1), vertical temperature series taken at this point were sufficient to characterize the lake without additional shallow-water observations. Water temperatures were measured at 10-foot intervals beginning at the surface, and air temperatures were taken in the shade 2 feet above the surface. A Foxboro resistance thermometer with 0.5° F. graduations was used for all temperature observations at the lake. A continuous air-temperature record was maintained at Convict Creek Station with a Taylor recording thermometer of 0.5° accuracy. These temperatures, which on a yearly basis were found to agree closely with those recorded at the lake, have been used to some extent in judging the effects of winter weather on heating of the lake.

CLIMATE AND THE GENERAL TEMPERATURE CYCLE

The eastern slope of the Sierras in the vicinity of Convict Lake is a moisture-deficient, sagebrush-covered upland where most of the precipitation occurs as snow during the winter. Daily air-temperature maxima usually range from 60° to 85° F. in summer, but occasionally reach 90°. Humidity is low in spring, summer, and fall because of the moisture-removing effect of the high mountains on easterly moving air masses. The primary influence on winter conditions in the area is the nature of a succession of Pacific storms, and winters vary accordingly in length and severity. The winter of 1950–51, preceding the first year of the Convict Lake observations, was relatively

mild as noted by Maciolek and Needham (1952). Prolonged periods of cold weather did not occur, and ice cover on the lake was intermittent and light. The 2 years of observations fortunately included an average winter and one of the most severe winters on record. In 1951–52, snowstorms kept the ground covered from November 18 to mid-April, and permanent ice was present on the lake from December 20 until the end of April, reaching a maximum thickness of 22 inches. In 1952–53, snowfall was relatively light, with the ice cover intermittent and reaching a thickness of only 4 inches. Although the mean air temperature of the period May 1951 to May 1952 was only 2.9° lower than that of the following 12-month period (41° and 43.9° F.), the first year contained 3,372 hours below freezing as compared with 2,750 such hours between May 1952 and May 1953 (table 1). The effects of a cold winter on subsequent heating of the lake are discussed under mean temperatures.

TABLE 1.—*Air temperatures at Convict Creek Station by months, May 1951 to April 1953*

[In degrees Fahrenheit]

Month	Monthly temperatures			Temperature range		Number of hours—	
	Mean maximum	Mean minimum	Mean	Maximum	Minimum	Above 32°	Below 32°
1951–52							
May	67.7	32.4	50.5	87	17	651	93
June	78.1	38.5	58.3	87.5	27	705	15
July	81.5	46.1	63.8	86	29	742	2
Aug	77.8	41.2	59.5	86	32.5	744	0
Sept	76.9	36.7	56.8	83.5	29	712	8
Oct	62.2	25.7	44	72.5	14	528	216
Nov	49.3	16.7	33	67.5	−8	308	412
Dec	28.9	10.3	19.6	42	−19	58	686
Jan	27.6	9.6	18.6	47.5	−12	36	708
Feb	35.8	8.3	22.5	45	−5	121	551
Mar	39.2	11.4	25.3	49	−5	277	467
Apr	55.3	26	39.8	69	15.5	506	214
Mean and total			41			5,388	3,372
1952–53							
May	70.3	32.1	51.2	82.	23	689	55
June	75.3	36.6	56	85	22	689	31
July	82.1	44.5	63.3	88.5	35	744	0
Aug	80.1	40.7	60.4	83.5	35.5	744	0
Sept	71.8	36.6	54.2	83	26	688	32
Oct	69.6	27.5	48.5	76	18.5	559	185
Nov	44.8	13.4	29.1	63	0	197	523
Dec	33.4	11.5	22.4	42.5	−8	72	672
Jan	43.1	19	31	52	4	361	383
Feb	47.8	24.7	31.3	57.5	5	270	402
Mar	54.5	19.2	36.9	66	0	425	319
Apr	60.9	24.6	42.8	82	3.5	572	148
Mean and total			43.9			6,010	2,750

The most notable aspect of the weather as it affects Convict Lake is the wind that sweeps the lake almost daily and varies from gusty breezes to prolonged gales that attain velocities of more than 70 miles an hour. Strong winds are especially frequent between October and May, when their action is the one factor that delays or, in mild years, prevents formation of a permanent ice cover. On several occasions in late 1952 the lake was cleared of 2 to 3 inches of ice in a few hours. Wind action is also of controlling importance in summer heat distribution, maintaining the lower limit of the epilimnion at roughly one-quarter to one-half the depth of the lake between July and October, and contributing to the weak and fluctuating nature of the thermocline.

In general, warming of the upper strata proceeds slowly until May, rapidly in late May and June, and more slowly again in July. Peak temperatures of the upper 20 feet are reached during August coincident with highest mean temperatures. Recognizable stratification developed in early July of 1951, following what may be regarded as a normal winter and spring. In 1952, after a heavy winter with resulting increased runoff, stratification was delayed until August. Owing to the constancy of wind agitation, much of the heat absorbed in early summer is transferred to the depths, overcoming the incipient thermal barrier, and the resulting lag in heat storage by the epilimnion places a short time limit on a stratified condition in any year. By the time the epilimnion nears the point of maximum heat, when sharply defined stratification is possible, the lake as a whole is about to lose heat.

Heat loss, as indicated by mean temperature, begins about the third week in August. Cooling becomes rapid in late October or early November, particularly in the upper strata. In this condition, there is only a small temperature decline with depth and little resistance to circulation. A drop in temperature of the upper strata, accompanied by a rise in temperature below 80 feet (table 2: Oct. 16 and 25, 1951), indicates that preliminary deep mixing occurs as early as mid-October, followed by stabilization and further cooling. Autumn overturns were recorded on November 30, 1951 (43.5° F.) and on December 4, 1952 (42.5° F.), but it may be noted from the temperature series preceding these dates (tables 2 and 3) that a homothermous condition at slightly higher temperatures could have been present several days earlier. Complete circulation begins with homothermy and continues until the lake

TABLE 2.—*Temperature readings at Convict Lake, May 7, 1951 to April 1, 1952*

[In degrees Fahrenheit]

Date	Air temperature	Water temperature at depth (feet) of—													
		0	10	20	30	40	50	60	70	80	90	100	110	120	130
1951															
May 7	58	45.5	44	43.5	43.5	43.5	43	43	43	42.5	42.5	42	42	42	42
14	53.5	46	45	44.5	44.5	44.5	44.5	44	43.5	43.5	43.5	43	43	42.5	42.5
21	59.5	50.5	50	48	47	46	45.5	44	44	43.5	43.5	43	43	43	43
28	70.5	56	53	52	50.5	49.5	47	46	45.5	44	44	43.5	43.5	43.5	43
June 4	60	53	52.5	51	50.5	49.5	48	46.5	45.5	44.5	44	43.5	43.5	43.5	43
11	64.5	54	52	51.5	50	49.5	48	47	45.5	44.5	44	43.5	43.5	43.5	43
14	69.5	58	55	53	52	50.5	48.5	46	45	44.5	44	43.5	43	43	43
18	69.5	58.5	56	53.5	52	49.5	48.5	47	45.5	44.5	44	43.5	43	43.	43
25	58.5	58	56	54	52.5	51.5	48.5	46.5	45	44	43.5	43	43	43	43
July 2	71	60.5	59.5	59.5	57	53.5	50	47	46	44.5	44.5	44	43	43	43
9	70	63.5	61	59	57.5	55.5	53	47	46	45	44.5	44	43	43	43
16	66	62.5	61.5	58.5	56	54	52	47	46	45.5	44.5	44	43	43	43
23	74.5	67	63	61	59.5	54	51.5	48.5	47	46	45	44.5	44.5	44	44
30	72	64	63.5	61.5	60.5	57	53	49	47	45	44.5	44	43	43	43
Aug. 6	66	63	62.5	62	61	57	53	49.5	48	46	45	44.5	44	43	43
13	74	63	63	62.5	60	51.5	48.5	46.5	45	44.5	44	43.5	43.5	43.5	43.5
21	62	62	61.5	61.5	61	58.5	52	49	47.5	46.5	45.5	45	45	44	44
28	62	60.5	60.5	60.5	60	59.5	53.5	48.5	47	46	45	44.5	44.	43.5	43.5
Sept. 4	68	61	60.5	60	59.5	59	55.5	49	47.5	46	45	44	43.5	43.5	43.5
11	65	61.5	60	59.5	59.5	59	56.5	49	47	46	45	44.5	44	44	44
18	63.5	61	61	61	60.5	60	59	53	48.5	46.5	45.5	44.5	44.5	44	44
25	62.5	59.5	59.5	59	59	59	58	51.5	48	46.5	45	44.5	44	44	44
Oct. 2	54	57	56	56	56	56	56	56	49.5	47	46	45	43.5	43.5	43.5
9	69.5	56.5	55.5	55.5	55.5	55.5	55.5	55.5	49.5	47.5	46.5	45.5	44.5	44	43.5
16	57.5	52.5	52.5	52.5	52.5	52.5	52	52	52	48	45.5	44	44	43.5	43.5
25	36	49.5	49.5	49.5	49	49	49	49	49	49	49	47.5	46.5	45	45
31	53	49	48.5	48.5	48.5	48.5	48.5	48.5	48.5	48	48	48	45.5	44.5	44
Nov. 2	53.5	51	50	49.5	49	49	49	49	49	49	49	48.5	46.5	45.5	45
9	49.5	48.5	48.5	48.5	48.5	48.5	48.5	48.5	48.5	48.5	48.5	48	47	44.5	44.5
16	52	46	46	45.5	45.5	45.5	45.5	45.5	45.5	45.5	45.5	45.5	45.5	45.5	45.5
23	23	44.5	44.5	44.5	44.5	44	44	44	44	44	44	44	44	44	44
30	52.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5	43.5
Dec. 7	22.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5	40.5
14	39	40	40	40	40	40	40	40	40	40	40	40	40	40	40
1952															
Feb. 6	45	33	36	36	36	36	36	36	36	36	36	36.5	36.5	36.5	36.5
14	39	33	36	36	36	36	36	36	36	36.5	36.5	36.5	36.5	36.5	36.5
21	37	32.5	35.5	36	36	36	36	36	36	36	36	36	36	36.5	36.5
Mar. 11	25.5	32	36	36	36	36	36	36	36	36	36	36	36	36	36
25	53	32	36	36	36	36	36	36	36	36	36	36.5	36.5	36.5	36.5
Apr. 1	49.5	32	36	36	36	36	36	36	36	36	36	36	36	36	36.5

has cooled uniformly to 39° F. or lower and surface ice has formed. If the ice is intermittent, circulation is maintained during periods of open water throughout the winter and spring at temperatures as low as 36° F.

The temperature series for March and April 1953 (table 3) show that warming of the lake in an ice-free spring was gradual and uniform up to about 40° F., at which point the warming of surface layers began to accelerate. Circulation during the early spring warmup of 1953 was thus almost continuous and no actual overturn occurred. In 1952, the late ice disappeared in the last week of April. By May 9, the earliest observation date in 1952, temperatures of deeper strata had risen 4° since April 1 (indicating some heating through the ice), and the surface had begun to warm additionally. It is likely that complete and thorough mixing occurs almost immediately after the breakup of permanent winter ice, and that the period of spring circulation at such a time is short, a week at the most.

DISTRIBUTION OF TEMPERATURE

SURFACE TEMPERATURES

Extremes of 32° F. (under ice) and 67° F. (at the surface) were recorded during the 2 years. The higher maximum occurred on July 23, 1951, following a mild winter and spring. The surface maximum of 1952, following a severe winter and late spring, was 3 weeks to a month later (August 16–21) and considerably lower (60° F.). The most rapid increases in surface temperature for both years were in late May, even though this is a period when mixing to a considerable depth is still in progress and insolation has not yet reached its full intensity. Increases were then gradual through June, and the data indicate that in a "normal" year the surface remains above 60° F. through the months of July, August, and Sep-

TABLE 3.—*Temperature readings at Convict Lake, May 9, 1952 to May 10, 1953*

[In degrees Fahrenheit]

Date	Air temperature	Water temperature at depth (feet) of—													
		0	10	20	30	40	50	60	70	80	90	100	110	120	130
1952															
May 9	55	42.5	42	41.5	41	41	41	41	40.5	40.5	40.5	40.5	40.5	40.5	40.5
16	49	44.5	44	44	44	42.5	42.5	42	41.5	41.5	41.5	41	40.5	40.5	40.5
23	58	48	45	44.5	44	43.5	43	42.5	42.5	42	42	41.5	41.5	41.5	41.5
29	60	50	48	47	45	44.5	44.5	44	43	42.5	42	42	42	42	41.5
June 6	60.5	51.5	49.5	48.5	47.5	47	46	45	43.5	42.5	42	42	42	41.5	41.5
16	62	49.5	47.5	47	46.5	46	45.5	45	44.5	44	43.5	43	43	42.5	42
24	57.5	49	49	48.5	48	47	47	45.5	45	44	43.5	43	43	43	42.5
July 1	69.5	52.5	50	49.5	48.5	48	47	46	45.5	45	44	43.5	43	43	43
9	64.5	53	52.5	51.5	50	48.5	47.5	46.5	45	45	43.5	43.5	43	43	43
16	61.5	56	53.5	52	51.5	50	49.5	47	45.5	45	44.5	44	44	43.5	43.5
23	75.5	58	56	55	54	52	50.5	48.5	46.5	46	45	44.5	44	43.5	43.5
30	58	57	56	55	54	53	49	47.5	46.5	45.5	44.5	44	44	43.5	43.5
Aug. 6	72.5	58	57	55.5	54.5	54	51	48.5	47	46	45.5	44.5	44	43.5	43.5
13	74	60	58.5	57	56.5	55.5	53	50.5	47.5	45.5	45	44.5	44	44	44
21	68	60	59.5	59	58	57	53	49.5	47.5	47	46	45.5	45	45	44.5
28	63.5	58	57.5	57	57	56.5	55	50	47.5	46.5	45.5	44.5	44.5	44	44
Sept. 5	58	57	57	57	57	56.5	54.5	50.5	49	47.5	45.5	44.5	44.5	44.5	44.5
10	42	55.5	55.5	55.5	55.5	55.5	54.5	53.5	48	46.5	45.5	45	44.5	44	44
17	67	56	55.5	55	55	54.5	54	54	49	47.5	46	45.5	44.5	44.5	44.5
26	62	55	55	55	55	55	54.5	54	52.5	46.5	46	44.5	44	44	44
Oct. 3	72	56	55	55	55	54.5	54	53.5	50.5	48	46	45	44	44	44
9	60.5	55.5	55	55	55	55	54.5	53.5	51	47.5	46	45	44.5	44	44
16	66	55.5	55	55	54.5	54.5	54.5	54	51	47.5	46.5	45.5	45	44	44
23	62.5	55	54	54	54	54	53.5	53.5	52.5	48	46	45	44.5	44.5	44
30	56.5	53	52.5	52.5	52.5	52.5	52.5	52.5	52	47.5	46	45	44.5	44	43.5
Nov. 7	46	51	51	51	51	51	51	51	51	50.5	46.5	45	44.5	44	44
18	36	46.5	46.5	46.5	46.5	46.5	46.5	46	46	46	46	46	46	44.5	43.5
24	43.5	45	45	45	45	45	44.5	44.5	44.5	44.5	44.5	44.5	44.5	44.5	44.5
Dec. 4	27	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5	42.5
11	36.5	39.5	40	40	40	40	40	40	40	40	40	40	40	40	40
17	40	40	40	40	40	40	40	40	40	40	40	40	40	40	40
23	27.5	39	39	39	39	39	39	39	39	39	39	39	39	39	39
1953															
Jan. 12	44	37	37	37	37	37	37	37	37	37	37	37	37	37	37
19	43	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5
30	52	36	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5
Feb. 11	47	34.5	35.5	36	36	36	36	36.5	36.5	36.5	36.5	36.5	36.5	36.5	36.5
19	34.5	35.5	36	36	36	36	36	36	36	36	36	36	36	36	36
Mar. 6	41	33.5	37	37	37	37	37	37	37	37	37	37.5	37.5	37.5	37.5
11	33.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5	37.5
31	50	39	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5
Apr. 8	35	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5
15	55.5	41.5	40.5	40.5	40	40	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5	39.5
22	53	42.5	41	41	41	41	41	41	40.5	40.5	40.5	40.5	40.5	40.5	40.5
May 2	48	42.5	42	41.5	41.5	41.5	41.5	41.5	41.5	41.5	41.5	41.5	41.5	41	41
10	38.5	43	43	43	43	43	43	42	42	42	42	42	42	41.5	41.5

tember. Rapid decline of surface temperatures began about October 9 in 1951 and near the end of October in 1952. A clear connection between surface and air temperatures at these times is indicated in tables 2 and 3. The continuation of surface cooling may be followed on figures 2 and 3, which were constructed to illustrate the seasonal variation of surface-to-bottom temperature ranges. Four weeks in 1952 and six weeks in 1951 were required to reduce the October surface temperatures from the beginning of rapid decline to 45° F., at which point the lake was essentially homothermous.

Although surface temperatures near the shore on calm days were sometimes found to be 1° or 2° higher than at the central station, the volume of shallow water involved is slight and the duration of calmness is usually brief. Water between the shoreline and a depth of 10 feet, which during favorable weather might be expected to attain slightly higher temperatures than the upper 10 feet at a distance from shore, amounts to less than 1 percent of the total lake volume. Vertical temperature series taken at a depth of 30 feet agreed regularly with the upper 30 feet of midlake temperatures. It is therefore evident that the entire lake may be considered as open water, and that wind action and the complete absence of sheltered shallow areas preclude any significant addition to surface heating from inshore areas.

DEEP TEMPERATURES

The seasonal course of temperatures at 130 feet, reported here as bottom temperatures, may be followed in tables 2 and 3 and on figures 2 and 3. Temperatures at this depth are affected very

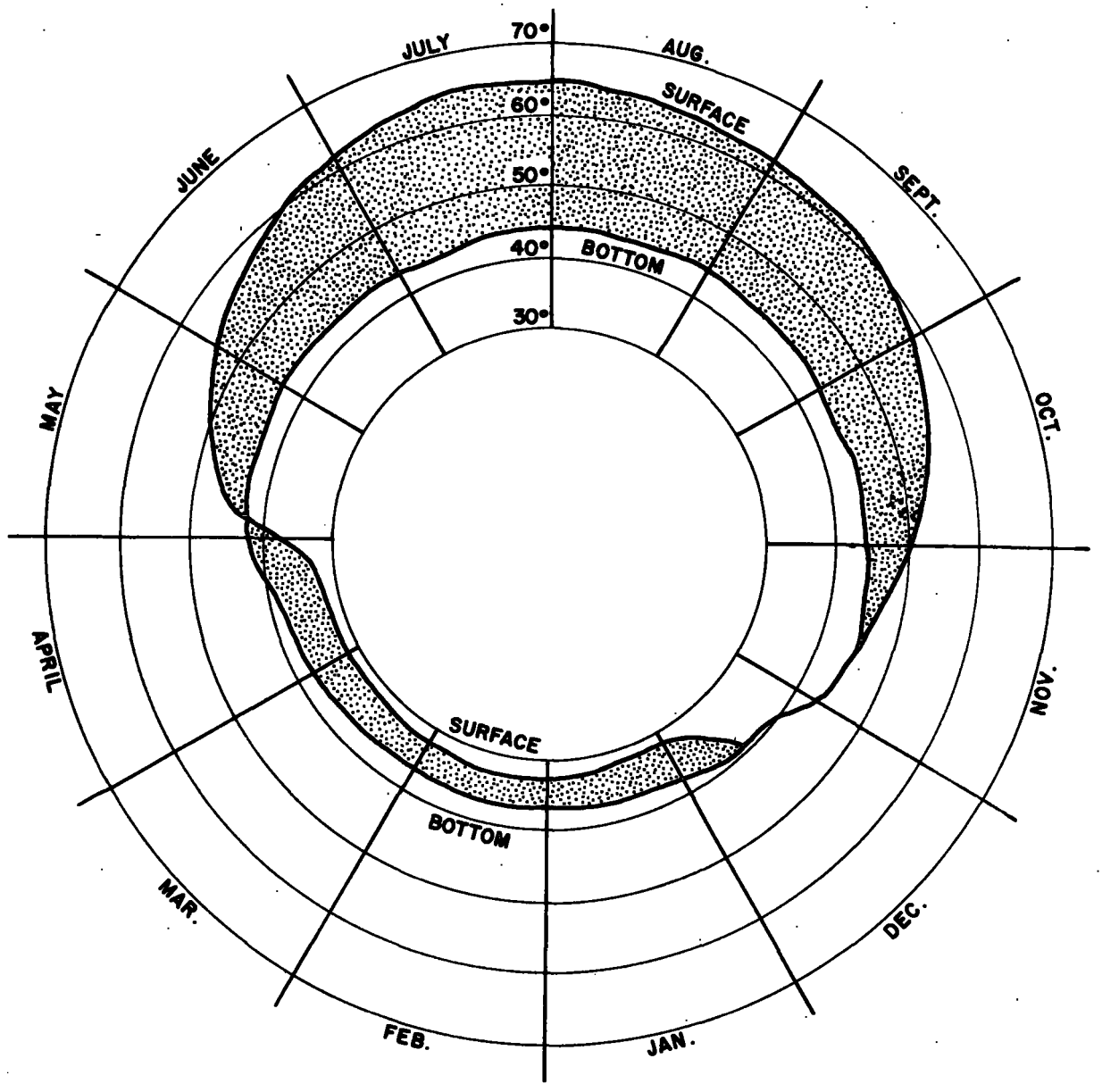

FIGURE 2.—Annual temperature cycle in Convict Lake, Calif., May 1951 to May 1952. (Temperatures in degrees Fahrenheit.)

little during the warming period, reaching a level of 40° to 43° F. in the spring circulation and rising only 2° to 4° through the summer and fall. Maximum bottom temperatures are attained at the beginning of complete autumn circulation, and are therefore brought about by cooling and mixing rather than by heating and mixing, as in upper and mid-depth zones. A seasonal range of temperature almost as narrow as that at the bottom is found through a hypolimnetic zone extending from the bottom to a depth of about 90 feet (tables 2 and 3). Above 90 feet, the effects of thermal stratification and occasional deep mixing are more pronounced, with the yearly temperature range of each stratum increasing steadily toward the surface.

MEAN TEMPERATURES

The best indication of time and degree of heat gains and losses attributable to yearly

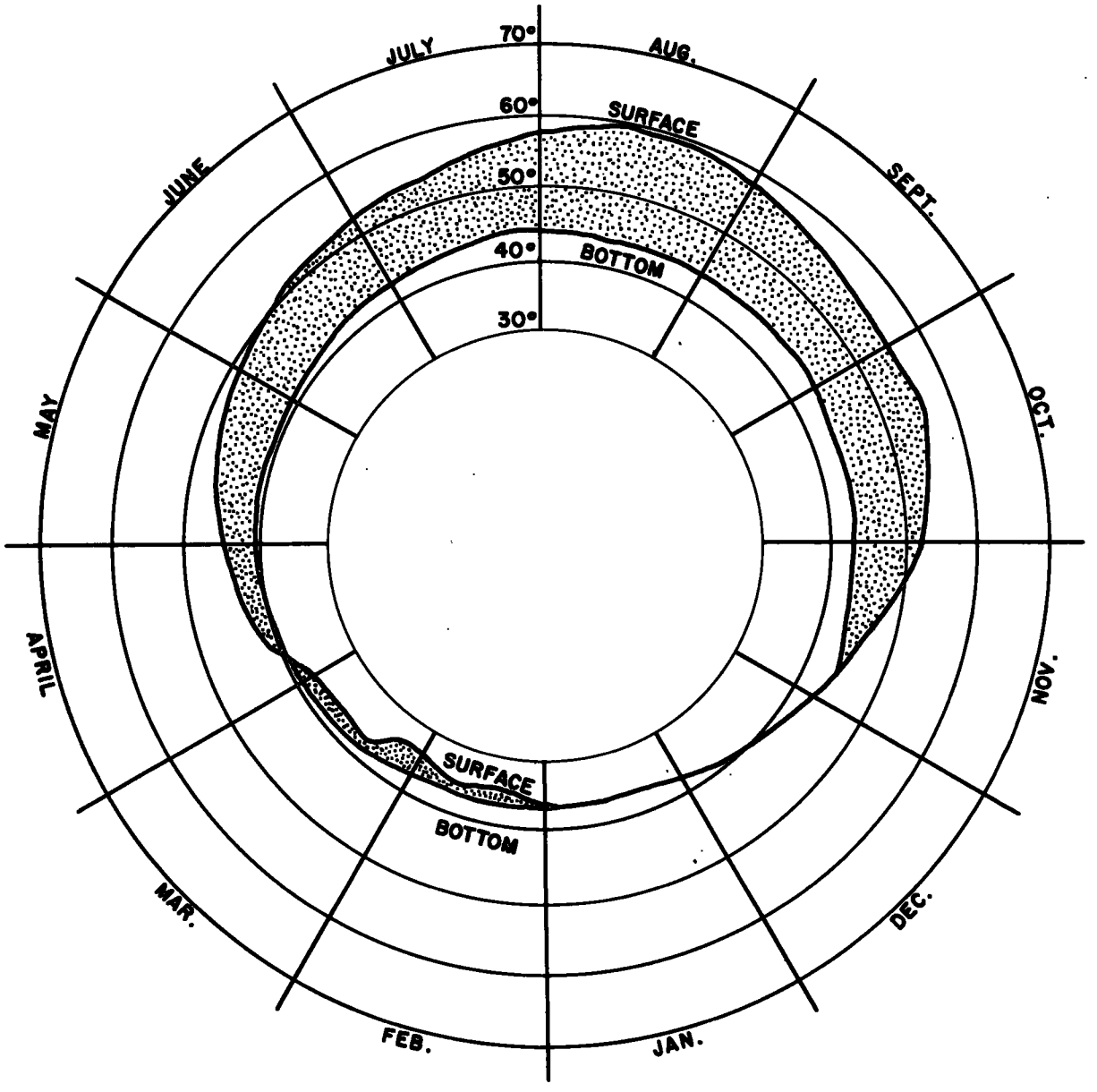

FIGURE 3.—Annual temperature cycle in Convict Lake, Calif., May 1952 to May 1953. (Temperatures in degrees Fahrenheit.)

weather, and of the probable average course of events, is found in the mean-temperature record. Table 4 lists the mean lake temperatures, calculated by 20-foot strata, for all observation dates. Figure 4 graphs the same data (smoothed by running averages of 3) for essential parts of 1951 and 1952, which followed radically different winter weather and ice conditions as previously noted, and for the first 4 months of 1953. The 1951–52 curve between April 1 and May 9 was extrapolated in two segments by estimate because it is certain that heating of the lake was somewhat slower under the ice than after the ice had broken up near the end of April. The figure demonstrates that in 1952, following a severe winter, heating of the lake as a whole lagged as much as a month behind the preceding year, and that for any given date between May 10 and October 5 the mean temperature was 1° to 4° lower than in the preceding year.

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TABLE 4.—*Mean temperatures at Convict Lake, May 7, 1951 to May 10, 1953*

[In degrees Fahrenheit; by 20-ft. strata]

Date of observation	Mean temperature	Date of observation	Mean temperature
1951		*1952—Con.*	
May 7	43.2	May 9	41.2
14	44.1	16	42.6
21	45.7	23	43.5
28	48	29	44.8
June 4	48	June 6	45.7
11	48	16	45.5
14	48.7	24	46
18	48.7	July 1	46.9
25	48.9	9	47.7
July 2	50.9	16	48.6
9	51.6	23	50.2
16	51.1	30	50
23	52.7	Aug. 6	50.7
30	52.9	13	51.7
Aug. 6	53.1	21	52.5
13	53.6	28	51.6
21	53.4	Sept. 5	51.8
28	52.9	10	51.7
Sept. 4	52.7	17	51.6
11	52.7	26	51.4
18	53.6	Oct. 3	51.7
25	52.9	9	51.5
Oct. 2	52.3	16	51.5
9	52.2	23	51.4
16	50	30	50.2
25	48.6	Nov. 7	49.8
31	48	18	46.1
Nov. 2	48.7	24	44.8
9	48	Dec. 4	42.6
16	45.5	11	40.1
23	44.1	17	40.1
30	43.5	23	39
Dec. 7	40.5	*1953*	
14	40.1	Jan. 12	37
1952		19	36.5
Feb. 6	35.8	30	36.4
14	35.8	Feb. 11	36.1
21	35.6	19	36
Mar. 11	35.6	Mar. 6	36.7
25	35.6	11	37.6
Apr. 1	35.6	31	39.5
		Apr. 8	39.6
		15	40.1
		22	40.9
		May 2	41.6
		10	42.4

General observations during March and April for 4 years (1951–54) indicate that a permanent ice cover may be present on the lake in March, but is definitely unusual in April. The normal course of spring heating is therefore believed to be similar to that shown for 1951 and 1953 in figure 4. On this basis, the daily gain after the disappearance of ice varies between 0.07° and 0.30° F. per day, with the most rapid rise in late May. The coarse average rise in mean temperature for the entire warming period (from a winter mean of 36° F.) is about 0.85° F. per week, and the highest summer mean is reached some time in August. The highest mean temperatures of 1951 and 1952 were 53.6° and 52.5° F. The mean temperature was above 50° for 15 weeks in 1951, and for 14 weeks in 1952. The average mean temperatures for these two periods were 52.5° and 51.3° F.

STRATIFICATION

Wind circulation and the inflow of cold water combine to prevent the formation of a sharp and well-sustained thermocline (1° C. per meter, or 0.549° F. per foot) in Convict Lake, but the three primary temperature regions nevertheless develop and remain distinct for 1 to 3 months of each year. Selected temperature series for 1951 and 1952, spaced 1 to 2 weeks apart, have been plotted (fig. 5), and illustrate the progress of stratification. On these charts, the temperature scale of each gradient is indicated at its point of origin (bottom) and termination (top). The points of origin of gradients are also time scaled to maintain the proper spacing of dates. Although the overlapping temperature scales and changing shapes of temperature gradients produce a slight horizontal distortion, the general movements of the thermocline can be followed clearly. In 1951, a thermocline was present as shown in the shaded area of the figure. Its thickness, though masked somewhat by the large depth interval of observations, was never greater than 15 feet, and the considerable depth of its first formation (50 feet) is a good indication of the extent of wind-mixing interference. Near the end of July 1951, the thermocline appears to have been overcome by a deeper mixing and to have re-formed shortly thereafter.

In 1952, an unusually large runoff strongly influenced summer thermal characteristics, as the inflow was several degrees colder than the epilimnial water of the lake. Stratification was weaker than in the preceding year, and a true thermocline was in existence only during the month of September, at depths ranging from 60 to 80 feet. The development of stratification in the 2 years is best illustrated by the seasonal progress of isotherms (figs. 6 and 7). In 1951, the rapid heat gains and regular development of strata are shown by closely spaced, parallel-tending isotherms. In 1952, the influence of colder water is evident in irregularly spaced and frequently divergent isotherms. The average summer condition would be a thick epilimnion and a slightly thicker hypolimnion, which account for over 90 percent of the depth of the lake and are separated by a thin, occasionally penetrable thermocline. With the progress of rapid autumn cooling, the already weakened thermocline follows the usual down-

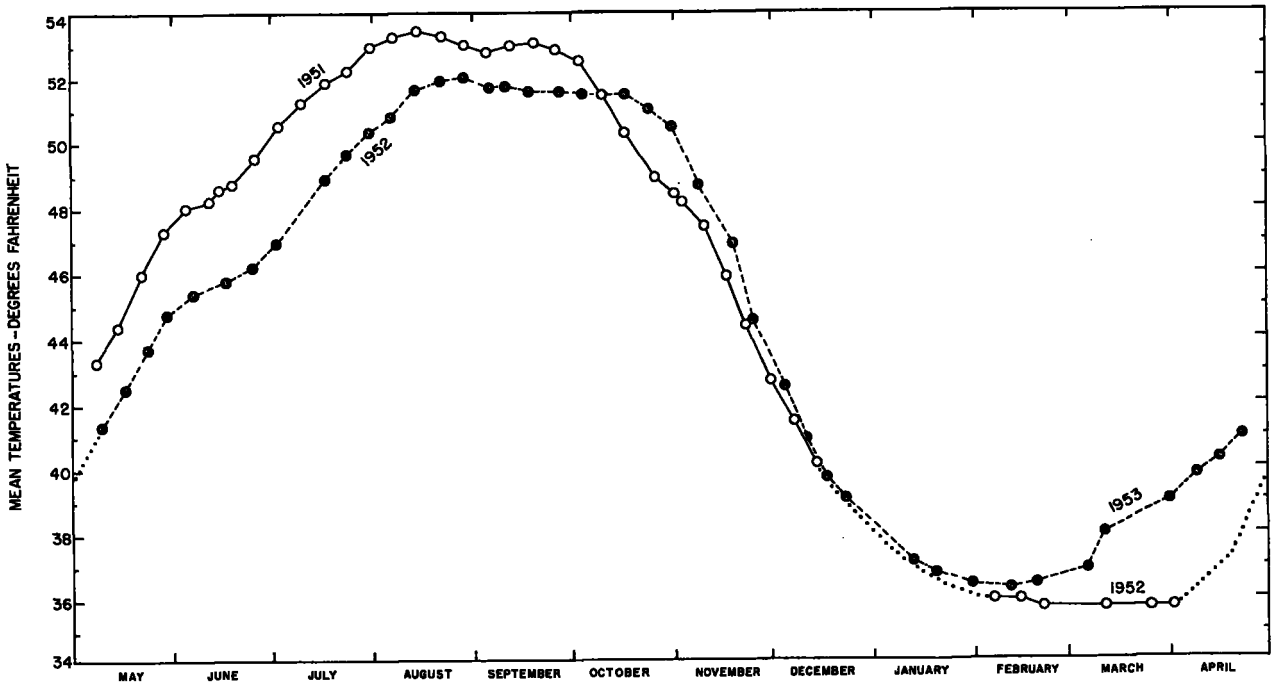

FIGURE 4.—Seasonal variation in the mean temperatures of Convict Lake, Calif., compared for 2 years, May 7, 1951 to May 10, 1953. Data were smoothed by running averages of 3 (open dots, 1951–52; solid dots, 1952–53).

ward course and is forced into mixing near the bottom, in November (fig. 5; upper chart).

ASSESSMENT OF HEAT IN LAKES

ENERGY BUDGETS AND HEAT BUDGETS

Juday (1940, p. 439) stated "The annual energy budget of a lake may be regarded as comprising the energy received from the sun and sky each year and the expenditures or uses which the lake makes of this annual income of radiation. In general the annual income and outgo substantially balance each other." The income of solar energy is expended in a number of ways, including evaporation, surface losses (reflection, scattering, absorption by snow and ice), conduction, convection, radiation, melting of ice, raising of water and bottom temperatures, and use by organisms.

The heat budget of a body of water is that portion of the energy income which is expended in raising the temperature of the water mass, or a convenient and representative sample of it, from a selected minimum to the summer maximum. As applied by Birge (1915) and later workers, the annual heat budget specifies the number of gram-calories required to warm a column of water of 1 square centimeter base, with height equal to the mean depth of the lake, from the mean winter minimum temperature to the highest mean summer temperature. Such a "budget," expressed in gram-calories per square centimeter of lake surface per year, represents the annual cycle of heat capacity of a lake which can be thermally characterized by single mean temperatures.

Limnological interest in total energy budgets has not been extensive. Except for its application to problems of computing evaporation, a knowledge of all energy values involved in the physical dynamics of a lake is of little more than academic usefulness. Aside from the question of application, the time and instrumentation required to evaluate the various energy expenditures all but limit energy-budget studies to long-term, multiphase investigations such as those which enabled Juday (1940) to describe the energetics of Lake Mendota. Heat budgets, however, are usually concerned only with the heating of the water itself, are relatively simple to determine, and are commonly included in physical descriptions of larger lakes for which sufficient temperature data are available.

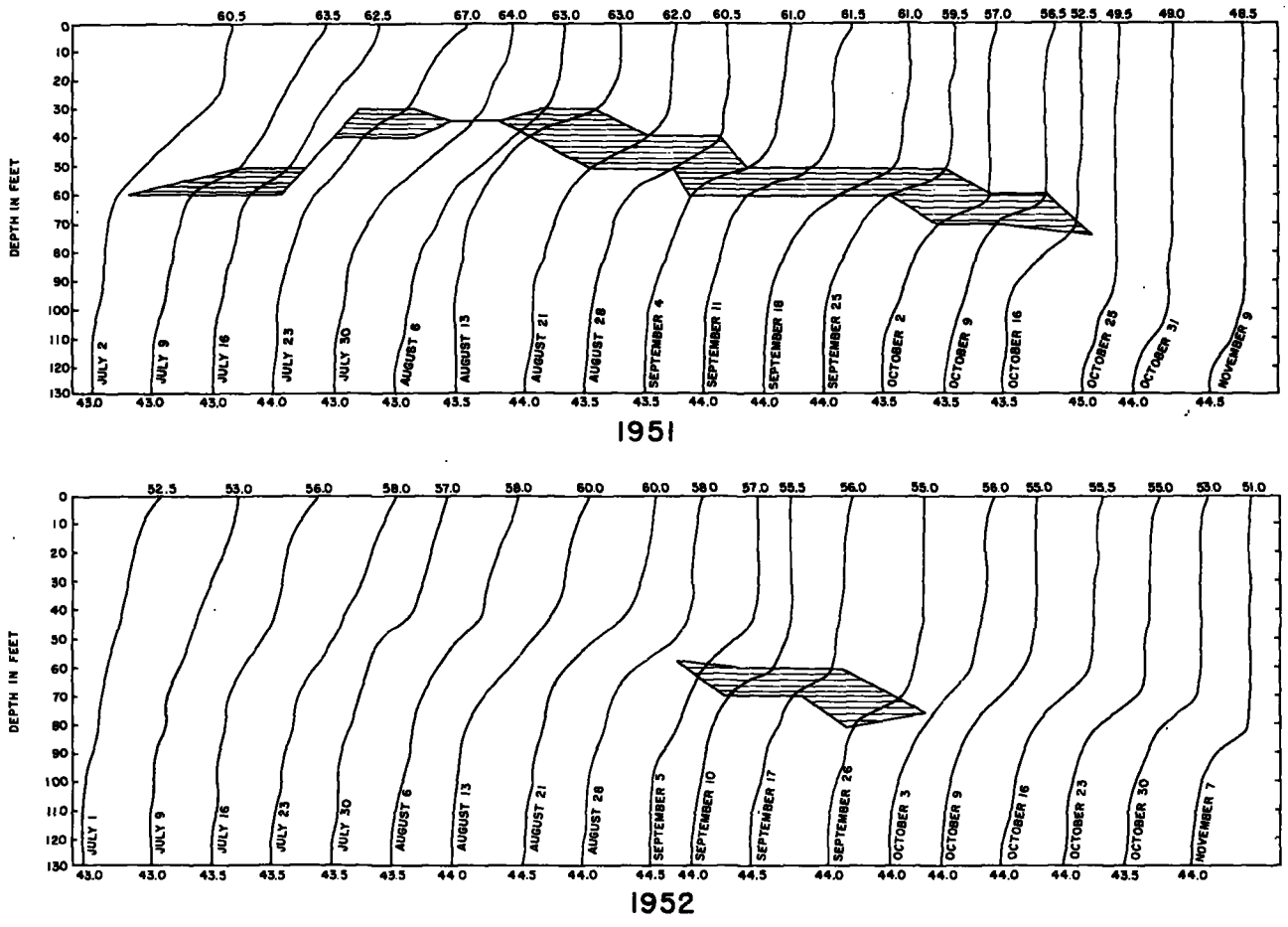

FIGURE 5.—Summer stratification in Convict Lake, Calif., compared for 2 years, 1951 (upper) and 1952 (lower). The thermocline is indicated by the shaded area. (Temperatures in degrees Fahrenheit.)

HEAT BUDGETS FOR CONVICT LAKE

Annual heat budgets were calculated for Convict Lake according to Birge, with heat expressed in gram-calories per square centimeter of lake surface derived from the product of temperature range and mean depth. To obtain heat budgets for 2 consecutive years (1952 and 1953), a few additional observations were made to determine the mean summer temperature of 1953. The highest mean, which is not reported elsewhere in this paper, was 53.9° F. (12.2° C.) and occurred on August 9.

Annual heat budgets for Convict Lake were 25,210 gram-calories in 1952 and 26,810 gram-calories in 1953. In view of the marked difference in winter and ice cover for the 2 years, and the general similarity of summers except for an excess of cold inflow in 1952, the difference between the two budgets (1,600 calories) represents the approximate range of variation in response to winter conditions. Summer heat incomes above 4° C. were 19,850 gram-calories (79 percent of annual) in 1952 and 21,990 gram-calories (82 percent of annual) in 1953. The average annual heat budget is estimated at between 26,000 and 27,000 gram-calories. Since the budget of 1952 represents an extreme winter, variations outside the range found for 1952 and 1953 would most likely be on the high side and due to exceptional summer weather.

LIMITATIONS OF THE HEAT BUDGET

In outlining dimensional and other limits used in heat-budget comparisons of American and European lakes, Birge (1915) described inland lakes of the "first class" as those which lie under ordinary conditions of topography and altitude, and whose size and depth (at least 10 km. by 2 km. by 30 meters mean depth in eastern United States) permit them to acquire the maximum heat

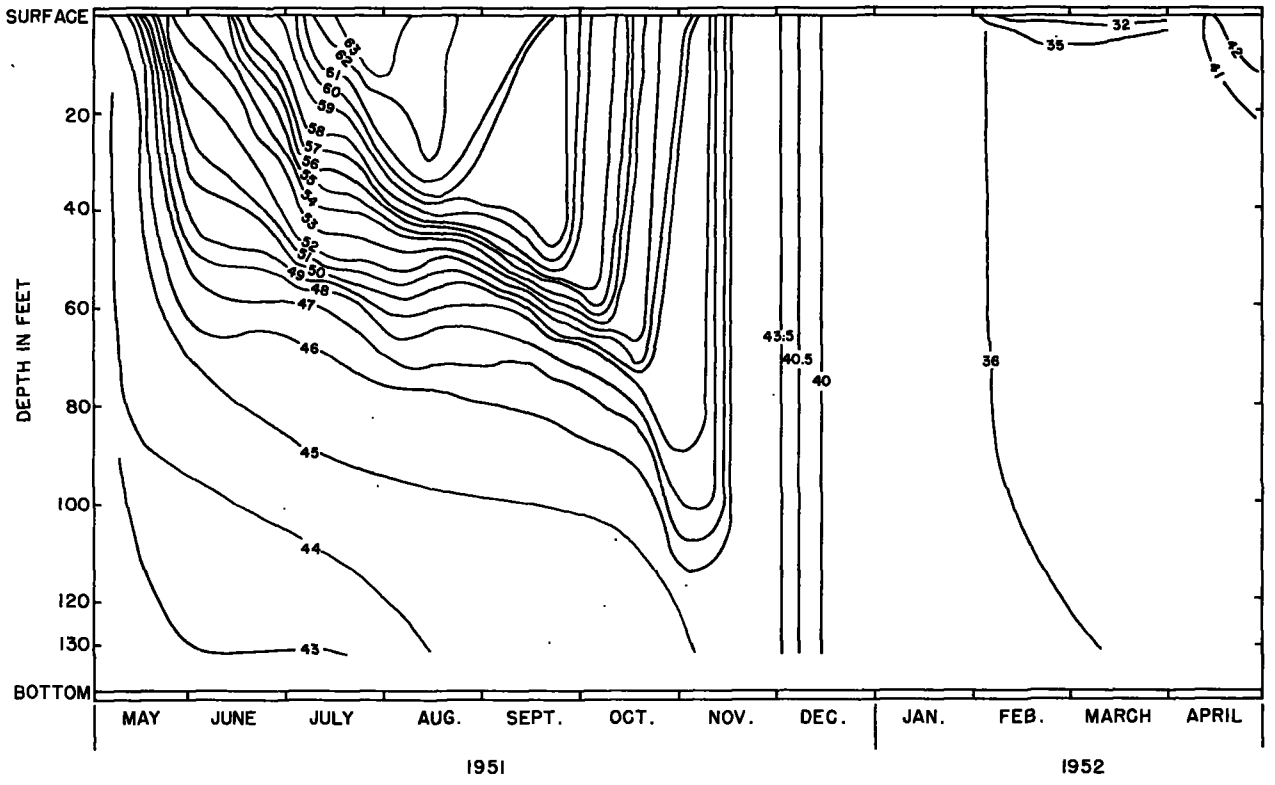

FIGURE 6.—Seasonal distribution of isotherms in Convict Lake, Calif., May 1951 to April 1952. (Temperatures in degrees Fahrenheit.)

possible under weather conditions of the season. Studies by Rawson (1936) indicated that in a series of Saskatchewan lakes shallower than the 30-meter requirement the heat budgets varied according to mean depth. Similar correspondence between mean depths and crude heat budgets was found among small lakes of the upper Convict Creek Basin (Reimers, Maciolek, and Pister, 1955), and this relationship is probably general among smaller, temperate lakes which are regionally related. It seems certain that a regional selection of lakes would show more variability in mean depth than in temperature range. Small or intermediate lakes, which are limited by area and depth to less than their climatic heat capacities, cannot properly be compared by heat budget with first class lakes, or with each other, except at the expense of explanations concerning relative size, depth, morphometry, or other factors which may bear on the magnitude of the heat budgets. With such added qualifications, heat budgets cannot represent lakes simply, as units, and are not satisfactory for index evaluations of thermal conditions.

Birge further excepted elevated lakes from heat-budget comparisons in the statement that "Lakes whose conditions of climate or location are exceptional, such as those of alpine lakes at considerable elevations, cannot be compared with those in lower and more normal situations." Climatic changes associated with a substantial increase in elevation may be comparable to those resulting from a large increase in latitude. Inflows of cold, snow-fed water have an unusual influence on the heating of many mountain lakes. Variability of these factors further impedes heat-budget comparisons among alpine lakes as a group, since heat budgets are more closely tied with the individual heating capacities of such lakes than with the sensible heat present in them from season to season.

The product of time and temperature is not considered in a heat budget, although this factor should be of great importance in comparative studies of thermal conditions, and particularly in studies of biological heat relations which involve temperature thresholds. In Convict Lake, for

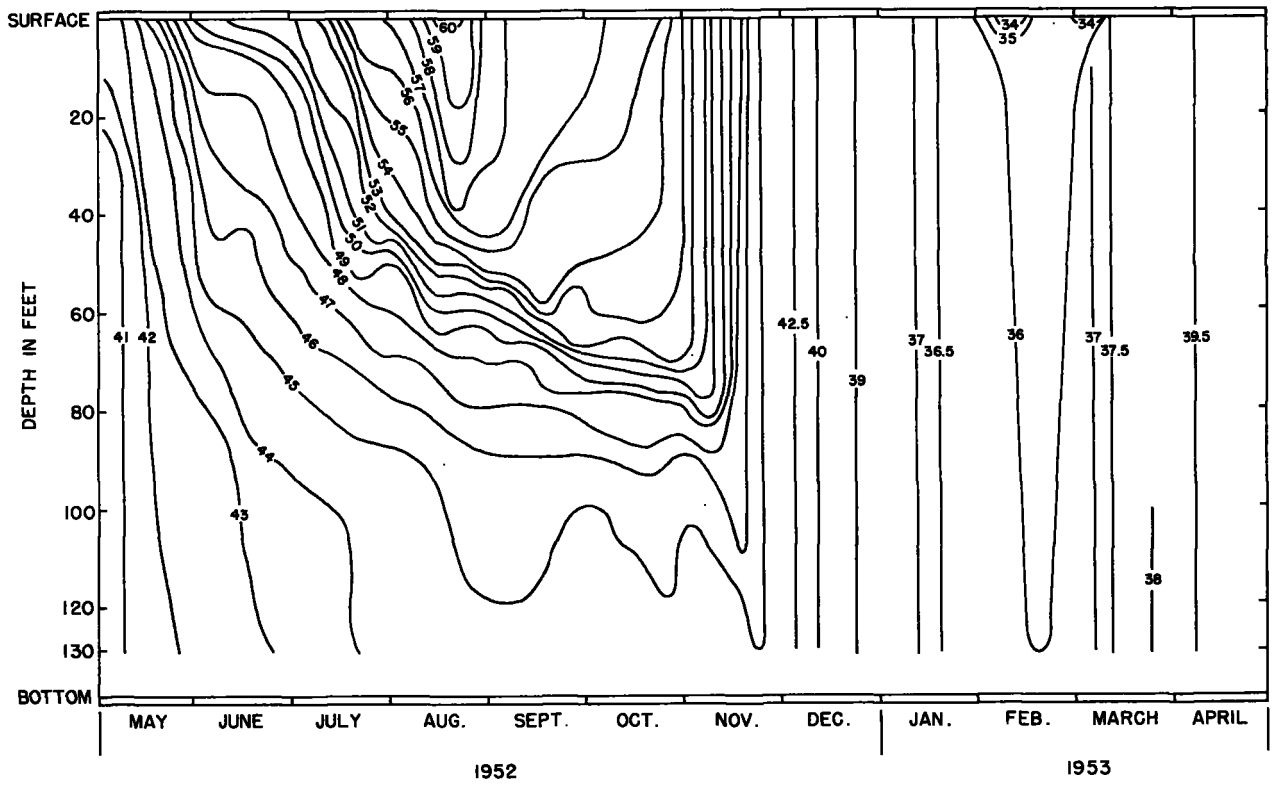

FIGURE 7.—Seasonal distribution of isotherms in Convict Lake, Calif., May 1952 to April 1953. (Temperatures in degrees Fahrenheit.)

example, comparisons of warming progress and the dates of highest mean temperature for two summers (fig. 4) suggest that the main effect of a severe winter is to delay heating in the following summer to the point where the usual mean-temperature peaks may not be reached. The difference in summer heat between the 2 years was due as much to the difference in the length of time that high temperatures were in existence as to the levels of temperature reached. This principle is applicable to comparisons of thermal conditions among lakes as well as among cycles in a single lake. Several lakes of comparable size may have similar heat budgets, yet differ considerably in heat actually in effect over a selected period of time by reason of variations in exposure, altitude, or morphometry, with resulting variations in rates and periods of heating.

Finally, the type of information yielded by the heat budget is not all that is desired in thermal evaluations of lakes or their parts. The actual heat condition of the water, expressed by temperature as the intensity factor, cannot be specified in caloric units. A description of the thermal character of a lake must be based on measurements of temperature, yet the only temperature data required for the calculation of a conventional heat budget are the lowest mean winter temperature (or an arbitrary base such as 0° C., 4° C.) and the highest mean summer temperature. A calculation based on these data, which amount to a gross range of temperature whether for annual or subannual periods, does not provide a cumulative estimate of sensible heat of the water; it only indicates the amount of energy expended to raise the water temperature to the maximum, or from one level to another.

TEMPERATURE SUMMATION AS A BASIS FOR HEAT EVALUATION

The use of temperature summations has a long history in phenology. Most applications have been concerned with the time relation between total accumulated heat above a base temperature and the completion of life-history stages of animals or plants. The base temperature may be the

experimentally determined temperature at or below which the process in question cannot be completed successfully, known as the ecological temperature zero, or it may be an arbitrarily selected point which approximates this threshold.

A summation is expressed in units of time× temperature, such as day-degrees or hour-degrees. With such units, "thermal constants" have been described for a wide variety of developmental processes whose rates are regulated by environmental temperatures and whose successful conclusions have been found to depend on reasonably consistent sums of heat within the effective temperature ranges. The theoretical basis of the concept, some applications, and some extensions to include the relation between length of life and metabolic rate as influenced by temperature are reviewed by Allee et al. (1949).

Fish hatcheries have for many years made use of day-degrees as "temperature units" (degrees per day in excess of 32° F.) to predict hatching times of eggs at various water temperatures. The freezing point of water is regarded as the ecological zero for egg development in this application. Development presumably cannot take place at the freezing point, but proceeds at rates which increase with temperatures above freezing.

Although their principal usefulness is in connection with such biological heat relations, temperature summations can also be of service as index measurements of thermal conditions alone in environmental units such as lakes or their biological regions, where the available heat varies throughout seasonal cycles and from lake to lake. A method for thermally comparing lakes and their divisions over selected periods of time is prerequisite to any understanding of possible relations between heat and aquatic productivity in terms of growth or incrementation. Summations provide information that neither caloric estimates nor temperature series alone can provide. They are capable of combining in simple form the two elements—temperature and time—that are essential to an adequate description of thermal character. The resulting thermal units are artificial rather than absolute heat values; however, they are valid as cumulative measurements of heat intensity and are suitable for purposes of comparison.

Since the principle of an experimentally determined "zero" cannot be applied to a lake, the base temperature for summations must necessarily be a constant chosen to represent the lower limit of biological activity in the waters and in the periods to be compared. Within a class such as alpine lakes, the freezing point of water is a logical and convenient base for annual summations. Winter mean temperatures approach the freezing point, and the flora and fauna consist of forms that are adapted to a relatively low range of water temperatures. In subannual comparisons that are to include periods of highest temperatures or other significant parts of the growing season, a higher base temperature may be desirable.

As the mean temperature of a lake represents the entire water body, with temperatures of various strata considered in ratio to their volumes, the summation for a lake as a unit should be made from the selected base temperature to the mean temperature to produce a result that is independent of volume and suitable for comparison with totals from other lakes. Similarly, summations should be made to the mean temperatures of the divisions or biological regions that are of interest in subtotal comparisons. Accurate knowledge of mean temperatures requires reasonably thorough hydrographic surveys, but such preliminary work is necessary for the calculation of acceptable morphometric values in any event.

One factor that limits summations to scheduled investigations is the need for a series of several mean temperatures distributed uniformly over the year. There is no escaping the fact that an annual accumulation of thermal units, sufficiently accurate to be used for comparing lakes, requires a number of observations on each lake that is adequate to represent the time and temperature cycle involved. Because seasonal changes in the mean temperatures of most lakes are notably slow and regular, the number of observations for the year may often be reduced to a feasible minimum. For example, reduction of the Convict Lake annual data to monthly intervals gave the same accuracy as weekly observations.

SUMMATION PROCEDURE

Trials of the summation method were conducted with 32° F. as a base point, and the day-degree values are accordingly referred to as temperature units.

With a series of mean lake temperatures at hand, the assembly of data is simple, since the only variables are the mean temperatures and numbers of days between temperature observations. The procedure used with the Convict Lake data is as follows:

1. Average the mean temperatures for each consecutive pair of observation dates to obtain the best estimate of the mean temperature for the interval.
2. Subtract 32 from the interval mean temperature to obtain temperature units per day.
3. Multiply temperature units per day by the number of days in the interval between observations.
4. Add the products for intervals through the desired period to obtain total temperature units.

Formulated,

total temperature units=

$$(T_m^{i(1)}-32)\,(TI_1)+(T_m^{i(2)}-32)\,(TI_2)+\ldots\ldots\ldots(T_m^{i(n)}-32)\,(TI_n),$$

in which T_m^i is the mean temperature for an interval between pairs of observation dates, TI is the length of a time interval in days, and n is selected to limit the summation to the desired period.

ANNUAL SUMS FOR CONVICT LAKE

Tables 5 and 6 present the summations of mean temperature for Convict Lake for the 2 years (May 1951 to May 1953) according to the procedure presented in the previous section. The results of both weekly and monthly intervals are tabulated to show separate totals for the year. The near identity of the weekly and monthly figures for each year is considered sufficient evidence of the adequacy of monthly observations in an annual cycle for any lake whose rates of heating and cooling are not radically greater than those observed for Convict Lake. As decimal selection in the computation of interval mean temperatures could cause bias in the product when temperature units are multiplied by days, particularly when the interval is large, these means and their temperature units (cols. 4 to 7) were carried to an extra decimal place where necessary to avoid such bias. The annual sums are therefore free of the influence of decimal selection at the weekly or monthly level, and the effect of such selection in

TABLE 5.—*Summations of mean temperatures above 32° F. in Convict Lake, by weekly and monthly intervals, May 1951 to May 1952*

Period	Time interval (TI) in days		Mean temperature of interval		Mean daily temperature units (TU)		Temperature units in time interval (TU × TI)	
	Weekly	Monthly	Weekly	Monthly[1]	Weekly	Monthly	Weekly	Monthly
May 7–14	7		43.65		11.65		81.6	
May 14–21	7		44.90		12.90		90.3	
May 21–28	7	35	48.85	45.60	14.85	13.60	104	476.0
May 28–June 4	7		48.00		16.00		112	
June 4–11	7		48.00		16.00		112	
June 11–18	7		48.35		16.35		114.4	
June 18–25	7		48.80		16.80		117.6	
June 25–July 2	7	28	49.90	49.80	17.90	17.80	125.3	498.4
July 2–9	7		51.25		19.25		134.8	
July 9–16	7		51.35		19.35		135.4	
July 16–23	7		51.90		19.90		139.3	
July 23–30	7	35	52.80	52.60	20.80	20.60	145.6	721.0
July 30–Aug. 6	7		53.00		21.00		147	
Aug. 6–13	7		53.35		21.35		149.4	
Aug. 13–21	8		53.50		21.50		172	
Aug. 21–28	7		53.15		21.15		148	
Aug. 28–Sept. 4	7	29	52.80	53.15	20.80	21.15	145.6	613.4
Sept. 4–11	7		52.70		20.70		144.9	
Sept. 11–18	7		53.15		21.15		148	
Sept. 18–25	7		53.25		21.25		148.8	
Sept. 25–Oct. 2	7	28	52.60	52.45	20.60	20.45	144.2	572.6
Oct. 2–9	7		52.25		20.25		141.8	
Oct. 9–16	7		51.10		19.10		133.7	
Oct. 16–25	9	31	49.30	50.10	17.30	18.10	155.7	561.1
Oct. 25–31	6		48.30		16.30		97.8	
Oct. 31–Nov. 9	9		48.00		16.00		144.0	
Nov. 9–16	7		46.75		14.75		103.2	
Nov. 16–23	7		44.80		12.80		89.6	
Nov. 23–30	7	28	43.80	44.25	11.80	12.25	82.6	343.0
Nov. 30–Dec. 7	7		42.00		10.00		70.0	
Dec. 7–14	7		40.30		8.30		58.1	
Dec. 14–Feb. 6	54	61	37.95	38.15	5.95	6.15	321.3	375.2
Feb. 6–14	8		35.80		3.80		30.4	
Feb. 14–21	7	33	35.70	35.70	3.70	3.70	25.9	122.1
Feb. 21–Mar. 11	18		35.60		3.60		64.8	
Mar. 11–25	14		35.60		3.60		50.4	
Mar. 25–Apr. 1	7	21	35.60	35.60	3.60	3.60	25.2	75.6
Apr. 1–May 9	38	38	38.40	38.40	6.40	6.40	243.2	243.2
Total	367						4,597.9	4,601.6

[1] Monthly interval mean temperatures are averages of initial and final monthly temperatures.

the product itself (last column) is negligible. Because of irregular intervals at certain times, the terms "weekly" and "monthly" are used somewhat loosely in the tabulations. The agreement of yearly totals on both interval bases, however, is again ample evidence that the slow seasonal change in mean temperature is capable of absorbing irregularities in intervals as well as reasonably large intervals. Intervals longer than a month do not appear to be adequate to follow the annual mean temperature curve. Results of trials with 9 and 7 observations a year (intervals of approximately 1½ and 2 months) were not consistent with those of monthly and weekly observations.

THERMAL COMPARISONS WITH TEMPERATURE UNITS

The difference in temperature units between the Convict Lake heat cycles of 1951 and of 1952 may be used to demonstrate the applicability of the summation method to annual or cyclic comparisons; but for this purpose it is necessary to adjust the time periods in tables 5 and 6. It has been shown that the severe winter of 1951–52 resulted in delayed heating as well as generally lower water temperatures in the following spring and summer, so that the 1952 cycle from winter minimum to winter minimum involved considerably less heat than the preceding cycle. However, the annual temperature unit totals in tables 5 and 6 were computed on a May-to-May basis to include all data for 2 noncalendar years. The below-normal temperatures of early 1952 (prior to May) are therefore actually appended to the 1951 cycle (table 5), and the relatively high, early spring temperatures prior to May 1953 are added to the 1952 cycle (table 6). This overlapping of cycles has a compensating effect on both "data

TABLE 6.—*Summations of mean temperatures above 32 ° F. in Convict Lake, by weekly and monthly intervals, May 1952 to May 1953*

Period	Time interval (TI) in days		Mean temperature of interval		Mean daily temperature units (TU)		Temperature units in time interval (TU × TI)	
	Weekly	Monthly	Weekly	Monthly[1]	Weekly	Monthly	Weekly	Monthly
May 9–16	7		41.90		9.90		69.3	
May 16–23	7	28	43.05	43.45	11.05	11.45	77.4	320.6
May 23–29	6		44.15		12.15		72.9	
May 29–June 6	8		45.25		13.25		106.0	
June 6–16	10		45.60		13.60		136.0	
June 16–24	8	33	45.75	46.70	13.75	14.70	110.0	485.1
June 24–July 1	7		46.45		14.45		101.2	
July 1–9	8		47.30		15.30		122.4	
July 9–16	7		48.15		16.15		113.0	
July 16–23	7		49.40		17.40		121.8	
July 23–30	7	35	50.10	49.70	18.10	17.70	126.7	619.5
July 30–Aug. 6	7		50.35		18.35		128.4	
Aug. 6–13	7		51.20		19.20		134.4	
Aug. 13–21	8		52.10		20.10		160.8	
Aug. 21–28	7	28	52.05	51.70	20.05	19.70	140.4	551.6
Aug. 28–Sept. 5	8		51.70		19.70		157.6	
Sept. 5–10	5		51.75		19.75		98.8	
Sept. 10–17	7		51.65		19.65		137.6	
Sept. 17–26	9	29	51.50	51.60	19.50	19.60	175.5	568.4
Sept. 26–Oct. 3	7		51.55		19.55		136.8	
Oct. 3–9	6		51.60		19.60		117.6	
Oct. 9–16	7		51.50		19.50		136.5	
Oct. 16–23	7	29	51.45	50.65	19.45	18.65	136.2	540.8
Oct. 23–30	7		50.80		18.80		131.6	
Oct. 30–Nov. 7	8		50.00		18.00		144.0	
Nov. 7–18	11		47.95		15.95		175.4	
Nov. 18–24	6	34	45.45	44.95	13.45	12.95	80.7	440.3
Nov. 24–Dec. 4	10		43.70		11.70		117.0	
Dec. 4–11	7		41.35		9.35		65.4	
Dec. 11–17	6		40.10		8.10		48.6	
Dec. 17–23	6	32	39.55	38.55	7.55	6.55	45.3	209.6
Dec. 23–Jan. 12	20		38.00		6.00		120.0	
Jan. 12–19	7		36.75		4.75		33.2	
Jan. 19–30	11	30	36.45	36.55	4.45	4.55	49.0	136.5
Jan. 30–Feb. 11	12		36.25		4.25		51.0	
Feb. 11–19	8		36.05		4.05		32.4	
Feb. 19–Mar. 6	15	28	36.35	36.85	4.35	4.85	65.2	135.8
Mar. 6–11	5		37.15		5.15		25.8	
Mar. 11–31	20	28	38.55	38.60	6.55	6.60	131.0	184.8
Mar. 31–Apr. 8	8		39.55		7.55		60.4	
Apr. 8–15	7		39.85		7.85		55.0	
Apr. 15–22	7	32	40.50	41.00	8.50	9.00	59.5	288.0
Apr. 22–May 2	10		41.25		9.25		92.5	
May 2–10	8		42.00		10.00		80.0	
Total	366						4,480.3	4,481.0

[1] Monthly interval mean temperatures are averages of initial and final monthly temperatures.

years" as tabulated, and the indicated temperature unit totals are not representative of the cycles.

To compare the cycles of the 2 years with present data, it is therefore necessary to eliminate the early spring temperatures, and to include in the summations only the temperature units between the initial May dates and winter dates chosen to represent near-minimum temperatures. Suitable periods from tables 5 and 6 are May 7 to December 14, 1951, and May 9 to December 16, 1952. Although temperatures had not reached the minimum at mid-December, these winter dates approximate the time when an ice cover forms on the lake, they permit equal comparison periods for the 2 years, and, on a weekly-interval basis, their mean temperatures are nearly identical for both years. Temperature-unit totals for the two periods (from tables 5 and 6) were 3,843.6 for 1951 and 3,566.8 for 1952. The difference of 277 units is significant. In a little over 7 months in 1951 there were roughly 6,650 more hour-degrees of heat above the freezing point than in a similar period in 1952. Moreover, a further comparison of two 4-month periods (May 7 to Sept. 11, 1951, and May 9 to Sept. 13, 1952) gives an almost equal difference of 273 temperature units, indicating quantitatively that the greatest difference in available heat between the two cycles was effective during late spring and summer months when higher temperatures prevailed.

In the same manner, annual, subannual, or shorter periods of interest may be compared among lakes in a given year. Data for 25-day periods in July and August 1953 are available for a short-term comparison among 10 lakes of the Convict Creek Basin, ranging in elevation from 7,583 feet (Convict Lake) to 10,950 feet (Lake Constance). In table 7, the lakes are arranged according to interval mean temperatures and summations above freezing for the 25-day intervals, which were as nearly simultaneous as travel conditions and other work permitted. These periods are too early to include highest summer mean temperatures, yet they are far enough advanced that the temperature differences among lakes would be changed but slightly by the amount of further heating to be expected during August.

It may be seen that there is sufficient variability of summations in such periods of representative summer temperatures to scale these related lakes for thermal comparison, or to correlate temperature sums with biological variables in a definite unit of time.

Also given for each lake (table 7) are mean depth, range of mean temperatures in the period, and number of gram-calories required to warm the standard "heat budget" unit of water (mean depth $\times$ 1 sq. cm.) from the freezing point to the interval mean temperature. The latter value may be represented as the energy content, above the freezing point, of a mean column of water at the interval mean temperature. This series of energy values, as influenced by the mean depths of the lakes, is in no way comparable with the series of summations of existing temperatures. The inclusion of mean depths essentially characterizes the lakes volumetrically and makes them noncomparable.

If the tabulated caloric values were factored by the mean depths, the result would be energy content per mean cubic centimeter, expressed in gram-calories as the number of degrees (centigrade) of the interval mean temperatures. Such values would be comparable by ratio to the temperature

TABLE 7.—*Thermal characteristics of 10 lakes in Convict Creek Basin, by 25-day periods, July and August 1953*

[Temperature in degrees Fahrenheit except in calculation of gram-calories]

Lake	Mean temperatures					Temperature units ((T^i_m-32) 25)	Gram-calories (T^i_m–0° C.)	Mean depth (feet)
	Initial		Final		Interval (T^i_m)			
	°F.	Date	°F.	Date				
Convict	51.8	7/15	53.9	8/9	52.9	522	31,007	88
Bighorn	45.7	7/13	51.5	8/7	48.6	415	4,471	16
Cloverleaf	43.9	7/15	52.5	8/9	48.2	405	3,276	12
Bright Dot	43.2	7/13	51.0	8/7	47.1	378	9,946	39
Genevieve	44.3	7/14	48.5	8/8	46.4	360	14,824	61
Mildred	44.0	7/13	48.1	8/7	46.1	352	6,478	27
Edith	42.6	7/14	46.3	8/8	44.5	312	12,544	59
Witsanapah	41.2	7/13	46.6	8/7	43.9	298	5,610	28
Dorothy	42.0	7/16	43.8	8/10	42.9	262	25,193	136
Constance	40.0	7/18	44.1	8/12	42.1	252	12,074	71

summation values, but they would have no connection with the 25-day period; they could apply to unequal periods, or to any given instant at the proper mean temperatures. If caloric evaluations were limited to the temperatures of the 25 days, based on initial and final mean temperatures and excluding mean depths, the results would be expressions not of energy content but of changes in energy storage. A period so situated as to indicate no change in mean temperature would then have no calories indicated.

In such comparisons of lakes, the central interest is in the heat of the water, with regard to time but without regard to volume. For this, temperature summations give adequate evaluations of heat. Caloric assessments are not suitable because gram-calories are intimately concerned with a unit volume of water (1 gram=1 cc.) and are expressible over a period of time only as rates of gain or loss.

TEMPERATURE AND PERIPHYTON PRODUCTIVITY IN CONVICT LAKE

In 1953 and 1954, continuous sampling of periphyton was attempted in Convict Lake as part of a current investigation to determine the suitability of this material as an indicator of basic productivity, primarily in oligotrophic alpine lakes. Techniques of periphyton sampling and analysis and results of preliminary 1952 sampling in the Convict Creek Basin lakes were reported by Nielson (1953). Briefly, the method consists of collecting and analyzing 25-day increments of attachment material on known areas of artificial substrate suspended in various depth strata. In deeper lakes, stations are located at appropriate depths to sample littoral, limnetic, and profundal zones. After controlled air drying, weighing, ignition, and reweighing, the material is represented as total dry residue, organic fraction, and ash fraction in milligrams per square decimeter of substrate corrected to mean values for the entire lake or for the division that is of interest.

In Convict Lake sampling, the relation between environmental temperature and periphyton production per time unit was of interest as a reference to the usefulness of periphyton for index purposes. Initial and final temperature series were recorded for each 25-day sampling period, and summations based on interval mean temperatures were used to determine a relationship. Except for a January to April gap when the periphyton sets were inaccessible, the five sampling periods in which sets remained undisturbed were consecutive and represent the transition from winter to summer temperatures. Temperature summation data and organic periphyton values for these periods are presented in table 8, and have been plotted on figure 8 with a regression line fitted by the method of least squares. The coefficient of correlation for the relationship (+0.966) was highly favorable, and from this it may be concluded that the periphyton assemblage is measurably sensitive to variations of temperature within the observed range.

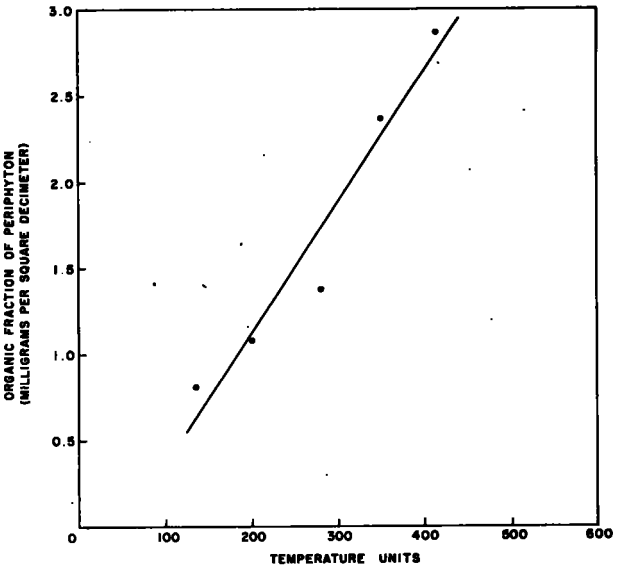

FIGURE 8.—Relation of organic periphyton increment to temperature sums above 32° F. for five 25-day periods in Convict Lake, Calif., November 1953 to July 1954. Line shown is least squares fit: $r=+0.966$; $y=-0.40+0.0076\,x$.

TABLE 8.—*Mean temperatures, temperature units, and mean periphyton quantities for five 25-day periods in Convict Lake, 1953 and 1954*

Sampling period	Mean temperatures			Temperature units	Organic periphyton [1]
	Initial	Final	Interval		
1953					
Nov. 17–Dec. 12	42	38	40	200	1.09
1954					
Dec. 12–Jan. 6	38	37	37.5	137.5	0.81
Apr. 22–May 17	41	45.5	43.2	280	1.38
May 17–June 11	45.5	46.6	46	350	2.36
June 11–July 6	46.6	50.7	48.6	415	2.87

[1] Lake mean values, expressed in milligrams per square decimeter of sample surface.

Of principal interest here, however, is the usefulness of temperature summations in determining such a relationship. Since the amount of attached material at the end of a 25-day period constitutes the sum of daily increments of attachment and daily increments of growth (of the material already attached), and since these two components are very difficult to separate (Newcombe 1950), it is desirable for the purpose of correlation to represent each periphyton sample as the total amount which has accumulated in a sampling period rather than as an indication of the rate of incrementation. In this connection, it is more accurate to represent the corresponding temperature structure as a sum than as the existing temperature condition. Temperatures alone do not characterize the periods quantitatively, whereas summations permit a direct quantitative association of temperature with the periphyton measurement on a time basis.

VALUE OF TEMPERATURE SUMMATION

In the continuing search for reliable indices of lake productivity, information indicative of the extent to which production is controlled by temperature may be of considerable importance, particularly in alpine situations. Rawson (1939) pointed out that in extreme oligotrophy low temperature is a major if not the limiting factor in production, and cited Lundbeck (1934) as a proponent of thermal oligotrophy in some lakes of the Alps. McCombie (1953) presented evidence of the controlling influence of temperature on phytoplankton growth and abundance. Rawson (1942) found a relation between the average standing crops of plankton and the mean temperatures of upper strata in a series of alpine lakes of western Canada, but he concluded (1953) that the standing crop of plankton is unlikely to provide a satisfactory index of basic productivity for lakes because of difficulties of sampling, rapid turnover and radical short-term changes in abundance of the crop, and small effective range of variation among lakes. Limitations of standing-crop measurements have been noted by others, and it is well recognized that an ideal measure of biological productivity should include the time factor and be expressible as a rate of production. Clearly, the temperature relations of any such index measurement should be known, for, to be valid, the index must conform with the known influences (heat, light, and nutrients) that act in combination to control or limit productivity in the larger sense.

It is suggested that the summation of temperatures constitutes a useful tool for the evaluation of heat intensity in lakes, both for problems of thermal comparison and for the investigation of biological temperature relations in which time is a factor. Advantages of the method for either purpose are (1) independence of depth, volume, and heat capacity factors which restrict the utility of caloric evaluations; (2) inclusion of the time factor, which in effect adds an extra dimension to temperature data; (3) applicability to selected comparison periods in accordance with objectives, seasonal limitations on field work, et cetera; and (4) adaptability to comparisons among selected parts of lakes (e. g., epilimnia of thermally complex lakes) as well as among entire lakes. In the study of temperature relations, the inclusion of time by the simple expedient of summing mean temperatures is perhaps less accurate than some situations require. Still, the biological assessments of lake productivity in general are far from a state of exactitude and a summation method would appear to be helpful in a further understanding of the role of temperature.

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GROWTH, MIGRATIONS, SPAWNING AND SIZE DISTRIBUTION OF SHRIMP *PENAEUS SETIFERUS*

BY MILTON J. LINDNER AND WILLIAM W. ANDERSON

FISHERY BULLETIN 106

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

In order to establish growth and migration patterns, approximately 45,000 shrimp were tagged and released between 1935 and 1939, in separate areas of the coast from North Carolina to Mexico. Of the shrimp released, more than 7,000 were recaptured, having been at liberty up to 200 days.

Tagged shrimp grow rapidly from March through September, but growth almost ceases from October through February. At the growth rate inferred from an analysis of the short-term increments of the shrimp recaptured, they grow from 10 cm. in length in April to 16 cm. in July, and to 19 cm. by November of a single year. Or, if they are 10 cm. long in July, they measure 16 cm. by November.

Tagged shrimp released along the south Atlantic coast in the fall were recovered consistently to the south of the area of release; those released in early spring tended to be retaken to the north. Large shrimp, those longer than 13 cm., moved more extensively than did the smaller ones.

Gulf-coast releases demonstrated no consistent migration pattern, other than the movement from inside waters to outside oceanic areas. The movement to outside waters was discovered at all areas of release, and pertains largely to small shrimp. Few large shrimp were found in inside waters.

Although the eggs and larvae of the white shrimp have rarely been taken, the location of females with ripe ovaries leads one to infer that spawning takes place offshore. Ripe females were obtained in most areas from April through August, but there may be separate populations spawning in different months.

On the basis of size distribution, both of commercially caught shrimp and of those taken by research vessels, at least two separate groups of young shrimp move from inside to outside waters each year. One group enters the offshore areas in June, the other in August or September. The latter group was probably spawned in the spring of the same year; the former, in the summer of the previous year.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

GROWTH, MIGRATIONS, SPAWNING AND SIZE DISTRIBUTION OF SHRIMP *PENAEUS SETIFERUS*

By Milton J. Lindner and William W. Anderson

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GROWTH, MIGRATIONS, SPAWNING, AND SIZE DISTRIBUTION OF SHRIMP, *PENAEUS SETIFERUS*

By Milton J. Lindner, *Technical Adviser, Fishery Mission to Mexico,* and William W. Anderson, *Fishery Research Biologist*

A steady increase in the production of shrimp along the Atlantic and Gulf coasts of the United States had by 1930 made canned shrimp the most valuable fishery product in the region. At that time, anxiety about the future of the expanding industry resulted in many requests for a biological study of the heavily exploited shrimp resources.

In February 1931 an investigation was initiated when F. W. Weymouth and M. J. Lindner visited the chief shrimp ports to make a brief survey of the fishery and to arrange the details of cooperation offered by the various States in which shrimping was carried on. As this fishery extends over more than 3,000 miles of coastline, it was necessary to have the cooperation of several States in order to obtain as complete information as possible with the limited funds available. Georgia, Louisiana, and Texas entered into the joint program and contributed in various ways. Headquarters were established at New Orleans, while various parts of the investigations were pursued at a number of places between Beaufort, N. C., and Port Aransas, Tex.

Although three species of shrimp occur in the fishery through most of its range from North Carolina to the Mexican border, the major effort was directed toward learning the life history of the common white shrimp of the United States, *Penaeus setiferus* (Linn.). This species was at that time by far the most important, and comprised more than 95 percent of the commercial catch.

The approach to the problem was as diversified as funds and facilities permitted and included investigations of the life history, including spawning, embryology and larval history, postlarval growth, longevity, and migrations; abundance analyses; biometrical studies with respect to racial determinations; and the effect of fishing, in relation to gear, localities, and time, on the composition of the catch. Experimental trawling provided data to supplement those gathered from the commercial catch. Temperature and salinity data were accumulated as a basis for interpreting shrimp behavior in relation to hydrographic factors; and certain life-history details and behavior patterns were checked under laboratory conditions.

In December 1934, experiments were initiated on the use of tags for marking shrimp. Experiments on shrimp retained in pens showed that the celluloid-disk type of tag affixed to the first abdominal somite of the shrimp was probably the best method, as it apparently interfered less with movements and molting and was retained better than other devices. During the latter part of 1935 this method of tagging was first used in the field and resulted in recoveries of almost 25 percent. This new method provided much needed direct evidence on growth and migrations, and the tagging program was continued with marked success until curtailed by World War II. Much of the material in this report is based on results produced by this technique.

Throughout the years in which we made this study of shrimp we had many colleagues and associates, who contributed in one way or another to this report. Among these were C. Howard Baltzo, Albert W. Collier, Jr., Forrest Durand, the late J. Nelson Gowanloch, Gordon Gunter, J. S. Gutsell, Joseph E. King, C. W. McPhail, Kenneth H. Mosher, John C. Pearson, and F. W. Weymouth. We appreciate their help, and we appreciate also the analytical assistance of George A. Rounsefell and the help given by the conservation agencies of the various States, particularly Georgia, Louisiana, and Texas. We are indebted to Martin D. Burkenroad, Theodore M. Widrig, and Rolf L. Bolin for critical review of the manuscript.

GROWTH

TAGGING

We obtained our growth data from shrimp tagged in various areas from North Carolina to Texas. Thus our results embrace the entire fishery.

The tag used consisted of two small celluloid disks and a nickel pin (fig. 1). The disks, one white and the other red, were perforated in the center. The white disks were numbered consecutively, and the red ones bore instructions for returning the shrimp. The disks were of opaque celluloid, ten one-thousandths of an inch thick, protected by a layer of transparent celluloid five one-thousandths of an inch thick. Most disks used were three-eighths of an inch in diameter, although some of the smaller shrimp were tagged with disks five-sixteenths of an inch in diameter. The pins were of pure nickel wire. A pin, with a white, numbered disk mounted, was thrust through the side of the first abdominal somite about midway between the dorsal and ventral surfaces; a red disk was slipped over the end of the pin protruding from the other side of the shrimp, and a loop was made in the pin with surgical forceps to prevent the disk from slipping off. Approximately ⅛-inch to ¼-inch play was left between the sides

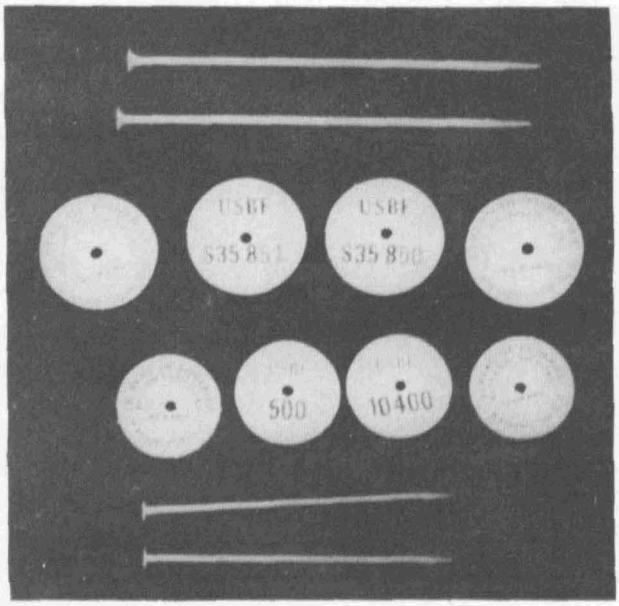


FIGURE 1.—Tags and pins used in marking experiments.

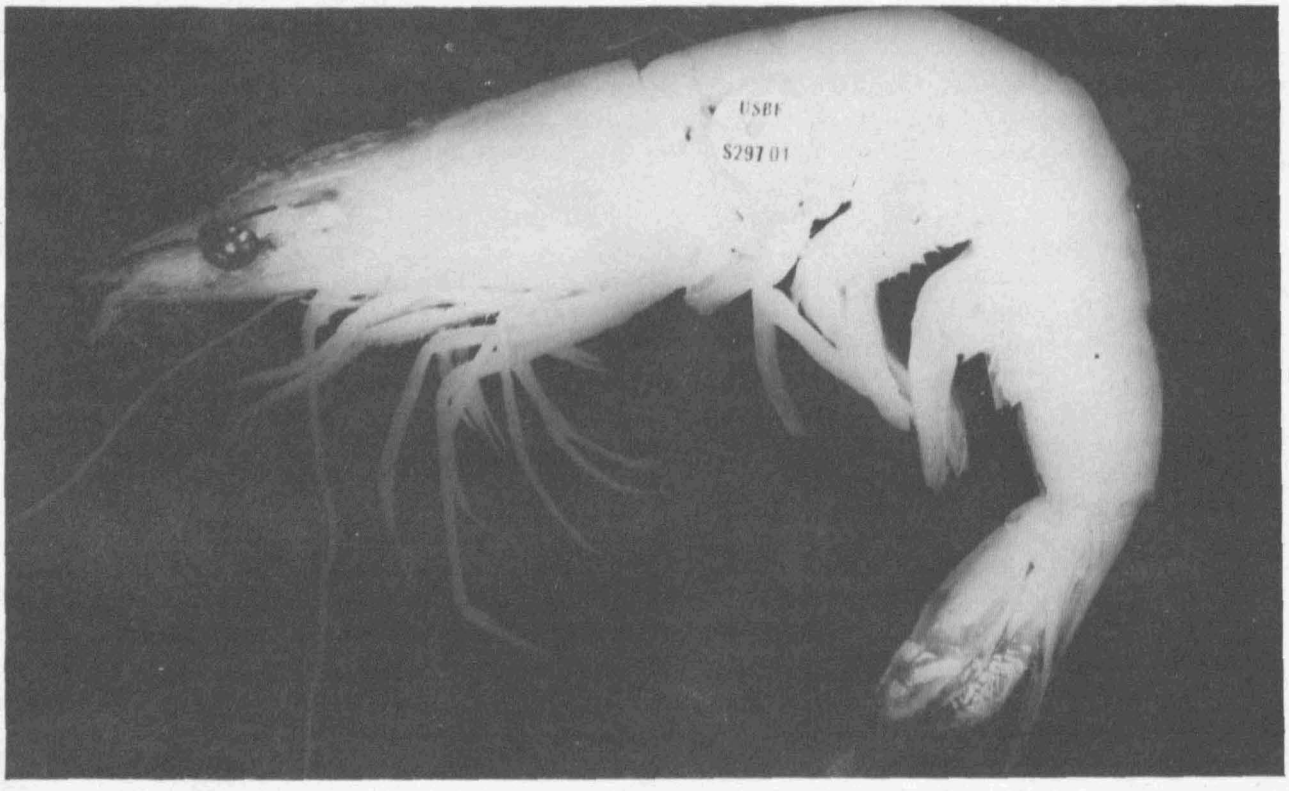


FIGURE 2.—A tagged specimen of the common or white shrimp of the United States, *Penaeus setiferus*.

FIGURE 3.—Tagging shrimp along the east coast of Mexico.

of the shrimp and each disk to allow for growth. The pin traversed the animal through muscle tissue only, and no vital organs were penetrated (fig. 2).

Several methods of capturing shrimp for tagging were tried, such as trapping and seining, and were discarded because they required too much time for the number of shrimp obtained. The commercial shrimp trawl, hauled slowly for a short time (15 to 20 minutes), provided animals in sufficiently good condition for tagging, and this gear was used exclusively.

Wooden or metal tubs were used for holding shrimp aboard the vessel. In addition, a conical net about 3 feet in diameter and 8 feet in length was suspended overboard for holding surplus shrimp not accommodated by the tubs. The live shrimp, as soon as they were hauled aboard, were separated from the fish, dead shrimp, and other organisms and placed in the tubs which had been previously filled with sea water. When this operation was completed, the shrimp that appeared to be in good condition were moved to other tubs of water. The water in the tubs was changed frequently, and dead or dying shrimp were discarded. A small deck pump supplied clean sea water.

Two men did the tagging and a third the recording (fig. 3). The two tubs in which the actual tagging occurred were placed side by side on a table of convenient height. A removable balsa-wood board was fastened to an arm extending vertically between the two tubs. The white, numbered disks were mounted on the pins and stuck on the balsa board in serial order so that either person tagging could remove the tags in sequence. A box of red disks was placed on the table within easy reach of both taggers. A floating measuring board, graduated in half-centimeter units, was placed in each tagging tub. A similar board, as well as the technique of measuring, has been described by Weymouth, Lindner, and Anderson (1933).

So far as possible, measuring and tagging were done under water. As the shrimp were tagged,

they were placed in another tub of water, and releases were made in batches of 50. When a batch had been tagged, the shrimp were examined, and substitutions were made for all that appeared to be in poor condition. They were then released by gently emptying the tub overside.

In all experiments a record was maintained of the date, time, and place of capture, the tag number, the sex and length (to the nearest half-centimeter) of each shrimp, and the date, time, and place of release.

Before tagging was begun, it was necessary to acquaint the industry with the work and to make arrangements for handling the returns. Trips were made to all landing ports, and dealers and fishermen were told of the program.

Each shrimp-receiving house was supplied with a jar of formalin for preserving tagged shrimp. Each was also given a book of printed forms on which could be recorded the tag number, the fisherman's name, the boat name, the date of capture, and the place of capture. Posters describing the program and giving instructions on the proper handling of tagged shrimp were placed in strategic places. A reward of 50 cents was given for the return of each whole, marked shrimp accompanied by information on date and place of capture. If the tag was returned without the shrimp, but with the required information, a reward of 25 cents was given. Trips were made at least once each month to collect the tagged shrimp and information, and to pay the rewards.

The success in obtaining tag returns depended on the cooperation of the dealers and fishermen. We were most fortunate in that this cooperation was excellent.

The white disk was always placed on the same side of the shrimp, and the pin from each return was examined carefully to see whether an attempt had been made to substitute another shrimp for one that had been tagged. These checks, together with the known sex of the tagged shrimp, served to prevent our obtaining fraudulent information. Attempts to substitute shrimp were made in very few instances, and these were always during the initial stages of an experiment in a new area. Whenever information was suspect or incomplete, the return was classified as uncertain.

Since it is conceivable that measurements of live shrimp and of those caught by fishermen and preserved in formalin might vary considerably, we ran an experiment to approximate conditions that would occur with marked shrimp caught in the commercial fishery. In this experiment, 300 shrimp were measured alive under water, allowed to die on deck and remain for 1 hour, then were iced down for 24 hours, placed in formalin for another 24 hours, and removed and measured. They were returned to the formalin solution for 1 week, measured again, and returned to the solution for 2 additional weeks, after which they were measured once more. All measurements were of whole shrimp, and to the nearest millimeter (table 1). The means indicate no significant differences between the various measurements. The small differences that occur are obviously the result of observational errors.

EFFECT OF TAGGING

Evidence indicates that some shrimp die as a result of tagging, and that the mortality rate is not uniform with respect to size. In figure 4 and table 2 we show the increasing percentage of recaptures with increasing length (up to about 13.5 cm.). These results we interpret to mean that the smaller the shrimp, the greater the initial tagging mortality.

TABLE 1.—*Effect of preservation in formalin on length of shrimp*

Size group	Number in size group, when measured—			
	Alive	After preservation in formalin for—		
		24 hours	1 week	3 weeks
96–100 mm	12	14	12	14
101–105 mm	28	26	25	24
106–110 mm	29	30	29	33
111–115 mm	23	25	21	24
116–120 mm	30	28	32	29
121–125 mm	29	28	29	26
126–130 mm	19	19	24	23
131–135 mm	28	30	23	22
136–140 mm	26	23	24	25
141–145 mm	27	29	28	30
146–150 mm	21	19	23	22
151–155 mm	15	15	13	14
156–160 mm	7	7	9	7
161–165 mm	5	6	7	6
166–170 mm	1	1	1	1
Total number of shrimp	300	300	300	300
Mean length	126.84	126.82	127.48	126.86

Since the curve levels off at about 13.5 cm., initial tagging mortality apparently is constant in sizes larger than this. It seems entirely logical that initial tagging mortality could be negatively correlated with size up to a certain limit, and be

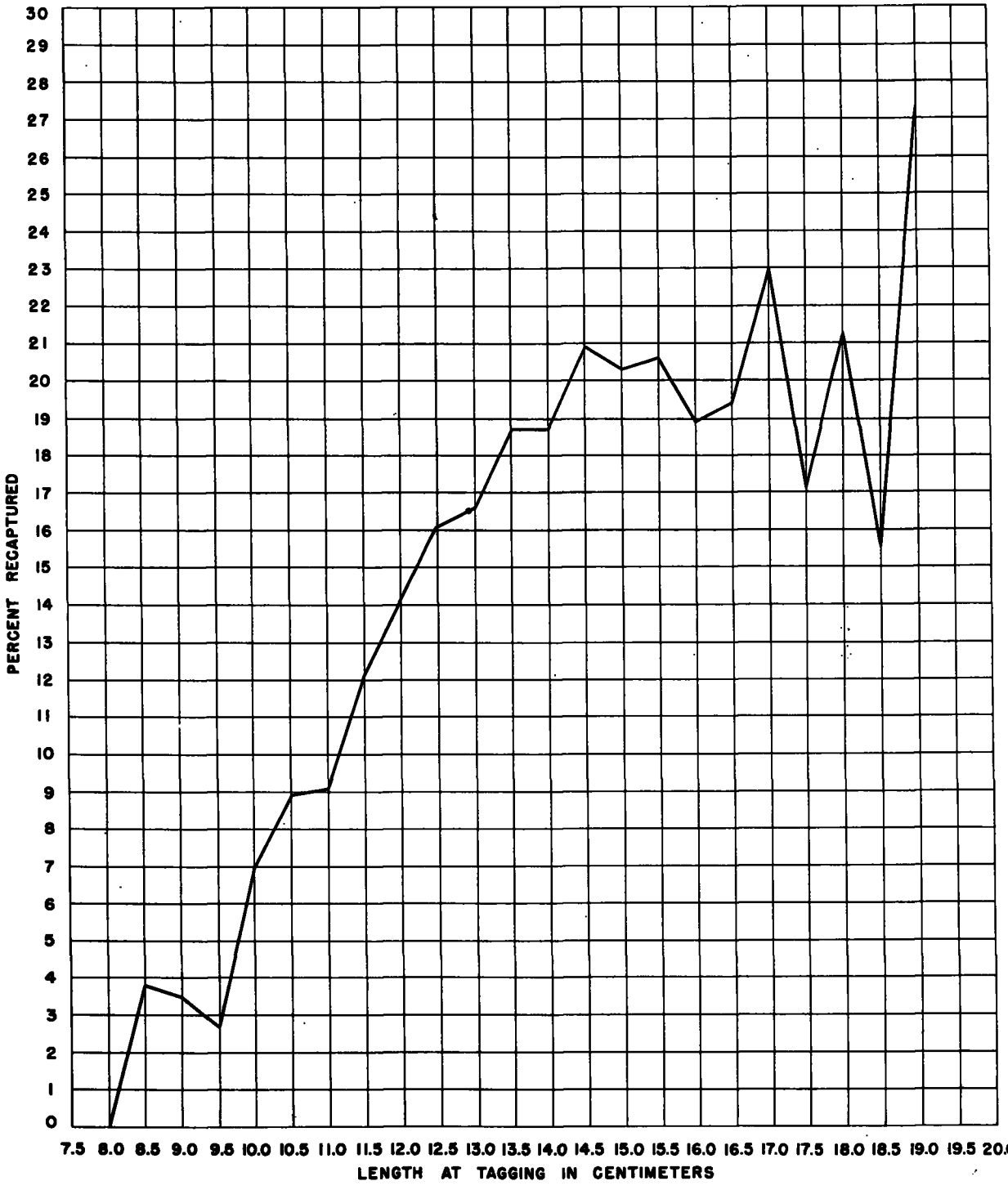


FIGURE 4.—Percentage of shrimp recaptured, according to size at time of tagging.

unaffected by increasing length from this size on. This same type of curve could also result from differential fishing intensity, based on the size of the shrimp, together with a high residual tagging mortality, or a high natural mortality, or both. However, from our experience with the fishery we do not believe that differential fishing appreciably affects the curve.

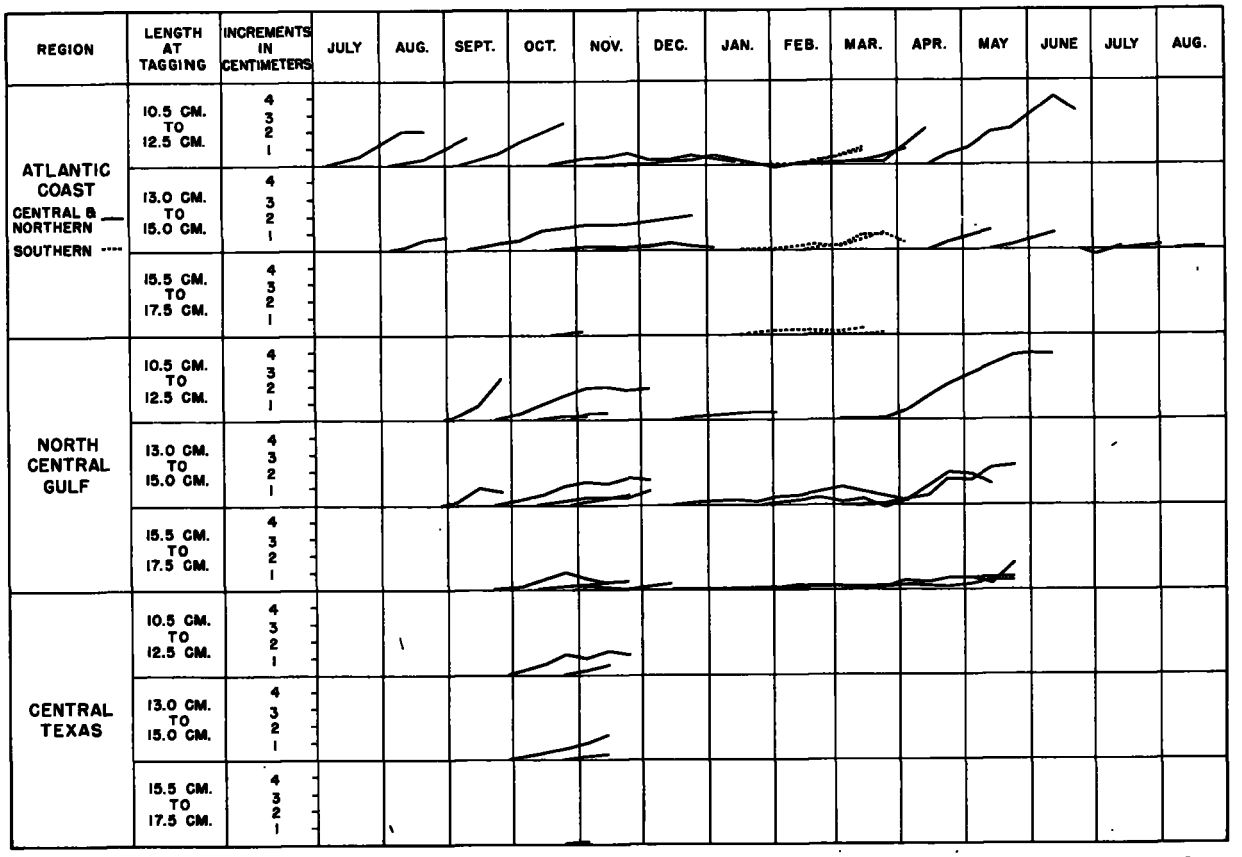


FIGURE 5.—Average growth of marked shrimp throughout the year. The curves begin at the base line on the date of release and follow the average increment, at approximate 10-day intervals, of all recoveries for each experiment. No 10-day interval contains fewer than three recoveries. If more than 1 day of release is included in an experiment, the beginning date is taken as midway between the release dates.

TABLE 2.—*Number of shrimp tagged and number and percentage recovered, according to size when tagged*

[Areas 1 to 38]

Length at tagging	Number released	Number recovered	Percent recovered
7.0 cm	2		0
7.5 cm	80		0
8.0 cm	20		0
8.5 cm	105	4	3.8
9.0 cm	227	8	3.5
9.5 cm	600	16	2.7
10.0 cm	1,372	96	7.0
10.5 cm	2,292	203	8.9
11.0 cm	3,202	292	9.1
11.5 cm	3,903	473	12.1
12.0 cm	4,175	591	14.2
12.5 cm	4,038	652	16.1
13.0 cm	3,665	610	16.6
13.5 cm	3,615	677	18.7
14.0 cm	3,142	588	18.7
14.5 cm	3,147	659	20.9
15.0 cm	3,204	650	20.3
15.5 cm	2,901	599	20.6
16.0 cm	2,246	424	18.9
16.5 cm	1,662	322	19.4
17.0 cm	868	200	23.0
17.5 cm	327	56	17.1
18.0 cm	141	30	21.3
18.5 cm	58	9	15.5
19.0 cm	22	6	27.3
19.5 cm	6	1	16.7
20.0 cm	1	1	100.0
20.5 cm	1		0
Total	45,022	7,167	

ANALYSIS OF RESULTS

The seasonal variations in rate of growth of marked shrimp, shown in figure 5,[1] could logically be expected to occur in unmarked individuals, and we therefore assume that the tagged specimens follow rather closely the course of growth of the entire population. It is apparent from figure 5 that growth is rapid during summer, slows down about the end of October, is slight during winter, and accelerates abruptly about the first of March or April, depending on the locality. This suggests that temperature is an important controlling factor, and if this is so we could expect the periods of rapid and slow growth to vary somewhat from year to year and with locality. The influence of locality is evident on the Atlantic coast, where the marked shrimp from the southern portion (Florida) started rapid growth in the

[1] See also tables 3 to 6 showing increments by approximate 10-day intervals of all measurable recoveries.

TABLE 3.—*Distribution by growth increments, of tagged shrimp recovered in northern and central Atlantic fishery*

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
July 6, 1938: [1]																
10.5–12.5 cm	July 6–July 17			1	2											3
	July 18–July 27			3	3	3	1									10
	July 28–Aug. 6					2	1									3
	Aug. 7–Aug. 16						3	4	3							10
	Aug. 17–Aug. 26						2	3	2							7
13.0–15.0 cm	Aug. 7–Aug. 16					1										1
	Aug. 17–Aug. 26						1									1
Aug. 3, 1938: [1]																
10.5–12.5 cm	Aug. 7–Aug. 16				2											2
	Aug. 17–Aug. 26			4	12											16
	Aug. 27–Sept. 5			1	1	4	1	1								8
	Sept. 6–Sept. 15					1	3	1	1							6
	Sept. 16–Sept. 25										1					1
13.0–15.0 cm	Aug. 7–Aug. 16		1	1	3											5
	Aug. 17–Aug. 26				2	1										3
	Aug. 27–Sept. 5				2	3										5
	Sept. 6–Sept. 15						1									1
Sept. 6–11, 1936:																
10.5–12.5 cm	Sept. 6–Sept. 20		3	27	8	3										41
	Sept. 21–Sept. 30			4	8	2	6									20
	Oct. 1–Oct. 10					1	4									5
	Oct. 11–Oct. 20						1									1
	Oct. 21–Oct. 30							2	1	1						4
	Oct. 31–Nov. 9							1		1						2
	Nov. 10–Nov. 19						1	1								2
	Dec. 30–Jan. 8									1						1
13.0–15.0 cm	Sept. 6–Sept. 20		5	39	11	2										57
	Sept 21–Sept. 30		1	8	23	2										34
	Oct. 1–Oct. 10			1	3	3										7
	Oct. 11–Oct. 20					6	2									8
	Oct. 21–Oct. 30					1	2									3
	Oct. 31–Nov. 9					2	1	2								5
	Nov. 10–Nov. 19					2	2	3								7
	Nov. 20–Nov. 29					1	1	1								3
	Dec. 10–Dec. 19							1								1
	Dec. 20–Dec. 29						2			1						3
	Dec. 30–Jan. 8						1									1
	Jan. 9–Jan. 18								1							1
	Jan. 19–Jan. 28						1									1
15.5–17.5 cm	Sept. 6–Sept. 20			2	1											3
	Sept. 21–Sept. 30			2	1											3
	Oct. 1–Oct. 20			1												1
	Oct. 21–Oct. 30						1	1								2
	Oct. 31–Nov. 9					1										1
Oct. 16–21, 1937:																
10.5–12.5 cm	Oct. 16–Oct. 30		9	65	33	6	1									114
	Oct. 31–Nov. 9		1	19	19	7	2	1								49
	Nov. 10–Nov. 19			4	6	4										14
	Nov. 20–Nov. 29			1	1	1	1									4
	Nov. 30–Dec. 9			3	1	1										5
	Dec. 10–Dec. 19		1		1	1										3
	Dec. 20–Dec. 29			1	2	2										5
	Dec. 30–Jan. 8					1										1
	Jan. 19–Jan. 28			3	1											4
	Feb. 18–Feb. 27		1			1										2
	Mar. 10–Mar. 19				1											1
13.0–15.0 cm	Oct. 16–Oct. 30		10	74	40	6										130
	Oct. 31–Nov. 9		9	22	18	5	1									55
	Nov. 10–Nov. 19			6	2	1										9
	Nov. 20–Nov. 29			4	1											5
	Nov. 30–Dec. 9		1													1
	Dec. 10–Dec. 19			3	2	3										8
	Dec. 20–Dec. 29		1	3	3	1										8
	Dec. 30–Jan. 8		1	2	2											5
	Jan. 9–Jan. 18			1	1											2
	Jan. 19–Jan. 28					1										1
	Jan. 29–Feb. 7					1										1
	Feb. 8–Feb. 17				1											1
15.5–17.5 cm	Oct. 16–Oct. 30		1	10	5											16
	Oct. 31–Nov. 9			3	2											5
	Dec. 20–Dec. 29			1												1
	Jan. 19–Jan. 28				1											1
	Jan. 29–Feb. 7			1												1
Nov. 9, 1937:																
10.5–12.5 cm	Nov. 9–Nov. 19		5	27	7											39
	Nov. 20–Nov. 29			2												2
	Nov. 30–Dec. 9		1	10	2											13
	Dec. 10–Dec. 19			7	3	1										11
	Dec. 20–Dec. 29			5	1			1								7
	Dec. 30–Jan. 8			1		2										3
	Jan. 9–Jan. 18			1	1											2
	Jan. 19–Jan. 28			3												3
13.0–15.0 cm	Nov. 9–Nov. 19			7	1											8
	Nov. 30–Dec. 9			3	2											5
	Dec. 20–Dec. 29				1					1						2
	Jan. 19–Jan. 28		1													1
15.5–17.5 cm	Nov. 9–Nov. 19		2													2

[1] Shrimp released on July 6 and Aug. 3, 1938, were immature, whereas those released on July 12 and Aug. 5–11, 1938, were mature.

TABLE 3.—*Distribution by growth increments, of tagged shrimp recovered in northern and central Atlantic fishery*—Continued

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Jan. 24, 1938:																
10.5–12.5 cm	Jan. 24–Jan. 28			1												1
	Jan. 29–Feb. 7		6	12	1											19
	Feb. 8–Feb. 17		3	31	5	1										40
	Feb. 18–Feb. 27		2	7				1								10
	Feb. 28–Mar. 9			1												1
	Mar. 10–Mar. 19		1	3	3											7
	Mar 20–Mar. 29		1		2											3
	Mar. 30–Apr. 8					2										2
13.0–15.0 cm	Apr. 9–Apr. 18						1		2							3
	Feb. 8–Feb. 17		1													1
	Mar. 10–Mar. 19			1												1
Feb. 23, 1938:																
10.5–12.5 cm	Feb. 23–Feb. 27			1												1
	Feb. 28–Mar. 9			2	1											3
	Mar. 10–Mar. 19		1	11	13	1										26
	Mar. 20–Mar. 29			5	17	5	1									28
	Mar. 30–Apr. 8				3	4		1								8
	Apr. 9–Apr. 18				1				1							2
	Apr. 19–Apr. 28								1		1					2
	Apr. 29–May. 8										1					1
	May 9–May 18							1								1
13.0–15.0 cm	Mar. 10–Mar. 19		1													1
	Mar. 20–Mar. 29				1	1										2
15.5–17.5 cm	Mar. 20–Mar. 29			2												2
Mar. 24, 1938:																
10.5–12.5 cm	Mar. 24–Mar. 29			1	2											3
	Mar. 30–Apr. 8			6	1											7
	Apr. 9–Apr. 18				2											2
	Apr. 19–Apr. 28						1	1								2
	Apr. 29–May 8							2								2
	May 9–May 18							1	1							2
	May 19–May 28								1							1
	June 8–June 17											1				1
13.0–15.0 cm	Mar. 24–Mar. 29			1												1
	Mar. 30–Apr. 8			1												1
	Apr. 9–Apr. 18				1											1
	Apr. 29–May 8									1						1
Apr. 14, 1938:																
10.5–12.5 cm	Apr. 14–Apr. 18		1	3	1	1										6
	Apr. 19–Apr. 28			6	13	16										35
	Apr. 29–May 8			2	9	7	4	3								25
	May 9–May 18					3	9	6	1	3	1					23
	May 19–May 28			1	1	1		1	1	2	2					9
	May 29–June 7											1				1
	June 8–June 17										1	2	1			4
	June 18–June 27								1		2					3
	June 28–July 7									1						1
	July 18–July 27														1	1
13.0–15.0 cm	Apr. 19–Apr. 28			3	3	1										7
	Apr. 29–May 8				2											2
	May 9–May 18				2		1	1								4
	May 19–May 28				1											1
	May 29–June 7					1										1
May 13, 1938:																
13.0–15.0 cm	May 13–May 18		5	14	8	1										28
	May 19–May 28		3	9	10	4										26
	May 29–June 7				1			1								2
	June 8–June 17				5	12	2	2								21
	June 18–June 27				1	1										2
	June 28–July 7						1									1
15.5–17.5 cm	May 13–May 18		1	1	1											3
	May 19–May 28		1		2											3
	June 8–June 17				1											1
June 24, 1938:																
13.0–15.0 cm	June 24–June 27		2	8	3											13
	June 28–July 7		2	2												4
	July 8–July 17			4	2											6
	July 18–July 27			1												1
	July 28–Aug. 6			1												1
15.5–17.5 cm	June 24–June 27		4	7												11
	June 28–July 7		1													1
	July 8–July 17		1	6	2											9
July 12, 1938:[1]																
13.0–15.0 cm	July 12–July 17			13												13
	July 18–July 27		1	5	3											9
	July 28–Aug. 6			3	2											5
	Aug. 7–Aug. 16			1	1											2
15.5–17.5 cm	July 12–July 17		6	11	3											20
	July 18–July 27		6	11	2											19
	July 28–Aug. 6		1	3												4
	Aug. 7–Aug. 16			1												1
Aug. 5–11, 1938:[1]																
13.0–15.0 cm	Aug. 5–Aug. 16		1	4	1											6
	Aug. 17–Aug. 26			5	1											6
	Aug. 27–Sept. 5				1											1
15.5–17.5 cm	Aug. 5–Aug. 16		3	9	1											13

[1] Shrimp released on July 6 and Aug. 3, 1938, were immature, whereas those released on July 12 and Aug. 5–11, 1939, were mature.

spring about one month earlier than in the central portion (Georgia).

A few 13- to 15-cm. shrimp from the central and northern Atlantic coast did not show the characteristic rapid growth during July and August; these are shown in the last two columns of figure 5. These shrimp were mature, whereas those from the same area depicted at the left were immature. The shrimp are not comparable, owing in part to the marked decrease in the rate of growth of the rostrum at maturity. This will be be discussed later.

TABLE 4.—*Distribution by growth increments, of tagged shrimp recovered in southern Atlantic fishery*

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Jan. 13–19, 1938:	Jan. 19–Jan. 28		3	18	7	1										29
	Feb. 8–Feb. 17		2	6	2											10
10.5–12.5 cm	Feb. 18–Feb. 27			1												1
	Feb. 28–Mar. 9		1		1	2										4
	Mar. 10–Mar. 19		1	1	2	1	2	1								8
	Jan. 19–Jan. 28		32	86	21	3										142
	Jan. 29–Feb. 7		2	8	5											15
	Feb. 8–Feb. 17		2	21	15	1										39
	Feb. 18–Feb. 27		1	11	5	2	1									20
13.0–15.0 cm	Feb. 28–Mar. 9		3	10	7	3										23
	Mar. 10–Mar. 19			3	14	6	3									26
	Mar. 20–Mar. 29			2	1	1	2		1							7
	Mar. 30–Apr. 8			1	1	1										3
	Jan. 19–Jan. 28		6	17	9	1										33
	Jan. 29–Feb. 7			2	2											4
	Feb. 8–Feb. 17			6	5	1										12
15.5–17.5 cm	Feb. 18–Feb. 27						1									1
	Feb. 28–Mar. 9		1	1	3											5
	Mar. 10–Mar. 19			2	4											6
	Mar. 20–Mar. 29			1												1
Feb. 13–20, 1938:																
	Feb. 13–Feb. 27			2	4		1									7
	Feb. 28–Mar. 9				4	1										5
10.5–12.5 cm	Mar. 10–Mar. 19			3	2	1	2	2								10
	Mar. 20–Mar. 29		1													1
	Feb. 13–Feb. 27		2	5	3											10
	Feb. 28–Mar. 9		2	5	5	3										15
13.0–15.0 cm	Mar. 10–Mar. 19			4	3	1	3	1	1							13
	Mar. 20–Mar. 29		1		3	1	2	1								8
	Feb. 13–Feb. 27		3	2	1											6
	Feb. 28–Mar. 9		2	9	4											15
15.5–17.5 cm	Mar. 10–Mar. 19		1	4	1											6
	Mar. 20–Mar. 29			3	1											4
	Mar. 30–Apr. 18		1													1

TABLE 5.—*Distribution by growth increments, of tagged shrimp recaptured in north-central Gulf fishery*

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Aug. 29–30, 1939:	Sept. 1–Sept. 10			3		1										4
	Sept. 11–Sept. 20			1	1		2									4
10.5–12.5 cm	Sept 21–Sept. 30							2	1	2						5
	Oct. 1–Oct. 10								1							1
	Oct. 11–Oct. 20										1					1
	Aug. 29–Aug. 31			1	6											7
	Sept. 1–Sept. 10			14	4	1										19
	Sept. 11–Sept. 20			1	3	7		1	1							13
	Sept. 21–Sept. 30			1		1	1									3
13.0–15.0 cm	Oct. 1–Oct. 10					1		1								2
	Oct. 21–Oct. 30							1								1
	Oct. 31–Nov. 9						1									1
	Nov. 10–Nov. 19							1								1
	Dec. 10–Dec. 19					1										1
Sept. 20–25, 1939:																
	Sept. 20–Sept. 30		5	58	22	4										89
	Oct. 1–Oct. 10			19	18	10	3									50
	Oct. 11–Oct. 20			2	6	8	6	1								23
	Oct. 21–Oct. 30			1	2	2	4	4	2							15
	Oct. 31–Nov. 9				1	1	4	4	2		1					13
10.5–12.5 cm	Nov. 10–Nov. 19						2	2	1							5
	Nov. 20–Nov. 29				1	1	4	4	3							13
	Nov. 30–Dec. 9					2	3	4	3							12
	Dec. 10–Dec. 19				1				1							2
	Dec. 30–Jan. 8									1						1
	Jan. 19–Jan. 28								1							1
	Sept. 20–Sept. 30	1	4	108	34	3										150
	Oct. 1–Oct. 10		2	13	23	3										41
	Oct. 11–Oct. 20			2	8		2									12
	Oct. 21–Oct. 30				2	1	3									6
13.0–15.0 cm	Oct. 31–Nov. 9				5	16	11	8	3							43
	Nov. 10–Nov. 19			1	1	5	3			1						11
	Nov. 20–Nov. 29				1	1	2	2	1							7
	Nov. 30–Dec. 9					3	1	2								6
	Dec. 10–Dec. 19						1									1
	Dec. 20–Dec. 29						1									1

TABLE 5.—*Distribution by growth increments, of tagged shrimp recaptured in north-central Gulf fishery*—Continued

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Sept. 20–25, 1939—Continued																
15.5–17.5 cm.	Sept. 20–Sept. 30		4	24	3											31
	Oct. 1–Oct. 10			8	2											10
	Oct. 11–Oct. 20			1	1											2
	Oct. 21–Oct. 30				1	1	1									3
	Oct. 31–Nov. 9			1	9	6										16
	Nov. 10–Nov. 19		1		1	1										3
	Nov. 20–Nov. 29				1											1
	Nov. 30–Dec. 19				1	1										2
Oct. 11–14, 1939:																
10.5–12.5 cm.	Oct. 11–Oct. 20			6												6
	Oct. 21–Oct. 30			6	4											10
	Oct. 31–Nov. 9			2	1											3
	Nov. 10–Nov. 19				1											1
	Nov. 20–Nov. 29				1											1
	Nov. 30–Dec. 9					1		1								2
13.0–15.0 cm.	Oct. 11–Oct. 20	1	4	21	6											32
	Oct. 21–Oct. 30	1	2	17	14	2	1									37
	Oct. 31–Nov. 9		2	21	31	10	1									65
	Nov. 10–Nov. 19		1	1	5	1										8
	Nov. 20–Nov. 29			3	6	1										10
	Nov. 30–Dec. 9			1	9	5	1		1							17
	Dec. 10–Dec. 19			1												1
	Dec. 30–Jan. 8				1											1
15.5–17.5 cm.	Oct. 11–Oct. 20		9	30	4											43
	Oct. 21–Oct. 30		1	7	3											11
	Oct. 31–Nov. 9	1	3	15	17	4										40
	Nov. 10–Nov. 19			3	1	2										6
	Nov. 20–Nov. 29			3	1	3										7
	Nov. 30–Dec. 9			1		1										2
	Dec. 10–Dec. 19					1										1
Oct. 27–28, 1939:																
10.5–12.5 cm.	Oct. 27–Oct. 30			3	7											10
	Oct. 31–Nov. 9			14	16	1										31
	Nov. 10–Nov. 19			2	3	1										6
	Apr. 28–May 7						1									1
13.0–15.0 cm.	Oct. 27–Oct. 30		1	6	4											11
	Oct. 31–Nov. 9		1	20	12	1										34
	Nov. 10–Nov. 19			1												1
	Nov. 20–Nov. 29			1	1	1										3
	Dec. 10–Dec. 19			1												1
	Dec. 30–Jan. 8			1												1
	Jan. 29–Feb. 7				1											1
	Feb. 8–Feb. 17				1											1
	Feb. 28–Mar. 8				1											1
	Mar. 29–Apr. 7						1									1
15.5–17.5 cm.	Oct. 27–Oct. 30			6	2	1										9
	Oct. 31–Nov. 9		1	25	7	3										36
	Nov. 20–Nov. 29		1	4	1											6
	Nov. 30–Dec. 9			2	1											3
	Dec. 10–Dec. 19			3	1	1										5
Nov. 10–15, 1939:																
10.5–12.5 cm.	Nov. 20–Nov. 29			1	2											3
	Nov. 30–Dec. 9					1										1
	Dec. 10–Dec. 19			1	1											2
	Jan. 29–Feb. 7				1											1
	Feb. 8–Feb. 17				1											1
	Feb. 28–Mar. 8				1											1
	Mar. 9–Mar. 18				1	1										2
	Mar. 29–Apr. 7				1	1										2
	May 8–May 17										1					1
13.0–15.0 cm.	Nov. 30–Dec. 9			3	2											5
	Dec. 10–Dec. 19			1												1
	Feb. 8–Feb. 17			1	1											2
	Feb. 18–Feb. 27					1										1
	Feb. 28–Mar. 8			1		1										2
Nov. 30, 1939:																
10.5–12.5 cm.	Nov. 30–Dec. 9			1												1
13.0–15.0 cm.	Nov. 30–Dec. 9			17	7											24
	Dec. 10–Dec. 19			2	1											3
	Dec. 30–Jan. 8		1													1
	Jan. 19–Jan. 28			1												1
	Mar. 19–Mar. 28			1												1
	Mar. 29–Apr. 7				1											1
	Apr. 8–Apr. 17				1											1
15.5–17.5 cm.	Nov. 30–Dec. 9		2	30	5											37
	Dec. 10–Dec. 19			2	1											3
Dec. 13–16, 1938:																
10.5–12.5 cm.	Dec 13–Dec. 19	2	4	49	14	1										70
	Dec. 20–Dec. 29	1		13	6											20
	Dec. 30–Jan. 8			1	1											2
	Jan. 9–Jan. 18				2											2
	Jan. 19–Jan. 28		1	1	5	1										8
	Jan. 29–Feb. 7			1	2											3
	Feb. 8–Feb. 17				1											1
	Apr. 19–Apr. 28							1								1

TABLE 5.—*Distribution by growth increments, of tagged shrimp recaptured in north-central Gulf fishery*—Continued

Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—													Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Dec. 13–16, 1938—Continued	Dec. 13–Dec. 19		1	19	9	1										30
	Dec. 20–Dec. 29			4	1											5
	Dec. 30–Jan. 8				1											1
	Jan. 9–Jan. 18			2	2											4
	Jan. 19–Jan. 28			2	1											3
	Jan. 29–Feb. 7			2	2	1										5
13.0–15.0 cm	Feb. 8–Feb. 17			2			1									3
	Feb. 28–Mar. 9					3										3
	Mar. 10–Mar. 19			1												1
	Mar. 30–Apr. 8		1	2		1										4
	Apr. 19–Apr. 28					1										1
	May 19–May 28								1							1
	May 29–June 7				1											1
	Dec. 13–Dec. 19		1	3												4
	Dec. 30–Jan. 8			1	1											2
	Jan. 9–Jan. 18			11												11
	Jan. 19–Jan. 28			1												1
	Jan. 29–Feb. 7		1	6	2											9
	Feb. 8–Feb. 17			10	1											11
	Feb. 18–Feb. 27			1												1
	Feb. 28–Mar. 9		1	8	3											12
	Mar. 10–Mar. 19		1	6	1											8
15.5–17.5 cm	Mar. 20–Mar. 29		1	5	3											9
	Mar. 30–Apr. 8			5	4											9
	Apr. 9–Apr. 18				1											1
	Apr. 19–Apr. 28		1	2	2											5
	Apr. 29–May 8			3		1										4
	May 9–May 18			2	2	2										6
	May 19–May 28			1	2	1										4
	June 8–June 17					1										1
	July 18–July 27						1									1
Jan. 20–26, 1939:																
	Feb. 28–Mar. 9				1	1										2
10.5–12.5 cm	Apr. 19–Apr. 28											1				1
	Jan. 20–Feb. 7			6	2	1										9
	Feb. 8–Feb. 17			4	3											7
	Feb. 18–Feb. 27			2	1	1										4
	Feb. 28–Mar. 9		2	10	5											17
	Mar. 10–Mar. 19			4	7											11
	Mar. 20–Mar. 29		1	5												6
13.0–15.0 cm	Mar. 30–Apr. 8			4	3											7
	Apr. 9–Apr. 18				1	1										2
	Apr. 19–Apr. 28						3	4	1							8
	Apr. 29–May 8				1	1		3		1						6
	May 9–May 18				1	1		1								3
	May 19–May 28					1	1									2
	June 8–June 17								1							1
	Jan. 20–Feb. 7			6	2											8
	Feb. 8–Feb. 17			7	6											13
	Feb. 18–Feb. 27			8	4											12
	Feb. 28–Mar. 9			18	4											22
	Mar. 10–Mar. 19			11	1											12
	Mar. 20–Mar. 29			8	2											10
15.5–17.5 cm	Mar. 30–Apr. 8			5	3	4										12
	Apr. 9–Apr. 18			2		1										3
	Apr. 19–Apr. 28			1	4	1	1									7
	Apr. 29–May 8			2	1	2	1									6
	May 9–May 18			1	2	3										6
	May 19–May 28			1	2	1	1									5
	Jun. 8–Jun. 17			1												1
Feb. 29–Mar. 6, 1940:																
	Feb. 29–Mar. 8		2	22	2											26
	Mar. 9–Mar. 18		14	68	7		1									90
	Mar. 19–Mar. 28	1	4	25	4	1										35
	Mar. 29–Apr. 7		1	1	7	3										12
	Apr. 8–Apr. 17				3	1	2	2	1							9
	Apr. 18–Apr. 27					1	1	1	1	1						5
10.5–12.5 cm	Apr. 28–May 7							3		3		1				7
	May 8–May 17									3	2					5
	May 18–May 27										3	1	1			5
	May 28–Jun. 6								1		1	1	1	1		5
	Jun. 7–Jun. 16									1		1	1			3
	Jun. 17–Jun. 26														2	2
	Jun. 27–Jul. 6											1	1			2
	Feb. 29–Mar. 8		1	1												2
	Mar. 9–Mar. 18		6	27	3											36
	Mar. 19–Mar. 28		2	7	2											11
	Mar. 29–Apr. 7		1	16	9	1										27
	Apr. 8–Apr. 17			1	1	1										3
	Apr. 18–Apr. 27				1	2	7	3	1							14
13.0–15.0 cm	Apr. 28–May 7			1	2	3	6	5		1						18
	May 8–May 17						2	2	1	1						6
	May 18–May 27					2	1	5	2	1	2					13
	May 28–Jun. 6					1			1							2
	Jun. 7–Jun. 16								1							1
	Jun. 17–Jun. 26											1				1
	Feb. 29–Mar. 8			2												2
	Mar. 9–Mar. 18		3	41	10											54
	Mar. 19–Mar. 28			10	2											12
	Mar. 29–Apr. 7		1	17	11											29
	Apr. 8–Apr. 17				5											5
15.5–17.5 cm	Apr. 18–Apr. 27			2	5	5										12
	Apr. 28–May 7			2	8	4	1									15
	May 8–May 17		1	3	8	1										13
	May 18–May 27				1		2	2								5
	Jun. 7–Jun. 16				1											1
	June 17–June 26			1												1

TABLE 6.—*Distribution by growth increments, of tagged shrimp recovered in central Texas fishery*

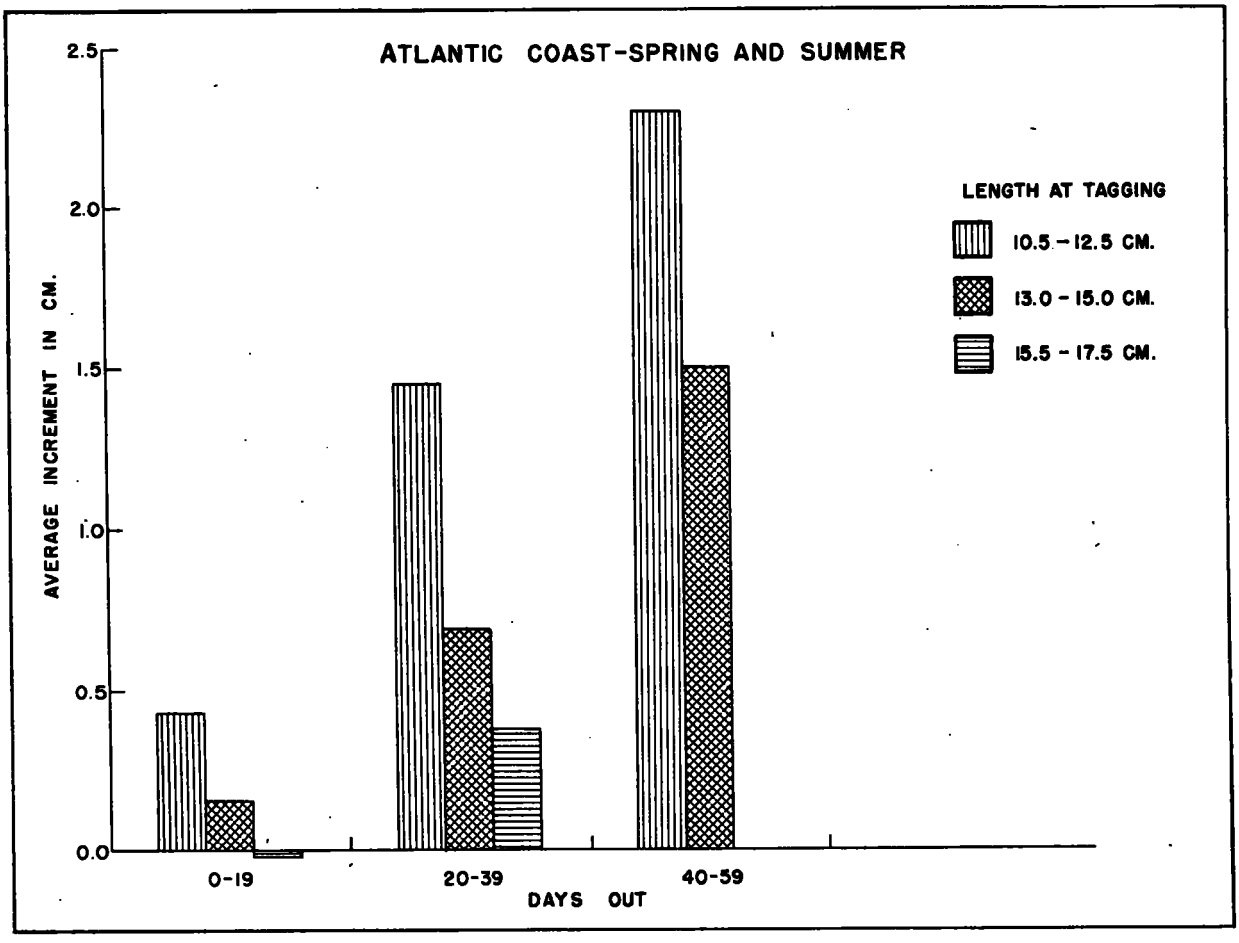
Date and size when released	Recovered in period—	Number with growth increments, in centimeters, of—														Total number
		−1.0	−0.5	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	
Aug. 27–31, 1937:																
10.5–12.5 cm	Aug. 27–Sept. 20			5	2											7
	Sept. 21–Sept. 30				1											1
	Oct. 1–Oct. 10								1							1
	Oct. 11–Oct. 20					1	1									2
	Oct. 31–Nov. 9								1							1
13.0–15.0 cm	Aug. 27–Sept. 20		5	5	1	1										12
	Sept. 21–Sept. 30				3	1										4
	Oct. 1–Oct. 10						2									2
	Oct. 21–Oct. 30			1												1
15.5–17.5 cm	Aug. 27–Sept. 20			2												2
	Sept. 21–Sept. 30			1												1
	Oct 1–Oct. 10			1												1
Sept. 23–Oct. 23, 1936:																
10.5–12.5 cm	Sept. 23–Oct. 10		11	35	7	1										54
	Oct. 11–Oct. 20			4	13	11										28
	Oct. 21–Oct. 30				1	5	6									12
	Oct. 31–Nov. 9				1	2	1									4
	Nov. 10–Nov. 19				2	3	6	1	1							13
	Nov. 20–Nov. 29				1	1	2									4
	Nov. 30–Dec. 9						1									1
	Dec. 10–Dec. 19							1								1
13.0–15.0 cm	Sept. 23–Oct. 10		9	23												32
	Oct. 10–Oct. 20			8	10	4										22
	Oct. 11–Oct. 30				8	3										11
	Oct. 21–Nov. 9				4	3	2									9
	Nov. 10–Nov. 19					2	1	1								4
	Nov. 20–Nov. 29					1										1
	Nov. 30–Dec. 9			1												1
	Dec. 10–Dec. 19					1										1
15.5–17.5 cm	Sept. 23–Oct. 10		3	3												6
	Oct. 11–Oct. 20		1	2	1											4
	Oct. 21–Oct. 30		1	1												2
	Oct. 31–Nov. 9				1											1
	Nov. 20–Nov. 29					1										1
	Nov. 30–Dec. 9				1											1
	Dec. 10–Dec. 19				1											1
	Dec. 20–Dec. 29				1											1
Oct. 20–28, 1937:																
10.5–12.5 cm	Oct. 20–Oct. 30		1	13	7	1										22
	Oct. 31–Nov. 9		1	12	7	3										23
	Nov. 10–Nov. 19				3	1										4
13.0–15.0 cm	Oct. 20–Oct. 30		9	29	11	1										50
	Oct. 31–Nov. 9		5	50	21	5										81
	Nov. 10–Nov. 19			3	3											6
15.5–17.5 cm	Oct. 20–Oct. 30		2	12	3											17
	Oct. 31–Nov. 9		3	14	4											21

The fact that we found soft-shelled, or recently molted, shrimp during winter indicates that some growth occurs during this season. Figure 6 also demonstrates this fact, but the winter growth is certainly negligible when compared with that of the spring, summer, and early fall. Of the shrimp released during winter (between November 1 and early February), the smallest and generally most rapidly growing group (10.5 to 12.5 cm.) had an average increment of only 5 mm. after 60 to 79 days, whereas during summer the same size group displayed a growth of more than 20 mm. in 40 to 59 days. No shrimp returned after February 28 were included in the calculations of the winter growth.

DESCRIPTION OF GROWTH

Not only does the rate of growth vary during different seasons, it also varies with the size of the shrimp. This is shown in tables 3 to 6. The data for spring and summer growth along the north and central Atlantic coast (typical also of other regions) (fig. 6) show that the smaller shrimp grow much more rapidly than do the larger ones. Walford (1946) described growth of this general type by plotting the length at a given age against the length at that age plus one unit of time, and applied the principle to several species of fishes and other animals. The same description of growth had previously been proposed by Von Bertalanffy (1938). It requires that the ratio of successive pairs of increments in length be constant for all sizes of the animal considered.

In the plot described, the growth data would appear as a straight line. While the straightness of the array of a given set of length measurements so plotted suggests that the animals are conforming to the principles that generate a straight line, this point is not necessarily proved by the plot alone. Such plots provide a convenient tool, however, since growth in this manner is simply described and is easy to illustrate and compute.



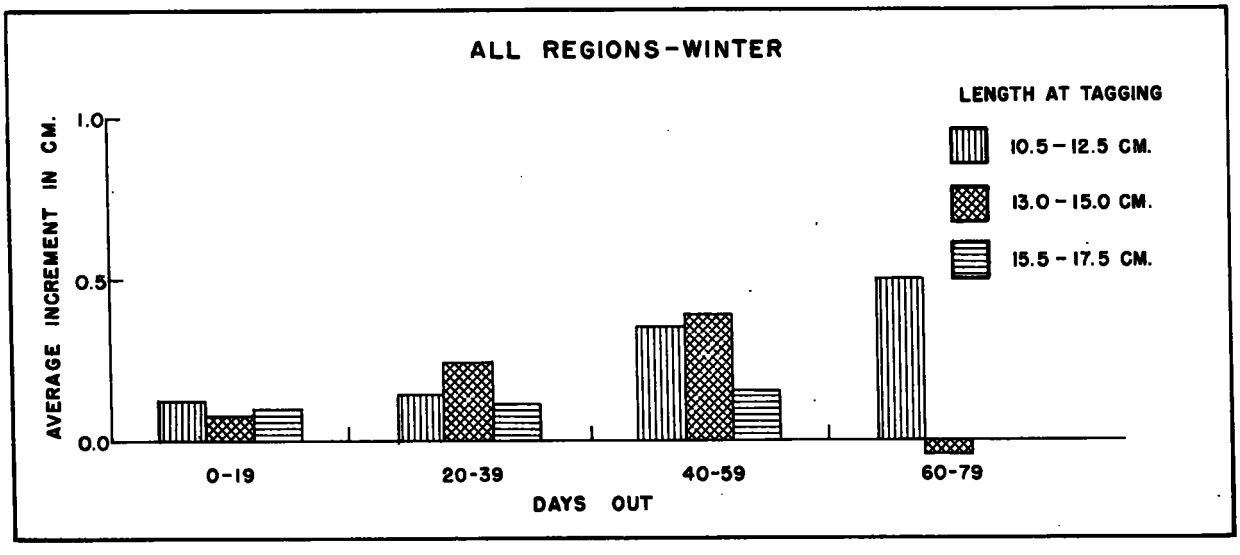


FIGURE 6.—Average growth of tagged shrimp; Atlantic coast, spring and summer, 545 individuals; all regions, winter, 1,183 individuals.

The length of an animal at a given age can be expressed, according to this description, as:

$$L_t = L_\infty(1-K^t)$$

where L_t is the length at age t
L is a constant, and
K is a constant.

The constant, L_∞ is the average ultimate length of animals growing in this fashion. The expression, $(1-K)$, can be interpreted as the fraction of the length yet to be attained in the animal's life that is attained during one unit of time. The constant, K, is an average ratio of successive pairs of length increments, accrued during constant intervals of time.

The same growth type can also be expressed as:

$$L_{t+1} = L_. + KL_t$$

where L_{t+1} is the length at age $(t+1)$

L_t is the length at age (t)

and L_1 is a constant, equal to $L_\infty\ (1-K)$

and K is a constant, as before.

This expression is a straight line when L_{t+1} is plotted against L_t. When the available length data are such as can be plotted in this fashion, a straight line fitted to the array describes the growth of the group from which the data were taken according to the principles given above. The slope of the fitted line will be an estimate of the parameter K, and, when $L_t=0$ the value of L_{t+1} will be an estimate of the parameter L_1. The parameter L_∞ can be estimated by dividing L_1 by $(1-K)$.

Having estimated the parameters K and L_∞, one can describe the growth pattern of the average animal with respect to age as given above:

$$L_t = L_\infty(1-K^t)$$

This would be the growth pattern if the animal grew throughout its life at the rate derived from the data.

Note that the plot, L_{t+1} against L_t, can be made even when the total age of the animals for which one has increments is unknown. Once the parameters K and L_∞ are estimated from such data, the age of the animals can be estimated, under the assumption that they grew at the observed rate throughout their life. For this reason the data here available on the growth increments of shrimp can conveniently be processed according to this growth type, to describe the size attained by the average individual at any given age.

A straight line was fitted to the data after tabulation as L_t (length at tagging) and the corresponding L_{t+r} (length at recovery) for each tagged shrimp. The lines were fitted under the criterion of "least squares." As an example, the data for males of the Atlantic coast, which had been released for a period of 40 to 49 days during summer and fall, are plotted in figure 7.

Since the shrimp were recovered at various time intervals after release, all those recovered after intervals of 0–9 days, 10–19 days, 20–29 days, and so on, were treated separately. The data were further classified by season, spring (March 31 to June 30), summer and fall (July 1 to October 31), and winter (November 1 to March 31), and as belonging to four regions of the coast: (1) Atlantic Coast, (2) Northern Gulf of Mexico east of the Mississippi Delta, (3) Gulf of Mexico west of the Mississippi Delta, and (4) Texas.

The slope (K_r) and L_{t+r} intercept $(L_{1,r})$ of the fitted lines are shown in figure 7. The L_∞ corresponding to the computed L_1 and K is also listed for each line.

TABLE 7.—*Dates of release of shrimp tagged for determining growth*

Atlantic coast		North central Gulf, east of Mississippi River: Summer and fall growth	Central Texas: Summer and fall growth
Spring growth	Summer and fall growth		
Mar. 24, 1938	Sept. 6, 1936	Sept. 20, 1939	Sept. 23, 1936
Apr. 14, 1938	Sept. 7, 1936	Sept. 21, 1939	Sept. 24, 1936
May 13, 1938	Sept. 8, 1936	Sept. 23, 1939	Sept. 25, 1936
June 24, 1938	Sept. 9, 1936	Sept. 24, 1939	Sept. 28, 1936
	Sept. 10, 1936	Sept. 25, 1939	Sept. 29, 1936
	Sept. 11, 1936	Oct. 11, 1939	Sept. 30, 1936
	Aug. 10, 1937	Oct. 12, 1939	Oct. 3, 1936
	Aug. 11, 1937	Oct. 13, 1939	Aug. 27, 1937
	Aug. 12, 1937	Oct. 14, 1939	Aug. 30, 1937
	Aug. 19, 1937		Aug. 31, 1937
	Sept. 7, 1937		Oct. 20, 1937
	Oct. 11, 1937		Oct. 21, 1937
	Oct. 12, 1937		Sept. 8, 1938
	Oct. 13, 1937		Sept. 14, 1938
	July 6, 1938		Sept. 15, 1938
	July 12, 1938		
	Aug. 3, 1938		
	Aug. 5, 1938		
	Aug. 11, 1938		

While the L_∞'s derived from data of several different time intervals are comparable, the K and L_1's are not. The K_{10} and $L_{1,10}$ given in the right-

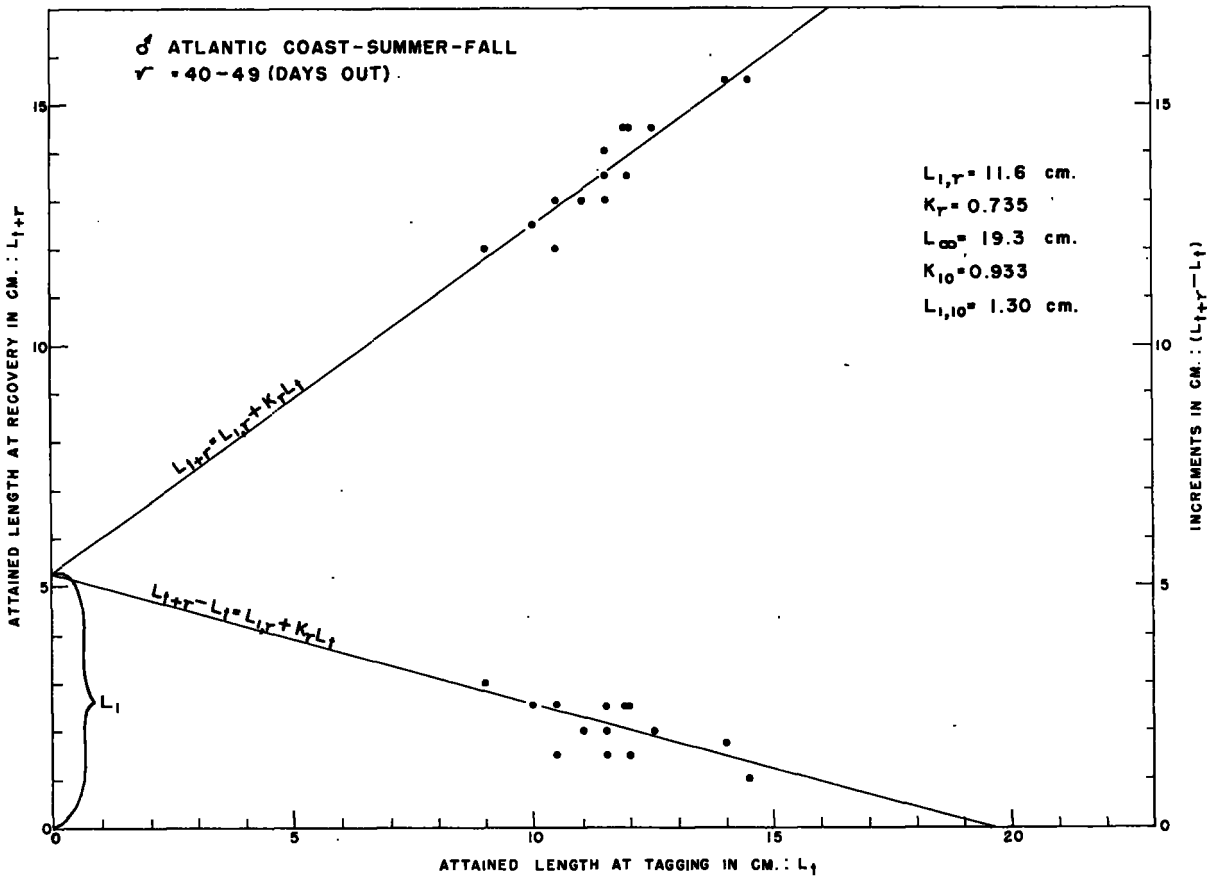


FIGURE 7.—Example of fitting a straight line to growth data from tagged shrimp.

hand columns of table 9 are derived from the K and L_1 of each time interval, from

$$\left(\frac{r}{r'}\right)$$

$$K_r = K_{r'}$$

where "r" and "r'" are any given intervals of time. The K_r (K for r days) is equivalent to the $K_{r'}$, which refers to a K for r' days. The values for $L_{1,10}$ are derived for each line from

$$L_{1,10} = L_\infty(1 - K_{10})$$

This relation follows from the original growth-type expression, as does the relation between the value of K for different time intervals given above.

DISCUSSION

Releases in the Northern Gulf of Mexico west of the Mississippi Delta were made only during winter, but some of these shrimp were recovered well into spring. Judging from figure 5, these shrimp grew very slowly until about the end of March, and rapidly thereafter. In table 9 the returns were treated as having been released on March 31, an arbitrarily chosen date. To the degree that these shrimp had grown before that date, the K_{10} and $L_{1,10}$ given for this region are too low and too high, respectively. A somewhat different method of estimating $L_{1,10}$ given by Lindner (1953) yields the following:

Number of days between release and recovery	*Male (length in cm.)*	*Female (length in cm.)*
0–9	3. 20	1. 88
10–19	3. 24	4. 80
20–29	. 42	4. 52
30–39	5. 94	2. 86
40–49	----------	1. 40
50–59		

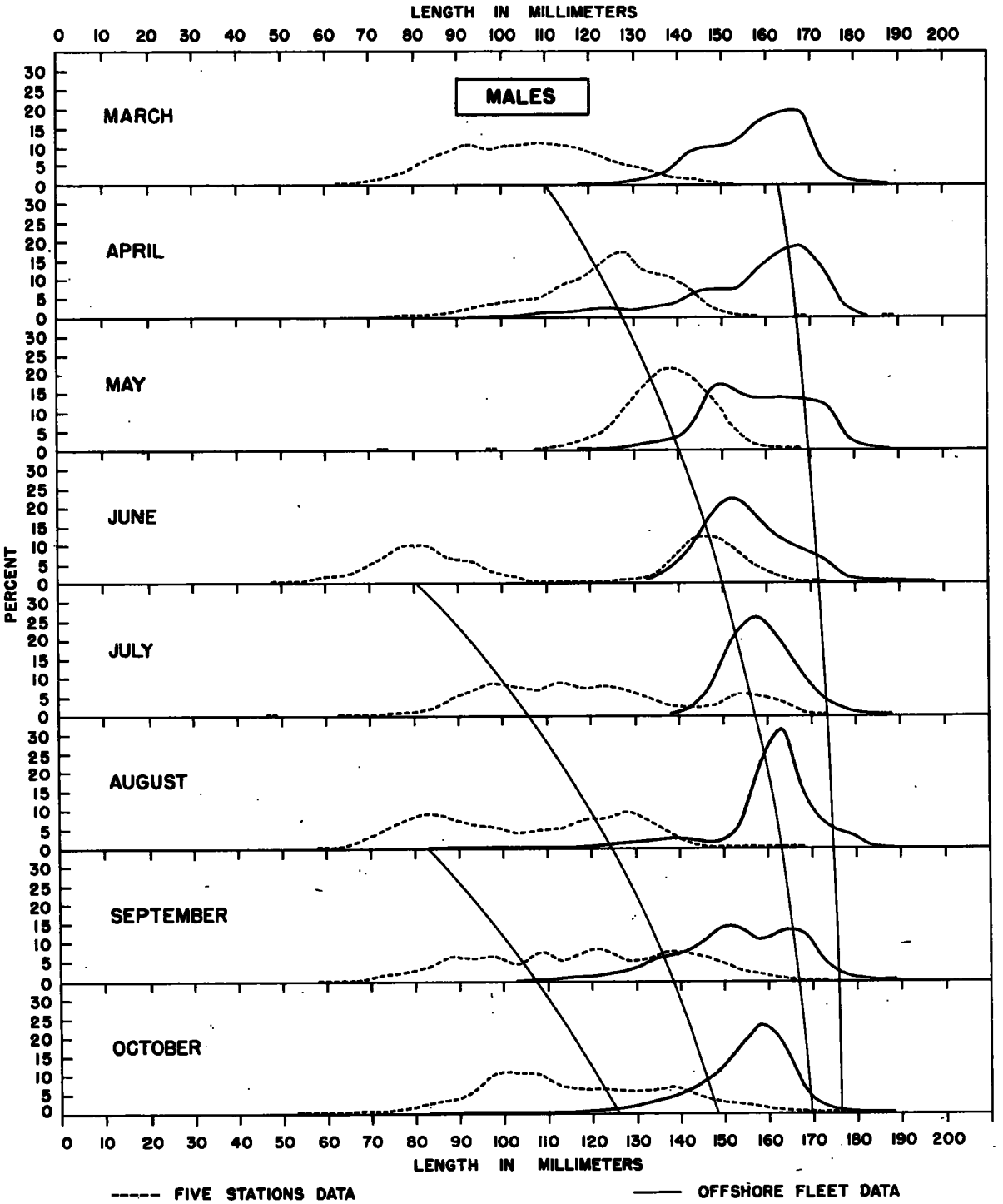


FIGURE 8.—Growth lines applied to Louisiana size distributions for males.

While this treatment does not give biased $L_{1,10}$'s, its results are not as precise as the method used for the other regions. The parameters are not estimated independently of each other, which results in more dispersion in these estimates than in those from data whose time of release occurred during a more uniform growing season. By March 31, these shrimp had grown an average of about one-half centimeter. Lines fitted to the length measurements of these shrimp as they were recovered between March 26 and April 5, irrespective of the time interval out, yielded an L_1 of 1.47, and a K of 0.923. These 61 shrimp were released between October 27 and March 6. Rather than try the several possible ways of correcting these measurements to obtain data comparable to those from other times and areas, the 281 recoveries from west of the Mississippi were not used in describing growth during spring.

The data concerning the release dates of the experiments from which shrimp were taken for determining growth are shown in table 7, while the lengths at release and recovery of all shrimp used for this purpose are presented in table 8.

TABLE 8.—*Lengths of shrimp at tagging and at recovery*

MALES—ATLANTIC COAST—SPRING

0–9 days out			10–19 days out			20–29 days out			30–39 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
11.0	11.0	2	11.0	11.5	1	10.5	12.5	1	11.5	13.5	1
11.5	12.5	1	11.0	12.0	4	11.5	13.0	2	12.0	13.5	2
12.0	11.5	1	11.5	12.0	4	11.5	13.5	1	12.0	14.0	1
12.0	12.0	1	12.0	12.0	1	11.5	14.0	1	12.0	15.0	1
12.0	12.5	2	12.0	12.5	2	12.0	13.5	3	12.5	13.0	1
12.0	13.0	2	12.0	13.0	4	12.5	13.5	2	12.5	14.0	1
12.5	12.5	3	12.0	13.5	1	12.5	14.0	1	12.5	14.5	1
12.5	13.0	2	12.5	12.5	5	13.0	13.5	3	13.5	14.5	1
13.0	13.0	2	12.5	13.0	2	13.0	14.5	1	14.0	14.5	1
13.0	13.5	1	12.5	13.5	2	13.0	15.0	1	14.5	15.5	1
13.5	13.5	4	12.5	14.5	1	13.5	14.5	5	15.0	15.0	1
13.5	14.0	4	13.5	13.5	3	13.5	15.5	1	16.0	16.5	1
13.5	14.5	1	13.5	14.0	2	14.0	14.5	4			
14.0	13.5	1	13.5	14.5	1	14.0	15.0	3			
14.0	14.0	5	14.0	14.0	1	14.0	15.5	1			
14.0	14.5	3	14.0	14.5	1	14.5	15.0	1			
14.5	14.0	2	14.5	14.0	1	15.0	15.0	2			
14.5	14.5	3	14.5	14.5	2	15.0	15.5	1			
14.5	15.0	2	14.5	15.0	1	15.5	15.0	1			
15.0	14.5	4	15.0	14.5	1	15.5	15.5	1			
15.0	15.0	6	15.0	15.0	1						
15.0	15.5	1	15.5	15.5	4						
15.5	15.0	3									
15.5	15.5	2									
798.5	804.5	58	581.0	601.0	45	478.5	515.0	36	170.0	187.0	13

FEMALES—ATLANTIC COAST—SPRING

11.0	12.0	1	10.0	10.5	1	11.0	12.5	1	11.0	11.0	1
11.5	12.5	1	10.5	11.0	1	11.5	12.5	1	11.5	13.0	1
12.0	12.0	1	11.0	11.0	1	12.0	14.0	3	11.5	14.5	1
12.0	12.5	5	11.5	11.5	1	12.0	15.5	1	11.5	15.0	1
12.5	12.5	1	11.5	12.0	5	12.5	14.5	1	12.0	13.5	1
12.5	13.5	1	11.5	12.5	2	14.5	15.0	1	12.0	14.0	1
13.0	13.0	1	11.5	13.5	1	14.5	16.0	1	12.0	14.5	1
13.0	13.5	1	12.0	12.0	1	14.5	16.5	1	12.0	15.0	1
14.0	14.0	2	12.0	12.5	3	15.0	15.5	1	12.5	15.5	1
14.0	14.5	2	12.0	13.0	3	15.0	16.0	2	13.0	16.0	1
14.0	15.0	1	12.5	12.5	1	16.0	16.5	2	14.0	16.0	1
14.5	14.0	1	12.5	13.0	2						
14.5	14.5	3	12.5	13.5	3						
15.0	14.5	1	12.5	14.0	1						
15.0	15.0	5	13.0	13.0	1						
15.0	15.5	2	13.0	13.5	2						
15.5	15.0	1	13.0	14.0	1						
15.5	15.5	3	13.5	13.5	2						
16.0	16.0	2	14.5	15.0	1						
16.5	16.0	1	14.5	15.5	1						
16.5	16.5	3	15.0	15.0	1						
			15.0	15.5	1						
			15.0	16.0	1						
			15.5	16.5	2						
			16.0	15.5	1						
			17.0	17.0	1						
553.5	560.5	39	523.5	546.5	41	203.5	225.0	15	133.0	158.0	11

Note that the L_∞'s in table 9 are often less than 15 cm. This implies that these tagged shrimp would reach an average maximum length of less than that figure during the course of their life. This may be true, but shrimp of 17.5 cm. were tagged, and lengths up to 20 cm. are not rare in the samples of the commercial catch. It is our opinion that the length-at-recovery measurements are too small. When the tagged shrimp were released only a few days before recovery, some would be recorded as having shrunk. This was particularly true for the large shrimp, whose growth rate is always less than that of the small ones. On preservation in formalin, the tendency of the fleshy part of the shrimp (the tails) to curl under and become stiff, we believe, results in underestimates of their actual length at recovery while alive. Moreover, one effect of tagging shrimp may be to cause them to shrink in length at their next molt. Very few tagged shrimp have been held long enough to molt, and those that did were apparently eaten by others while in the soft condition. The question of shrinkage remains in doubt, but we believe the growth rate of the tagged shrimp as reported here to be minimal in comparison with that of the untagged animals.

TABLE 8.—*Lengths of shrimp at tagging and at recovery*—Continued

MALES—ATLANTIC COAST—SUMMER AND FALL

0–9 days out			10–19 days out			20–29 days out			30–39 days out			40–49 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
10.0	10.0	2	9.5	9.5	1	10.0	11.0	1	9.5	11.0	1	9.0	12.0	1
10.5	10.5	8	9.5	10.0	1	10.5	11.5	1	10.0	11.0	1	10.0	12.5	1
11.0	11.0	9	10.0	11.0	1	11.5	12.5	1	10.0	11.5	1	10.5	12.0	1
11.0	11.5	5	10.5	10.5	1	12.0	12.5	1	10.0	12.5	1	10.5	13.0	1
11.0	12.0	1	10.5	11.0	1	12.0	13.5	1	10.5	12.0	1	11.0	13.0	1
11.5	11.5	14	10.5	12.0	1	12.5	13.0	1	10.5	12.5	1	11.5	13.0	1
11.5	12.0	4	11.0	11.0	2	12.5	13.5	3	10.5	13.0	1	11.5	13.5	1
11.5	12.5	2	11.0	11.5	3	12.5	14.0	1	11.0	12.0	1	11.5	14.0	1
12.0	11.5	2	11.0	12.0	1	13.0	13.0	1	11.0	12.5	1	12.0	13.5	1
12.0	12.0	13	11.0	12.5	1	13.0	13.5	2	11.0	13.0	1	12.0	14.5	2
12.0	12.5	11	11.5	12.0	3	13.5	13.5	1	11.5	13.5	1	12.5	14.5	1
12.0	13.0	1	11.5	12.5	1	13.5	14.0	2	12.0	13.5	1	14.0	15.5	1
12.5	12.5	9	12.0	12.0	1	13.5	14.5	2	12.5	14.0	1	14.5	15.5	1
12.5	13.0	7	12.0	12.5	3	14.0	14.5	1	13.0	14.0	1			
12.5	13.5	1	12.0	13.5	2	14.0	15.0	1	13.5	13.5	2			
13.0	13.0	14	12.5	12.5	1	14.5	14.5	1	14.0	15.0	1			
13.0	13.5	4	12.5	13.0	6	14.5	15.0	1	14.5	15.5	2			
13.0	14.0	1	12.5	13.5	1	14.5	15.5	1						
13.5	13.0	1	12.5	14.0	1	15.0	15.0	2						
13.5	13.5	8	13.0	13.0	2	15.0	15.5	3						
13.5	14.0	6	13.0	13.5	4	15.5	15.5	1						
13.5	14.5	1	13.5	13.5	2									
14.0	14.0	8	13.5	14.0	6									
14.0	14.5	3	14.0	14.0	3									
14.0	15.0	1	14.0	14.5	3									
14.5	14.0	2	14.0	15.0	1									
14.5	14.5	15	14.5	14.5	4									
14.5	15.0	1	14.5	15.0	5									
15.0	14.5	3	15.0	14.5	1									
15.0	15.0	29	15.0	15.0	7									
15.0	15.5	3	15.0	15.5	6									
15.5	15.0	12	15.5	15.0	5									
15.5	15.5	24	16.5	15.5	5									
15.5	16.0	2	16.0	16.0	4									
16.0	15.5	2												
16.0	16.0	9												
16.0	16.5	4												
3,281.5	3,303.5	242	1,211.5	1,241.5	102	387.0	405.5	29	223.0	249.0	19	162.5	191.0	14

TABLE 8.—*Lengths of shrimp at tagging and at recovery*—Continued

FEMALES—ATLANTIC COAST—SUMMER AND FALL

0–9 days out			10–19 days out			20–29 days out			30–39 days out			40–49 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
10.5	10.0	1	10.0	11.5	2	10.5	11.5	1	11.0	12.0	2	10.0	12.5	1
10.5	10.5	3	10.0	11.0	1	11.5	11.5	1	11.0	12.5	1	10.5	12.5	2
10.5	11.0	2	10.5	11.0	4	11.5	12.0	1	11.0	13.5	1	11.0	13.0	1
11.0	10.5	1	10.5	11.5	1	12.0	12.5	2	11.5	13.0	1	11.5	15.0	1
11.0	11.0	4	10.5	12.0	1	12.0	13.0	3	12.0	14.0	1	12.5	14.5	1
11.0	11.5	2	11.0	11.0	2	12.0	13.5	2	12.5	13.0	1	13.0	14.5	1
11.0	12.0	1	11.0	11.5	5	12.5	12.5	1	12.5	14.0	4	14.0	15.5	1
11.5	11.0	3	11.0	12.0	1	12.5	13.5	2	12.5	15.0	1	15.0	16.0	1
11.5	11.5	6	11.5	11.5	7	12.5	14.0	1	13.0	14.0	3	15.5	16.5	1
11.5	12.0	4	11.5	12.0	7	13.0	13.5	1	13.0	14.5	1			
12.0	11.5	2	11.5	12.5	2	13.5	13.5	1	14.0	15.5	2			
12.0	12.0	7	11.5	13.0	1	13.5	14.0	1	15.0	16.0	1			
12.0	12.5	3	12.0	11.5	1	13.5	14.5	1	16.5	17.0	1			
12.0	13.0	1	12.0	12.0	5	14.0	14.5	1						
12.5	12.0	4	12.0	12.5	7	14.0	15.5	1						
12.5	12.5	6	12.0	13.0	1	15.0	15.0	1						
12.5	13.0	6	12.0	13.5	1	15.0	15.5	2						
13.0	13.0	7	12.5	12.0	1	15.5	15.5	1						
13.0	13.5	3	12.5	12.5	8									
13.5	13.0	4	12.5	13.0	10									
13.5	13.5	6	12.5	13.5	3									
13.5	14.0	1	13.0	12.5	1									
14.0	14.0	5	13.0	13.0	3									
14.0	14.5	2	13.0	13.5	17									
14.5	14.0	1	13.0	14.0	1									
14.5	14.5	5	13.5	13.5	5									
15.0	15.0	2	13.5	14.0	10									
15.0	15.5	1	13.5	14.5	3									
15.5	15.5	5	14.0	13.5	1									
16.0	16.0	1	14.0	14.0	3									
16.0	16.5	3	14.0	14.5	7									
16.5	16.0	2	14.5	14.5	8									
16.5	16.5	3	14.5	15.0	5									
17.0	16.5	2	15.0	14.5	1									
17.0	17.0	4	15.0	15.0	2									
			15.0	15.5	2									
			15.5	15.5	3									
			15.5	16.0	2									
			16.0	16.0	2									
			16.0	16.5	2									
			16.5	16.0	1									
			16.5	16.5	2									
			16.5	17.0	1									
			17.0	17.0	3									
			17.0	17.5	2									
			17.5	17.5	1									
1,491.0	1,496.0	113	2,088.0	2,144.0	159	309.5	326.5	24	254.0	281.5	20	123.5	143.5	10

FEMALES—WEST OF MISSISSIPPI RIVER—SPRING

0–9 days out			10–19 days out			20–29 days out			30–39 days out			40–49 days out			50–59 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
12.0	12.0	1	10.5	11.0	1	11.5	14.0	1	11.5	14.5	1	12.5	15.5	2	11.0	15.5	1
12.0	12.5	2	12.0	12.5	1	11.5	15.5	1	12.5	15.5	2	12.5	16.0	2	11.5	16.0	1
12.0	13.0	1	12.0	14.5	1	12.0	14.0	1	12.5	16.5	1	13.0	16.0	2	11.5	16.5	1
12.5	13.0	2	12.5	14.0	1	12.5	13.5	1	13.0	15.0	2	13.0	16.5	1	12.0	15.5	1
13.0	13.0	1	13.5	14.5	1	12.5	14.5	1	13.0	15.5	1	13.5	15.5	1	12.0	16.0	1
13.0	13.5	1	15.0	15.5	1	13.5	15.0	1	13.0	16.0	1	14.5	15.5	1	12.5	16.0	1
13.5	13.5	1	16.5	16.5	1	13.5	15.5	1	13.5	15.5	1	14.5	16.0	1	13.0	15.0	1
13.5	14.0	1	16.5	17.0	3	13.5	16.0	1	13.5	16.5	1	15.0	15.5	1	13.0	16.0	1
13.5	14.5	1				14.5	16.0	2	14.0	15.5	1	15.5	16.0	1	13.5	16.0	1
14.0	14.5	1				14.5	16.5	3	14.0	16.0	1	15.5	17.0	1	14.0	16.0	1
14.5	14.5	2				14.5	17.0	1	14.5	16.5	1	15.5	17.5	1	14.0	16.5	1
14.5	15.0	1				15.0	16.0	2	15.0	15.5	1	16.0	17.0	4	14.5	16.5	1
15.0	15.5	3				15.0	16.5	2	15.0	16.0	1	16.0	17.5	1	14.5	17.0	1
15.5	15.5	4				15.0	17.0	1	15.0	17.0	2	16.5	17.0	1	14.5	18.0	1
15.5	16.0	1				15.5	16.5	2	15.5	16.0	1	17.0	17.5	2	15.0	16.0	1
15.5	16.5	1				16.0	16.5	1	15.5	16.5	1				15.0	16.5	1
16.0	16.0	3				16.5	16.5	1	15.5	17.0	1				16.0	16.5	2
16.0	16.5	2				16.5	17.5	5	16.0	16.5	1				16.5	18.0	1
16.0	17.0	1				17.0	17.0	1	17.0	17.5	1				16.5	18.5	1
16.5	16.5	1				17.0	17.5	1	17.0	18.0	1				17.0	17.5	1
16.5	17.0	2				17.0	18.0	2									
17.0	17.0	3				17.5	17.5	1									
17.0	17.5	1				17.5	18.0	1									
17.5	17.5	2															
583.5	596.0	39	141.5	149.5	10	511.5	558.0	34	327.0	370.5	23	323.5	362.0	22	493.5	346.0	21

TABLE 8.—*Lengths of shrimp at tagging and at recovery*—Continued

MALES—WEST OF MISSISSIPPI RIVER—SPRING

0–9 days out			10–19 days out			20–29 days out			30–39 days out			40–49 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
10.5	11.0	1	11.0	13.0	1	10.5	12.0	1	12.5	14.0	1	12.0	15.0	1
11.5	12.5	1	12.0	14.0	1	11.0	14.0	1	12.5	14.5	3	12.0	15.5	1
11.5	13.0	1	12.5	13.5	1	13.0	15.0	1	13.5	15.0	2	13.0	15.0	1
12.0	11.5	1	14.0	14.0	1	13.5	15.5	2	13.5	15.5	1	13.5	15.5	1
12.0	12.5	2	15.0	15.5	1	14.0	15.0	1	14.0	15.5	1	14.5	16.0	1
12.5	13.0	2	15.5	16.0	1	14.0	15.5	1	14.5	15.5	2	15.0	16.0	1
13.5	13.5	2	16.0	16.5	1	14.5	15.0	1	14.5	16.0	1	15.0	17.0	1
13.5	14.0	1	16.0	17.0	1	14.5	16.0	3	15.0	15.5	2	15.5	16.0	1
13.5	14.5	1	16.5	16.5	1	15.0	15.0	1	15.0	16.5	1	15.5	16.5	2
14.0	14.0	1	17.0	17.5	1	15.0	16.0	1	15.5	16.0	2	16.0	16.0	2
14.5	14.5	5	----------	----------	----------	15.0	16.5	1	15.5	16.5	2	16.0	16.5	4
15.0	14.5	2	----------	----------	----------	15.5	15.5	2	15.5	17.0	1	16.5	16.5	1
15.0	15.0	3	----------	----------	----------	15.5	16.0	3	16.0	16.5	1	16.5	17.0	2
15.5	15.5	1	----------	----------	----------	15.5	16.5	2	16.0	17.0	1	17.0	17.0	3
15.5	16.0	2	----------	----------	----------	16.0	16.5	4	16.5	16.0	1	17.0	17.5	1
16.0	16.0	1	----------	----------	----------	16.5	16.0	1	16.5	16.5	3	----------	----------	----------
16.0	16.5	2	----------	----------	----------	16.5	16.5	1	16.5	17.0	3	----------	----------	----------
16.0	17.0	1	----------	----------	----------	16.5	17.0	3	17.0	17.0	1	----------	----------	----------
16.5	16.0	1	----------	----------	----------	17.0	17.0	1	----------	----------	----------	----------	----------	----------
16.5	16.5	4	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.5	17.0	1	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.0	17.0	2	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.5	17.5	1	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
18.0	17.5	1	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
588.0	596.5	40	145.5	153.5	10	464.5	491.5	31	435.0	462.0	29	355.0	376.0	23

FEMALES—EAST OF MISSISSIPPI RIVER—SUMMER AND FALL

0–9 days out			10–19 days out			20–29 days out			30–39 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
8.5	9.0	1	10.0	11.5	1	11.0	13.0	1	11.0	13.5	1
10.0	10.0	1	10.5	11.0	1	11.5	12.5	3	11.5	13.5	3
10.5	11.0	1	11.5	12.5	1	11.5	13.0	2	12.0	13.0	1
11.0	11.0	2	12.0	12.0	2	12.0	12.0	1	12.5	13.5	1
11.0	11.5	2	12.0	12.5	4	12.0	13.0	1	12.5	14.0	1
11.5	11.0	2	12.0	13.0	3	12.0	13.5	1	13.0	14.0	1
11.5	11.5	5	12.0	13.5	1	13.0	14.5	1	13.5	15.0	1
11.5	12.0	3	12.5	12.5	6	13.5	14.0	2	14.0	15.5	1
11.5	12.5	1	12.5	13.5	1	13.5	15.0	1	14.5	15.5	1
12.0	12.0	11	13.0	13.0	3	14.0	14.5	3	15.0	16.0	2
12.0	12.5	4	13.0	13.5	2	15.5	16.0	1	15.5	16.0	1
12.5	12.0	1	13.0	14.0	1	----------	----------	----------	15.5	16.5	2
12.5	12.5	17	13.5	13.5	1	----------	----------	----------	15.5	17.0	1
12.5	13.0	7	13.5	14.0	4	----------	----------	----------	----------	----------	----------
13.0	12.0	1	14.0	13.5	1	----------	----------	----------	----------	----------	----------
13.0	12.5	2	14.0	14.0	4	----------	----------	----------	----------	----------	----------
13.0	13.0	11	14.0	14.5	1	----------	----------	----------	----------	----------	----------
13.0	13.5	8	14.5	14.5	3	----------	----------	----------	----------	----------	----------
13.0	14.0	1	14.5	15.0	3	----------	----------	----------	----------	----------	----------
13.5	13.0	2	14.5	15.5	1	----------	----------	----------	----------	----------	----------
13.5	13.5	18	15.0	15.0	4	----------	----------	----------	----------	----------	----------
13.5	14.0	8	15.0	15.5	2	----------	----------	----------	----------	----------	----------
14.0	14.0	12	15.5	15.5	3	----------	----------	----------	----------	----------	----------
14.0	14.5	2	15.5	16.0	1	----------	----------	----------	----------	----------	----------
14.5	14.0	2	16.0	16.0	3	----------	----------	----------	----------	----------	----------
14.5	14.5	10	16.5	16.5	2	----------	----------	----------	----------	----------	----------
14.5	15.0	9	----------	----------	----------	----------	----------	----------	----------	----------	----------
15.0	15.0	11	----------	----------	----------	----------	----------	----------	----------	----------	----------
15.0	15.5	3	----------	----------	----------	----------	----------	----------	----------	----------	----------
15.5	15.0	2	----------	----------	----------	----------	----------	----------	----------	----------	----------
15.5	15.5	19	----------	----------	----------	----------	----------	----------	----------	----------	----------
15.5	16.0	4	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.0	15.5	2	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.0	16.0	11	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.5	16.0	3	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.5	16.5	7	----------	----------	----------	----------	----------	----------	----------	----------	----------
16.5	17.0	4	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.0	16.5	1	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.0	17.0	4	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.0	17.5	1	----------	----------	----------	----------	----------	----------	----------	----------	----------
17.5	17.5	1	----------	----------	----------	----------	----------	----------	----------	----------	----------
3,025.5	3,046.5	217	803.5	822.0	59	215.5	232.0	17	275.5	252.5	17

TABLE 8.—*Lengths of shrimp at tagging and at recovery*—Continued

MALES—EAST OF MISSISSIPPI RIVER—SUMMER AND FALL

0–9 days out			10–19 days out			20–29 days out			30–39 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
8.5	8.5	2	10.0	10.0	1	10.0	11.5	1	10.5	12.0	1
9.5	9.5	1	10.0	10.5	1	11.5	12.0	1	11.0	13.5	1
10.0	10.0	1	10.5	11.0	1	12.0	12.5	3	11.5	12.0	1
10.5	10.5	3	11.0	11.5	1	12.0	13.0	2	11.5	13.0	1
11.0	10.5	1	11.5	12.0	1	12.0	13.5	1	11.5	13.5	1
11.0	11.0	2	11.5	12.5	2	12.5	13.5	2	12.0	12.5	1
11.0	11.5	1	12.0	12.5	2	13.0	13.0	1	12.0	13.0	1
11.5	11.5	4	12.0	13.0	3	13.0	13.5	1	12.0	13.5	1
11.5	12.0	1	12.0	13.5	1	13.5	13.5	1	12.5	13.0	1
11.5	12.5	1	12.5	12.5	7				12.5	13.5	1
12.0	12.0	6	12.5	13.0	4				13.0	15.5	1
12.0	12.5	7	13.0	13.0	2				13.5	15.0	1
12.5	12.5	25	13.0	13.5	3				14.5	15.0	1
12.5	13.0	5	13.5	13.0	1				14.5	16.0	1
12.5	13.5	2	13.5	13.5	1				15.0	15.5	1
13.0	12.5	2	13.5	14.0	5				15.5	16.0	2
13.0	13.0	24	13.5	15.0	1				15.5	16.5	1
13.0	13.5	5	14.0	13.0	1						
13.5	13.5	18	14.0	14.5	3						
13.5	14.0	3	14.5	14.5	4						
13.5	14.5	2	14.5	15.0	2						
14.0	13.5	2	15.0	15.5	4						
14.0	14.0	10	15.0	16.0	1						
14.0	14.5	8	15.5	15.5	1						
14.0	15.0	2	15.5	16.0	1						
14.5	14.5	11	16.0	16.0	1						
14.5	15.0	2	16.0	16.5	1						
15.0	14.0	1	16.5	16.5	1						
15.0	14.5	2	17.0	16.5	1						
15.0	15.0	11									
15.0	15.5	6									
15.0	16.0	1									
15.5	15.0	1									
15.5	15.5	12									
16.0	15.0	3									
16.0	16.0	2									
16.0	16.5	1									
16.5	16.0	1									
16.5	16.5	3									
2,625.5	2,646.0	195	773.0	794.5	58	158.0	167.5	13	234.0	255.0	18

FEMALES—TEXAS—SUMMER AND FALL

0–9 days out			10–19 days out			20–29 days out			0–9 days out			10–19 days out			20–29 days out		
Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens	Tagging length	Recovery length	Number of specimens
Cm.	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*		*Cm.*	*Cm.*	
10.5	10.0	1	11.0	11.5	1	11.5	12.0	1	13.5	14.0	2	15.0	14.5	1			
10.5	10.5	1	11.0	12.0	1	11.5	12.5	1	13.5	14.5	1	15.0	15.0	1			
10.5	11.0	1	11.5	11.5	3	11.5	13.0	2	14.0	13.5	1	15.5	15.0	1			
11.0	10.5	1	11.5	12.0	1	12.0	12.5	1	14.0	14.0	4	15.5	15.5	2			
11.0	11.0	2	11.5	12.5	1	12.0	13.0	3	14.0	14.5	1						
11.0	11.5	3	12.0	12.5	1	12.0	13.5	2	14.5	14.0	2						
11.5	11.5	6	12.0	13.0	1	12.5	13.5	3	14.5	14.5	4						
11.5	12.0	1	12.5	12.5	1	13.5	14.0	1	15.0	14.5	1						
12.0	11.5	2	12.5	13.0	1	14.0	14.5	2	15.0	15.0	8						
12.0	12.0	9	12.5	13.5	1	14.0	15.0	1	15.5	15.0	2						
12.0	12.5	2	13.0	13.0	2	15.0	16.0	1	15.5	15.5	3						
12.5	12.0	1	13.0	13.5	2	16.0	16.0	1	16.0	16.0	1						
12.5	12.5	5	13.0	14.0	1	16.5	16.5	1	16.5	16.0	1						
12.5	13.0	3	13.5	13.5	1	18.0	18.0	1	16.5	16.5	2						
13.0	12.5	2	13.5	14.0	3				16.5	17.0	1						
13.0	13.0	3	14.0	14.5	1				17.5	17.5	1						
13.0	13.5	1	14.0	15.0	2												
13.5	13.0	3	14.5	14.5	1												
13.5	13.5	2	14.5	15.5	2				1,115.5	1,115.5	84	422.0	435.0	32	276.5	294.0	21

MALES—TEXAS—SUMMER AND FALL

10.0	9.5	1	10.5	11.5	1	11.5	12.0	1	13.0	13.0	4	15.5	16.0	1			
10.0	10.0	1	11.5	11.0	1	12.5	13.0	1	13.5	13.0	2						
10.0	10.5	1	11.5	12.0	1	12.5	13.5	1	13.5	13.5	3						
10.5	10.0	1	11.5	12.5	1	12.5	14.0	1	13.5	14.0	2						
10.5	10.5	3	12.0	12.5	5	13.0	14.0	1	14.0	13.5	2						
11.0	10.5	1	12.0	13.0	1	13.5	14.0	1	14.0	14.0	7						
11.0	11.0	3	12.5	12.5	3	14.5	15.0	4	14.5	14.0	1						
11.5	11.0	1	12.5	13.0	1	15.0	15.5	2	14.5	14.5	3						
11.5	11.5	6	12.5	13.5	2	16.0	15.5	1	15.0	14.5	1						
11.5	12.0	1	13.0	13.0	1	16.0	16.0	1	15.5	15.0	1						
11.5	12.5	1	13.0	13.5	1				15.5	15.5	1						
12.0	12.0	5	13.5	13.5	3				15.5	16.0	1						
12.0	12.5	2	13.5	14.0	3				16.0	15.5	1						
12.5	12.0	2	13.5	14.5	1				16.0	16.0	2						
12.5	12.5	4	14.0	14.5	2												
12.5	13.0	2	14.5	14.5	1												
13.0	12.5	2	15.0	15.0	2				869.5	867.0	68	400.5	413.0	31	195.5	203.0	14

TABLE 9.—*Growth characteristics derived from tagged shrimp: single experiments*

Time out (in days)	L_1	K	L_∞	K_{10}	$L_{1,10}$	n
MALES						
Atlantic coast:						
Spring:	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	
0–9	2.25	0.8440	14.40	0.686	4.52	58
10–19	3.30	.7788	14.90	.842	2.36	45
20–29	6.78	.5661	15.65	.792	3.26	36
30–39	7.06	.5599	16.05	.845	2.49	13
Total			61.00	3.165	12.62	152
Mean			15.25	.791	3.16	
Summer and fall:						
0–9	.85	.9437	15.2	.874	1.91	242
10–19	2.19	.8623	15.9	.903	1.54	90
20–29	3.04	.8202	16.9	.922	1.32	29
30–39	4.39	.7427	17.0	.806	3.31	19
40–49	5.11	.7352	19.3	.933	1.29	14
Total			84.3	4.438	9.38	394
Mean			16.8	.888	1.88	
East Mississippi: Summer and fall:						
0–9	.47	.9728	17.4	.940	1.04	195
10–19	1.40	.9224	18.1	.946	.98	58
20–29	5.22	.6304	14.1	.828	2.42	13
30–39	3.54	.8177	19.4	.943	1.10	18
Total			69.0	3.657	5.54	284
Mean			17.2	.914	1.38	
Texas: Summer and fall:						
0–9	.36	.9693	11.6	.933	.78	68
10–19	1.76	.8954	16.8	.926	1.24	31
20–29	3.71	.7728	16.4	.900	1.64	14
Total			44.8	2.759	3.66	113
Mean			14.9	.920	1.22	
West of river: Spring: [1]						
0–9	1.90	.8853	16.9	.762	4.02	40
10–19	4.62	.7379	17.6	.811	3.32	10
20–29	6.99	.5917	16.1	.807	3.30	31
30–39	7.37	.5708	17.2	.850	2.58	29
40–49	10.44	.3831	16.9	.805	3.30	23
Total			85.6	4.035	16.52	133
Mean			17.2	.807	3.30	
FEMALES						
Atlantic coast: Spring:						
0–9	2.54	.8337	15.2	.667	5.08	39
10–19	1.60	.9187	19.7	.943	1.12	41
20–29	5.64	.6893	18.2	.859	2.06	15
30–39	−1.62	[2] 1.3224	0			11
Total			53.1	2.469	8.76	106
Mean			17.7	.823	2.92	
Summer and fall:						
0–9	.38	.9745	15.0	.944	.84	113
10–19	1.26	.9305	18.2	.952	.88	159
20–29	2.50	.8612	18.0	.941	1.06	24
30–39	3.34	.8454	21.6	.952	1.04	20
40–49	4.20	.8216	23.6	.957	1.02	10
Total			96.3	4.746	4.82	326
Mean			19.2	.949	.96	
East Mississippi: Summer and fall:						
0–9	.55	.9677	17.0	.929	1.21	217
10–19	2.14	.8660	16.0	.906	1.50	59
20–29	3.92	.7673	16.8	.898	1.72	17
30–39	4.39	.7753	19.6	.929	1.39	17
Total			69.4	3.662	5.82	310
Mean			17.4	.916	1.46	
Texas: Summer and fall:						
0–9	.44	.9669	13.3	.927	.97	84
10–19	1.75	.8981	17.2	.928	1.24	32
20–29	3.58	.7910	17.2	.908	1.58	21
Total			47.6	2.763	3.78	137
Mean			15.8	.921	1.26	
West of river (not corrected): Spring: [1]						
0–9	1.26	.9371	20.0	.865	2.70	39
10–19	2.97	.8465	19.4	.892	2.09	10
20–29	7.18	.6130	18.6	.819	3.36	34
30–39	10.10	.4230	17.5	.779	3.87	23
40–49	11.10	.3644	17.4	.796	3.56	22
50–59	11.70	.3413	17.8	.821	3.18	21
Total			110.6	4.972	18.76	149
Mean			18.4	.829	3.12	

[1] Shrimp from this locality, although tagged at various times during the winter, were treated as if released on March 31, the approximate date of resumption of growth in the spring.

[2] One shrimp, 11.5 cm when tagged, was recorded as having not grown in more than 30 days out.

RESULTS

The data from which table 9 was prepared have been pooled, and the results of the growth description of all of these animals, 1,822 individuals, are contained in table 10. The data from west of the Mississippi have been omitted, for reasons previously given. The K_{10} and $L_{1,10}$ from the several regions and from the different "time-out" intervals are quite similar. Variances of the several individual parameter estimates were not computed, but in combining the several K_{10}, $L_{1,10}$, and L_∞'s, two schemes of weighting were employed: (1) The several parameter estimates were given equal weight for each "time-out" period, and (2) they were weighted according to the square root of the size of the sample from which they came. The latter procedure is equivalent to weighting inversely as their standard errors, if the standard deviation of their original distributions in the regressions were all equal. Since there was little difference among the several parameters, these two schemes of weighting produce very similar averages. For convenience in comparing monthly modes in the length frequency distribution with the growth pattern here derived for tagged shrimp, the K_{10} and $L_{1,10}$ were converted to K_{30} and $L_{1,30}$. This is accomplished, as given above, by cubing the K_{10}'s to get K_{30}'s and by using K_{30} and L_∞ to get $L_{1,30}$, as described.

	K_{30}	$L_{1,30}$	L_∞
Females:			
Weighted equally	0.817	3.5	19.0
Weighted to $\sqrt{n}$	.810	3.3	17.6
Males:			
Weighted equally	.761	4.0	17.0
Weighted to $\sqrt{n}$	.756	4.0	16.3

The growth lines shown in figures 8 and 9 were calculated from the formulas: [2]

		L_∞
Males	$Y=4.58+0.7427\ X$,	17.80
Females	$Y=5.64+\ .7225\ X$,	20.30

We chose the initial points to approximate the modes of the distributions. The remaining points were then determined by calculation (table 11).

Judging from the modes, there is some indication that the young shrimp appearing in June increase more rapidly in total length than do those resuming rapid growth at the beginning of March. This difference may well be actual, since the March shrimp are approaching maturity more rapidly than are those which appear in June, and as the shrimp approach maturity various morphological changes occur. The result of one of these changes is that mature shrimp have a shorter rostrum in comparison with immature shrimp of the same total length.

TABLE 10.—*Growth characteristics derived from tagged shrimp: Combined single experiments*

[All localities except West of the Mississippi River and all seasons pooled, sexes separated]

Time out and sex	a	b	L_∞	K_{10}	$L_{1.10}$	$\sqrt{n}$	n
0–9 days:							
Females	0.52	0.967	15.8	0.928	1.1	21.3	453
Males	.58	.963	15.6	.920	1.2	23.7	563
10–19 days:							
Females	1.65	.910	17.4	.937	1.1	17.1	291
Males	2.15	.866	16.0	.905	1.5	15.0	224
20–29 days:							
Females	3.35	.815	18.1	.920	1.4	8.8	77
Males	4.28	.736	16.2	.882	1.9	9.6	92
30–39 days:							
Females	4.23	.793	20.4	.935	1.3	6.9	48
Males	4.30	.759	17.8	.923	1.3	7.1	50
40–49 days:							
Females	4.20	.822	23.5	.957	1.0	3.2	10
Males	5.11	.735	19.3	.933	1.3	3.7	14
Averages:							
Females:							
Unweighted			19.1	.935	1.2		
Weighted			17.6	.932	1.2		
Males:							
Unweighted			17.0	.913	1.4		
Weighted			16.3	.911	1.4		
Totals:							
Females							879
Males							943

Figure 10, showing the 30-day growth line for males and females combined, has been drawn so that the solid part represents the range covered by our data (100 to 180 mm.), and the broken parts are extensions beyond this range. The equation of this line is noted on the figure. We realize that it is not sound to extend the line to L_o, but we have done so because the growth of the shrimp seems to approximate that represented by this line. In other words, we believe that shrimp reach about 80 mm. in length approximately 2 months after spawning. Perhaps this is fortuitous, since it indicates a growth considerably more rapid than that obtained by Pearson (1939) with shrimp in aquariums. However, his aquarium conditions did not duplicate the natural environment, nor was the food the same as that found naturally.

[2] These lines, very similar to those represented by the parameter estimates given, were those included in the first draft of this manuscript. Although a reexamination of the original data yielded slightly different results, the original growth lines were not changed. These results are used primarily for checking the advance in length of modes in monthly length frequencies, for which they are adequate, in the opinion of the authors.

TABLE 11.—*Calculated growth of shrimp, derived from single experiment*

Sex and month	Length, in millimeters					
Males:						
March	105.0	110.0	163.0			
April	123.8	127.5	166.9			
May	137.7	140.5	169.8			
June	148.1	150.1	171.9	81.0		
July	155.8	157.3	173.5	106.0	113.0	
August	161.5	162.6	174.7	124.5	129.7	83.0
September	165.7	166.6	175.5	138.3	142.1	107.4
October	168.9	169.5	176.1	148.5	151.3	125.6
Females:						
March	105.0	168.0				
April	132.2	177.7	128.0			
May	151.9	184.7	148.8			
June	166.1	189.8	163.9	78.0		
July	176.4	193.5	174.8	112.7		
August	183.8	196.2	182.6	137.8	83.0	128.0
September	189.1	198.1	188.3	155.9	116.3	148.8
October	193.0	199.5	192.4	169.0	140.4	163.9

To use this line we proceed thus: Choose the size of shrimp we wish to follow, say 100 mm., on the X axis and continue vertically until the growth line is intersected. This gives us about 125 mm. Hence, a shrimp 100 mm. long (from tip of rostrum to end of telson) will in 1 month have grown to about 125 mm. Following the same procedure with 125 mm. on the X axis, we find that at the end of 2 months the shrimp will have grown from 100 mm. to about 141 mm. This line, of course, can be used only for the rapid growing season, from about March until the end of October.

MIGRATIONS

In any tagging experiment one must assume, unless there is evidence to the contrary, that the unmarked individuals follow a pattern similar to that of the marked individuals. Since the size distributions (treated in a later section) suggest no difference in the movements of the two groups, and since we have encountered no evidence which would lead us to suspect any abnormal behavior of the tagged shrimp, we make this assumption.

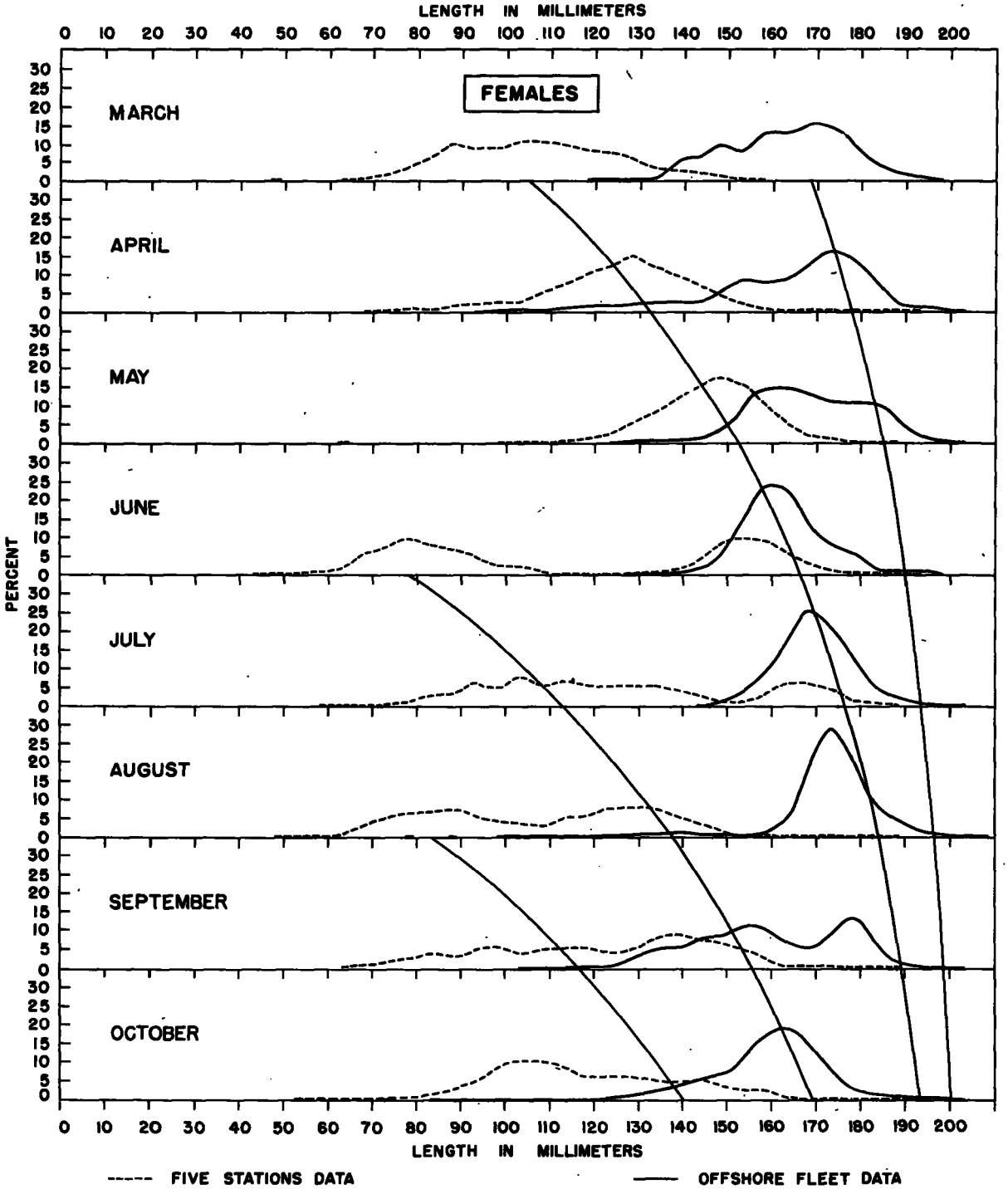


FIGURE 9.—Growth lines applied to Louisiana size distributions for females.

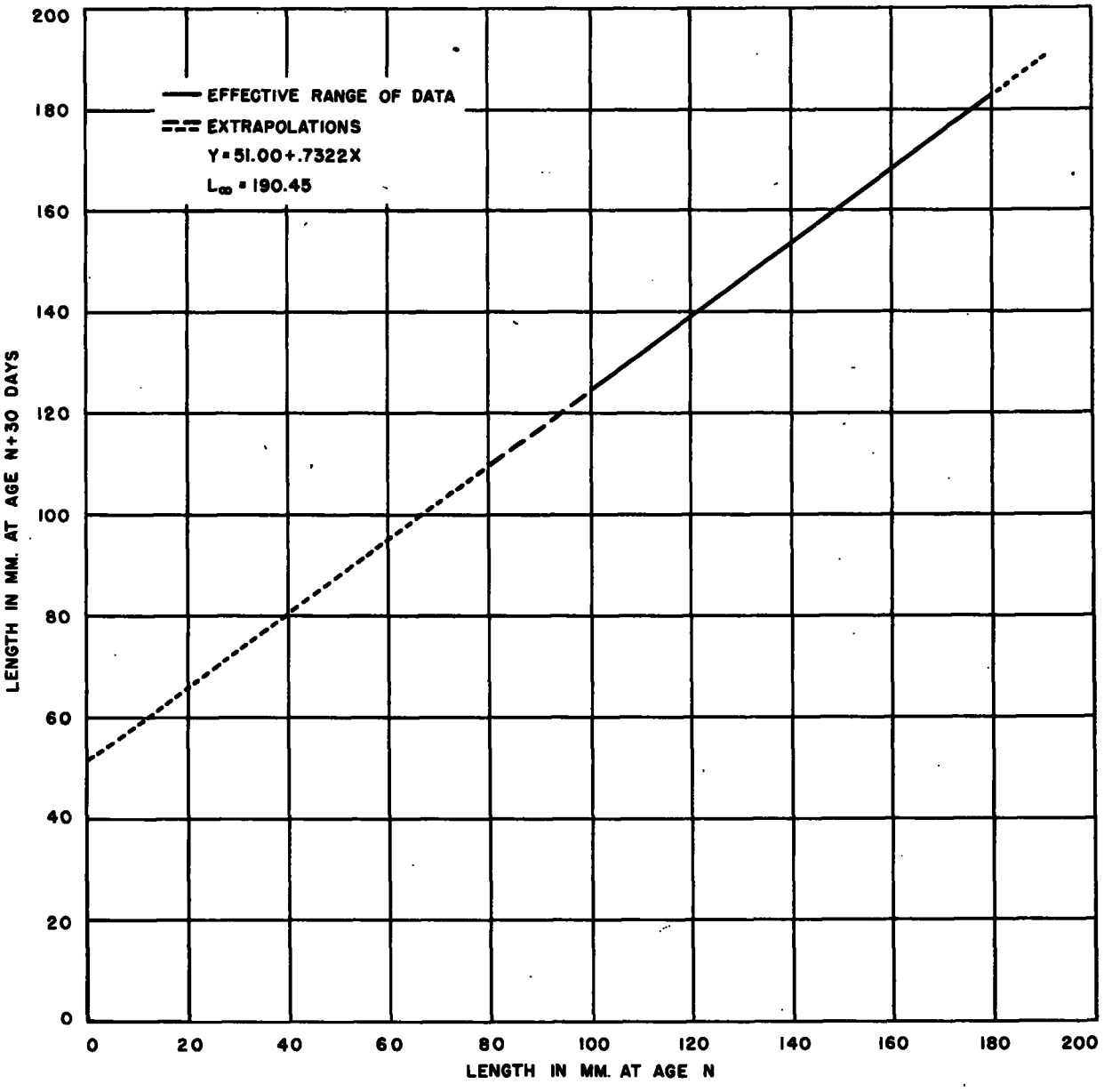


FIGURE 10.—Transformed growth line in 30-day intervals, calculated from marked shrimp.

With few exceptions, we always marked random samples of shrimp as we found them on the fishing grounds. The exceptions occurred now and then when small individuals were abundant. On these occasions we would not mark shrimp less than about 9 cm. in length, since we had found that our technique failed on small shrimp (see table 2 and fig. 4).

For convenience in analysis and interpretation of our data, we divided the coast into sections about 50 miles long. Our divisions are shown in figures 11 and 12. The extent of the present-day fishery for white shrimp off the coast of the United States is shown in these figures by stippling.[3]

We marked 46,532 shrimp. Our conclusions are based on 7,055 returns for which we know the date and locality of recapture. The longest time between release and recapture was that of a shrimp marked at Cape Canaveral in January and recaptured off the Georgia coast 257 days later.

[3] A description of the boats, gear, fishing methods, and localities can be found in Anderson, Lindner, and King (1949).

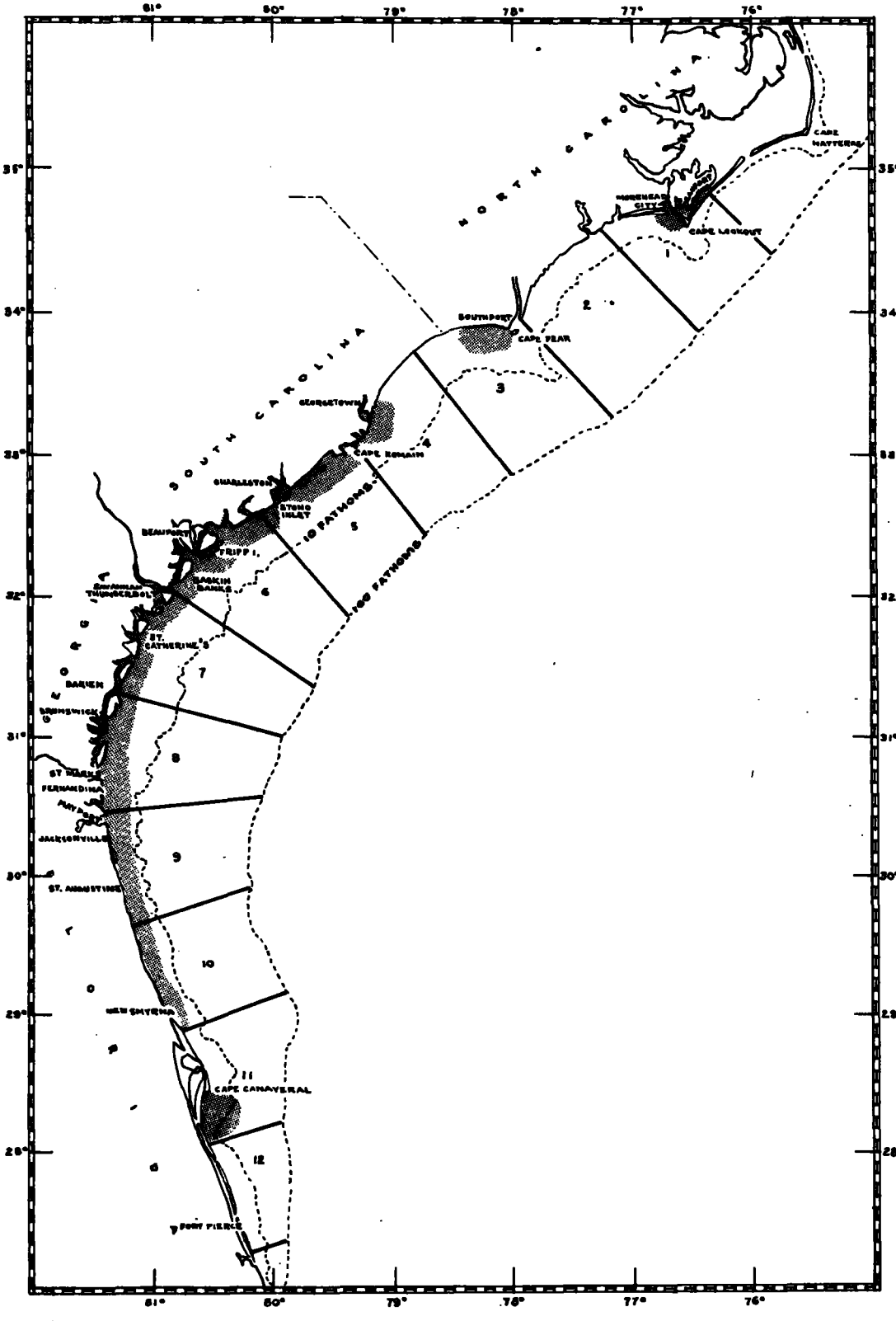


FIGURE 11.—Shrimp-fishing grounds and reference areas for tagging analyses along the Atlantic coast. Fishing grounds are shown by stippling.

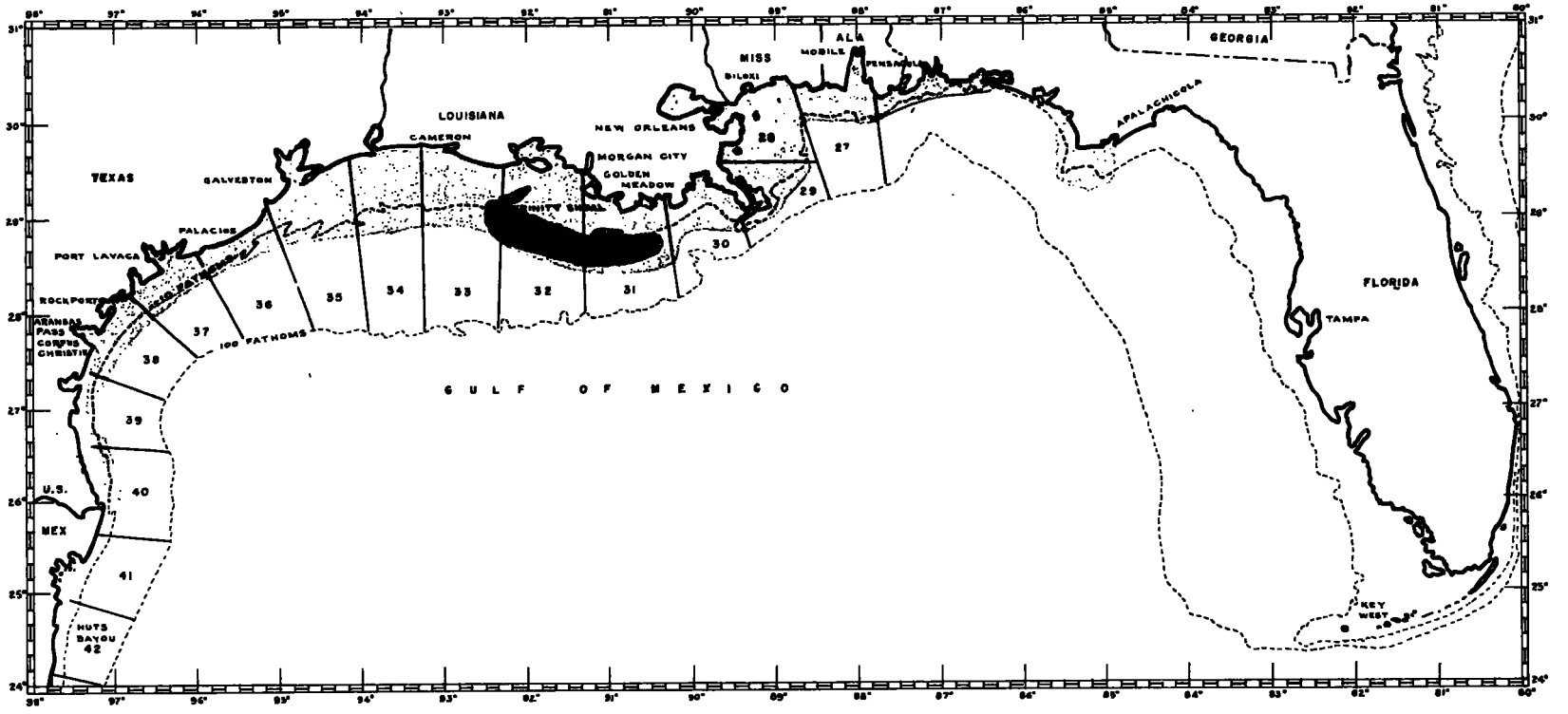


FIGURE 12.—Shrimp-fishing grounds and reference areas for tagging analyses along the coast of the Gulf of Mexico. Fishing grounds are shown by stippling.

In table 12 we give for each experiment, the date and locality of release and the number of returns for all our marking experiments.

MIGRATIONS FROM INSIDE WATERS TO OUTSIDE WATERS

The common or white shrimp has very definite patterns of movement, but these vary in different areas. However, in one respect the movements of marked shrimp were similar in all localities studied between North Carolina and Texas, that is, after the young shrimp first made their appearance on the inland fishing grounds they gradually worked their way towards the sea.

If the shrimp move from inside waters (those landward of the outer beach line, the marshes, bays, sounds, rivers, creeks, and bayous) to outside waters (the littoral waters beyond the outer beach line) and remain subject to recapture, we should expect that with the passage of time increasing proportions of inside releases would be encountered in outside waters. Eventually, we should expect to find the recaptures coming only from outside waters. We found this to happen along the Atlantic coast and in the north-central Gulf of Mexico. However, if the marked shrimp moved from inside waters to outside waters and then beyond the range of the fishing fleet we should expect relatively poor returns from outside waters, although the recaptures from inside waters should decline progressively at a rate greater than could be explained on the basis of mortality alone. We found that our central-Texas recaptures of inside releases behaved in this fashion. They were soon lost to the fishery once they moved to outside waters. They obviously moved beyond the range of the fishery.

The data substantiating these statements are contained in table 13 and are arranged so that the months after release represent calendar months, with 0 month the month of release. For instance,

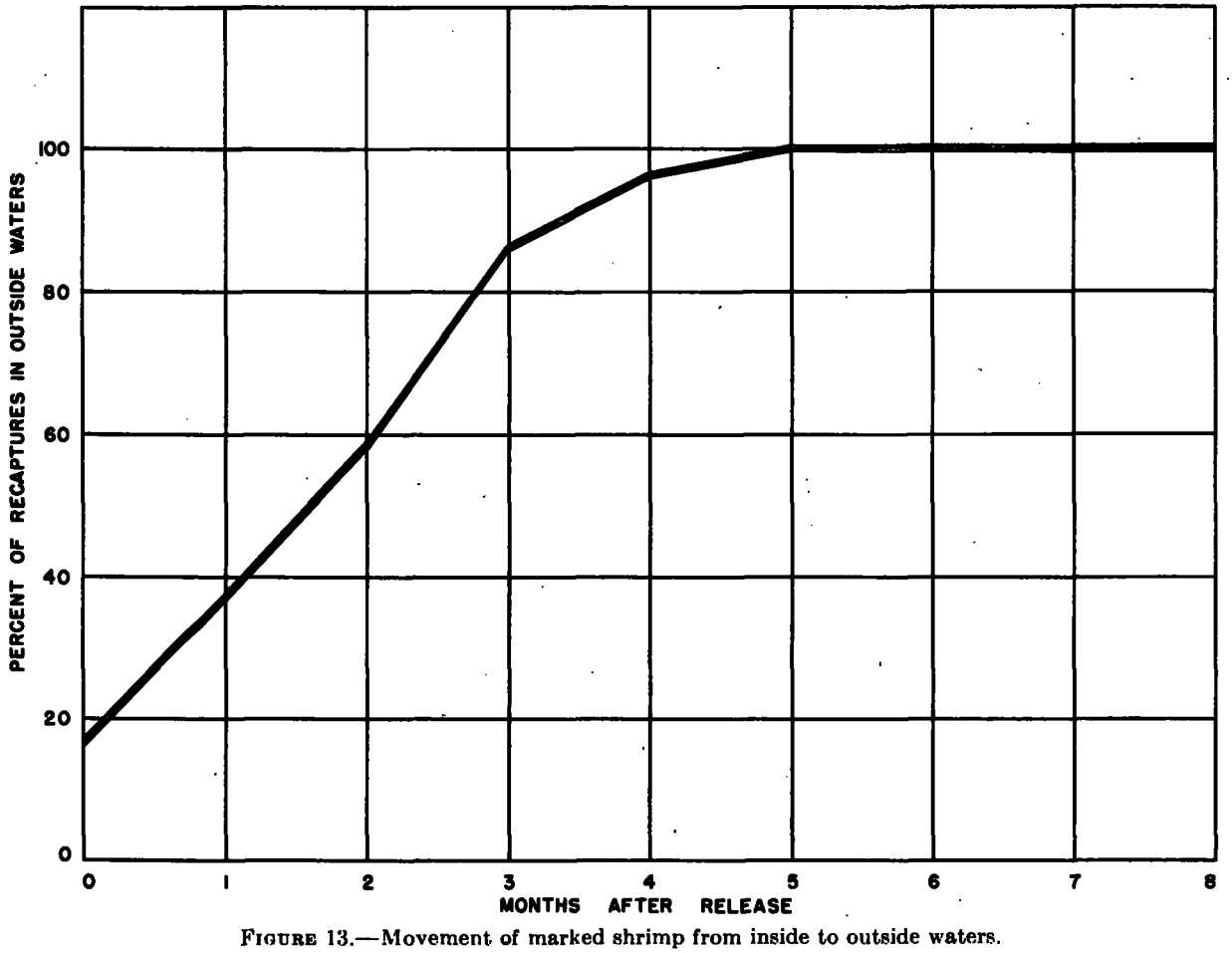


FIGURE 13.—Movement of marked shrimp from inside to outside waters.

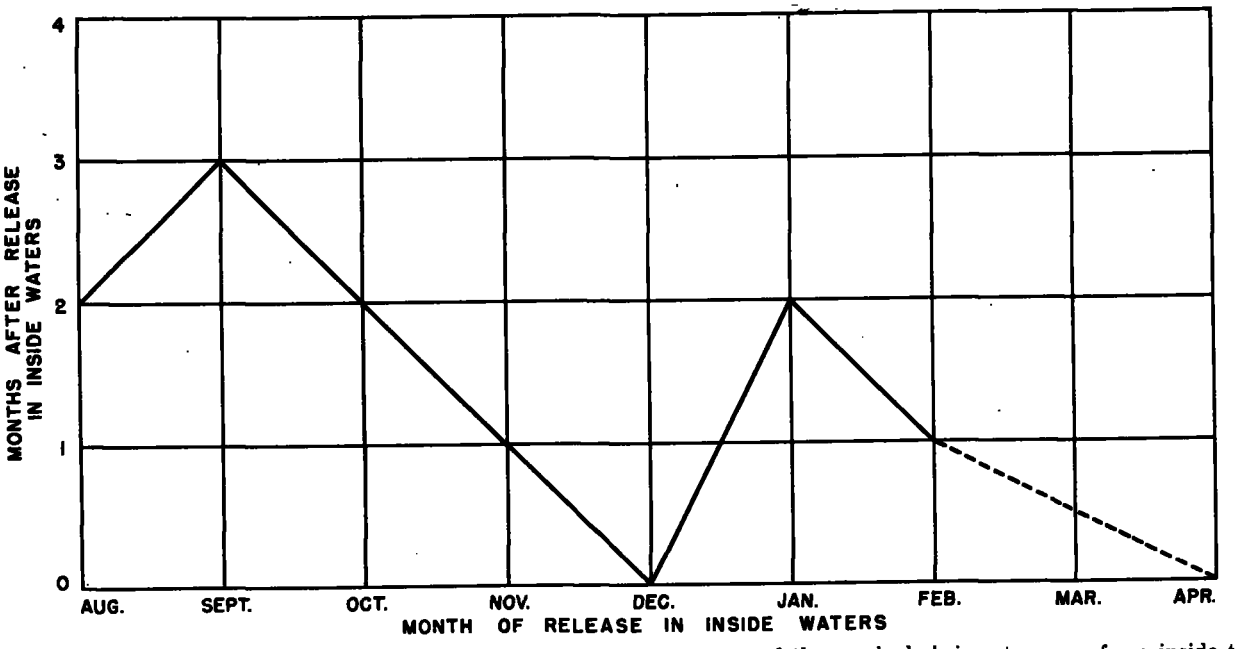


FIGURE 14.—Seasonal changes in length of time required for 60 percent of the marked shrimp to move from inside to outside waters.

recaptures any time during September of shrimp released any time in September were recorded as month 0 returns. Recaptures any time in October from September releases were recorded as month 1 returns.

Figure 13 (based on the data for all areas except Texas) shows the monthly percentage of marked shrimp, recaptured in outside waters, which originally were caught, marked, and released in inside waters. During 0 month, 16.5 percent of all recaptures were in outside waters. The month following the release month, 37.2 percent of all recaptures were taken in outside waters. After the fourth month none of these shrimp was recaptured in inside waters.

The movement of marked shrimp from inside to outside waters is not uniform throughout the year. We can obtain a rough estimate of the seasonal changes in the rapidity of this migration by noting the number of months required for outside recaptures of shrimp tagged in inside waters to reach, or to exceed and maintain, a level of 60 percent of the total recaptures for each month. The data on this point are given in tables 14 and 15, from which we have omitted Texas data for reasons previously given. We have depicted the data graphically in figure 14. The September releases in inside waters required 3 months before 60 percent or more of the recaptures were found in outside waters. In December and April, more than 60 percent were caught in outside waters during the same month in which they were released. We made no releases in inside waters during March, May, or June. July is not included in figure 14 since all of the recaptures from releases made during this month were caught in July or August, and in neither month did the returns from outside waters equal 60 percent.

It is obvious that the movement from inside waters to outside waters speeds up during two periods of the year, at the onset of winter and in the spring. As we shall demonstrate later, these two periods seem to be associated with two groups of shrimp, one an early-spawned group, and the second a later-spawned group. The first group spawned apparently was almost completely in outside waters by December, and the second was rapidly moving out in April.

Of course these data are only rough approximations, but they do corroborate (as will be demonstrated in the section on size distribution) conclusions reached by other means. These conclusions are as follows:

1. After the young shrimp appear on the inside fishing grounds they move toward the sea.

2. This movement becomes more rapid during two seasons, with the approach of winter and during spring.

TABLE 12.—*Releases and recoveries of tagged shrimp*

Area No.	Experiment No.	Date released	Released in locality of—	Number released	Total (each experiment)	Number recovered
		Oct. 11, 1937	Beaufort Fisheries Station, N. C.	197		
		Oct. 12, 1937	Off Beaufort Bar, N. C.	149		
1	1	do	Near Gallant Point, N. C.	34	834	60
		do	Gallant Point, N. C.	248		
		Oct. 13, 1937	Off Beaufort Bar, N. C.	206		
		Oct. 16, 1937	Off Oak Island, N. C.	442		
3	1	do	Inside Southport Entrance, N. C.	493	935	388
		Oct. 6, 1936	Mouth of Key Creek, S. C.	178		
	1	do	Mouth of Bull Creek, S. C.	214		
		do	Bull Creek, S. C.	174	941	35
5		Oct. 7, 1936	Mouth of Bull Creek, S. C.	375		
	2	Oct. 18, 1937	Mouth of Warf Creek, S. C.	97		
		Oct. 18-19, 1937	Warf Creek, S. C.	841	938	37
		Sept. 8, 1936	Off Sandy Point, S. C.	399		
6	1	do	Off Trenchard Inlet, S. C.	289		
		Sept. 9, 1936	Mouth of Trenchard Inlet, S. C.	108	1,188	107
		do	Off Point of Hilton Head, S. C.	392		
		Oct. 1, 1935	Sapelo Sound, Ga.	236		
	1	Oct. 2, 1935	Off south end of St. Catherines Island, Ga.	59		
		do	Julienton River, Ga.	142	603	163
		do	Mud River, Ga.	166		
		Oct. 23, 1935	Off south end of Sapelo Island, Ga.	499		
7	2	Oct. 24, 1935	Off south end St. Catherines Island, Ga.	390	1,185	345
		do	Near mouth of Sapelo Sound, Ga.	296		
	3	Sept. 10, 1936	South end of Ossabaw Island, Ga.	396	396	105
	4	Oct. 21, 1937	Sapelo Sound, Ga.	398	398	125
	1	Sept. 10, 1935	North end Cumberland River, Ga.	7	7	5
		Sept. 20, 1935	Off south end St. Simon's Island, Ga.	118		
	2	do	Jekyll Creek, Ga.	25	210	33
		Sept. 23, 1935	St. Simons Sound, Ga.	67		
	3	Oct. 16, 1935	St. Simons Sound, Ga.	23	23	7
		Oct. 21, 1935	Off St. Simons sea buoy, Ga.	370		
	4	do	Off north end Jekyll Island, Ga.	280	1,143	299
		Oct. 22, 1935	Near mouth St. Andrew's Sound, Ga.	493		
	5	Sept. 11, 1936	St. Simons Sound Entrance, Ga.	495	495	78
		Aug. 10, 1937	Umbrella Creek, Ga.	389		
	6	Aug. 11, 1937	St. Simons Sound, Ga.	294	733	129
		Aug. 12, 1937	St. Simons Sound Entrance, Ga.	50		
	7	Aug. 19, 1937	Off south end of St. Simon's Island, Ga.	423	423	16
8		Sept. 7, 1937	St. Simons Sound Entrance, Ga.	397		
	8	do	St. Simons Sound, Ga.	75	472	59
	9	Nov. 9, 1937	do	398	398	109
	10	Jan. 24, 1938	do	543	543	128
	11	Feb. 23, 1938	do	395	395	83
	12	Mar. 24, 1938	Off St. Simons Island bar, Ga.	396	396	26
	13	April 14, 1938	St. Simons Sound, Ga.	397	397	136
	14	May 13, 1938	Off St. Simons Island bar, Ga.	393	393	92
	15	June 24, 1938	do	260	260	51
		July 6, 1938	Jekyll Jetties, St. Simons Sound, Ga.	426	895	124
	16	July 12, 1938	Off south end Jekyll Island, Ga.	469		
		Aug. 3, 1938	Jekyll Jetties, St. Simons Sound, Ga.	200		
	17	do	Eastfield River, near St. Simons Sound, Ga.	197	592	76
		Aug. 5, 1938	Off St. Simons bar, Ga.	165		
		Aug. 11, 1938	do	30		
		Nov. 12, 1935	Off Mayport Jetties, Fla.	136		
	1	do	Off Mayport can buoy, Fla.	262	598	79
9		Nov. 13, 1935	Off St. Augustine sea buoy, Fla.	200		
	2	Jan. 19, 1938	St. Augustine Entrance, Fla.	772	772	211
	3	Feb. 13, 1938	Off St. Augustine Inlet, Fla.	99	99	25
	4	Mar. 18, 1938	St. Augustine Inlet, Fla.	198	198	7
	1	Jan. 17, 1936	Off New Smyrna bar, Fla.	300	300	18
		Jan. 17, 1938	do	507	656	142
10	2	do	Inside New Smyrna Entrance, Fla.	149		
	3	Feb. 20, 1938	Off New Smyrna bar, Fla.	196	393	58
		do	Inside New Smyrna bar, Fla.	197		
	1	Jan. 16, 1936	Cape Canaveral, Fla.	399	399	168
	2	Feb. 15, 1936	do	55	55	13
		Jan. 13, 1938	do	348	582	132
11	3	Jan. 14, 1938	do	234		
		Feb. 15, 1938	do	392	491	35
	4	Feb. 16, 1938	do	99		
	1	Sept. 20, 1939	Bon Secours Bay in Mobile Bay, Ala.	493	493	89
	2	Sept. 21, 1939	Mobile Bay, upper portion, Ala.	489	489	96
27	3	Oct. 11, 1939	Bayou La Batre, outer beacon, Ala.	324	324	103
	4	Oct. 12, 1939	Grants Pass, Ala.	363	363	34
		Sept. 23, 1939	Three miles off Gulfport, Miss.	298		
	1	Sept. 24, 1939	East Beach, Gulfport, Miss.	596	894	259
	2	Sept. 25, 1939	Vicinity of Grand Island, Mississippi Sound, Miss.	922	922	303
28	3	Oct. 12, 1939	Off Belle Fontaine Point, Miss.	392	392	36
	4	Oct. 13, 1939	Near Gulfport, Mississippi Sound, Miss.	378	378	83
	5	Oct. 14, 1939	Sundown Island, near Isle au Pitre, Miss.	479	479	109
	6	Dec. 1, 1939	Mitchell Keys Light, Chandeleur Sound, La.	247	247	1
29	1	Nov. 30, 1939	Breton Sound near Breton Island, La.	688	688	84
	1	Dec. 13, 1938	Four Bayou Pass, La. (inside)	495	495	26
	2	Dec. 14, 1938	Shell Island, La.	771	771	164
	3	Jan. 19, 1939	Four miles W. of Caminada Pass, La.	169	169	0
	4	Aug. 29-30, 1939	Barataria Bay, La. (inside)	978	978	88
30	5	Oct. 27, 1939	Two miles north of Shell Reef Light, Barataria Bay, La. (inside)	970	970	102
		Oct. 28, 1939	Seven miles off Caminada Pass, La.	189	770	124
	6	do	Caminada Pass, La.	581		
	7	Nov. 10, 1939	Four Bayou Pass (inside), La.	50	50	3
	8	Nov. 11, 1939	Three miles off Four Bayou Pass, La.	444	444	9

TABLE 12.—*Releases and recoveries of tagged shrimp*—Continued

Area No.	Experiment No.	Date released	Released in locality of—	Number released	Total (each experiment)	Number recovered
	1	Dec. 16, 1938	Eleven miles southwest of Ship Shoal Light, La	957	957	17
	2	Jan. 20, 1939	Whiskey Pass, La	806	806	4
	3	Nov. 12–15, 1939	Inside Wine Island, near Pt. Mast, La	928	928	27
	4	Jan. 17, 1940	One mile off Whiskey Pass, La	348	348	4
31	5	Feb. 29, 1940	Ten miles south-southeast of Ship Shoal Light, La	589	589	65
	6	Mar. 1, 1940	Northeast of Ship Shoal Light, La	1190	1190	194
	7	do	Eight miles northwest of Ship Shoal Light, La	199	199	42
	8	Mar. 6, 1940	Eight miles west-northwest of Ship Shoal buoy, La	589	589	107
		Jan. 25, 1939	Thirty miles south of Atchafalaya beacon, La	394		
	1	Jan. 26, 1939	Twenty-five miles south of Atchafalaya beacon, La	344	738	64
	2	Dec. 15–16, 1939	Thirty miles south of Marsh Island, La	1, 133	1, 133	128
32	3	Jan. 30, 1940	Ten miles southeast of Trinity Shoal buoy, La	1, 241	1, 241	194
	4	Feb. 29, 1940	Ship Shoal Light, La	593	593	73
	5	Mar. 5, 1940	South-southwest of Atchafalaya Beacon, La	793	793	195
	1	Oct. 2, 1936	Two miles east of Signal Island, San Antonio Bay, Tex	200	200	0
37	2	Oct. 3, 1936	One mile east of Sand Point Beacon and 2 miles west of Gallinipper Pt. Beacon, Matagorda and Lavaca Bays, Tex	380	380	5
		Sept. 23, 1936	One mile S. of Half Moon Reef, Aransas Bay, Tex	98		
	1	Sept. 24, 1936	Ship Island, Aransas Bay, Tex	296	490	34
		do	Cool Coast Camp, Tex	96		
	2	Sept. 25, 1936	Copano Bay, Tex	296	296	5
	3	Sept. 28, 1936	Mud Island, Aransas Bay, Tex	199	298	21
		do	Harbor Island Light, Aransas Bay, Tex	99		
	4	Sept. 29, 1936	Shamrock Cove, Corpus Christi Bay, Tex	490	882	206
		Sept. 30, 1936	Off Ingleside, Corpus Christi Bay, Tex	392		
		Aug. 27, 1937	Mouth Allen's Bight, Aransas Bay, Tex	99		
	5	Aug. 30, 1937	Allen's Bight, Aransas Bay, Tex	196	391	18
		do	Off Ranch House, Mud Island, Aransas Bay, Tex	96		
38		Aug. 31, 1937	Shamrock Point, Corpus Christi Bay, Tex	189	283	21
	6		Ingleside Beacon, Corpus Christi Bay, Tex	94		
		Oct. 20, 1937	Rockport Basin, Aransas Bay, Tex	404		
	7	Oct. 21, 1937	Three-quarter mile E. of Mud Island Point, Aransas Bay, Tex	100	701	157
		Oct. 26, 1937	Rockport Basin, Aransas Bay, Tex	197		
		Oct. 27, 1937	Inside south jetty, Aransas Pass, Tex	249	793	78
	8	Oct. 28, 1937	Four miles off, 3 miles S. of jetties, Aransas Pass, Tex	544		
	9	do	Docks at Port Aransas, Tex	195	195	31
		Sept. 8, 1938	Just west of drawbridge, Copano Causeway, Tex	177		
	10	Sept. 14, 1938	Two miles SW. of Jordan Pass, Copano Bay, Tex	100	472	10
		Sept. 15, 1938	One mile N. of Port Bay Channel, Copano Bay, Tex	195		
41	1	Mar. 17–22, 1947	Fifteen to 35 miles S. of Rio Grande River, Mexico	616	616	118
42	1	Mar. 17, 1947	Off Huts Bayou, Mexico	379	379	19
1	All		North Carolina		834	60
3	do		do		935	388
5	do		South Carolina		1, 879	72
6	do		do		1, 188	107
7	do		Georgia		2, 582	738
8	do		do		7, 775	1, 451
9	do		Florida		1, 667	322
10	do		do		1, 349	218
11	do		do		1, 527	348
27	do		Alabama		1, 669	322
28	do		Mississippi and Louisiana		3, 312	791
29	do		Louisiana		688	84
30	do		Inside waters, Louisiana	2, 493	4, 647	516
			Offshore, Louisiana	2, 154		
31	do		Inside waters, Louisiana	928	5, 606	460
			Offshore, Louisiana	4, 678		
32	do		Offshore, Louisiana		4, 498	654
37	do		Central Texas		580	5
38	do		do		4, 801	581
41	do		Northern Mexico		616	118
42	do		do		379	19
1–11	do		Atlantic coast	19, 736		3, 704
27–29	do		Northern Gulf, east of Mississippi River	5, 669		1, 197
30–32	do		Northern Gulf, west of Mississippi River (inside)	3, 421		246
			Northern Gulf, west of Mississippi River (offshore)	11, 330		1, 384
37–38	do		Central Texas	5, 381		586
41–42	do		Off Mexico, south of Rio Grande	995		137
All	do		North Carolina to northern Mexico	46, 532		7, 254

Apparently, once the shrimp reach outside waters they tend to remain there unless driven out before their normal time by sudden environmental changes. Of those shrimp we tagged in outside waters along the Atlantic coast, only two were recaptured in the inside waters of another area. Along the Louisiana coast, 118 of our marked shrimp released in outside waters were later recaptured in inside waters. However, all but nine of these were small shrimp from late February and early March releases following an unusual cold spell. These shrimp had sought refuge in deeper water, but later when the inland waters became warmer they returned there, probably almost immediately to move offshore to spawn.

TABLE 13.—*Movement of tagged shrimp from inside waters to outside waters*

Locality of recapture	Number recaptured in month								
	0	1	2	3	4	5	6	7	8
Atlantic Coast:									
Inside waters	334	185	12		1				
Outside waters	139	263	94	33	11	1		2	
Northern Gulf east of Mississippi River:									
Inside waters	518	386	100	8					
Outside waters	2	90	58	10	5	2			
Northern Gulf west of Mississippi River:									
Inside waters	16	101	2						
Outside waters	30	45	7	7	10	3	2	1	1
Texas:									
Inside waters	83	221	48	7					
Outside waters	49	94	1	1					
Total all localities except Texas:									
Inside waters	868	672	114	8	1				
Outside waters	171	398	159	50	26	6	2	3	1
Total (excluding Texas)	1,039	1,070	273	58	27	6	2	3	1
Percent outside (excluding Texas)	16.5	37.2	58.2	86.2	96.3	100.0	100.0	100.0	100.0

TABLE 14.—*Numbers of tagged shrimp released in inside waters, arranged according to locality and time of recapture*

[Atlantic coast and northern Gulf of Mexico; Texas omitted]

Locality of recapture and month of release	Number recaptured in month								
	0	1	2	3	4	5	6	7	8
Inside waters:									
January	3	71	4						
February		16	1						
April	11	10	2						
July	8	18							
August	106	80	1						
September	358	230	102	8					
October	331	232	3		1				
November	49	15	1						
December	2								
Outside waters:									
January	6	23	12	7	2				
February		55	8	3					
April	49	52	8	1	1				
July	11	12							
August	34	23	8	3	1				1
September	2	20	39	15	8				
October	39	100	71	17	4	3	1	3	
November	10	112	13	4	10	3	1		
December	20	1							
Total inside	868	672	114	8	1				
Total outside	171	398	159	50	26	6	2	3	1

TABLE 15.—*Monthly percentages of recaptures of inside releases recaptured in inside and outside waters*

[Data from table 17]

Month and locality of release	Percent recaptured in month								
	0	1	2	3	4	5	6	7	8
January:									
Inside waters	33.3	75.5	25.0						
Outside waters	66.7	24.5	75.0	100.0	100.0				
February:									
Inside waters		22.5	11.1						
Outside waters		77.5	88.9	100.0					
April:									
Inside waters	18.3	16.1	20.0						
Outside waters	81.7	83.9	80.0	100.0	100.0				
July:									
Inside waters	42.1	60.0							
Outside waters	57.9	40.0							
August:									
Inside waters	75.6	77.7	11.1						
Outside waters	24.4	22.3	88.9	100.0	100.0				100.0
September:									
Inside waters	99.4	92.0	72.3	34.8					
Outside waters	.6	8.0	27.7	65.2	100.0				
October:									
Inside waters	89.5	69.9	4.1		20.0				
Outside waters	10.5	30.1	95.9	100.0	80.0	100.0	100.0	100.0	
November:									
Inside waters	83.1	11.8	7.1						
Outside waters	16.2	88.2	92.9	100.0	100.0	100.0	100.0		
December:									
Inside waters	9.1								
Outside waters	90.9	100.0							

TABLE 16.—*Months in which tagged shrimp were released along the Atlantic coast*

Released in month of—	Released in area No.—								
	1	3	5	6	7	8	9	10	11
January						x	x	x	x
February						x	x	x	x
March						x	x		
April						x			
May						x			
June						x			
July						x			
August						x			
September			x	x	x	x			
October	x	x	x		x	x			
November						x	x		

Once the shrimp reached the outside waters their movements varied with the size of the shrimp and the locality, and apparently also the time of the year.

The small shrimp, 13 cm. or less in total length, did not make any extensive movements. Once they reached the outside waters they remained there, almost immediately adjacent to their inland nursery grounds. The large shrimp, more than 13 cm. in total length, showed distinct behavior patterns which, since they varied with locality, must be discussed on a geographical basis.

ATLANTIC COAST

Weymouth, Lindner, and Anderson (1933) demonstrated that the larger shrimp disappeared from the Georgia coast during fall and winter. We later found that a decrease in abundance of large shrimp also occurred at about the same time along the North and South Carolina coasts. Concomitant with the decline in catch and the disappearance of larger shrimp from the northern and central sections, we found that in the southern section (Florida) the catches increased (fig. 15),[4] and that the shrimp caught were comparable in length to those missing from the north. These facts suggest the possibility of a southward migration during fall.

Throughout the winter, small shrimp remained in varying numbers from North Carolina to northern Florida. They were most abundant in southern Georgia and northern Florida. In Georgia and the Carolinas, after the winter low, the catches increased during April, May, and June, before the appearance of the new spring-spawned shrimp on the fishing grounds. This was primarily due to the growth and entrance into the fishery of small shrimp that wintered in these areas.

The catch records for the various States, mostly based on tax receipts, cannot be considered entirely accurate. However, from intimate association with the fishery, we believe that figure 15 roughly represents both relative seasonal abundance and relative fishing effort. In general, there was more effort expended when and where the shrimp were abundant than when and where they were not.

At the time we ran our marking experiments (1935–38), part of the fishing fleet would move along the coast in accordance with the shifting abundance of shrimp and operate in South Carolina and Georgia during late summer and fall and along the Florida coast during winter. Many of the boats would return to Georgia and South Carolina for the spring run of shrimp. North Carolina did not permit fishing by boats from other States. In all the States, there were fleets of small boats that fished the entire year from their home ports, but the majority of these were in Georgia and northern Florida.

Except in area 3, North Carolina boats would fish only occasionally in outside waters during winter and early spring. There was no fishing in area 2 at any time. Winter and early spring fishing in outside waters of South Carolina (areas 4, 5, and 6) was more frequent than in areas to the north, but it still was casual. It was only along the coasts of Georgia and northern Florida (areas 7, 8, and 9) that fishing occurred with a fair degree of intensity throughout the year. Fishing in central Florida (areas 10 and 11) was limited almost exclusively to late fall, winter, and spring.

Because of these conditions, and also because of our facilities, we concentrated our efforts on the one area (area 8) where throughout the year fairly intensive fishing occurred both to the north and to the south; here we tagged shrimp each month of the year, except December. In the other areas, we tagged only when the shrimp were most abundant. Table 16 shows the months in which we released marked shrimp in each area.

In figure 16 (based on data presented in table 17) we show graphically, by months, the percentage of total recaptures for each month taken in areas north or south of the areas of release. In this figure the lines begin with the month in which the

[4] The data for this figure are from Anderson, Lindner, and King (1949).

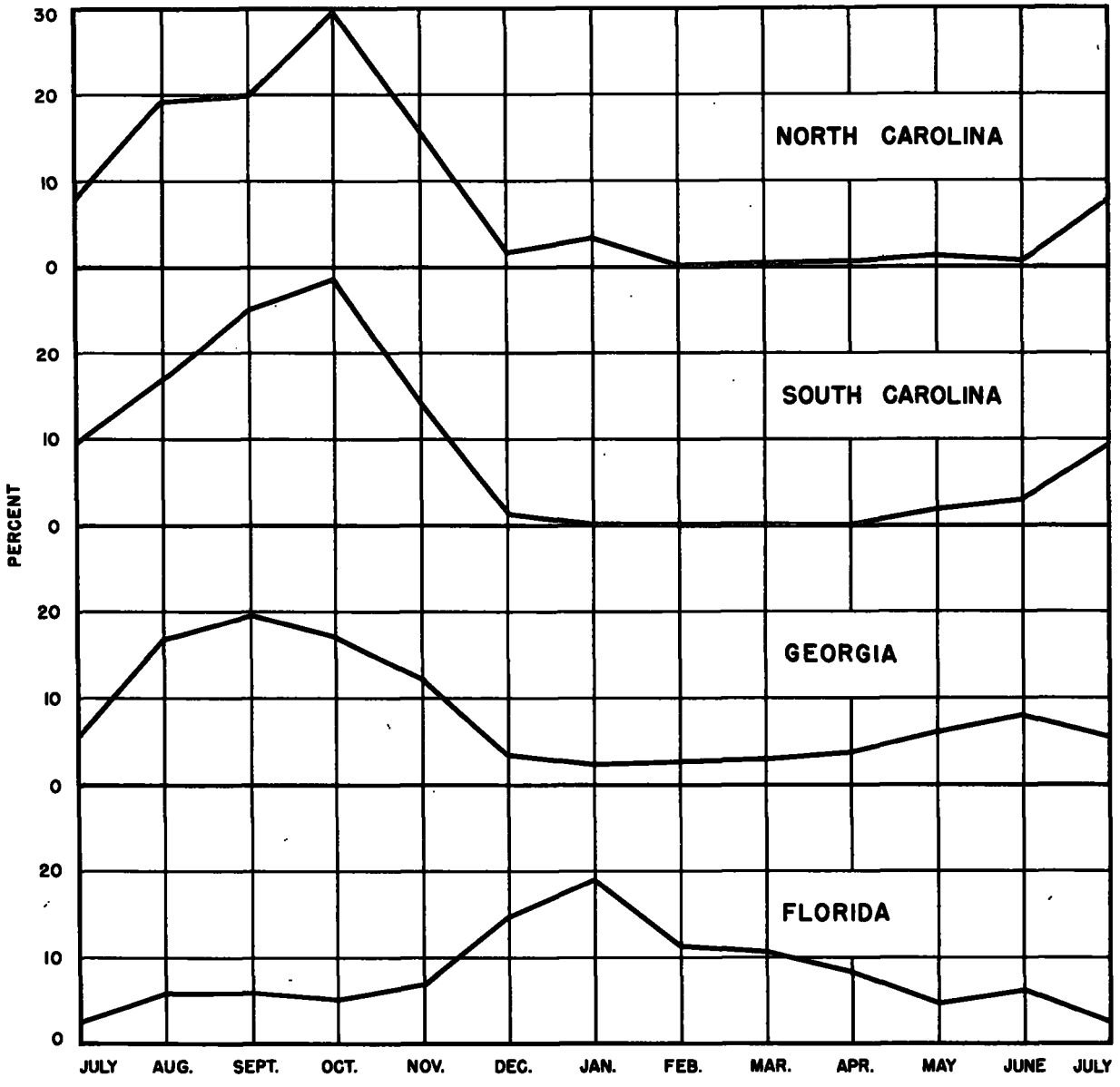


FIGURE 15.—Average monthly percentage of annual shrimp catch for the Atlantic coast, by States.

shrimp were released and follow (from top to bottom) the recaptures from the releases of this month until fewer than eight of these shrimp were recaptured in any following month. The points falling within the 0–0 section of this graph indicate that no recaptures were made in areas other than the release area. For example, from releases made during May all recoveries during both May and June were from the area of release. However, we find that about 12 percent of all October releases that were recaptured during the same month were taken south of the release areas. Following these October releases month by month, we see that each month the percentage of recoveries in areas south of the release areas increased until, in February, all recaptures were to the southward. When recaptures were made in the same month both north and south of the release area, the line shows only the direction in which the predominant recaptures were made. We believe that this figure tells the general story of shrimp movements along the Atlantic coast: a southward movement

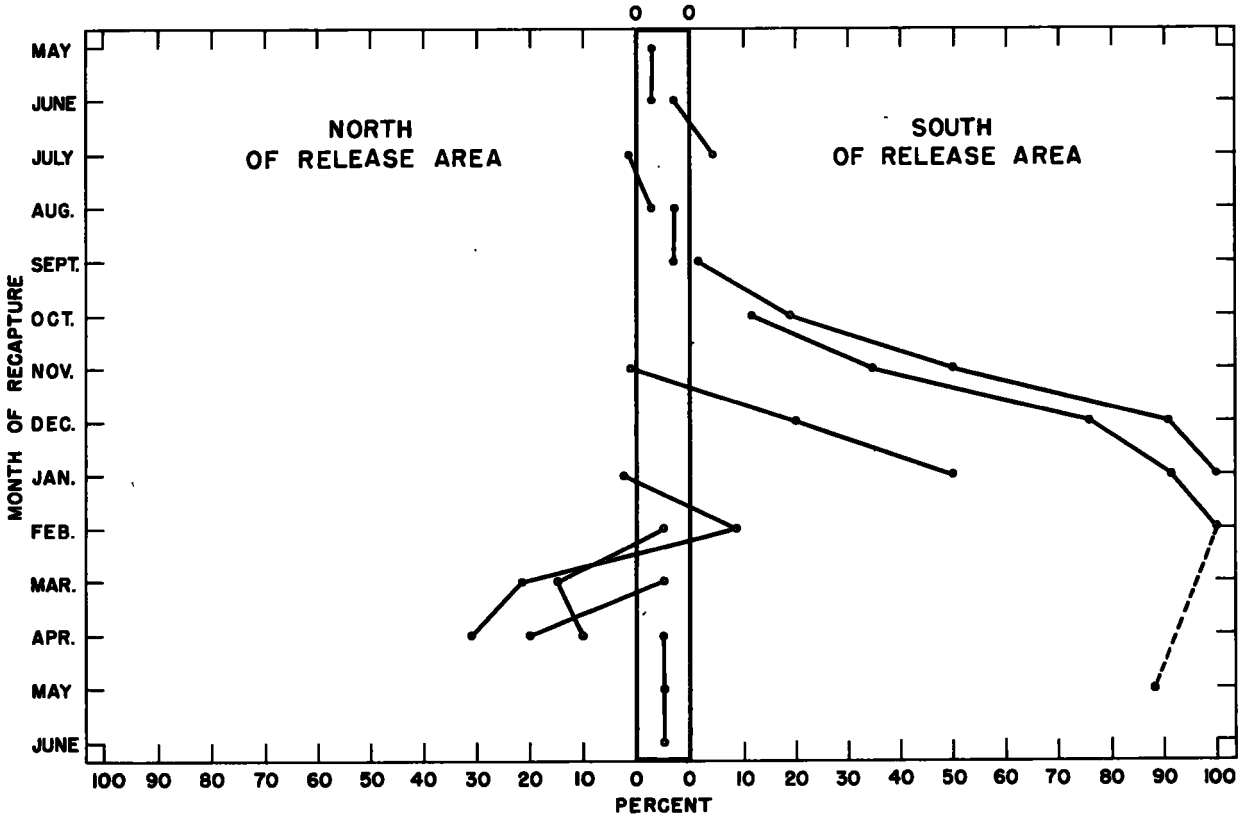


FIGURE 16.—Monthly percentage of total monthly recaptures of marked shrimp recovered in areas north and south of release area.

during fall and early winter, a return northward in late winter and early spring, and no coastwise movement during late spring and summer.

Of the 10 shrimp recaptured between July and December (of releases made during these same months) in areas north of the release area, only one was retaken as far as 35 miles from the place of release. These certainly cannot be considered to indicate a migration pattern. During the same period, 425 shrimp were recaptured south of the release areas. Some of these shrimp had migrated more than 200 miles, and one was recaptured 290 miles from where it had been released.

The movements can be followed in greater detail in tables 17 and 18 and are diagramed in figures 17 to 19. In table 17 we interpret the apparent shaped pattern of recoveries from the October markings to indicate a southward movement and then a later northward return.

Our January to March releases of tagged shrimp, in contrast to the fall releases, show a definite northward trend. In discussing this matter, we can eliminate from consideration releases made in area 11, since recoveries from outside this area could only be from the north. If we then follow through April, the January and February releases made in the other areas (after April there was little fishing in areas 10 and 11), we find that in February about 37 percent and in March about 78 percent of those shrimp recaptured outside the release area were taken in areas to the north of that in which they were liberated (table 19).

Similarly, when we consider the releases from area 8, to the north and south of which relatively equally intensive fishing occurred throughout the year, we find (table 20) that the recaptures to the south and to the north of this area follow the same general pattern as already described. They show that the shrimp move south during fall and early winter, north during late winter and early spring, and remain relatively stationary from mid-spring until fall.

None of the shrimp marked in area 8 were recaptured north of area 7. It should be noted, however, that shrimp released in area 8 during the period January to March, when the northern

TABLE 17.—*Monthly recaptures of Atlantic-coast tagged shrimp, arranged according to month of release and distance (in areas) shrimp were recaptured north and south of release area*

[Areas are 50 miles wide]

Released in month of—	Recaptured in month of—	Number recaptured in areas north or south of release area in geographical sequence													Total
		North					Area of release	South							
		5	4	3	2	1	0	1	2	3	4	5	6	7	
May	May						62								92
	June						29								
	July						1								
June	June						26								49
	July						21	1							
	August						1								
July	July					1	84								123
	August						38								
August	August						179								220
	September						36								
	October						2	1							
	November							1							
	January							1							
September	September					2	282	3	1						412
	October					3	53	12			1				
	November						18	13	2	1	2				
	December						1	3		2	4	1			
	January							2		3	3				
October	October					2	578	73	3						1366
	November						326	158	13	1					
	December						38	69	30	12	6	2			
	January						3	3	7	11	6	1	2	1	
	February								3	3	2	1			
	March								3					1	
November	May						1	7							180
	November					1	95								
	December					1	52	9	2	2					
	January						8	6	2						
	February							1							
	March								1						
January	January				5	5	420		1						785
	February				5	11	180	19							
	March				3	22	84	8							
	April				1	3	8	1							
	May						2	1							
	July	1			2	1									
	August					1									
	September			1											
February	February						36								210
	March				1	22	136	1							
	April					1	9								
	May				1	1	2								
March	March						11								31
	April					3	11	1							
	May					1	3								
	June						1								
April	April						60								134
	May						62								
	June						10								
	July						1								
	August						1								

migration is at its height, were mostly small shrimp which normally do not migrate far.

Since some of our releases from areas 5 and 6 were recaptured in September in areas south of the release area, and none from areas 7 and 8 were recaptured in more southerly regions until October, it is probable that the fall migration begins earlier in South Carolina than it does in Georgia.

The shrimp have completed their southern migration by January or February. The northward return appears to begin at the southern extremity (area 11) as early as January, but not until February in areas 8 to 10. Our data do not indicate precisely when the northward migration terminates, but apparently there is little or no coastwise movement of shrimp between April and August. Since temperature is probably one of the principal factors influencing these coastal movements, we may expect some changes in their timing from year to year. The longest southward migration was by a shrimp released near Beaufort, N. C., in October, and recaptured 95 days later off the east coast of Florida, about 360 miles south of where we released it. The greatest northward migration was recorded for a specimen released at Cape Canaveral, Fla., in January, and recaptured 168 days later off the coast of South Carolina. It had traveled about 260 miles.

TABLE 18.—*Recaptures, by area, month, and size, of tagged shrimp released along the Atlantic coast from 1935 to 1938, inclusive*

Area, and month of release, and size [1] when released	Recaptured in month of—	Number recaptured in area—											All areas	Total
		1	2	3	4	5	6	7	8	9	10	11		
Area 1:														
October:														
Small	October	45											45	45
Large	October	9		1									10	14
	November	1		2									3	
	January								1				1	
Area 3:														
October:														
Small	October			98									98	146
	November			46									46	
	December			1									1	
	February								1				1	
Large	October			167									167	249
	November			60									60	
	December			4					2				6	
	January			2					1	2			5	
	February							1					1	
	March										1		1	
Area 5:														
September:														
Small	October					2				1			2	4
	December												1	
	January								1				1	
Large	September					7		1					8	29
	October				3	1				1			5	
	November					4	2	1	1				8	
	December								1	3	1		5	
	January									3			3	
October:														
Small	December								3	1			4	10
	January								5				5	
	February							1					1	
Large	November					2	3		1				6	24
	December							1	7	5			13	
	January								2	2			4	
	February								1				1	
Area 6:														
September:														
Small	September						26	1					27	33
	October						1	3					4	
	November							1			1		2	
Large	September						51	2					53	71
	October						6	5					11	
	November						2	3			1		6	
	December									1			1	
Area 7:														
September:														
Small	September						1	54					55	58
	October							2					2	
	November								1				1	
Large	September							41					41	46
	October							2	2				4	
	November								1				1	
October:														
Small	October							55					55	105
	November							32	4				36	
	December							1	7	3			11	
	March									1			1	
	May								2				2	
Large	October							98	69	2			169	508
	November							124	110	11			245	
	December							19	26	25	2		72	
	January								1	6	2	4	13	
	February									1	2	1	4	
	May								5				5	
Area 8:														
January:														
Small	January								9				9	125
	February							1	91				92	
	March								15				15	
	April							1	6				7	
	May								2				2	
Large	February								2				2	3
	March								1				1	
February:														
Small	March							1	65				66	78
	April							1	8				9	
	May							1	2				3	
Large	March							1	4				5	5
March:														
Small	March								6				6	21
	April							2	8				10	
	May							1	3				4	
	June								1				1	
Large	March								1				1	4
	April							1	1	1			3	

[1] Small shrimp are those less than 13 cm.; large shrimp are those 13 cm. and longer.

TABLE 18.—*Recaptures, by area, month, and size, of tagged shrimp released along the Atlantic coast from 1935 to 1938, inclusive*—Continued

Area, and month of release, and size [1] when released	Recaptured in month of—	Number recaptured in area—												Total
		1	2	3	4	5	6	7	8	9	10	11	All areas	
Area 8—Continued														
April:														
Small	April								51				51	
	May								56				56	
	June								9				9	118
	July								1				1	
	August								1				1	
Large	April								9				9	
	May								6				6	16
	June								1				1	
May: Large	May								62				62	
	June								29				29	92
	July								1				1	
June: Large	June								26				26	
	July								21	1			22	49
	August								1				1	
July:														
Small	July								19				19	
	August								29				29	48
Large	July							1	65				66	
	August								9				9	75
August:														
Small	August								103				103	
	September								24				24	
	October									1			1	129
	November									1			1	
Large	August								76				76	
	September								12				12	
	October								2				2	91
	January									1			1	
September:														
Small	September								40				40	
	October								10				10	
	November								2				2	54
	January									1		1	2	
Large	September							1	63				64	
	October								29	2			31	
	November								10	5	1		16	117
	December								1	3			4	
	January									1		1	2	
October:														
Small	December									2			2	2
Large	October							2	106	4			112	
	November								61	41			102	
	December								13	34	1		48	
	January								1	2	1	2	6	272
	February										1		1	
	March										2		2	
	May								1				1	
November:														
Small	November								41				41	
	December								29	3	1		33	
	January								7	3			10	85
	March										1		1	
Large	November								12				12	
	December								4	2	1	2	9	23
	January									2			2	
Area 9:														
January:														
Small	January									20			20	
	February									2	1		3	
	March									5	2		7	30
Large	January									105		1	106	
	February								2	16	16		34	
	March								1	30	4		35	178
	April								1	1			2	
	July								1				1	
February:														
Small	February									1			1	
	March									13	1		14	15
Large	February									2			2	
	March									7			7	9
March:														
Small	March									1			1	
	April									1			1	2
Large	March									3			3	
	April									1			1	4
November: Large	November								1	42			43	
	December								1	19	4		24	
	January									1	1	2	4	72
	February										1		1	

[1] Small shrimp are those less than 13 cm.; large shrimp are those 13 cm. and longer.

TABLE 18.—*Recaptures, by area, month, and size, of tagged shrimp released along the Atlantic coast from 1935 to 1938, inclusive*—Continued

Area, and month of release, and size [1] when released	Recaptured in month of—	Number recaptured in area— 1	2	3	4	5	6	7	8	9	10	11	All areas	Total
Area 10:														
January:														
Small	January										8		8	18
	February										6		6	
	March									1	3		4	
Large	January										58		58	142
	February								2	6	33	2	43	
	March									16	17	2	35	
	April									1		1	2	
	May											1	1	
	July								2				2	
	August									1			1	
February:														
Small	February										1		1	1
Large	February										18		18	57
	March									12	27		39	
Area 11:														
January:												11	11	
Small	January											3	3	18
	February									2	1	1	4	
	March									5	5	209	219	
Large	January									3	2	27	32	271
	February									1	3	12	16	
	March									1		1	2	
	April						1						1	
	July								1				1	
	September													
February:														
Small	February											8	8	18
	March										3	7	10	
Large	February											6	6	27
	March									1	5	13	19	
	April											1	1	
	May									1			1	

[1] Small shrimp are those less than 13 cm.; large shrimp are those 13 cm. and longer.

TABLE 19.—*Recaptures north and south of release area, of shrimp tagged in areas 8, 9, and 10 during January and February*

[Small and large shrimp combined]

Recaptured in month of—	Number recaptured in areas— North of release area	South of release area
January		1
February	11	19
March	31	9
April	4	1

TABLE 20.—*Recaptures, other than in area 8, of tagged shrimp released in area 8*

[Small and large shrimp combined]

Recaptured in month of—	Number recaptured in— Area 7	Area 9	Areas south of 9
August			
September	1		
October	2	7	
November		47	1
December		44	5
January		10	5
February	1		1
March	2		3
April	5	1	
May	2		
June			
July	1	1	

TABLE 21.—*Tagged small shrimp (less than 13 cm.) recaptured along southern Atlantic coast*

[Both sexes included, 1935-38 experiments]

Distance captured from point of release	Direction	Number recaptured, of shrimp released in area— 1	3	5	6	7	8	9	10	11	All areas
335-360 miles	South										
305-330 miles	do										1
275-300 miles	do		1								
245-270 miles	do										1
215-240 miles	do			1							2
185-210 miles	do			1	1						8
155-180 miles	do			7			1				4
125-150 miles	do			3			1				1
95-120 miles	do						1				7
65-90 miles	do					4	3				22
35-60 miles	do				1	10	11				
0-30 miles	Local	45	145	2	31	149	643	47	18	26	1,106
35-60 miles	North								1	3	4
65-90 miles	do									2	2
95-120 miles	do									1	1
125-150 miles	do										
155-180 miles	do										
185-210 miles	do										
215-240 miles	do										
245-270 miles	do										
Total		45	146	14	33	163	660	47	19	32	1,159

The proportion of large shrimp that move is much greater than that of the small ones. In tables 18, 21, and 22, we have divided the marked shrimp into two size groups, small and large, with 13 cm. as the arbitrarily selected dividing line between them. The different behavior of the two size groups may be ascertained from table

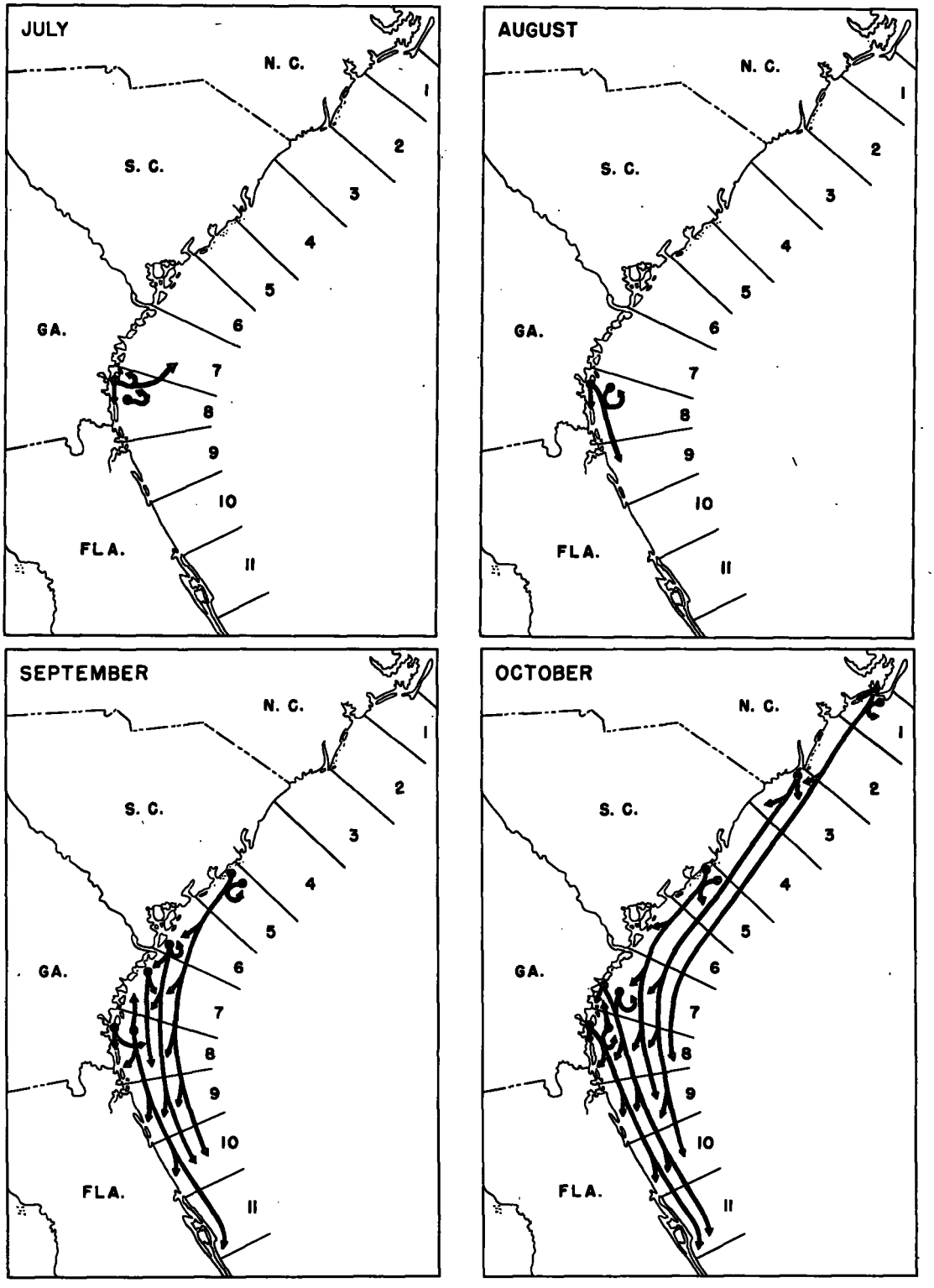


FIGURE 17.—Movements of marked shrimp released along the Atlantic coast during July, August, September, and October. These diagrams (also figs. 18–26) show where marked shrimp were recovered. They do not indicate quantity, or length of time between release and recovery, but merely where the shrimp went. The dot at the beginning of each arrow indicates locality of release.

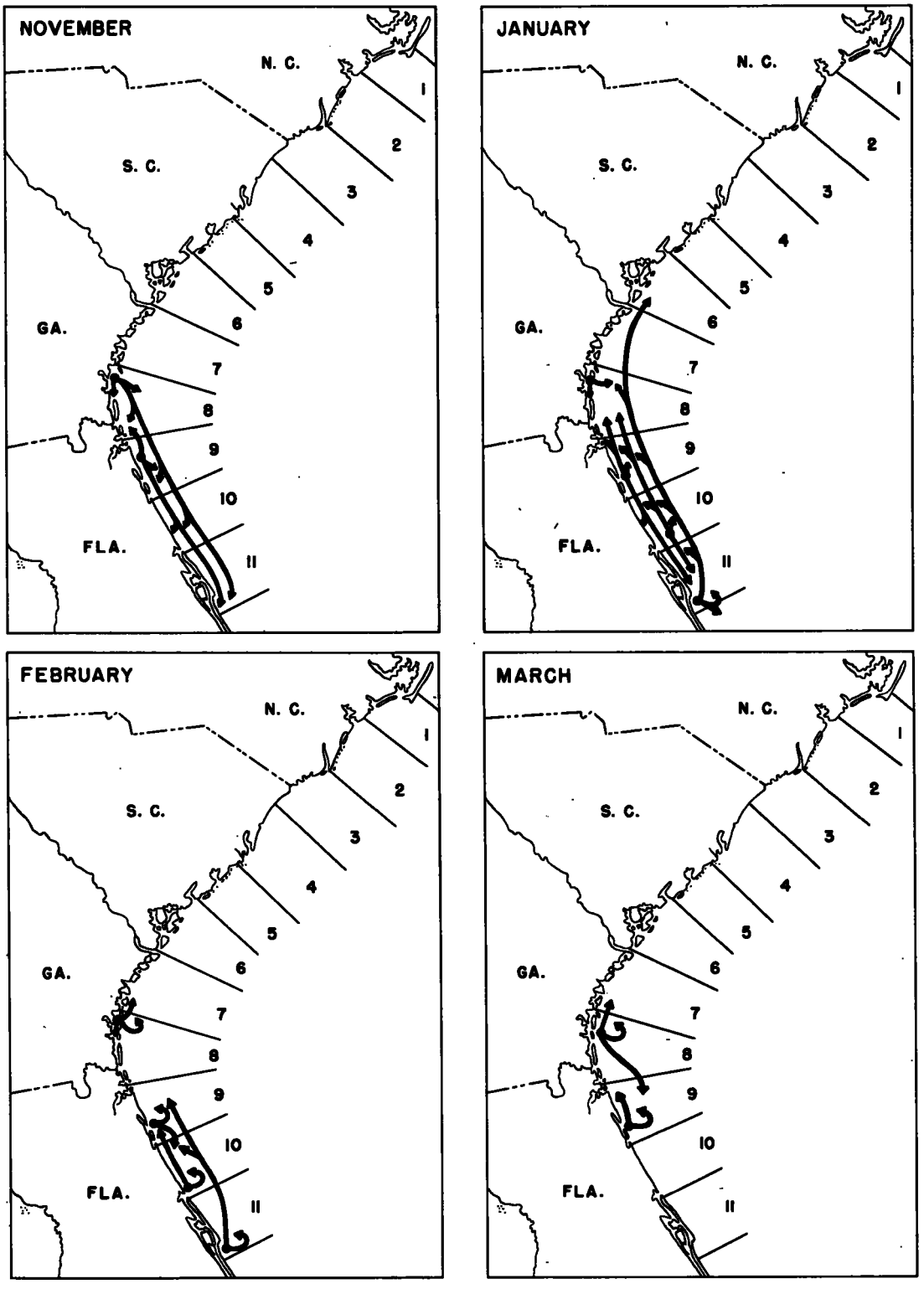


FIGURE 18.—Movements of marked shrimp released along the Atlantic coast during November, January, February, and March. See figure 17 for further explanation.

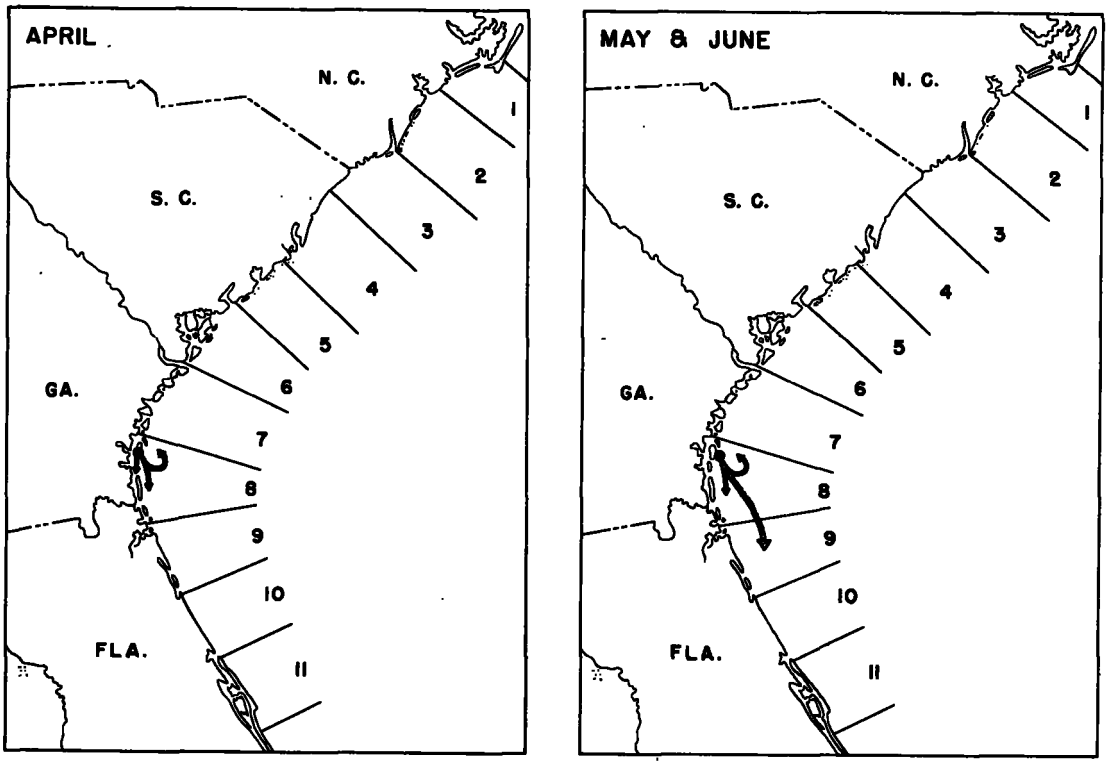


FIGURE 19.—Movements of marked shrimp released along the Atlantic coast during April, May, and June. See figure 17 for further explanation.

18, and a comparison of table 21 with 22, but the very definite correlation between migratory tendency and size is most clearly displayed in table 23.

With respect to the southward migrations along the Atlantic coast during fall and early winter, we do not claim that all the large shrimp move south, but we think the vast majority do. Our data cannot be considered conclusive for the most northern section because in this region we tagged shrimp only during 1 year (there was almost no winter fishing north of area 3), and our returns from this section were few.

If the shrimp are affected by temperature, it is possible, because of the effects of the Gulf Stream on this stretch of the coast (Parr 1933), that both a northward and a southward winter migration might occur, with southern South Carolina or northern Georgia as the center from which the dispersion takes place. Apparently, to a limited and variable extent, there is a northward movement along the Carolina coasts during winter, but the numbers of shrimp involved are few, since the bulk of the population of large shrimp has migrated to the Florida coast. Our tagging would not show such a northward movement, since we did not tag in South Carolina during midwinter. (See p. 621 for additional discussion.)

We believe the migrations of the common shrimp, as presented here, represent the pattern followed by the bulk of the shrimp along the Atlantic coast.

Before we began our marking experiments along the Atlantic coast, the information we had available (length-distribution records and production figures), although highly indicative, was not conclusive evidence of coastwise migration. The decline in abundance and decrease in length of the shrimp in the central and northern sections of the fishery during late fall and early winter might be caused by factors other than a southward migration. Similar symptoms could be caused by the large shrimp burying in the mud and hibernating, or by an offshore migration.

We believe that the evidence we have presented here effectively disposes of these other possibilities. However, we do have additional information.

Shrimp which we kept in aquariums would bury themselves on occasion but never for long periods—a few days at the most, never for weeks or months.

TABLE 22.—*Tagged large shrimp (13 cm. and longer) recaptured along southern Atlantic coast*

[Both sexes included, 1935-38 experiments]

Distance captured from point of release	Direction	Number recaptured, of shrimp released in area—									
		1	3	5	6	7	8	9	10	11	All areas
335–360 miles	South	1	1								2
305–330 miles	do										
275–300 miles	do		4								4
245–270 miles	do		1								1
215–240 miles	do		1	5							6
185–210 miles	do			10	1	5					16
155–180 miles	do			5			5				10
125–150 miles	do			8	1	5	2	1			17
95–120 miles	do			3		10	4	2			19
65–90 miles	do	3		2		34	46	4			89
35–60 miles	do			5	6	67	58	9	6		151
0–30 miles	Local	10	233	15	63	432	632	242	153	274	2,054
35–60 miles	North					1		4	32	11	48
65–90 miles	do							1	6	6	13
95–120 miles	do								2	7	9
125–150 miles	do									2	2
155–180 miles	do									1	1
185–210 miles	do										
215–240 miles	do										
245–270 miles	do									1	1
Total		14	240	53	71	554	747	263	199	302	2,443

TABLE 23.—*Effect of length on migratory tendencies of shrimp from Atlantic coast*

[Migratory shrimp are those recaptured 35 or more miles from release point]

Length	Number recaptured	Number migratory	Percent migratory
10.5 cm. and smaller	199	4	2.0
11 to 12.5 cm.	960	49	5.1
13 cm. and larger	2,443	389	15.9

We have considerably more information, all negative, on the subject of large shrimp moving offshore. During the winter and early spring of 1940 we explored the area from Cape Hatteras to Cape Canaveral in depths between 5 and 100 fathoms and, although we caught other species of shrimp, we did not find a single specimen of *P. setiferus* more than about 8 miles from the coast. Furthermore, despite the intensive commercial fishing, our own exploratory fishing, and that of Springer and Bullis (1952) in the Gulf of Mexico out to 100 fathoms, the greatest known depth in which *P. setiferus* has been taken is 43 fathoms. This record was reported by Springer and Bullis. The white shrimp is usually taken by the commercial fishery in the Gulf of Mexico in depths of less than 20 fathoms, and these shallow waters seem to be its normal habitat. On the Atlantic coast this species does not appear to frequent the depths attained by it in the Gulf. The probable explanation for this is the lack of suitable feeding grounds in the deeper waters along the Atlantic coast.

Our findings lead us to conclude that the bulk of the shrimp of the Atlantic coast, after migrating from inshore to offshore waters, do not move into very deep water far from the coast. Instead, they execute seasonal migrations parallel to the shoreline, moving southward during the fall and early winter, and northward in late winter and early spring. During late spring and summer, their movements are limited and random, so that they remain relatively stationary. The larger specimens are much more prone to move considerable distances than are the smaller ones.

NORTHERN GULF EAST OF THE MISSISSIPPI RIVER

In areas 27 to 29, between Mobile Bay and the mouth of the Mississippi River (fig. 20), we released marked shrimp only during September, October, November, and December; consequently our remarks refer only to the fall and winter movements of the shrimp in these areas. Only one shrimp from the December releases was recaptured, and this in zone *c* in December.[5] Hence, the remaining recaptures during December and later were from September, October, and November releases. All of our releases were in inside waters.

In 1939, when we carried out our tagging program in this area, fishing occurred throughout the year, but the intensity shifted towards the mouth of the Mississippi River during winter, as the shrimp were more abundant there at that time. Our exploratory fishing did not reveal concentrations of white shrimp in depths greater than those covered by the commercial fishery.

Most of the ocean bottoms of the outside littoral waters off the Alabama and Mississippi coasts (other than those immediately adjacent to the outlying islands, and principally the passes between the islands) are barren wastes of sand and shell. There probably is little or no food

[5] In our discussion of movements in the northern Gulf of Mexico and in Texas we have subdivided each area into depth zones. Zone *a* represents inside waters as we have already defined them; zones *b* to *f* are outside waters with depths as follows: *b*, 0 to 4½ fathoms; *c*, 5 to 8½ fathoms; *d*, 9 to 12½ fathoms; *e*, 13 to 16½ fathoms; *f*, 17 fathoms and deeper.

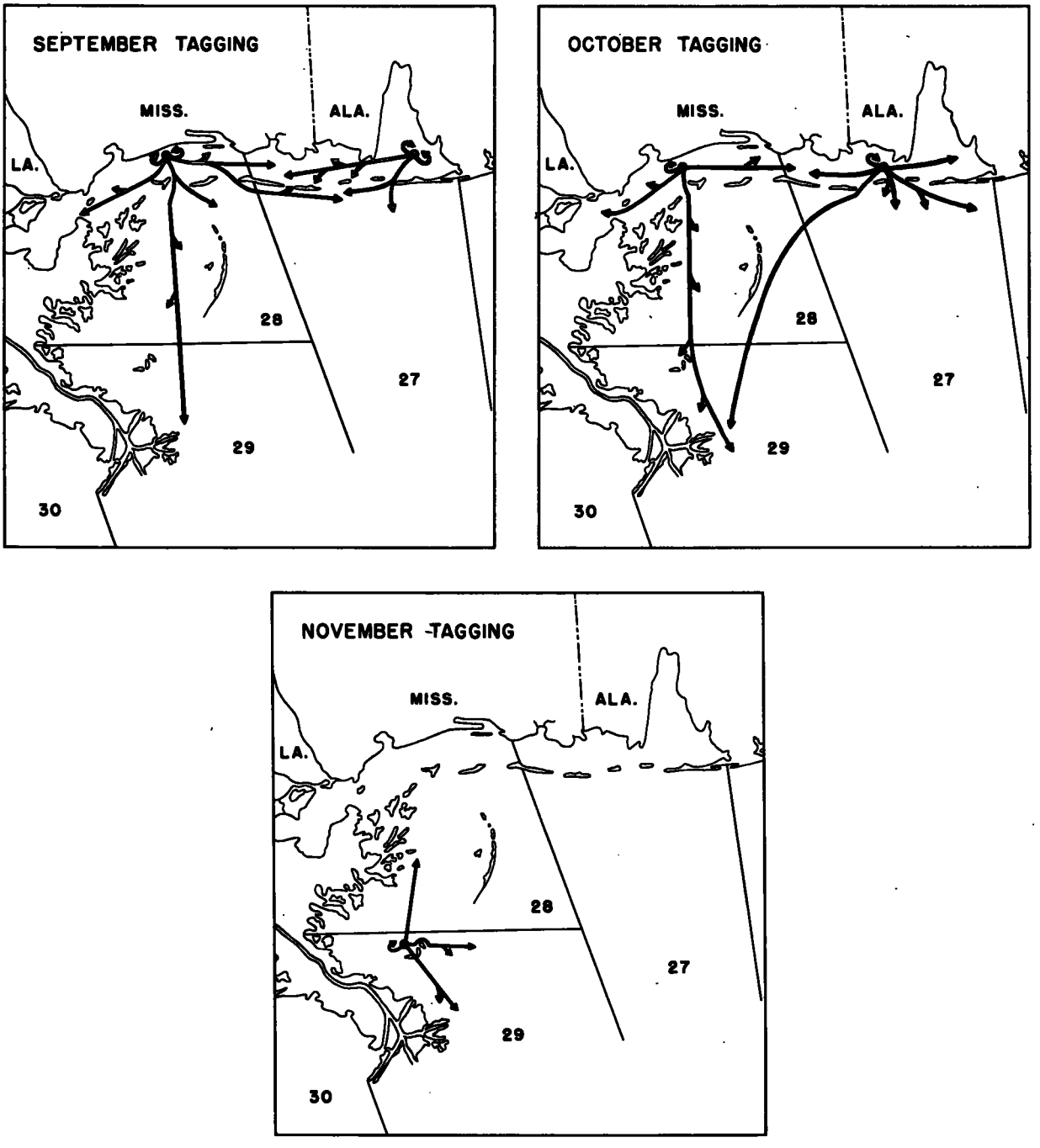


FIGURE 20.—Movements of marked shrimp released in the northern Gulf of Mexico east of the Mississippi River during September, October, and November. See figure 17 for further explanation.

for large shrimp in these areas. Near the delta of the Mississippi River, the bottom, although it shelves off rapidly, consists mostly of mud with an abundance of food. Probably because of this, the large shrimp in this region tend to seek the deeper waters near the mouth of the Mississippi River as winter progresses. Tables 24 and 25 indicate this tendency of the large shrimp, and some of the small ones, to invade area 29. The data presented in tables 26 and

TABLE 24.—*Recaptures of small shrimp (less than 13 cm.) released in Gulf of Mexico, by area of release and by month and area of recapture*

Released in—	Recaptured in month—	Number recaptured in area—														Total
		27	28	29	30	31	32	33	34	35	36	37	38	Unknown	All areas	
Area 27	September	43													43	141
	October	54													54	
	November	31													31	
	December	10													10	
	January	3													3	
Area 28	September		92												92	200
	October		86												86	
	November		16	3											19	
	December		1	2											3	
Area 30	September				16										16	215
	October				13	1									14	
	November				42	6									48	
	December				117										117	
	January				12										12	
	February				2									2	4	
	March					1									1	
	April					1	1								2	
	May					1									1	
Area 31	November					4									4	278
	December					2									2	
	January						2								2	
	February						3								3	
	March					199	4	1							204	
	April					30	4								34	
	May					12	11								23	
	June					5	1								6	
Area 32	March					32	3								35	45
	April					3	1							1	5	
	May					1	3								4	
	June							1							1	
Area 37	November											4			4	4
Area 38	August												3		3	211
	September												29		29	
	October												127		127	
	November												50		50	
	December												2		2	

TABLE 25.—*Recaptures of large shrimp (13 cm. and longer) released in Gulf of Mexico, by area of release and by month and area of recapture*

Released in—	Recaptured in month—	Number recaptured in area—																Total
		27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	All areas	
Area 27	September	22																22	179
	October	71																71	
	November	72																72	
	December	12		2														14	
Area 28	September		197															197	576
	October	4	181	1														186	
	November	34	129	9														172	
	December	1		20														21	
Area 29	December			78														78	83
	January		1															1	
	March			2														2	
	April			2														2	
Area 30	August				2													2	271
	September				57													57	
	October				38	6												44	
	November				82	11												93	
	December				54	1												55	
	January				10													10	
	February				3	2	1											6	
	March					2	1											3	
	April						1											1	
Area 31	December					5												5	159
	January					2	2	1										5	
	February					3	2											5	
	March				1	44	15											60	
	April					21	19	2										42	
	May					25	13											38	
	June					1	2	1										4	
Area 32	December						3											3	588
	January					3	24	2										29	
	February					21	54											75	
	March				1	72	174	12										259	
	April					46	71	7										124	
	May				1	29	50	8										88	
	June					1	5	2										8	
	July						1											1	
	August						1											1	

TABLE 25.—*Recaptures of large shrimp (13 cm. and longer) released in Gulf of Mexico, by area of release and by month and area of recapture*—Continued

Released in—	Recaptured in month—	Number recaptured in area—																	Total
		27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	All areas	
Area 37	November											1						1	1
Area 38	August												3					3	365
	September												36					36	
	October												186					186	
	November												134					134	
	December												6					6	
Area 41	March														26			26	118
	April														63	3		66	
	May													7	16			23	
	June												1	1	1			3	
Area 42	March														2			2	19
	April														4	1		5	
	May												1		2			3	
	June													3	1		1	5	
	July														2	2		4	

27 demonstrate quite clearly the movement from zone *a* to offshore zones during fall and early winter.

No tagged shrimp from areas 27 to 29 were recaptured west of the mouth of the Mississippi River.

At present, all that can be said about the movements of the shrimp in this region is that during the fall and winter they tend to move into deeper water and toward the mouth of the Mississippi River.

NORTHERN GULF WEST OF THE MISSISSIPPI RIVER

Between the mouth of the Mississippi River and western Louisiana (areas 30 to 32), we released marked shrimp from the latter part of August until March (table 28). In this region, therefore, our remarks pertain only to the fall, winter, and spring movements of shrimp (figs. 21–24).

During the years we tagged, the inside waters were closed to fishing from about mid-June until mid-August, but during the rest of the year they were subjected to relatively heavy fishing. In the outside waters, fishing occurred throughout the year, although it was probably most intense during winter and spring, when a part of the inshore fleet moved into outside waters. Fishermen in this region (judged by the depths to which the fleet fished and the maximum depths at which we caught white shrimp in our exploratory fishing), fished the entire population of adult and subadult shrimp.

The specimens we marked in inside waters displayed the typical movement to outside waters (tables 26 and 27). Once the shrimp reached outside waters they tended to move offshore and then mill about. Tables 29 and 30 demonstrate this behavior of the shrimp for August, October, and November releases.

TABLE 26.—*Recaptures of small shrimp (less than 13 cm.) released in Gulf of Mexico, by depth of release and by month and depth of recapture*

[Depth zones are as follows: *a*, inside waters, *b* outside waters, 0–4½ fathoms; *c*, outside waters, 5–8½ fathoms; *d*, outside waters, 9–12½ fathoms; *e*, outside waters, 13–16½ fathoms; and *f*, outside waters, 17 fathoms and deeper]

Area and depth of release	Recaptured in month—	Number recaptured in depth zone—							Total
		a	*b*	*c*	*d*	*e*	*f*	All depths	
Areas 27–29: Depth zone *a*	September	135						135	343
	October	140						140	
	November	44	4	4				52	
	December	6	1	5	1			13	
	January		3					3	
Areas 30–32: Depth zone *a*	September	16						16	109
	October	7	3					10	
	November	19	18	10				47	
	December	2	18	4				24	
	January		1					1	
	February					2		2	
	March		5		1			6	
	April		1					1	
	May			1	1			2	
Depth zone *b*	November		1					1	193
	December		93	3				96	
	January		8	3				11	
	February			2				2	
	March	24	46					70	
	April	3	2					5	
	May		2	4	1			7	
	June				1			1	
Depth zone *c*	October		3	2				5	234
	November	4	1					5	
	January		2					2	
	February		1					1	
	March	53	103	4	1			161	
	April	16	18		1			35	
	May	2	4	8	5			19	
	June			4	2			6	
Depth zone *d*	March			1	1			2	2
Areas 37–38: Depth zone *a*	August	3						3	202
	September	29						29	
	October	96		24	1			121	
	November	39		8				47	
	December	2						2	
Depth zone *b*	October			2				2	7
	November			5				5	
Depth zone *d*	October			4				4	6
	November			2				2	

Our tables also show an inshore movement during March and April, and a tendency for the shrimp to move offshore again in May and June. We think that the return to shallower waters during spring is an anomaly which is emphasized in the data by the fact that many of our releases were made during the winter of 1939–40, in which an unusual cold wave occurred in January. After the cold wave, the fishermen reported many dead shrimp in inside waters and small shrimp much further offshore than usual for that time of year.

The observations of the fishermen were corroborated by our own investigations when, on the last day of February and early in March 1940, we marked random samples consisting of 3,160 of these small shrimp in depths *b* and *c*. According to random samples of shrimp from the commercial fishery, in this region we should normally expect to find, in depth *c*, less than 1 percent of the shrimp to be smaller than 13 cm. in total length in February; in March the normal value is about 2 percent. In depth *b* we should expect about 2.5 percent of the shrimp to be less than 13 cm.

TABLE 27.—*Recaptures of large shrimp (13 cm. and longer) released in Gulf of Mexico, by depth of release and by month and depth of recapture*

[Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0–4½ fathoms; *c*, outside waters, 5–8½ fathoms; *d*, outside waters, 9–12½ fathoms; *e*, outside waters, 13–16½ fathoms; and *f*, outside waters, 17 fathoms and over]

Area and depth of release	Recaptured in month—	Number recaptured in depth zone—							Total
		a	*b*	*c*	*d*	*e*	*f*	All depths	
Areas 27–29:									
Depth zone *a*	September	219	----	----	----	----	----	219	836
	October	251	5	----	----	----	----	256	
	November	202	9	30	2	----	----	243	
	December	14	19	78	2	----	----	113	
	January	1	----	----	----	----	----	1	
	March	----	1	1	----	----	----	2	
	April	----	----	----	2	----	----	2	
Areas 30–32:									
Depth zone *a*	August	1	1	----	----	----	----	2	117
	September	56	1	----	----	----	----	57	
	October	6	3	2	1	1	----	13	
	November	11	10	4	----	----	----	25	
	December	1	8	----	----	----	----	9	
	January	----	2	----	1	----	----	3	
	February	----	----	----	2	1	----	3	
	March	----	3	----	----	----	----	3	
	April	----	1	----	1	----	----	2	
Depth zone *b*	October	----	16	8	1	----	----	25	180
	November	----	50	7	3	1	----	61	
	December	----	41	2	3	----	----	46	
	January	----	7	2	----	----	----	9	
	February	----	----	3	----	----	----	3	
	March	2	19	2	1	----	----	24	
	April	----	6	----	----	----	----	6	
	May	----	2	1	1	----	----	4	
	June	----	1	----	1	----	----	2	
Depth zone *c*	October	----	3	1	----	----	----	4	182
	November	1	3	3	----	----	----	7	
	December	----	5	----	----	----	----	5	
	January	----	2	1	1	----	----	4	
	February	----	----	1	7	2	3	13	
	March	5	43	4	13	1	----	66	
	April	4	17	8	12	----	----	41	
	May	2	7	19	11	----	----	39	
	June	----	----	1	2	----	----	3	
Depth zone *d*	December	----	----	----	3	----	----	3	537
	January	----	2	5	12	10	----	29	
	February	----	1	17	40	8	----	66	
	March	1	73	79	74	5	----	232	
	April	----	43	31	39	2	----	115	
	May	1	22	42	17	2	----	84	
	June	----	----	1	5	----	----	6	
	July	----	----	----	1	----	----	1	
	August	----	----	----	1	----	----	1	
Areas 37–38:									
Depth zone *a*	August	3	----	----	----	----	----	3	272
	September	36	----	----	----	----	----	36	
	October	109	----	47	----	----	----	156	
	November	36	----	35	----	----	----	71	
	December	5	----	1	----	----	----	6	
Depth zone *b*	October	----	----	20	----	----	----	20	76
	November	3	----	53	----	----	----	56	
Depth zone *d*	October	----	----	11	----	----	----	11	18
	November	----	----	7	----	----	----	7	

TABLE 28.—*Depths and dates of release of tagged shrimp in areas 30 to 32*

[Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0–4½ fathoms; *c*, outside waters, 5–8½ fathoms; *d*, outside waters, 9–12½ fathoms]

Released in month of—	Years in which releases were made in depth zone—			
	a	*b*	*c*	*d*
August	1939	----------	----------	----------
October	1939	1939	1939	----------
November	1939	----------	1939	----------
December	1938	1938	1938	1939
January	----------	1939, 1940	1939	1939, 1940
February	----------	1940	1940	----------
March	----------	1940	1940	1940

TABLE 29.—*Monthly recaptures of tagged shrimp, arranged according to month of release and number of depth zone shrimp were recaptured inshore and offshore from release depth*

[Release depth is zero. Releases in depth zones *a* (inside waters) and *b* (outside waters, 0–4½ fathoms) only. Areas 30–32]

Released in month of—	Recaptured in month of—	Depth zones from release zone						Total
		Inshore	Release depth	Offshore				
		1	0	1	2	3	4	
August	August	------	1	1	----	----	----	85
	September	------	72	1	----	----	----	
	October	------	1	3	----	1	1	
	November	------	------	2	----	----	----	
	December	------	------	1	----	----	----	
	April	----	------	1	----	----	----	
October and November	October	------	28	11	3	----	----	214
	November	------	81	33	17	1	----	
	December	------	5	10	3	----	----	
	January	----	------	2	----	1	----	
	February	----	------	..	----	2	3	
	March	----	------	8	1	1	----	
	April	----	------	1	----	1	----	
	May	----	------	..	1	1	----	
December and January	December	------	131	20	4	----	----	188
	January	------	15	6	----	----	----	
	February	------	------	5	----	----	----	
	March	----	4	----	----	----	----	
	April	1	1	----	----	----	----	
	June	----	1	----	----	----	----	
February and March	March	26	61	2	----	----	----	112
	April	2	7	----	----	----	----	
	May	------	4	5	2	----	----	
	June	------	1	----	2	----	----	

TABLE 30.—*Monthly recaptures of tagged shrimp, arranged according to month of release, and number of depth zones shrimp were recaptured inshore and offshore from release depth*

[Release depth is zero. Releases in depth zones *c* (outside waters, 5-8½ fathoms) and *d* (outside waters, 9-12½ fathoms) only. Areas 30-32]

Released in month of—	Recaptured in month of—	Depth zones from release zone							Total
		Inshore			Release depth	Offshore			
		3	2	1	0	1	2	3	
October and November.	October			6	3				29
	November		5	4	3				
	December			5					
	February					1			
	March					1			
	April		1						
December and January.	December				3				391
	January		2	9	13	11			
	February		1	18	41	14	2	3	
	March	1	40	37	45	15	1		
	April		26	21	22	6			
	May	1	13	26	11	2			
	June and August.			1	6				
February and March.	March		91	190	37	3			535
	April		36	45	25	9			
	May		13	27	33	16			
	June				6	4			

long in March (we have no data for February). In February of 1940, however, 81 percent of our marked shrimp taken in depth *c* were less than 13 cm. in length, while in March 94 percent were of this small size. In depth *b*, these small specimens constituted 62 percent of the catch in February and 23 percent in March.

The migrations of these small shrimp are clearly shown by our tagging results. From the data presented in table 31 it is evident that the small shrimp were the ones that went towards the shore after release. They had evidently been driven offshore by the excessively low temperatures of the inshore waters during the cold wave, but they returned to their usual habitat when the temperatures became normal in March (fig. 37). Then in May and June they made the typical spawning movement and reentered the deeper waters (table 32).

Probably a more nearly typical spring distribution is demonstrated by shrimp marked in offshore waters before January (table 33). In the outside waters, though the shrimp move about in all depths (mostly between depths *b* and *d*), there is a tendency for the largest shrimp to seek the deepest waters. During fall, winter, and spring, only occasionally will shrimp less than 13 cm. in length be found in depths greater than 5 fathoms (table 34).

TABLE 31.—*Recaptures by depth and by size of shrimp released in depths* b *and* c *during February and March 1940*

[Areas 30-32. Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0-4½ fathoms; *c*, outside waters, 5-8½ fathoms; *d*, outside waters, 9-12½ fathoms]

Recaptured in depth zone—	Number recaptured, of shrimp whose lengths at tagging were—				Percentage recaptured, shrimp whose lengths at tagging were—		
	10 cm. and less	10.5-12.5 cm.	13-15 cm.	15.5 cm. and more	10.5-12.5 cm.	13-15 cm.	15.5 cm. and more
a	2	94	13		32.1	10.1	
b	2	170	74	19	58.0	57.4	57.6
c	1	19	22	9	6.5	17.1	27.3
d		10	20	5	3.4	15.5	15.2
Total	5	293	129	33	100.0	100.1	100.1

TABLE 32.—*Recaptures, by depth and month, of tagged shrimp released in depths* b *and* c *during February and March 1940*

[Areas 30-32. Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0-4½ fathoms; *c*, outside waters, 5-8½ fathoms; *d*, outside waters, 9-12½ fathoms]

	Number recaptured in month of—			
	March	April	May	June
Released in depth zone *b* and recaptured in depth zone—				
a	26	2		
b	61	7	4	1
c	2		5	
d			2	2
Total	89	9	11	3
Released in depth zone *c* and recaptured in depth zone—				
a	58	19	4	
b	146	35	11	
c	5	8	26	5
d	3	8	16	4
Total	212	70	57	9

TABLE 33.—*Recaptures, by depth of release and by month and depth of recapture, of shrimp tagged before January*

[Areas 30-32. Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0-4½ fathoms; *c*, outside waters, 5-8½ fathoms; *d*, outside waters, 9-12½ fathoms; *e*, outside waters, 13-16½ fathoms; *f*, outside waters, 17 fathoms and deeper]

	Number recaptured in depth zone—						Total recaptured
	a	*b*	*c*	*d*	*e*	*f*	
Released in depth zones *a*, *b*, and *c* and recaptured in month of—							
December	3	165	9	3			180
January		22	6	2			30
February		1	5	4	4	1	15
March		8	1	6			15
April	1	2		2			5
May			2	1			3
Released in depth zone *d* and recaptured in month of—							
December				3			3
January		2	4	12	1		19
February			11	12	1		24
March		6	17	10	4		37
April		5	9	8			22
May		2	11	3	1		17
June				1			1
July				1			1

TABLE 34.—*Recaptures, by depth and by size, of shrimp for three different release depths*

Areas 30–32. Depth zones are as follows: *a*, inside waters; *b*, outside waters, 0–4½ fathoms; *c*, outside waters, 5–8½ fathoms; *d*, outside waters, 9–12½ fathoms]

Released in depth zone—	Released in *month* of—	Recaptured in depth zone—	Number recaptured, of shrimp whose lengths at tagging were—				Percent recaptured, of shrimp whose lengths at tagging were—			
			10 cm. and less	10.5–12.5 cm.	13–15 cm.	15.5 cm. and more	10 cm. and less	10.5–12.5 cm.	13–15 cm.	15.5 cm. and more
b	October, December, and January	*a*		1				1.0		
		b	13	92	69	48	100.0	91.1	85.2	71.6
		c		8	10	12		7.9	12.3	17.9
		d and deeper			2	7			2.5	10.4
		All	13	101	81	67	100.0	100.0	100.0	99.9
c	October, November, December, and January	*a*		5	1			38.5	4.2	
		b		6	6	8		46.2	25.0	25.8
		c		1	5	5		7.7	20.8	16.1
		d and deeper		1	12	18		7.7	50.0	58.1
		All		13	24	31		100.1	100.0	100.0
d	December, January, and March	*a*			1	1			0.6	0.3
		b			64	77			37.9	21.0
		c		1	46	128		50.0	27.2	34.9
		d and deeper		1	58	161		50.0	34.3	43.9
		All		2	169	367		100.0	100.0	100.1

No shrimp marked in areas 30 to 32 were recaptured east of the mouth of the Mississippi River, or in Texas waters. They concentrated mostly in areas 31 and 32 and the eastern part of 33 (tables 24 and 25). This section between Ship and Trinity Shoals probably provides the most favorable outside feeding grounds for shrimp in this region. We believe the more or less aimless wanderings of the shrimp (but not the offshore and onshore movements) represent a search for food.

In brief, along the Louisiana coast west of the Mississippi River the large shrimp move offshore and scatter during fall and winter. At all times they appear to be drifting about, like cattle on open rangeland. The only definite patterns were those of the offshore and onshore movements, which evidently were associated with temperature changes and spawning, and a tendency to concentrate between Ship and Trinity Shoals, probably because of better feeding conditions.

There appeared to be a natural barrier at the Mississippi River, for we found neither east-west nor west-east crossings.

CENTRAL TEXAS

At the time we ran our tagging experiments in central Texas there was no fishing along the Mexican coast and no outside fishing during winter near the mouth of the Rio Grande, and the outside fishing near Port Aransas was limited to an area of narrow radius near the pass. There was no more or less continuous coastwise fishing along the entire coast, as there has been in recent years. Consequently, all of our recaptures were made close to the points of release (fig. 25, tables 24–27) and once our marked shrimp left the restricted area covered by the fishing fleet we could no longer follow them. As a matter of fact, for this very reason we discontinued tagging in Texas, once we had established that the shrimp were moving from inside waters to outside waters in accordance with the evidence we had obtained from the size-distribution pattern.

The fact that the larger of our marked specimens disappeared soon after reaching outside waters off Port Aransas, indicates only that they left this area; they could have gone farther offshore or to the north or south beyond the range of the fishing fleet. We believe it most likely that they went south, because in winter the waters are warmer to the south and because there appears to be a northward return of the shrimp in spring, as is suggested by a tagging experiment along the coast of Tamaulipas, Mexico, to be discussed in the next section.

Probably the migration pattern, for at least part of the western Gulf, is comparable to that along the southern Atlantic coast. We also think it probable that the shrimp reared in the vicinity of Galveston, Tex., move as do those in areas 30–32.

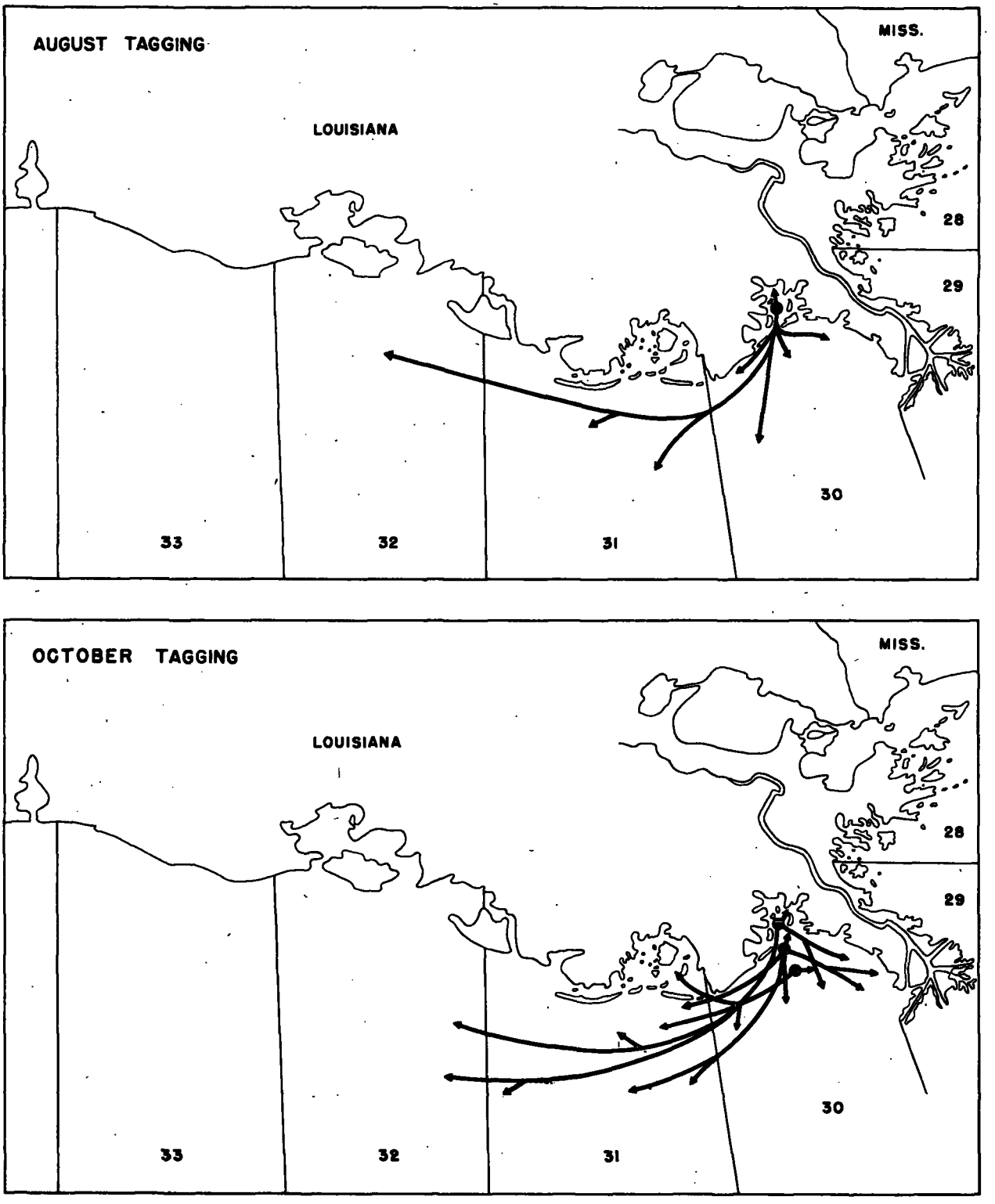


FIGURE 21.—Movements of marked shrimp released in the northern Gulf of Mexico west of the Mississippi River during August and October. See figure 17 for further explanation.

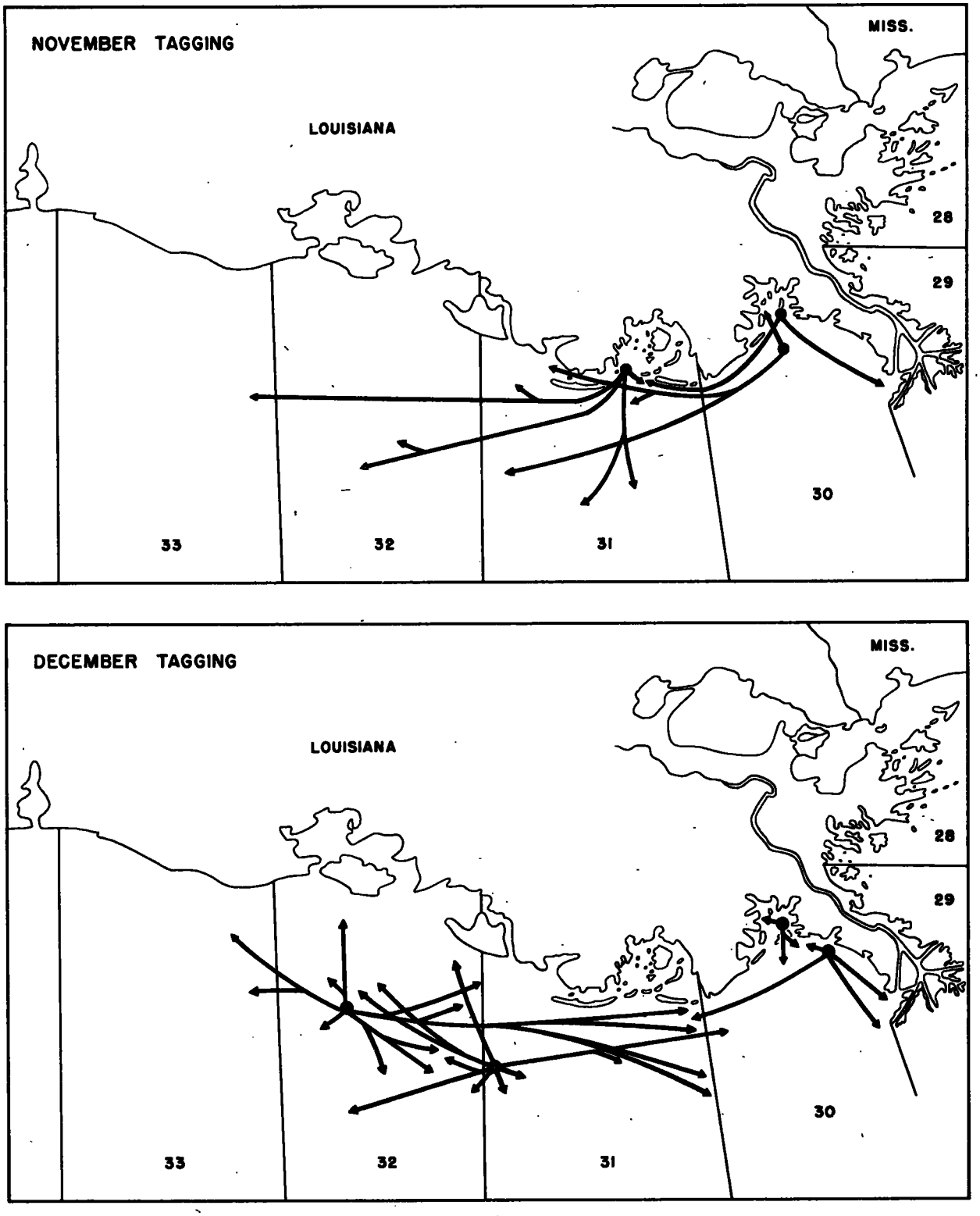


FIGURE 22.—Movements of marked shrimp released in the northern Gulf of Mexico west of the Mississippi River during November and December. See figure 17 for further explanation.

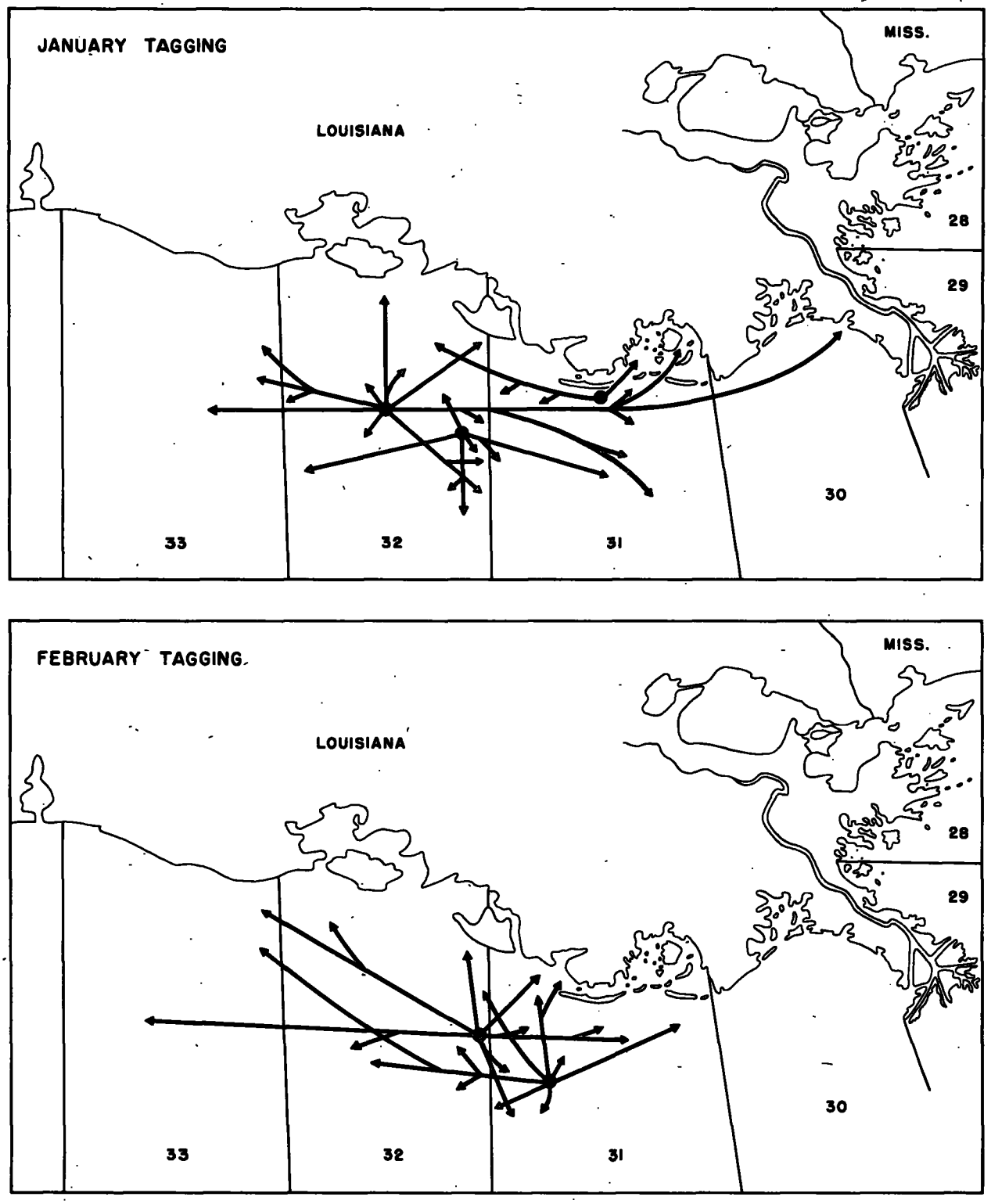


FIGURE 23.—Movements of marked shrimp released in the northern Gulf of Mexico west of the Mississippi River during January and February. See figure 17 for further explanation.

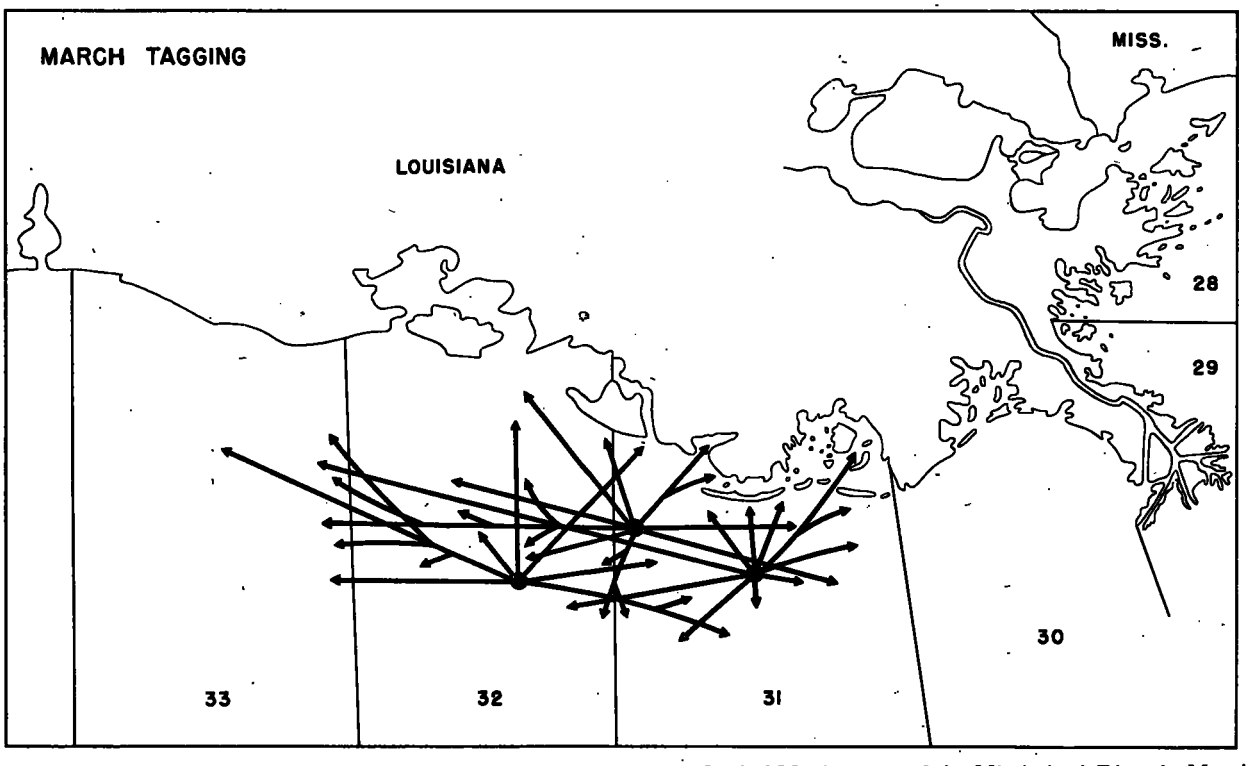


FIGURE 24.—Movements of marked shrimp released in the northern Gulf of Mexico west of the Mississippi River in March. See figure 17 for further explanation.

NORTHERN MEXICO

At the time we tagged shrimp along the coast of Tamaulipas, Mexico (March 1947), there was a large fleet of shrimp boats operating out of Brownsville, Tex. Fishing was intense near the mouth of the Rio Grande. For this reason our returns were mostly from near the mouth of this river (area 40). Perhaps more returns are shown as coming from near the mouth of the Rio Grande than actually occurred, as it is probable that some shrimp caught in Mexican waters were reported as having been captured north of the border.

Inasmuch as there was no fishing (or very little) to the south of area 40, returns would have to come from area 40 and to the north. Consequently, the movements of the shrimp released in areas 41 and 42 (table 25 and fig. 26) might be merely normal feeding movements. Area 41 is closer to the region of heavy fishing than is area 42; this would account for the difference in the percentage of returns from the releases in area 42 (5 percent) and those from area 41 (19.2 percent). Although the large majority of recaptures from these areas had moved considerable distances and appear to indicate a migratory population, it must be remembered that they represent a small percentage of the releases.

Therefore, the majority of the shrimp tagged in March could have been local or nonmigratory shrimp reared in Laguna Madre, Tamaulipas, which were not recaptured because of the total lack of fishing in these areas. Yet (1) in recent years there has been a spring run of shrimp striking first (about March) near the Rio Grande and later (about May) near Aransas Pass, Tex. (2) Of the recaptured shrimp marked in areas 30 to 32 (Louisiana) less than 1 percent moved more than 75 miles, whereas about 17 percent of those recaptured after tagging in Mexico moved more than this distance; the greatest distance between release and recapture along the Louisiana coast was about 110 miles, whereas 5 of the recoveries from our Mexican releases were taken at distances greater than this (the greatest distance, about 175 miles). (3) The water temperatures during winter off the coast of Mexico are warmer than they are

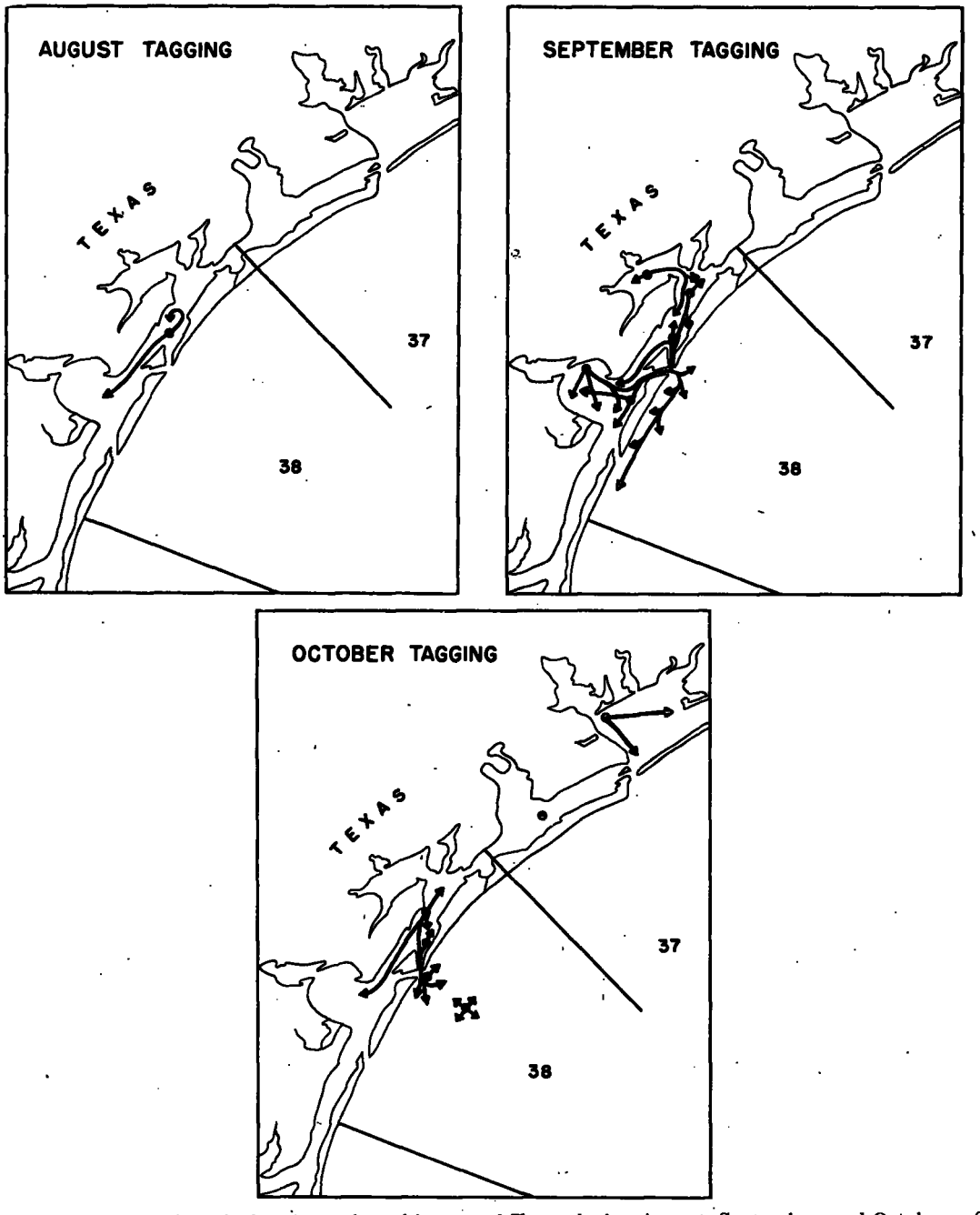


FIGURE 25.—Movements of marked shrimp released in central Texas during August, September, and October. See figure 17 for further explanation.

in Texas. The evidence, therefore, seems to favor a springtime south-to-north migration.

Our data are not adequate to establish this point, but if such a spring migration occurs it is also likely that during the fall and winter there is a reciprocal southward movement of larger shrimp from central and southern Texas into northern Mexico.

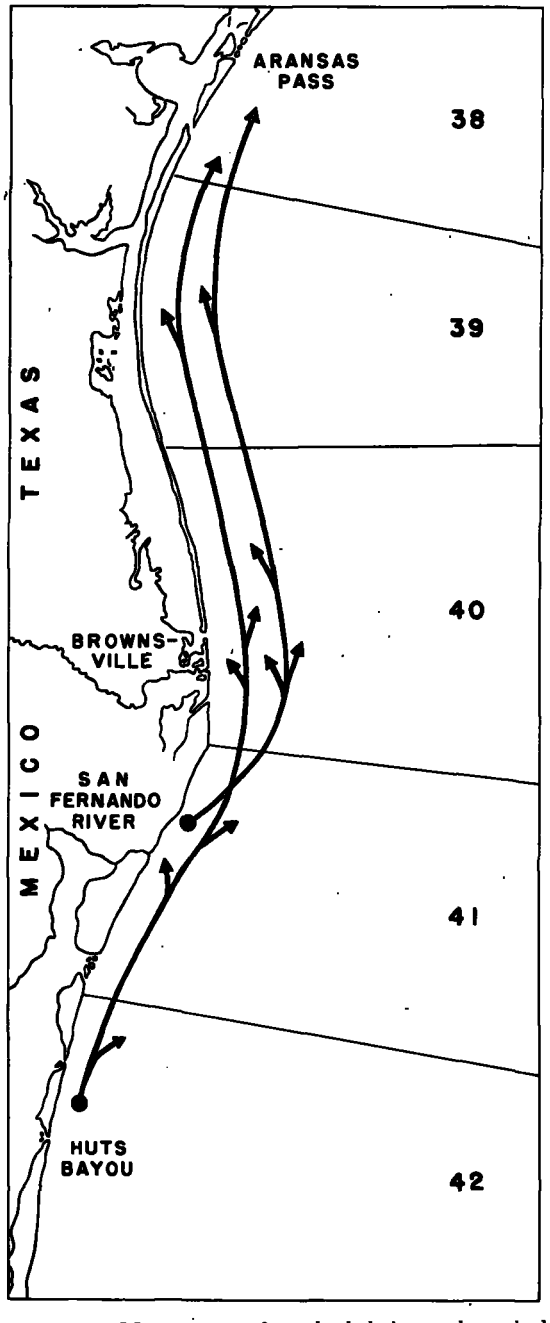


FIGURE 26.—Movements of marked shrimp released along the northern coast of Mexico during March. See figure 17 for further explanation.

SPAWNING AND LONGEVITY

Weymouth, Lindner, and Anderson (1933) have shown that when the young (spring-spawned) shrimp first appear on the inside fishing grounds (in June or July, depending on the locality) they can readily be distinguished from the spawning population both by size and by sexual development. By September, the largest of the spring-spawned shrimp have attained the length of the smallest of the mature shrimp spawned the previous summer, and the two groups overlap in total length. At the same time, many of the mature females have completed spawning and are beginning to enter a stage in which it is impossible, by ovarian examination alone, to distinguish them from the larger spring-spawned females. With the approach of maturity, various morphological changes took place in the shrimp, which made it possible to separate immature spring-spawned individuals from spent mature shrimp until December, but by January the spring-spawned specimens began assuming the adult characteristics and we could no longer distinguish them.

SPAWNING

In the field we recognized five successive stages of ovarian development: Undeveloped; developing; yellow; ripe; and spent.[6] Unfortunately, most of our field records of ovarian development are incomplete, as we were unable to work out a satisfactory technique for field determination of spent shrimp until late in 1941. Before December 1941, recently spent shrimp, during and immediately following the spawning season, usually were classed by us as "developing" or in an early "yellow" stage; those not recently spent, the ovaries of which during fall and early winter were actually more or less dormant, were usually classed as "undeveloped," but when they began to approach a second spawning season were classed as "developing."

Louisiana

Because of the complications just mentioned, we have only one year (December 1941 to November 1942) for the Louisiana offshore fishery[7] in which we believe our records are complete with

[6] See King (1948) for a description of these various stages.

[7] We have divided the Louisiana fishery into two sections (Anderson, Lindner, and King, 1949) based on fishing grounds. The inshore fishery includes the inside waters (bays and bayous) and the outside waters out to about 5 fathoms. This area was fished by shallow-draft luggers, and it also represents the area covered by our research boat *Black Mallard*. About the beginning of 1938, a group of Florida-type trawlers migrated to Louisiana and began fishing the offshore area (outside waters from about 5 to 35 fathoms, although the boats usually did not go much beyond 20 fathoms). This area had never been fished extensively by the inshore fleet. After the offshore fishery was developed, some of the larger boats from the inshore fleet would fish offshore on occasions. The offshore fleet, however, never fished the inside or estuarine waters. Generally the areas fished by the two fleets were quite distinct.

respect to maturation and spawning. In figure 27 we show the size distribution of the five different ovarian stages from random samples taken from the offshore fleet during this period. This figure is plotted in percentages, with the total number of females examined in any month equal to 100 percent. Inasmuch as the ripe and spent shrimp were only a small percentage of the population and difficult to follow in figure 27, we have shown these separately and by actual numbers in figure 28.

Following the progression of these curves (fig. 27), we find that in December the largest females had spent ovaries, although most of them were in a resting stage and appeared undeveloped. The majority of these were probably summer spawners. These spent shrimp constituted less than 2½ percent of the specimens in our samples; all of the others were spring-spawned and had undeveloped ovaries. By January (we could no longer distinguish between shrimp which had previously spawned and those which were maturing for the first time) many had developing ovaries and a few were in the yellow stage. The first ripe shrimp appeared in March and the first spent ones in April. No shrimp with undeveloped ovaries remained in April. In May a second group of females approaching spawning began making their appearance in the shallow waters of the offshore fishery. These were smaller than their predecessors. Most of them had undeveloped or developing ovaries, and some had yellow ovaries. By June this second group of spawners dominated the offshore fishery which had now largely moved into comparatively shallow water; many were ripe, and a number were spent. In August the immature spring-spawned shrimp began making their appearance offshore. By September the spring-spawned shrimp dominated the fishery, the majority of the mature shrimp were spent, and there were none with developing ovaries. By October there were neither developing nor ripe shrimp and very few with yellow ovaries. Almost all the mature shrimp were spent by October.

The duration of the spawning season in Louisiana can be seen best in figure 29, which shows the percentage of females for each month with developing, yellow, ripe, and spent ovaries. We have eliminated (on the bases previously described) all immature shrimp from August through November; consequently this figure follows mature individuals only. It is apparent that the first ripe shrimp appear in March and the first spent ones in April. It is also evident that spawning is almost completed by the end of September. Since we did encounter (in selected samples) recently spent shrimp in late March and ripe shrimp as late as October, we believe that the earliest spawning occurs during the latter part of March, and that it may extend into October. Judging from the appearance of the young (which we shall treat later, and which is discussed to some extent in Anderson, King, and Lindner, 1949), spawning later than September probably is not effective. For all practical purposes the spawning season extends from the latter part of March or early in April through September.

The sequential appearance of the various ovarian stages (table 35) indicates that the developing stage occupies a period of 1 month or less, the yellow stage persists for from 1 to 2 months, and ripe ovaries become spent in less than a month. Assuming that an ovary may develop from the newly spent stage into the yellow stage in a period of a few days, it may take as much as 3 months or it may take less than 2 months to prepare for a new spawning, if such should occur.

If shrimp spawned but once a year and remained available to the fishery after spawning, we could expect the percentage of spent shrimp to increase markedly month by month. The summer-spawning shrimp, appearing in the shallower waters in June, form the main basis for the fishery almost from the time of their appearance and are detectable in the catches until well after the end of the spawning season. It is interesting that in this well-sampled population the percentage of spent ovaries remained low during June, July, and August; it was not until September that a rapid rise occurred. This phenomenon can easily be explained by assuming that these shrimp spawn twice. The persistence of a low percentage of spent shrimp in the population for 3 months suggests that after spawning these individuals enter a second yellow stage preparatory to production of another batch of eggs.

It is unfortunate that our data are not complete for the spring-spawning shrimp throughout the year. These shrimp, which initiate the spawning season in the deeper waters, were not taken in as large numbers after June as previously, and they became indistinguishable from the summer spawn-

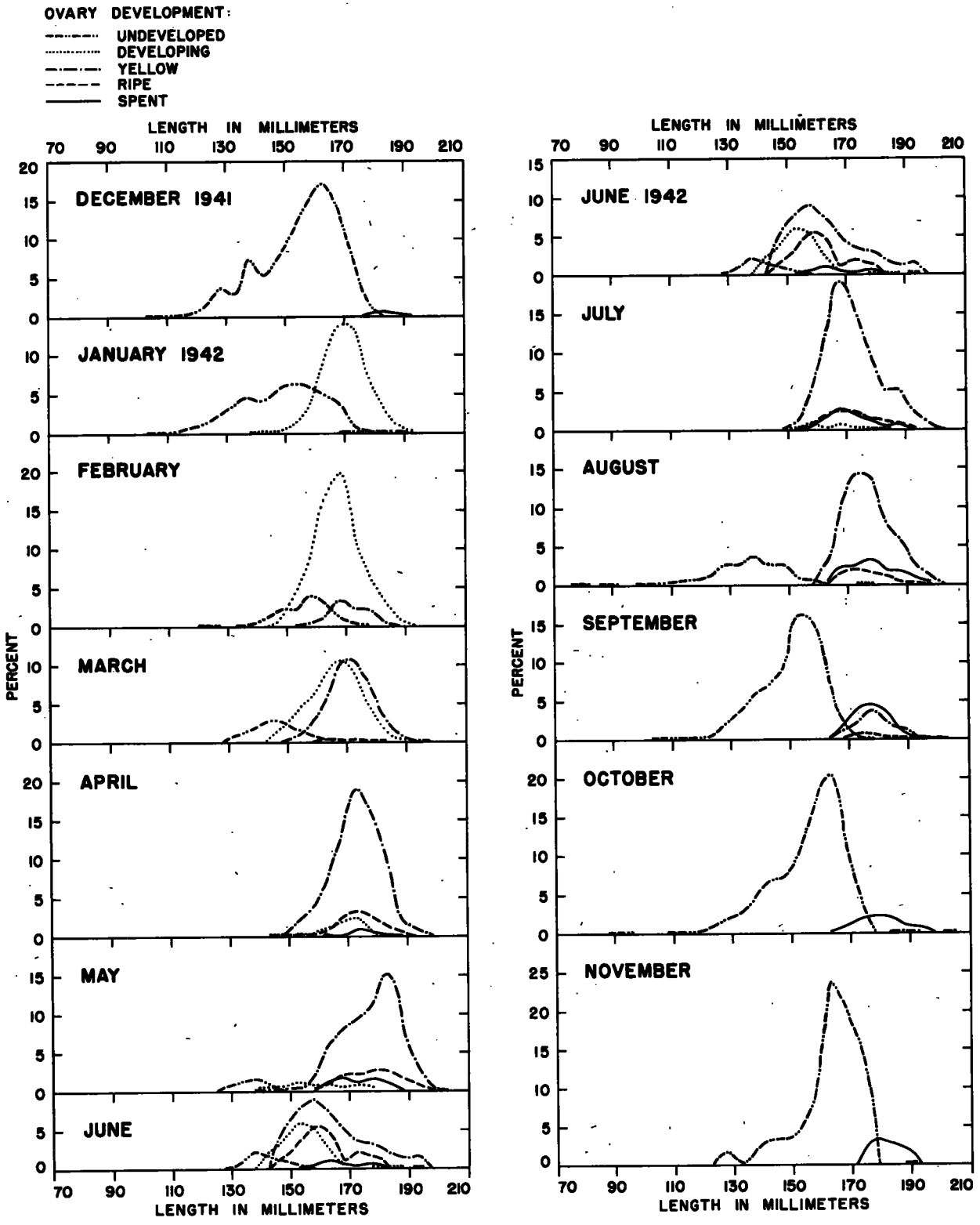


FIGURE 27.—Size distribution of female shrimp according to stage of ovarian development, for the Louisiana offshore fishery from December 1941 to November 1942. The curves represent percentages of the total population each month.

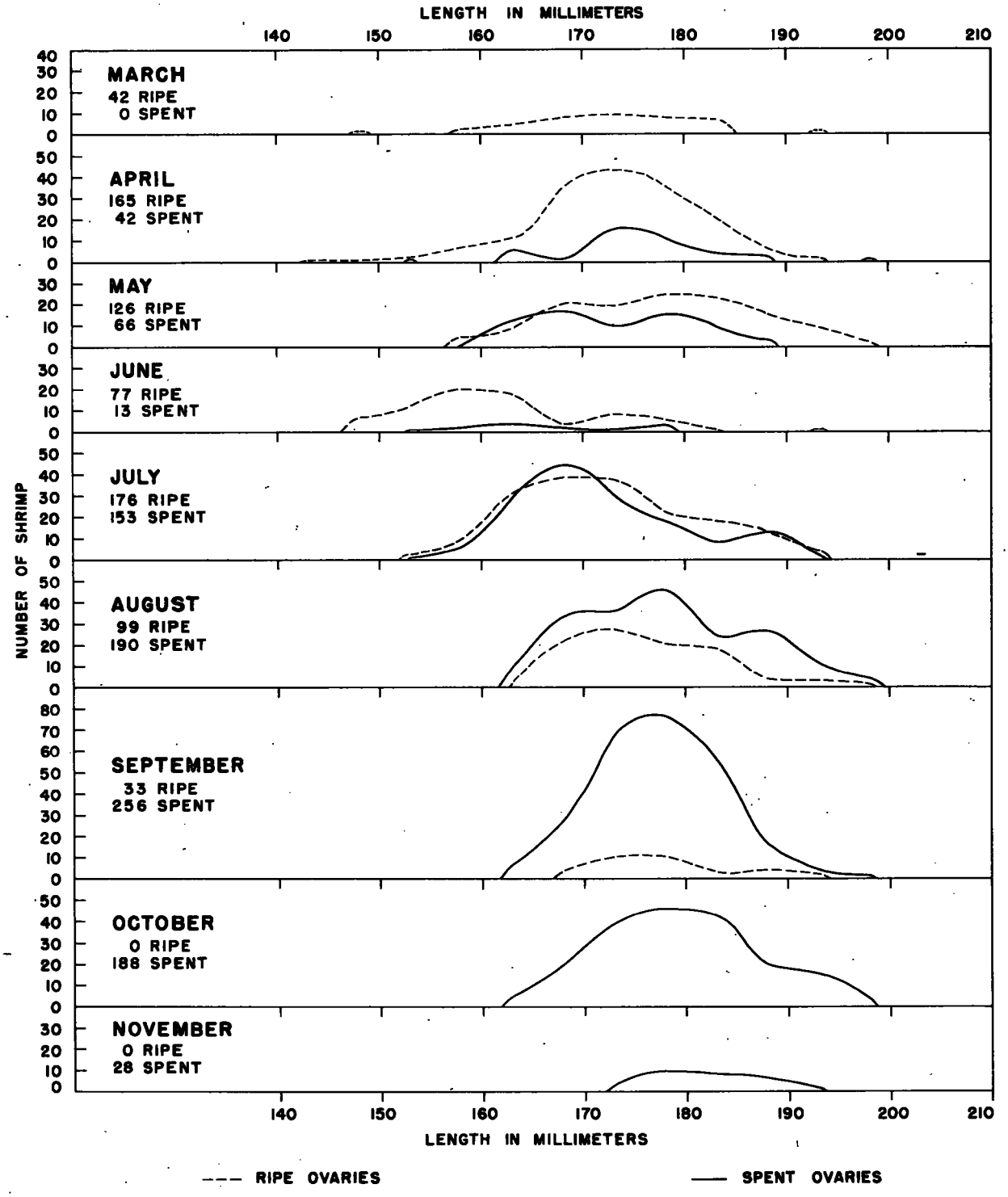


FIGURE 28.—Size distributions by numbers of ripe and spent female shrimp in the Louisiana offshore fishery from March to November 1942.

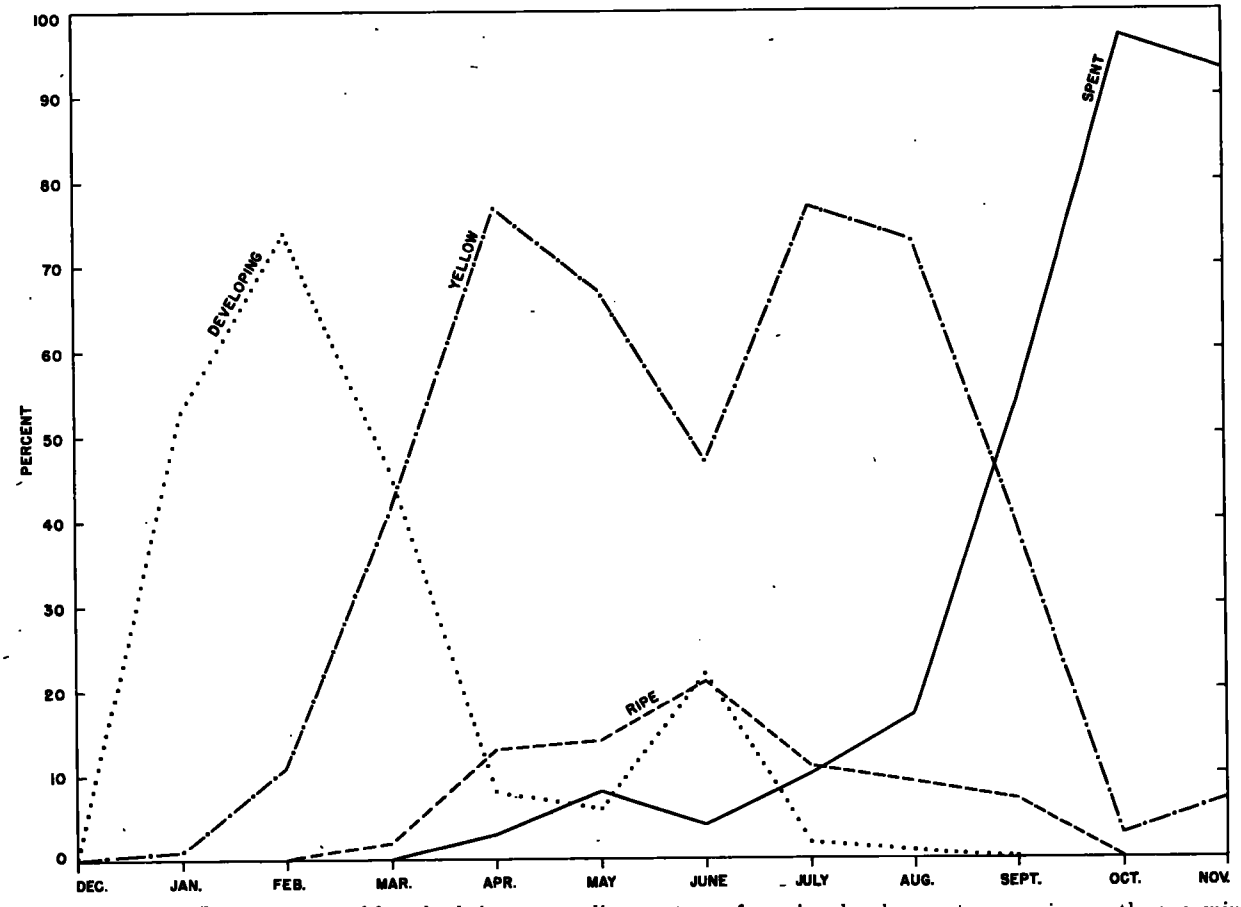


FIGURE 29.—Monthly percentage of female shrimp, according to stage of ovarian development, appearing on the spawning grounds in the Louisiana offshore fishery. The data are from the period December 1941 to November 1942. After August 1942 this figure includes only shrimp approximately 1 year old or more.

ers when the latter group became the mainstay of the fishery. Lack of material on this group in later months makes it impossible to determine the exact proportion of spent individuals during the summer.

How many times an individual shrimp spawns in a single season is unknown; while we have no definite proof that a shrimp spawns more than once, it is possible that the spring-spawning shrimp could spawn as many as four times in a season, if the proportion of spent shrimp in this population remained low throughout summer. King (1948), from histological studies, also believed that a female might spawn more than once during the spawning season, and the evidence of Burkenroad (1939) is not in disagreement.

On the basis of the presence of ripe and recently spent shrimp it may be stated that practically all spawning in Louisiana occurs offshore in depths greater than 4.5 fathoms. Probably most of it takes place between 5 and 17 fathoms (tables 35 and 36). The second group of spawners appearing in May obviously came from a more inshore area (table 35). They first appeared in May in depths under 5 fathoms; by June they were found as deep as 9 to 12½ fathoms. The immature spring-spawned shrimp appearing in August behaved in a similar fashion: they were found only in the shallowest depth in August, but by September they moved out to at least 9 to 12½ fathoms. This latter group, however, did not mature until the following year. We shall follow these various groups in detail when we discuss the size distributions. Here, we are merely trying to establish the location of spawning.

We believe that tables 35 and 36 suggest that the spring spawners deposit their eggs in the deeper waters well offshore early in the season,

but that the summer spawners complete the process in lesser depths.[8] It is also suggested that the summer-spawning shrimp, when they have completed spawning, return to lesser depths. Viosca (1920) presented a number of major conclusions with respect to the life history of *P. setiferus* in Louisiana which are in accord with our own findings; it is unfortunate that he never published his data so that they could be compared in detail with ours.

TABLE 35.—*Distribution by stages of ovarian development and by depths, of female shrimp in Louisiana offshore fishery, December 1941 to November 1942*

Month, and stage of ovarian development	Number taken at depth of—						Total
	0–4½ fathoms	5–8½ fathoms	9–12½ fathoms	13–16½ fathoms	17 fathoms and deeper	All depths	
1941							
December:							
Undeveloped	280	633	22			935	
Developing						0	
Yellow						0	958
Ripe						0	
Spent	1	22				23	
1942							
January:							
Undeveloped		979	181	22		1,182	
Developing		997	351	15		1,363	
Yellow		13	2			15	2,560
Ripe						0	
Spent						0	
February:							
Undeveloped		19	71	19	42	151	
Developing		16	410	264	58	748	
Yellow			50	49	13	112	1,011
Ripe						0	
Spent						0	
March:							
Undeveloped			62	190	35	287	
Developing			230	461	471	1,162	
Yellow			304	260	476	1,040	2,531
Ripe				10	32	42	
Spent						0	
April:							
Undeveloped						0	
Developing			3	33	65	101	
Yellow			39	442	533	1,014	1,322
Ripe			4	49	112	165	
Spent			7	7	28	42	
May:							
Undeveloped	40					40	
Developing	22		10	18	6	56	
Yellow	14		167	333	80	594	882
Ripe			39	85	2	126	
Spent			17	43	6	66	
June:							
Undeveloped	25					25	
Developing	74	5				79	
Yellow	45	95	31			171	365
Ripe		66	11			77	
Spent		8	5			13	
July:							
Undeveloped	1			1		2	
Developing	1	32	4	1		38	
Yellow	23	655	360	174		1,212	1,581
Ripe	1	113	21	41		176	
Spent	22	70	50	11		153	
August:							
Undeveloped	259		2			261	
Developing			5	2		7	
Yellow		94	453	266		813	1,370
Ripe		9	59	31		99	
Spent	1	6	106	77		190	
September:							
Undeveloped	385	223	600			1,208	
Developing						0	
Yellow		12	172			184	1,681
Ripe		1	32			33	
Spent	12	19	225			256	

[8] It is obvious that in June 1942 our sampling did not cover the entire spawning population.

TABLE 35.—*Distribution by stages of ovarian development and by depths, of female shrimp in Louisiana offshore fishery, December 1941 to November 1942*—Continued

Month, and stage of ovarian development	Number taken at depth of—						Total
	0–4½ fathoms	5–8½ fathoms	9–12½ fathoms	13–16½ fathoms	17 fathoms and deeper	All depths	
1942—Continued							
October:							
Undeveloped	1,307	455				1,762	
Developing						0	
Yellow	2	4				6	1,956
Ripe						0	
Spent	121	67				188	
November:							
Undeveloped		167	76			243	
Developing						0	
Yellow		2				2	273
Ripe						0	
Spent		20	8			28	

TABLE 36.—*Percentage of ripe and spent females in Louisiana offshore fishery December 1941 to November 1942, arranged according to depth*

[0-class spring-spawned shrimp not included after July]

Month	Ovarian stage	Percent taken at depth of—				
		0–4½ fathoms	5–8½ fathoms	9–12½ fathoms	13–16½ fathoms	17 fathoms and deeper
1941						
December	Ripe	0.0	0.0	0.0		
	Spent	4.3	95.7	0		
1942						
January	Ripe		0	0	0.0	
	Spent		0	0	0	
February	Ripe		0	0	0	0.0
	Spent		0	0	0	0
March	Ripe			0	.4	1.3
	Spent			0	0	0
April	Ripe			.3	3.7	8.5
	Spent			.5	.5	2.1
May	Ripe	0		4.4	9.6	.2
	Spent	0		1.9	4.9	.7
June	Ripe	0	18.1	3.0		
	Spent	0	2.2	1.4		
July	Ripe	.1	7.1	1.3	2.6	
	Spent	1.4	4.4	3.2	.7	
August	Ripe	0	.8	5.3	2.8	
	Spent	.1	.5	9.5	6.9	
September	Ripe	0	.2	6.8		
	Spent	2.5	4.0	47.6		
October	Ripe	0	0			
	Spent	62.4	34.5			
November	Ripe	0	0	0		
	Spent	0	66.7	26.7		

Other localities

If we judge the spawning season by the presence of shrimp with yellow and ripe ovaries (table 37),[9] we find that—

1. In South Carolina, spawning probably begins in May and extends into September (our sampling was poor in April and August, and by September the spring-spawned shrimp dominated the fishery to such an extent that the mature shrimp were barely represented).

[9] Since we did not satisfactorily recognize spent shrimp throughout most of our collections, we have omitted these from our Louisiana data in this table. In interpreting the table, allowances must be made for our sampling technique (see section on size distributions).

2. In Georgia and northern Florida, spawning extends from April into September.

3. In central Florida (between St. Augustine and Cape Canaveral), spawning occurs from March until October.

4. In Louisiana, spawning takes place from March until October or November.

5. Near Galveston, Tex., it extends from April until September.[10]

6. Near Aransas Pass, Tex., spawning occurs from March or April until October.

TABLE 37.—*Distribution by months and by stages of ovarian development of female shrimp in Atlantic and Gulf coast fisheries*

Locality and month	Number whose ovaries were—				Monthly total	Total for locality
	Undeveloped	Developing	Yellow	Ripe		
South Carolina: Outside waters:						
January	701				701	
February	617				617	
March	559				559	
April	192	15	1		208	
May		83	319	54	456	
June		144	361	38	543	7,689
July	195	50	178	18	441	
August	286	4	5		295	
September	861	5	4		870	
October	888	6			894	
November	1,006	3			1,009	
December	1,094	2			1,096	
Georgia and northern Florida:						
Creeks and rivers:						
January	1,311				1,311	
February	1,242				1,242	
March	1,764	74	6		1,844	
April	1,855	886	302	4	3,047	
May	702	855	767	6	2,330	
June	86	739	436	15	1,276	22,919
July	1,184	105	48		1,337	
August	2,323	1	1		2,325	
September	2,350				2,350	
October	1,923				1,923	
November	2,157				2,157	
December	1,777				1,777	
Sounds:						
January	1,701				1,701	
February	1,764				1,764	
March	2,069	18	4		2,091	
April	1,358	821	574	11	2,764	
May	270	606	434	3	1,313	
June	24	642	772	27	1,465	22,662
July	578	113	155	43	889	
August	1,802	12	14		1,828	
September	2,779	1			2,780	
October	2,193				2,193	
November	1,902				1,902	
December	1,972				1,972	
Outside waters less than 1 mile offshore:						
January	932				932	
February	1,306				1,306	
March	740	19	4		763	
April	746	380	190	4	1,320	
May	112	442	235	8	797	
June		231	446	28	705	11,276
July	191	64	181	86	522	
August	516	62	34	4	616	
September	937				937	
October	1,169				1,169	
November	1,124				1,124	
December	1,085				1,085	

[10] Our data with respect to ovarian development are in error for Texas as our observer there (who covered both Galveston and Aransas Pass) tended to confuse shrimp in a late yellow stage with ripe shrimp. As a consequence our records for Texas show a greater number of ripe shrimp than existed.

TABLE 37.—*Distribution by months and by stages of ovarian development of female shrimp in Atlantic and Gulf coast fisheries*—Continued

Locality and month	Number whose ovaries were—				Monthly total	Total for locality
	Undeveloped	Developing	Yellow	Ripe		
Georgia and northern Florida—Continued						
Outside waters more than 1 mile offshore:						
January	1,500				1,500	
February	2,238				2,238	
March	190	5	3		198	
April	238	158	199	104	699	
May	138	251	659	90	1,138	
June		156	391	104	651	15,704
July	141	197	391	85	814	
August	989	87	158	42	1,276	
September	1,938	17	5		1,960	
October	1,637	9			1,646	
November	1,622	1			1,623	
December	1,959	2			1,961	
Florida: Central outside waters between St. Augustine and Cape Canaveral:						
January	1,120	23			1,143	
February	881	152	21		1,054	
March	154	172	213	2	541	
April	7	143	430	127	707	
May		51	225	34	310	
June	6	12	85	12	115	9,467
July	3	87	388	9	487	
August	144	35	213	11	403	
September	972	57	64	2	1,095	
October	1,157	51	7		1,215	
November	1,159	5			1,164	
December	1,227	6			1,233	
Louisiana:						
Inside waters, *Black Mallard* collections:						
January	851	1			852	
February	679	6			685	
March	1,128	179			1,307	
April	515	743	5		1,263	
May	119	530	31		680	
June	551	112	4		667	13,398
July	814	14	3		831	
August	1,061	1		1	1,063	
September	938	2			940	
October	2,406				2,406	
November	1,172				1,172	
December	1,532				1,532	
Outside waters, *Black Mallard* collections:						
January	962	21			983	
February	795	115	9		919	
March	336	453	154		943	
April	2	327	68		397	
May	14	451	188		653	
June	1	252	108	2	363	10,306
July	386	119	153		658	
August	758	15	19	6	798	
September	686	69	3		758	
October	1,991	34			2,025	
November	845	2			847	
December	960	2			962	
Outside waters, offshore fleet and *Pelican* collections:						
0–4½ fathoms:						
January						
February						
March	412	98	1		511	
April	361	46	49		456	
May	61	56	30		147	
June	25	105	135	3	268	4,774
July		2	121	17	140	
August	259				259	
September	460				460	
October	1,757	1	2		1,760	
November	288				288	
December	477	8			485	
5–8½ fathoms:						
January	979	997	13		1,989	
February	158	101	13		272	
March	16	22	9		47	
April	47	19	88	3	157	
May	1	401	1,150	184	1,736	
June		188	892	240	1,320	12,121
July	1	138	1,164	395	1,698	
August		44	334	52	430	
September	359	38	137	11	545	
October	1,482	3	8	5	1,498	
November	1,591	3	3		1,597	
December	816	16			832	

TABLE 37.—*Distribution by months and by stages of ovarian development of female shrimp in Atlantic and Gulf coast fisheries*—Continued

Locality and month	Number whose ovaries were—				Monthly total	Total for locality
	Undeveloped	Developing	Yellow	Ripe		
Louisiana—Continued						
Outside waters, offshore fleet and *Pelican* collections—Con.						
9–12½ fathoms:						
January	722	391	2	-------	1,115	
February	226	702	158	-------	1,086	
March	89	290	400	59	838	
April	7	115	488	48	658	
May	1	307	1,297	201	1,806	
June	1	291	1,034	172	1,498	10,047
July	-------	57	643	63	763	
August	2	61	711	85	859	
September	600	-------	172	32	804	
October	210	9	-------	4	223	
November	108	-------	-------	-------	108	
December	207	82	-------	-------	289	
13–16½ fathoms:						
January	268	20	-------	-------	288	
February	19	264	49	-------	332	
March	190	520	393	65	1,168	
April	-------	72	576	89	737	
May	-------	19	334	85	438	
June	-------	15	63	13	91	4,289
July	1	1	174	41	217	
August	-------	2	266	31	299	
September	-------	-------	-------	-------	-------	
October	-------	-------	-------	-------	-------	
November	3	-------	-------	-------	3	
December	684	32	-------	-------	716	
17 and more fathoms:						
January	79	17	-------	-------	96	
February	43	58	13	-------	114	
March	35	492	562	43	1,132	
April	-------	65	533	112	710	
May	-------	17	100	4	121	
June	-------	-------	-------	-------	-------	2,287
July	-------	-------	-------	-------	-------	
August	-------	-------	-------	-------	-------	
September	-------	-------	-------	-------	-------	
October	-------	-------	-------	-------	-------	
November	10	-------	-------	-------	10	
December	4	100	-------	-------	104	
Texas:						
Outside waters near Galveston:						
January	782	-------	-------	-------	782	
February	822	4	-------	-------	826	
March	182	442	18	-------	642	
April	80	350	183	245	858	
May	148	491	120	159	918	
June	-------	482	96	77	655	8,418
July	-------	273	164	156	593	
August	183	12	14	5	214	
September	190	80	-------	-------	270	
October	1,074	11	-------	-------	1,085	
November	814	-------	-------	-------	814	
December	761	-------	-------	-------	761	
Inside waters near Aransas Pass:						
January	154	-------	-------	-------	154	
February	204	-------	-------	-------	204	
March	1,032	155	1	-------	1,188	
April	263	206	112	35	616	
May	94	209	583	159	1,045	
June	7	53	136	49	245	16,345
July	387	7	1	-------	395	
August	1,669	86	8	1	1,764	
September	2,758	35	4	-------	2,797	
October	2,983	15	1	-------	2,999	
November	3,315	10	-------	-------	3,325	
December	1,613	-------	-------	-------	1,613	
Outside waters near Aransas Pass:						
January	870	1	-------	-------	871	
February	1,051	39	3	-------	1,093	
March	566	270	119	57	1,012	
April	486	415	206	210	1,317	
May	22	728	470	456	1,676	
June	-------	317	321	529	1,167	12,943
July	4	406	328	520	1,258	
August	382	340	215	322	1,259	
September	283	65	6	9	363	
October	1,188	38	3	-------	1,229	
November	757	29	-------	-------	786	
December	911	1	-------	-------	911	

TABLE 38.—*Mature females appearing in random samples from Louisiana offshore fishery at Morgan City, La., July–November 1942 and December 1941*

Month	Total females	Mature females	Percent mature
July 1942	1,581	1,581	100.0
August 1942	1,370	1,111	81.1
September 1942	1,681	473	28.1
October 1942	1,956	194	9.9
November 1942	273	30	11.0
December 1941	958	23	2.4

When we consider sampling technique and errors, it appears probable that there is little, if any, difference between the spawning seasons in any of the localities we covered between South Carolina and Texas. There probably is not more than about 2 weeks' difference in the beginning of spawning between any of the localities. Spawning may start later and end earlier in South Carolina and Georgia than it does in Florida, Louisiana, and Texas, but in all of the localities it probably begins either during the latter part of March or early in April and may possibly continue on into November, though probably it is completed by the end of September.

Wherever evidence is available, it appears that the shrimp of other areas select spawning grounds similar to those frequented by the Louisiana population. Judging by the presence of ripe shrimp and their proportion in the population, most spawning in Georgia and northern Florida is in outside waters more than 1 mile from shore, although some spawning may actually occur in inside waters in this area. Similarly, near Aransas Pass, Tex., most, if not all, spawning is in outside waters (table 37).

LONGEVITY

Immature and mature shrimp of the same total length can usually be distinguished by body proportions. Apparently, on approaching maturity, various irreversible changes take place in the body of the shrimp. Viosca (1920) showed the increase in width and Burkenroad (1934) mentions others.[11] In figure 30 we show the relation between rostrum length and total length for immature (which are spring-spawned) and mature female shrimp for the Louisiana offshore fishery in October 1941.

[11] We suspect, as possibly did Burkenroad, that most of the differences Burkenroad (1934) mentions between North Carolina and Louisiana shrimp are actually differences between immature North Carolina and mature Louisiana shrimp.

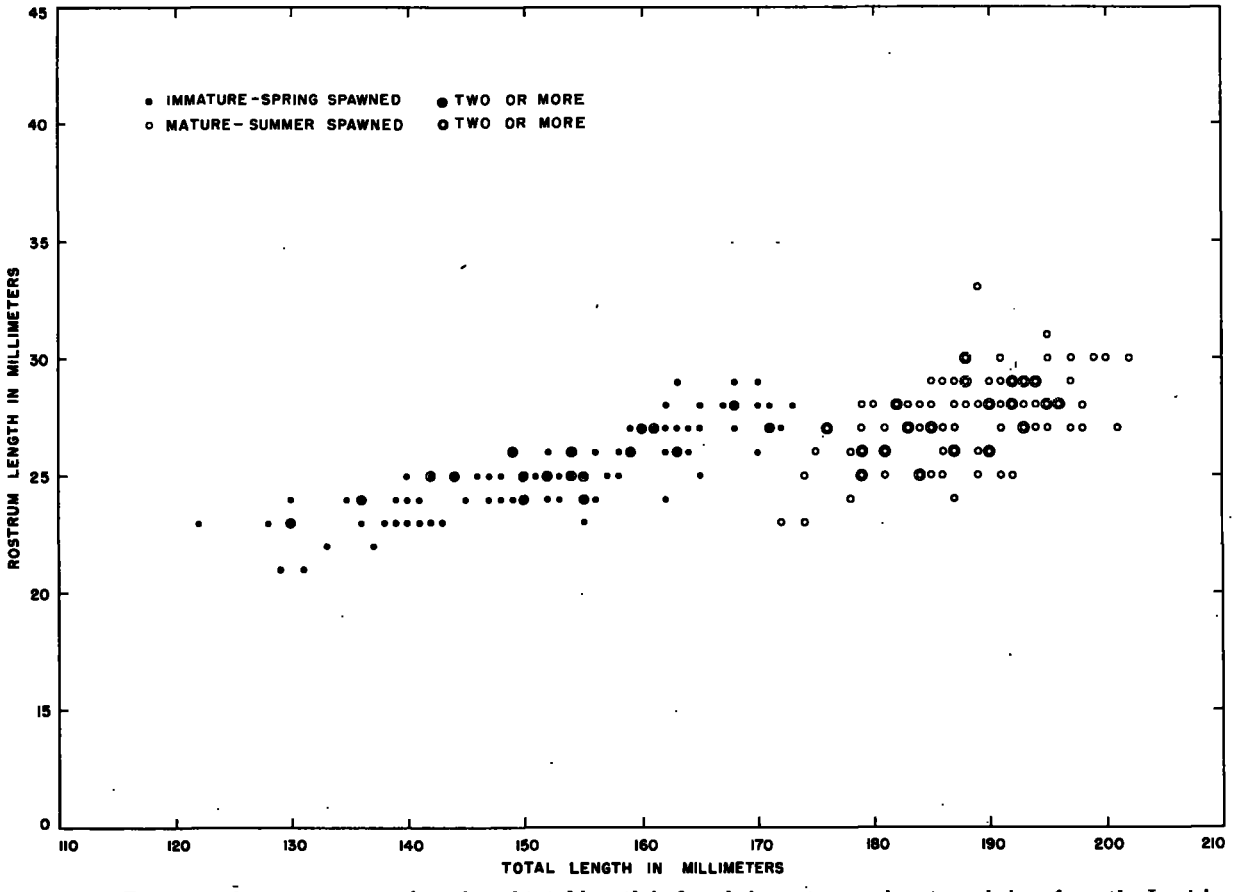


FIGURE 30.—Difference between rostrum length and total length in female immature and mature shrimp from the Louisiana offshore fishery in October.

Through body proportions and observations on the condition of the ovaries of the females, we were able to follow the mature group (which probably were mostly summer-spawned shrimp) until December (fig. 27). After this we lost them as they became indistinguishable from the spring-spawned animals which were beginning to mature. However, the summer-spawning group formed a conspicuous mode at about 90 mm. in the previous December (fig. 39), so there can be no doubt that they live more than 1 year. As will be shown in the section on size distributions, some of these shrimp were spawned in or before August; thus it may be stated that some shrimp live at least 16 months. Since the mortality is apparently high, the number that do live more than 1 year is small with respect to the total population. In figure 31 we show the percentage of mature female shrimp in the Louisiana offshore fishery from July to

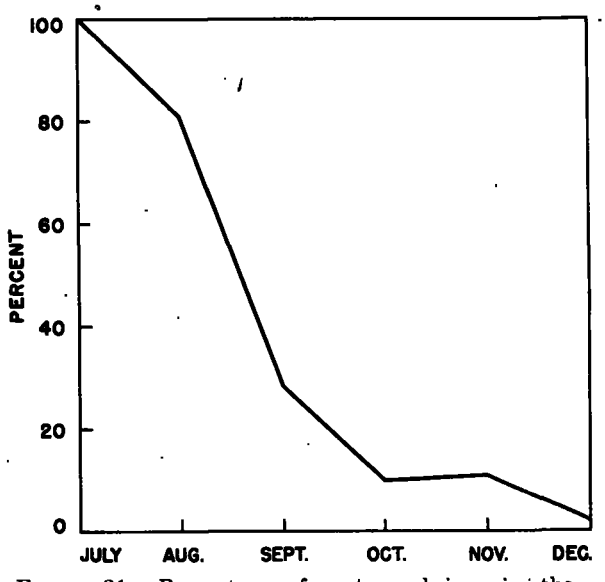


FIGURE 31.—Percentage of mature shrimp in the Louisiana offshore samples from July to December.

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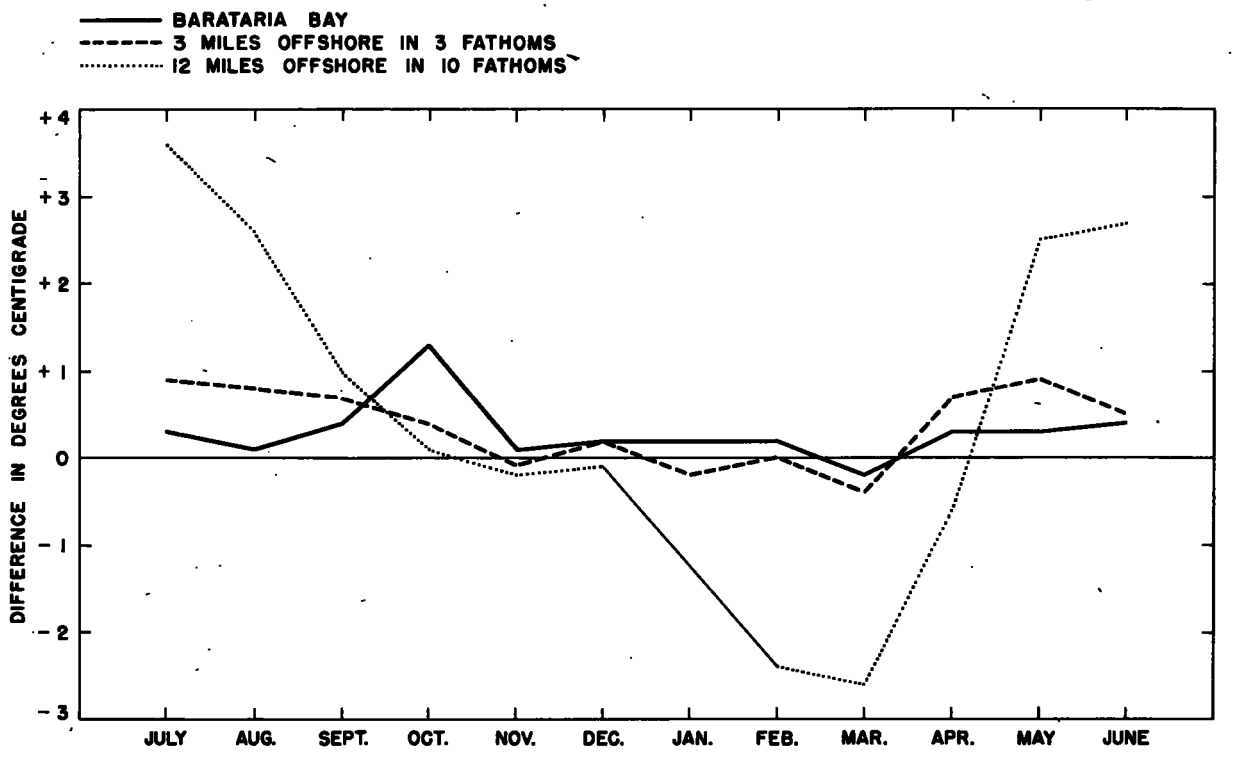

FIGURE 32.—Average monthly deviation of surface water temperature from bottom temperature (simultaneous observations) for three localities in Louisiana. We have no data for the 12-mile station during January.

November 1942 and in December 1941. The actual numbers of shrimp, from which this figure was derived, are presented in table 38. As can be seen, our sampling in November 1942 was poor, which probably accounts for the rather high percentage of mature shrimp during that month. In December, according to our samples, less than 3 percent of the offshore population was composed of mature shrimp. These December samples were taken from comparatively shallow areas out to 12½ fathoms. Undoubtedly, there were some shrimp in greater depths, many of which would be mature, but even if we doubled the number of mature shrimp to compensate for the incomplete sampling we would only have about 5 percent. When we consider the second group of immature shrimp which will move into the offshore fishery during the following April through July we are forced to conclude that after December the mature shrimp more than 1 year of age are not of great practical importance.

Weymouth, Lindner, and Anderson (1933) stated that on the Georgia coast shrimp disappeared from the fishery after 1 year, and these authors presumed that they died. We believe the data we present in this section prove Burkenroad's (1934, 1939) contention that shrimp live more than 1 year.

TEMPERATURE AND SALINITY RELATIONS

In Louisiana, we took surface and bottom water temperatures and salinities with each trawl haul made with the *Black Mallard* from 1931 to 1934. Along the Atlantic coast, where hauls were made with *Launch 58* from 1931 to 1935, we generally took only surface observations. For Texas, we have only the average surface water temperatures taken at Port Aransas Lighthouse, based on readings which were usually taken twice a day, at 8 a. m. and at 6 p. m., by the various lighthouse keepers from 1930 to 1936.

At times, even in the shallow water inhabited by shrimp, there are appreciable differences between surface and bottom temperatures (table 39, figs. 32 and 34), and comparable differences in salinities also occur (fig. 33). Since the shrimp is primarily a bottom form, we restrict our discussion of the influence of temperature and salinity as much as possible to the Louisiana area west of

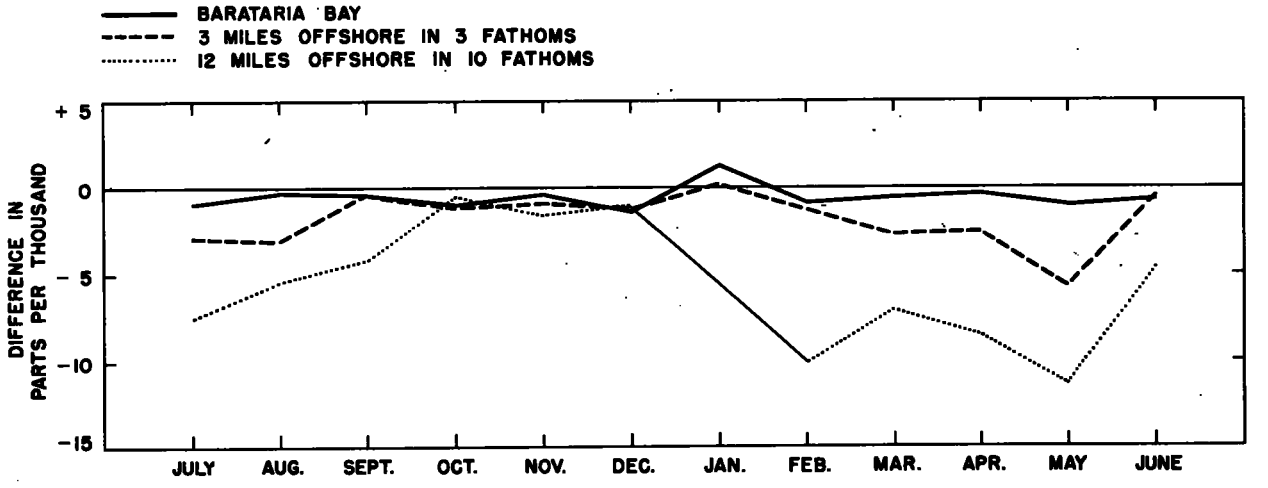

FIGURE 33.—Average monthly deviation of surface water salinity from bottom salinity for three localities in Louisiana. We have no data for the 12-mile station during January.

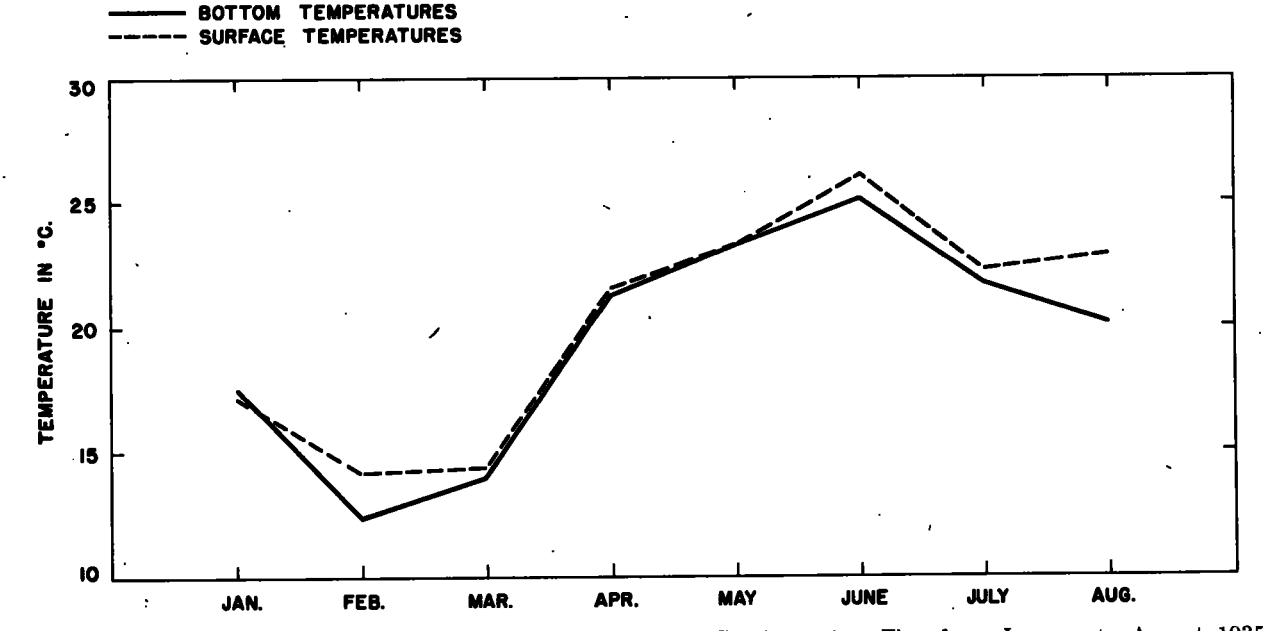

FIGURE 34.—Outside surface and bottom-water temperatures at St. Augustine, Fla., from January to August 1935.

the Mississippi River, the only region for which we have an appreciable amount of bottom data.

TEMPERATURE AND GROWTH

It is well established that temperature affects metabolism and hence the growth of all cold-blooded animals, such as shrimp. In table 40 and figure 35 we show the monthly average bottom water temperatures for three adjacent localities in Louisiana. These data were collected during the period 1932 to 1934. Unfortunately, no similar hydrographic data are available for the period 1939 to 1942 when the data on growth and spawning were collected. Although we fully realize that the marine climate may have changed somewhat in the intervening decade and that our conclusions may, as a result, not be valid, certain correlations between water temperatures in the early 1930's and growth and spawning of shrimp almost 10 years later are so interesting that we deem it advisable to discuss these correlations, assuming that the hydrographic conditions remained rela-

tively stable. Although the temperature records may not reflect the exact conditions during the period in which the biological observations were made, there is an equal chance that they represent an average. If we accept these temperatures as representing the average and use them to interpret the periods of growth and dormancy, it appears that growth slows to almost nil near the end of October (see fig. 5), when the temperature drops to about 20° C., and is resumed in the spring when the temperature again reaches approximately that value.

TABLE 39.—*Deviation of average surface-water temperatures from bottom temperatures along Atlantic coast, November 1934 to August 1935*

[These represent temperatures taken in outside waters within 5 miles of shore in depths between 2 and 10 fathoms, and are recorded in ° C. The averages are from 2 or 3 surface and bottom samples taken simultaneously in each locality. The stations are: 1, Cape Romain, S. C.; 2, Stono Inlet, S. C.; 3, Gaskins Bank, S. C.; 4, St. Catherines Island, Ga.; 5, Brunswick, Ga.; 6, Fernandina, Fla.; 7, St. Augustine, Fla.; 8, New Smyrna, Fla.; 9, Cape Canaveral, Fla.]

Month	Deviation at station No.—								
	1	2	3	4	5	6	7	8	9
1934									
November	−1.0	+0.4	−0.5	−0.1	−0.2	−0.1	−0.1	+0.1	−0.4
December	+0.6	+.1	−.3	−.4	+.4	0	−2.0	+.6	+.2
1935									
January	+.4	−.2	−.2	+.1	+.3	0	−.4	−.5	+.7
February	−.1	0	−.2	+.5	−.2	+2.2	+1.8	−.1	+2.8
March	−.3	0	−1.1	+.4	−1.2	+.5	+.4	−.5	0
April	−.4	−.4	+.2	+.4	+.7	+.3	+.3	+.8	0
May	+.5	+.1	+.9	−.2	+.1	+.5	0	+.6	+.9
June	+.1	+.7	+.1	+.2	+.2	+1.1	+1.0	+.6	+1.3
July	+.5	−.1	+.2	0	+.2	+2.5	+.6	+1.3	+3.4
August	------	------	------	------	------	−2.3	+2.8	+2.4	------

TEMPERATURE AND SPAWNING

Spawning in Louisiana appears to be more closely associated with rising and falling temperatures than with absolute temperature. As we have shown, it begins in the greater depths during the latter part of March or early April and is nearly completed by the end of September. In figure 35 there is an indication that the rise in temperature from the winter low begins later in the deeper waters than in shallow areas closer to shore. If this is true it is probable (though we cannot establish this from our meager temperature data) that the bottom temperatures on the spawning grounds begin to rise about the first of April and are falling rapidly by the end of September. Thus, the comparatively abrupt rise in the spring temperature coincides rather closely with the beginning of the spawning season and may, indeed, initiate it, while the season seems to terminate as soon as the temperatures begin to decline rapidly in the fall, even though they are at that time appreciably higher than those which evidently induced spawning in the spring.

TEMPERATURE AND MIGRATIONS

At first glance, it seems that there is little relation between temperature and migrations. In Louisiana, spring-spawned shrimp appear first in the trawl catches in inside waters in June, in outside waters adjacent to the coast in July, and offshore in August. This well-defined outward movement cannot be temperature-induced, since it occurs well before there is any appreciable drop in temperature. Judging from the behavior of the shrimp during this period, we believe the offshore movement is primarily associated with the approach of adulthood and spawning. However, this offshore movement is later accelerated by falling temperatures. The phenomenon, evidently initiated by physiological changes in the organism itself, seems to be hastened and intensified during fall and winter by the external factor of declining temperatures.

Concomitant with the accelerated fall and winter offshore movement of the adults and subadults, the smaller, more immature shrimp move from the very shallow inland waters toward the Gulf of Mexico. These very small shrimp, which during summer are most abundant toward the heads of the bays, are during midwinter more abundant near the mouths of the bays and in the Gulf adjacent to the shore, where the temperatures are not so readily depressed.

The change in habitat caused by winter temperatures can probably best be described as a general shift toward warmer waters, but with all sizes of shrimp still maintaining their size-locality separations. In Louisiana this shift is toward the Gulf because the bottom temperatures are warmer offshore.

Along the coast of Louisiana during winter there is an offshore belt of warm bottom water, on either side of which the bottom water becomes progressively colder. The shallower inshore waters reflect the temperature of the land, whereas the thermal belt reflects the temperature of the tropical oceanic waters of the Gulf of Mexico. Figure 35 shows the progression in winter bottom temperatures from the land toward, and probably into, the thermal belt.

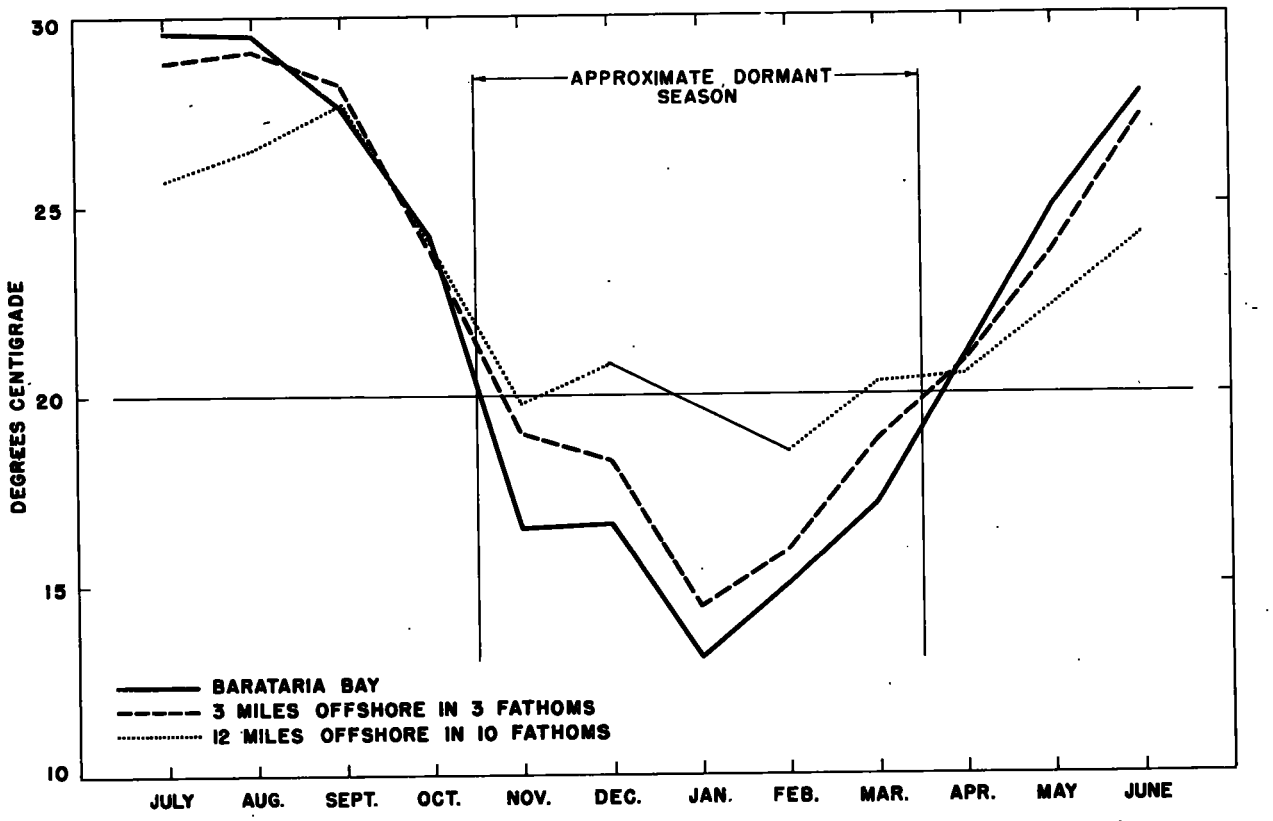

FIGURE 35.—Seasonal changes in bottom temperatures in three parts of the shrimp habitat in Louisiana.

Between midsummer and midwinter there is a complete reversal of bottom-temperature gradients between the estuarine waters and the inner littoral waters of the more stable thermal belt. We do not know to what depths offshore this belt extends, but on the basis of the depths at which shrimp have been taken in midwinter we believe that it does not normally extend much beyond 30 or 35 fathoms, if that far.

In central Texas there is probably a winter offshore gradient in temperature similar to that along the Louisiana coast. At least, the temperature records of Springer and Bullis (1952) indicate that such a gradient existed in November 1950. In addition to this there undoubtedly is also a coastal temperature gradient with increasing temperatures toward the south. During winter, larger shrimp from this section disappear from the shallower waters near the coast. They go offshore or southward. The greatest depth at which we encountered shrimp off central Texas in winter was 18 fathoms.

In Georgia and northern Florida, the spring-spawned shrimp appear almost simultaneously in the trawl catches in the inside and outside waters in July, although initially they are relatively much more abundant in the inside waters.[12] This summer movement from inside to outside waters is comparable to that in Louisiana and does not appear to be influenced by temperature. However, when the temperature begins to decline rapidly in the fall the large shrimp move southward along the coast rather than offshore as they do in Louisiana. We suspect their failure to go offshore results from the lack of suitable bottoms for feeding in this area along the Atlantic coast. As a consequence of this southward movement of the larger shrimp, with the largest tending to go farthest south, there is in midwinter a correlation along the Georgia and Florida coasts

[12] We suspect that the almost simultaneous appearance of spring-spawned shrimp in both inside and outside waters in this area results from the very narrow inside nursery-ground belt in this section of the Atlantic coast as compared with the Louisiana nursery grounds and those of central Texas. The nursery grounds in Georgia and northern Florida average about 10 miles in width, those near Aransas Pass, Tex., about 20 miles, and those in the vicinity of Barataria Bay, La., about 40 miles. Near Aransas Pass, Tex., the spring-spawned shrimp first appear in the inside trawl catches in July and in the outside catches in August. See Collier and Hedgpeth 1950 for details on hydrography of a Texas bay.

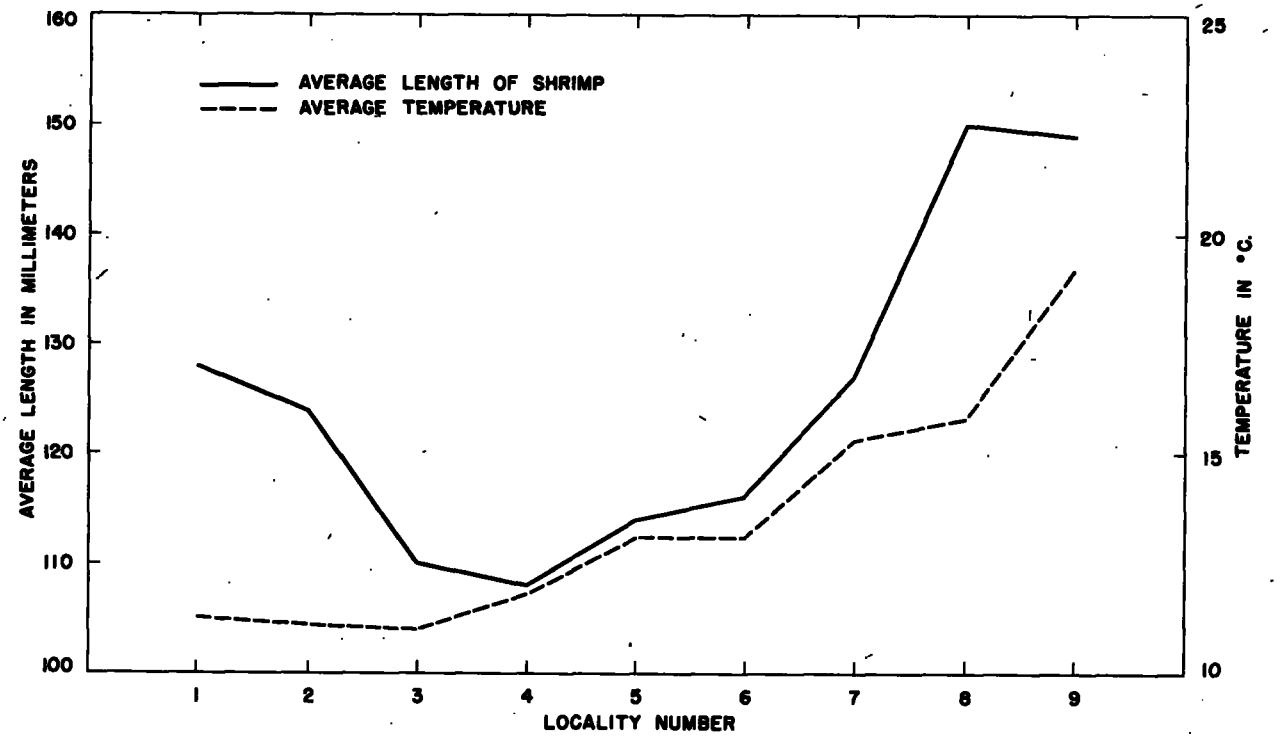

FIGURE 36.—Average outside surface water temperature and average median lengths of shrimp along the Atlantic coast during January and February, 1934 and 1935. The localities are (1) Cape Romain, S. C., (2) Stono Inlet, S. C., (3) Gaskins Bank and Fripp Island, S. C., (4) St. Catherines Island, Ga., (5) Brunswick, Ga., (6) Fernandina, Fla., (7) St. Augustine, Fla., (8) New Smyrna, Fla., (9) Cape Canaveral, Fla.

between water temperature and the average length of shrimp (fig. 36).

Apparently, some of the migrants from farther north become trapped along the South Carolina coast and a northward movement of these shrimp may occur in this section in midwinter. This is suggested by the progressive increase in the average length of shrimp to the north of St. Catherines Island. Our tagging would not show this northward movement, since we did not tag in South Carolina during midwinter. The numbers of shrimp which become winter-trapped in South Carolina are relatively few and variable from year to year. The bulk of the population of larger shrimp is along the coast of Florida at that time.[13]

Burkenroad (1949) reports sporadic offshore trawler catches of large shrimp in winter between Capes Hatteras and Lookout. Broad (1951) mentions finding them offshore near Diamond Shoals during winter but not in commercial quantities, and Gutsell (our records) also once encountered a school of large shrimp in this area in January. Apparently some of the North Carolina shrimp go offshore in winter in an attempt to escape the rigorous temperatures close to shore, although the majority go south. The proportion of the North Carolina shrimp population that goes south, north, and offshore in the fall and winter undoubtedly varies considerably from year to year.

In table 39 we give the differences between surface and bottom temperatures for nine stations along the Atlantic coast. Atlantic temperatures between Cape Canaveral and Fernandina, Fla., are interesting since they indicate the probable occurrence of a mass of cold bottom water striking the coast in this area during July and August. This was particularly noticeable in 1935 (fig. 34). An examination of table 41 suggests that the mass of cold water was also present in 1933 and 1934. Green (1944) attributes this phenomenon to upwelling. This mass of cold water may be one of the causes for the scarcity of shrimp during summer, between St. Augustine and Cape Canaveral.

[13] Parr (1933) foresaw the possibility of a winter northward migration of fishes in this general area.

Although the fall and winter migrations of shrimp appear to be primarily related to temperature, they also seem to be regulated by the type of bottom, which implies food. In general, along the Atlantic coast between Capes Lookout and Canaveral and between the 10- and 100-fathom contours the bottom is a marine desert of sand, shell, and coral. Along the Alabama and Mississippi coasts the same condition prevails. Near the mouth of the Mississippi River, however, the bottom changes to mud and apparently the large shrimp east of the Mississippi winter near its mouth, because both food and suitable temperatures are available. Along the Louisiana coast west of the Mississippi River these same suitable conditions are met between Ship and Trinity Shoals.

WINTER KILL

Sudden, severe drops in temperature in some localities will kill shrimp and in other localities will cause them to move offshore considerably beyond their normal range. We mentioned, in our discussion of migrations in Louisiana, the occurrence of such a drop in temperature in January 1940. This cold wave was general throughout the south Atlantic and Gulf areas of the United States.

In figure 37, we show (based on data from Local Climatological Summary for New Orleans, La., 1951, published by the U. S. Weather Bureau) the average monthly air temperatures at New Orleans for the winter of 1939–40 compared with the 78-year average. Lindner (1936) has shown a rather close relation between the New Orleans air temperatures and the surface water temperatures at Oyster Bayou Light, La.; consequently, we believe the temperatures of the shallow inland and coastal waters of Louisiana had a drop in January somewhat comparable to that shown for the New Orleans air temperatures.

Immediately after this January freeze, fishermen reported finding dead shrimp in the inland and adjacent coastal waters of Louisiana. However, in Louisiana we received no reports of great mass mortalities of fishes and shrimp, such as were reported by Gunter (1941) for Texas. We believe Gunter and Hildebrand (1951) have the correct explanation for the Texas mortalities when they state (p. 736) that, "The shallowness of Texas bay waters, their practically landlocked condition and the rapidity with which cold northers strike the coast are factors making the marine life of this area particularly subject to mortality from cold waves every few years." In Louisiana, on the other hand, the numerous passes between bays and the Gulf permit ready escape of the shrimp from the shallow inland areas to the deeper and warmer waters offshore. Although many small shrimp were killed in inside waters by the January freeze of 1940, the majority of them were undoubtedly driven off the coast by the cold and sought refuge in deeper waters, where we found and marked them in February and March.

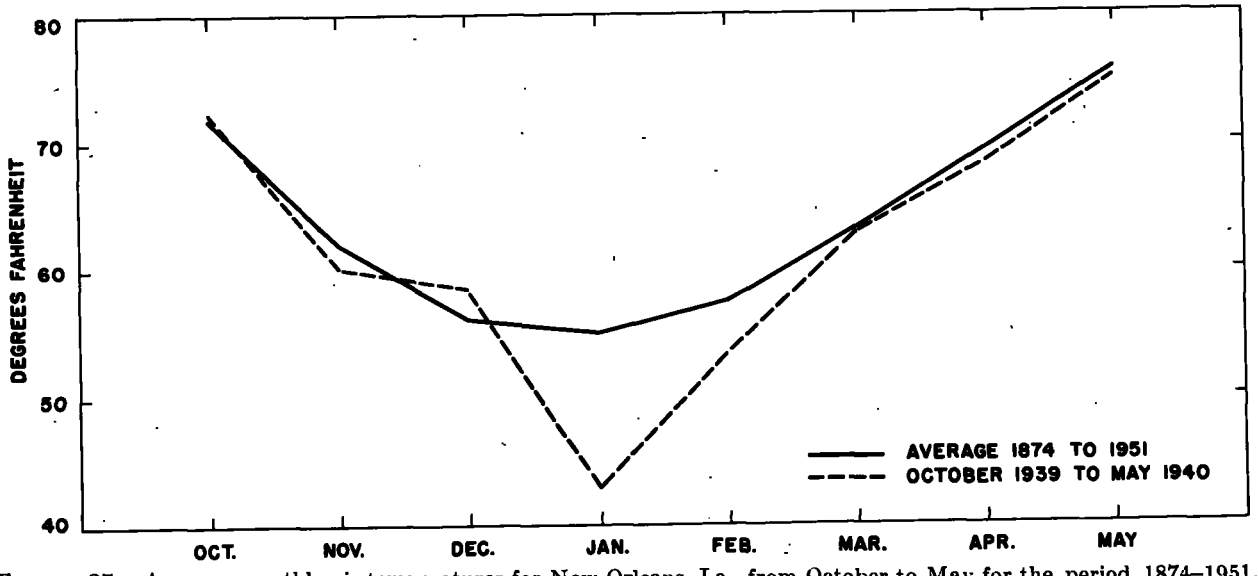

FIGURE 37.—Average monthly air temperatures for New Orleans, La., from October to May for the period 1874–1951, and from October 1939 to May 1940.

Along the Atlantic coast, the 1940 cold wave decimated the shrimp in South Carolina and Georgia to about as far south as Brunswick, but apparently had little effect in Florida. The effects of this cold wave were so severe that there were scarcely any shrimp during the spring in South Carolina and Georgia.

We were so concerned about a complete failure of the fishery at the time, that we recommended the immediate cessation of all shrimp fishing. The recommendation was not needed, as the fishermen, unable to catch enough shrimp to pay operating costs, stopped of their own accord. Owing to the scarcity of shrimp, the Brunswick, Ga., fleet was tied up so long that sparrows nested in the rigging of one boat. The occasional Georgia fishing boat that was sent out that spring to search for shrimp along the northern coast of the State would catch only 5 or 6 shrimp in an entire day's fishing.

The results of our experimental trawling corroborated those of the commercial fishermen in every respect. Immediately after the cold wave, we conducted trawling operations along the Atlantic coast between the 2- and 100-fathom contours from Fort Pierce, Fla., to Cape Hatteras, N. C. We used a 10-foot (spread at mouth) shrimp trawl, and the hauls were 30 minutes each. We usually covered between 3 and 3½ miles of bottom per haul. At about the same time we were operating offshore, the State of Georgia very kindly provided us with a launch so that we could also survey the inland waters. Here the hauls were also 30 minutes each and were made with the same type of 10-foot trawl that we used offshore. With the launch we averaged about 3 miles per haul.

The results of these operations are shown in tables 42, 43, and 44 and indicate that the catastrophe had almost completely depopulated the northern shrimp grounds. Apparently a few of the North Carolina shrimp moved offshore into warmer waters and did not perish. (See Parr, 1933, for average temperature contours.) In South Carolina very few shrimp survived the freeze. Inasmuch as all our hauls in this State in depths of 10 fathoms or less were on known fishing grounds that usually had shrimp during that time of year, and (1) our trawls covered between 80 and 100 miles of these bottoms, (2) our offshore trawling extended out from the known fishing grounds, and (3) we caught other peneid shrimps which normally were much less abundant than *P. setiferus*, we believe that had there been *P. setiferus* in any quantity we would have found them. Judging from our data and from firsthand knowledge of the experience of the Georgia fishermen, we think that there were scarcely any spawners left along the South Carolina and northern Georgia coasts that spring. All the *P. setiferus* we caught in inside waters were south of Sapelo Sound, Ga. We caught none in outside waters north of Jekyll Island, Ga., except one specimen taken in North Carolina southwest of Cape Fear in 13 fathoms. So far as we know, this specimen represents a depth record for *P. setiferus* off the Atlantic coast.

The migrants that had gone into Florida waters during the fall and early winter had been greatly depleted by fishing and few were left to return northward. There was very little spawning stock left north of central Georgia and practically none in South Carolina.

The results from the spawning of this depleted fishery were most interesting. In North Carolina, the 1940 fall fishery, although about 90 percent of normal as compared to the 2 previous years, was based not on the white shrimp (*Penaeus setiferus*) but almost entirely on "brownies" (Burkenroad's [1939] Division II of *Penaeus*).[14] In South Carolina, the 1940 calendar-year catch was down to only about 46 percent of the average of the previous two years. In Georgia and Florida it was about 90 percent of the previous 2-year average, which probably was well within the range of normal fluctuation; the limited drop could be caused by the lack of South Carolina migrants and a poor catch that spring. In 1941, fishermen reported their catches to be normal along the entire coast. The depopulated northern areas, as well as the more fortunate southern regions, had in this short period of time recovered completely from the catastrophe, and shrimp were as numerous as ever.

The remarkable thing about the shrimp and the 1940 cold wave is not the kill but the recuperative powers of the shrimp. The evidence of the Atlantic coast, incomplete as it may be, is certainly highly indicative that a normal crop may be produced by a few spawners. It seems doubtful

[14] The information on the composition of the North Carolina catch was furnished us at the time in a personal communication by Dr. H. F. Prytherch, who was then Director of the Beaufort, N. C., Fishery Station. See Anderson, Lindner, and King (1949) table 2, for catch statistics.

whether man, by fishing, could reduce the shrimp to a level where there was a direct relation between the number of spawners and the resultant crop. Apparently, except under most unusual conditions such as the 1940 cold wave, there is always a superabundance of spawners.

There was no indication that the January 1940 cold wave had any effect on the shrimp catches for that year in either Louisiana or Texas. In Louisiana the shrimp apparently escaped offshore. In central Texas during midwinter (as Gunter, 1950, has shown, and we confirm) there were very few shrimp in the bays, and probably even if all were killed it would have made no appreciable difference in the spawning population.

Gunter (1947) has demonstrated that smaller fishes are less susceptible to lower temperatures than are the larger ones. It appears from the winter distributions of shrimp, as shown by our data, that the smaller shrimp, like the smaller fishes, are probably better able to withstand cold than are the larger ones.

SALINITY

The reaction of the shrimp to salinity is not clear-cut. The young apparently seek the inland areas of low salinity, and on approaching adulthood they move towards the more saline waters of the sea to spawn. It seems that the shrimp (at least the subadults) are rather insensitive to large fluctuations in salinity but that they are very sensitive to small changes in temperature.

SIZE IN RELATION TO SALINITY AND TEMPERATURE

In every locality there was a general progression, from inside to outside waters, in the size of the trawl-caught shrimp; the smallest ones were taken in the waters of lowest salinity farthest from the sea, the largest ones were captured in the outside waters where the salinity was highest. Superficially this appeared to be a high positive correlation between salinity and size of the shrimp, but there were certain anomalies. In Louisiana, for instance, we would on occasions find much larger shrimp in Little Lake and Lake Salvador than we would in the upper reaches of Barataria Bay, although the salinity was much less in Little Lake. With a seine, we would also find very small shrimp along the banks of Bayou Rigaud (near the mouth of Barataria Bay) and along the edges of the marsh and among the mangroves bordering the bay where the salinity was relatively high.

To test the significance of the apparent relation between size of trawl-caught shrimp and salinity and temperature, we selected 17 sets of data we

TABLE 40.—*Average monthly bottom temperatures and salinities for 3 localities in Louisiana, 1932 to 1934*

[Temperatures in degrees centigrade; salinities in parts per thousand]

Month	Barataria Bay			3 fathoms			10 fathoms		
	Number of observations	Temperature	Salinity	Number of observations	Temperature	Salinity	Number of observations	Temperature	Salinity
January	[1] 17	13.1	11.7	5	14.4	26.7			
February	16	15.0	10.4	4	15.9	24.9	1	18.5	33.6
March	22	17.1	8.0	7	18.8	26.5	3	20.3	34.6
April	31	21.0	11.6	8	20.8	28.3	6	20.5	34.4
May	[2] 27	24.9	12.7	5	23.8	26.9	6	22.3	34.0
June	24	27.9	11.4	6	27.3	23.8	3	24.2	35.6
July	[3] 14	29.6	16.7	[4] 7	28.8	32.1	4	25.7	35.6
August	11	29.5	13.7	3	29.1	29.5	[6] 3	26.5	34.0
September	[3] 13	27.6	16.7	3	28.2	29.7	3	27.7	33.3
October	20	24.2	17.8	6	23.8	30.9	3	24.0	32.5
November	13	16.5	13.6	[5] 4	19.0	31.9	[7] 2	19.8	33.5
December	17	16.6	15.7	3	18.3	29.3	2	20.8	34.5

[1] Only 16 salinity observations.
[2] Only 23 temperature observations.
[3] Only 12 temperature observations.
[4] Only 6 salinity observations.
[5] Only 3 salinity observations.
[6] Only 2 temperature observations.
[7] Only 1 salinity observation.

TABLE 41.—*Mean surface temperatures in °C for nine stations along Atlantic coast, May 1933 to August 1935*

[The stations are: 1, Cape Romain, S. C.; 2, Stono Inlet, S. C.; 3, Gaskins Bank and Fripp Island, S. C.; 4, St. Catherines Island, Ga.; 5, Brunswick, Ga.; 6, Fernandina, Fla.; 7, St. Augustine, Fla.; 8, New Smyrna, Fla.; 9, Cape Canaveral, Fla.]

Month	Mean temperature at station No.—								
	1	2	3	4	5	6	7	8	9
1933									
May	------	24.2	23.7	24.3	25.6	25.7	25.7	26.4	26.4
June	------	27.5	27.2	28.7	29.0	26.7	25.7	27.8	26.7
July	------	26.8	27.2	28.6	27.9	27.3	26.8	25.6	26.7
August	------	28.4	28.9	29.6	28.9	28.9	27.5	26.4	28.3
September	------	28.9	29.0	26.4	27.3	27.5	26.7	30.8	29.4
October	------	20.6	21.1	21.6	25.0	22.2	24.7	26.4	26.1
November	------	17.3	16.7	16.8	16.7	19.3	21.1	21.6	21.1
December	------	15.4	14.5	14.1	14.7	16.7	19.2	20.4	20.7
1934									
January	------	12.8	12.7	12.9	12.8	13.6	15.8	16.8	19.6
February	------	9.0	9.0	10.2	11.9	11.1	13.6	15.7	18.3
March	------	12.1	14.3	13.8	12.5	------	17.2	18.3	20.0
April	------	18.6	17.3	16.6	19.3	16.8	17.9	21.7	23.3
August	------	28.9	28.3	28.2	29.6	26.7	23.9	28.1	------
September	27.1	26.8	27.2	28.2	28.7	27.5	27.2	28.4	28.6
October	21.6	21.1	20.7	23.4	23.9	26.6	27.3	27.5	27.8
November	13.6	14.3	13.1	15.0	16.4	18.9	22.3	23.6	23.2
December	13.6	12.7	12.3	13.1	15.6	16.1	18.3	21.6	22.2
1935									
January	12.7	12.5	12.2	12.8	14.6	15.7	17.2	17.1	21.0
February	10.0	10.0	10.0	11.3	13.2	12.5	14.2	13.4	17.8
March	13.8	12.8	14.9	13.6	14.3	12.8	14.4	16.9	17.2
April	16.6	16.7	19.3	19.7	21.0	20.4	21.6	23.1	23.4
May	23.6	23.3	24.7	24.4	26.0	24.3	23.3	24.4	25.4
June	25.8	26.7	26.4	26.7	26.7	26.0	26.1	25.6	26.8
July	27.8	27.1	27.7	27.3	27.2	26.6	22.3	24.7	24.9
August	------	------	------	------	------	24.0	22.9	22.7	------

had for Louisiana which met the following requisites: (1) Almost simultaneous observations for all of four stations; (2) not less than 20 shrimp caught per haul; and (3) both bottom temperature and salinity observations at the time and place of each haul. We show these data in table 45. Most of the months of the year are represented, although we lack data for March, May, and June. Gunter (1938) gives the location of the stations.

TABLE 42.—*Percentage at each depth grouping, of hauls with* P. setiferus *present following January 1940 cold wave*

Depth	North Carolina	South Carolina	Georgia	Florida
2–5 fathoms	0	0	10	75
6–10 fathoms	0	0	9	28
11–20 fathoms	[1] 2	0	0	[2] 2
21–50 fathoms	0	0	0	0
51 fathoms and deeper	0	0	0	0

[1] One shrimp caught in 13 fathoms.
[2] One shrimp caught in 11 fathoms.

TABLE 43.—*Number of trawl hauls along Atlantic coast following January 1940 cold wave, showing presence or absence of shrimp*

Locality and depth	Number of trawl hauls		
	Total	With *P. setiferus*	With other peneids
North Carolina: [1]			
2–5 fathoms	1	0	1
6–10 fathoms	27	0	3
11–20 fathoms	46	1	4
21–50 fathoms	13	0	0
51 fathoms and deeper	4	0	0
Total	91	1	8
South Carolina: [2]			
2–5 fathoms	5	0	3
6–10 fathoms	18	0	2
11–20 fathoms	27	0	4
21–50 fathoms	16	0	4
51 fathoms and deeper	4	0	0
Total	70	0	13
Georgia: [3]			
2–5 fathoms	20	2	6
6–10 fathoms	22	2	4
11–20 fathoms	30	0	11
21–50 fathoms	15	0	6
51 fathoms and deeper	2	0	1
Total	89	4	28
Florida: [4]			
2–5 fathoms	4	3	2
6–10 fathoms	94	26	15
11–20 fathoms	52	1	7
21–50 fathoms	19	0	6
51 fathoms and deeper	7	0	0
Total	176	30	30

[1] All hauls between February 13 and March 8.
[2] 45 hauls between February 3 and February 13; 25 hauls between March 9 and March 13.
[3] 47 hauls between January 26 and February 2; 24 hauls between March 14 and March 16; 18 hauls between April 17 and April 18.
[4] 71 hauls between January 17 and January 25; 105 hauls between March 27 and April 17.

If we range these data from 1 to 4, giving the value 1 to the lowest or smallest observation and 4 to the highest or largest, we obtain the results shown in table 46. By this method we find an almost perfect correlation between size of trawl-caught shrimp and salinity, and rather good correlations between size and temperature and between temperature and salinity. However, when we eliminate the effect of locality by means of partial correlations we find the correlation between length and salinity to be only +0.0622, which is not significant, and the correlation between length and temperature to be +0.2184, which is significant.

TABLE 44.—*Average number of shrimp per haul in inside waters along Georgia and northern Florida coast following January 1940 cold wave*

[Localities are from north to south and all hauls were made between April 24 and May 8, 1940]

Locality	Number of hauls	Average number of *P. setiferus* per haul
Wassaw Sound to Sapelo Sound	15	0.0
Sapelo Sound to St. Simons Sound	13	2.1
St. Simons Sound to St. Marys Entrance	22	14.9
St. Marys Entrance to St. Johns Inlet	11	17.7

Our interpretation of the foregoing is that the apparent relation between size of shrimp and absolute salinity within relatively large ranges of salinity does not exist for these four stations. The relation normally is between size and locality. That is, certain sizes of shrimp will be found in certain localities at certain seasons regardless of what the salinity may be (within relatively large ranges) at that particular locality and time. This does not mean, however, that there is no relation between size and salinity. Why is it that as the shrimp increase in size they move toward the sea? We suspect this to be a reaction to salinity, related to spawning, or maturity. We have observed that if the salinity becomes too low in an area, the shrimp will leave. Figure 38, based on the data presented in table 40, shows the marked differences in salinity between the nursery grounds in Barataria Bay and the offshore spawning areas. The salinity gradient indicated is certainly abrupt enough to lead us to suspect that it might serve as an effective stimulant for migration.

TABLE 45.—*Median size of shrimp captured, bottom temperature, and bottom salinity for four stations in Louisiana*

Inclusive dates of sampling	Data [1] for St. Mary's Point station				Data [1] for Middle Ground station				Data [1] for Four Bayou Pass station				Data [1] for station 3-6 miles southeast of Fort Livingston			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
1932																
Sept. 28–30	200	105	25.3	6.6	200	122	25.4	24.4	200	129	27.2	27.2	200	130	27.2	30.4
Oct. 1–4	199	110	26.2	9.9	200	122	25.2	23.5	185	142	25.6	29.1	200	141	26.7	30.5
Oct. 12–15	195	96	21.2	10.3	200	125	23.6	30.4	200	131	22.7	31.3	200	135	23.8	31.6
Oct. 16–18	200	102	22.0	9.6	200	117	23.0	29.8	200	128	25.6	34.4	200	140	22.6	31.0
Oct. 28–31	200	86	18.9	2.3	200	123	21.2	18.5	200	135	22.6	31.1	195	149	22.1	32.5
Nov. 1–4	200	83	20.1	1.5	200	116	19.3	23.1	82	124	19.4	30.6	200	127	21.0	32.3
Dec. 1–4	112	63	11.7	14.8	200	83	15.7	28.4	200	102	14.7	30.9	200	129	16.1	32.1
1933																
Jan. 29–31	56	64	13.9	1.2	200	85	14.4	21.5	200	102	15.6	24.4	200	111	15.4	24.5
Feb. 2–4	200	79	16.3	2.9	200	87	15.7	23.5	200	106	15.9	22.9	200	113	15.8	24.0
Apr. 16–18	113	115	18.0	.8	200	130	20.3	15.9	33	133	20.5	30.9	20	135	21.0	34.7
Apr. 28–29	122	127	25.1	3.2	200	139	25.6	17.4	200	141	23.6	13.8	200	145	24.3	18.3
July 12–14	200	111	26.2	7.2	200	104	28.4	13.2	118	116	27.5	34.3	200	122	27.6	32.4
July 19–20	200	110	29.4	11.0	200	118	30.2	29.7	200	125	31.1	30.9	47	141	28.3	34.2
Aug. 9–11	83	121	28.8	7.5	26	125	28.6	18.5	200	129	29.3	23.8	200	126	28.8	25.9
Nov. 18–19	200	94	18.2	15.9	200	117	18.0	23.9	200	120	18.6	32.3	200	120	19.1	31.2
Dec. 14–16	200	89	20.1	15.2	200	95	19.4	25.0	200	99	20.3	28.9	200	110	20.3	30.9
1934																
Jan. 12–13	200	79	12.0	15.9	200	95	12.9	28.5	200	97	16.0	32.1	200	99	16.4	32.6

[1] A=number of specimens; B=median length of the shrimp in millimeters; C=bottom temperature in degrees centigrade; and D=bottom salinity in parts per thousand.

TABLE 46.—*Relations between median size of shrimp captured, bottom temperature, and bottom salinity for four stations in Louisiana*

[Data were ranked from 1 to 4 for each of 17 periods; 1 is smallest or lowest and 4 is largest or highest]

Item	Rank	Rank 1	Rank 2	Rank 3	Rank 4
		Bottom salinity			
Median size	4			4.5	12.5
Do	3		2	10.5	4.5
Do	2	1	14	2	
Do	1	16	1		
		Bottom temperature			
Do	4	1	5	3.5	7.5
Do	3	2.5	3.5	4.5	6.5
Do	2	6	5	5	1
Do	1	8	3.5	3.5	2
		Bottom salinity			
Bottom temperature	4	1	1	7	8
Do	3	4.5	5	3	4.5
Do	2	3.5	5	6	2.5
Do	1	8	6	1	2

The correlation which our data shows between size and temperature is caused by the large number of cold-weather observations. In winter there is a definite relation between size and temperature, with the largest shrimp seeking the warmest temperatures. This correlation does not exist during summer. In fact the summer size-temperature relation is negative, but we can see no cause-and-effect connection.

INFLUENCE OF SALINITY AND TEMPERATURE ON MOVEMENTS

We wish to refer the reader to Gunter's papers on the distribution of fishes and invertebrates both in Louisiana and Texas. In general we agree with his conclusions on the relation between shrimp and both temperature and salinity. We do not entirely agree, however, with his statement that, "This general exodus of shrimp and other invertebrates as well as fishes from the bays is correlated with the annual temperature cycle and not with salinity changes or any other phenomenon." (Gunter 1950, p. 44.) Our data indicate that the shrimp normally leave the Texas bays as they approach adulthood. This movement is started in summer, long before there is any appreciable drop in temperature, and in spring with rising temperatures, and in some way seems to be related to salinity as well as to maturity or spawning. Dropping temperatures merely hasten and tend to obscure the other causes of this normal movement.

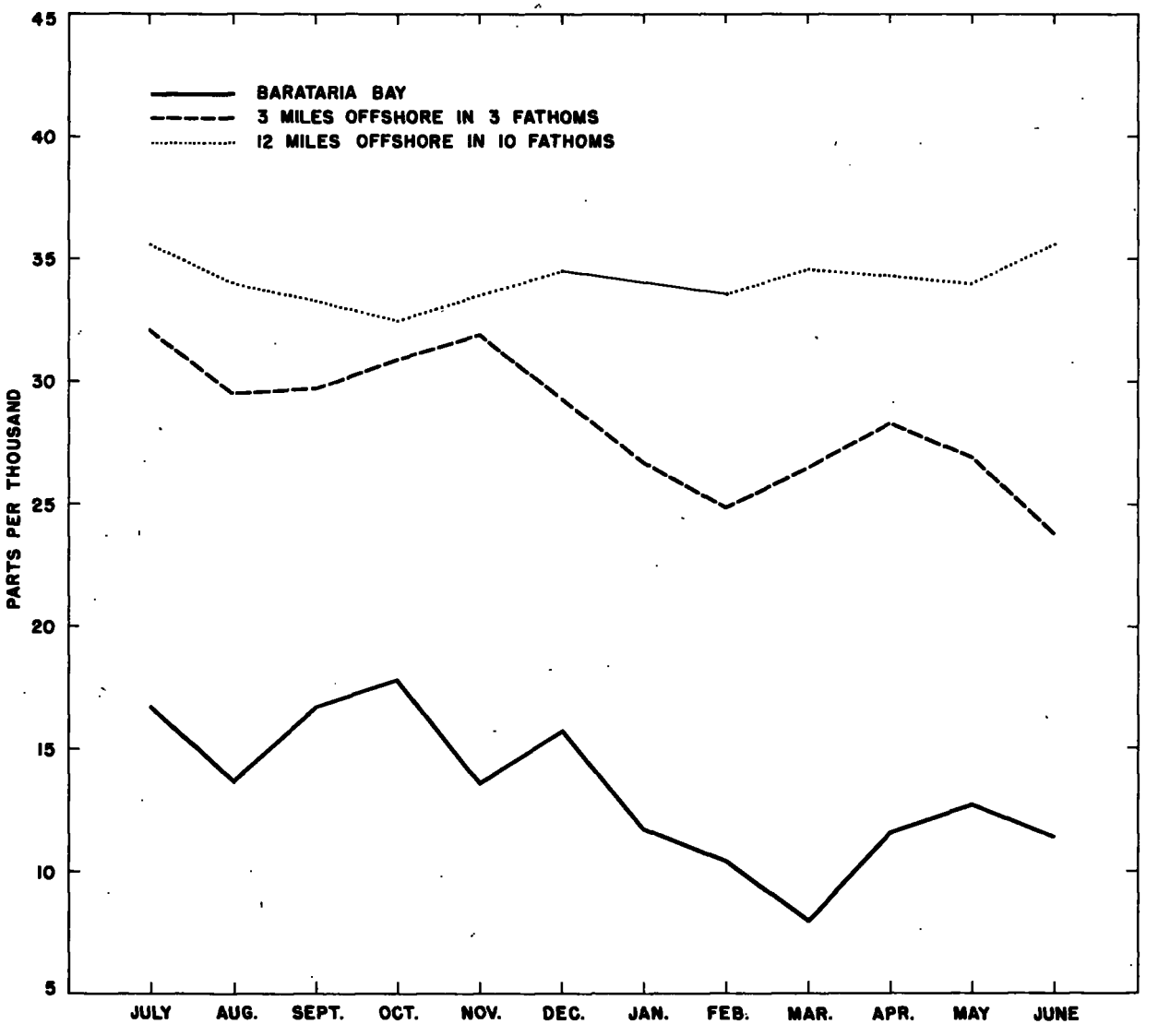

FIGURE 38.—Seasonal changes in bottom salinities in three parts of the shrimp habitat in Louisiana. We have no data for the 12-mile station during January.

SIZE DISTRIBUTIONS

SAMPLING PROCEDURE

Since Lindner (1933), Weymouth, Lindner, and Anderson (1933), and Gunter (1938) have described our sampling procedures in detail we shall not discuss them at length here. There are, however, certain rather obvious things connected with the sampling that should be pointed out. In the first place, in any fishery it is extremely difficult, if not impossible, to get samples that represent the population in its entirety. Our samples deal only with trawl-caught shrimp after they appear on the fishing grounds.

In samples taken from boats which we operated, there was a tendency for some of the smaller shrimp (about 60 mm. or less) to escape through the meshes of the trawl when fish and shrimp were not abundant. We do not believe this to be a serious factor in our sampling, since shrimp smaller than 60 mm. generally were not abundant on the fishing grounds. The small post-larval shrimp inhabit the marginal areas of the inland waters and apparently do not move to the inland fishing grounds until about 50 mm. or more in length (Anderson, King, and Lindner, 1949).

Along the Atlantic coast, from February 1931 through April 1933, our samples included only shrimp caught by our own boat in Georgia and northern Florida.[15] Numerous hauls were made each month in both the inside and outside waters in localities frequented by the commercial fishery. From each haul a random sample of 200 shrimp was measured. If less than 200 shrimp were caught, the entire catch was used as a sample. In May 1933 we changed our sampling procedure but not the number of shrimp measured in each haul. We curtailed our operations in Georgia and extended them to cover South Carolina and central Florida. In Georgia we usually made only four hauls each month in inside waters. All our remaining hauls were in outside waters on known fishing grounds that were close to shore. We made two hauls each month in each locality. The localities and months we fished were as follows:

South Carolina:

1. Cape Romain, September 1934 through July 1935.
2. Stono Inlet, May 1933 through July 1935 with exception of May through August 1934.
3. Gaskins Bank or Fripp Inlet, same as locality 2.

Georgia:

4. St. Catherines Island, same as locality 2.
5. Brunswick, same as locality 2.

Florida:

6. Fernandina, same as locality 2.
7. Mayport, May 1933 through April 1934, and August 1934.
8. St. Augustine, May 1933 through April 1935 with the exception of May through July 1934.
9. New Smyrna, same as locality 8.
10. Cape Canaveral, same as locality 8.

Our original objective (not always attained) was to sample on a semimonthly basis. After May 1933, when the area under study was expanded, the procedure was modified, and monthly samples became the goal for the remaining period of the work.

The numbers of shrimp upon which the size-distribution curves for this section of the coast are based are shown in tables 47 and 48. In all instances, data called "Georgia and northern Florida" include the entire Georgia coast and northern Florida as far south as Mayport.

[15] We have always appreciated the difficulties inherent in one-boat samples as recently pointed out by Gunter (1950), but we believe that the size selectivity generally exerted by the commercial fleet in inside waters, both from choice of fishing localities and from sorting, probably is equally bad.

TABLE 47.—*Numbers of shrimp in random samples used for determining Georgia and northern Florida size-distribution curves shown in figure 45*

Source and month	1931	1932	1933	1934	1935	Total
Inside waters:						
January	----	1,463	2,590	800	799	5,652
February	1,417	408	2,400	800	800	5,825
March	2,086	1,780	2,400	800	501	7,567
April	3,149	4,343	2,518	730	456	11,196
May	3,736	1,474	788	----	800	6,798
June	1,706	1,255	730	----	141	3,832
July	1,090	1,934	788	----	782	4,584
August	3,623	3,232	800	800	679	9,134
September	5,199	3,201	800	800	----	10,000
October	3,016	3,200	800	611	----	7,627
November	2,792	3,200	800	800	----	7,592
December	2,599	3,045	800	800	----	7,244
Total	30,413	28,535	16,204	6,941	4,958	87,051
Outside waters:						
January	----	558	1,321	1,600	1,143	4,622
February	2,290	849	1,280	1,525	714	6,658
March	139	224	1,294	43	287	1,987
April	53	1,179	1,720	422	679	4,053
May	1,099	256	1,753	----	650	3,758
June	400	692	1,679	----	227	2,998
July	574	441	1,747	----	305	3,067
August	944	1,310	1,244	1,040	----	4,538
September	1,091	1,800	1,600	1,240	----	5,731
October	1,118	1,680	1,600	1,200	----	5,598
November	1,000	1,800	1,600	957	----	5,357
December	600	1,832	1,600	1,200	----	5,232
Total	9,308	12,621	18,438	9,227	4,005	53,599

TABLE 48.—*Numbers of shrimp in random samples used for determining Atlantic-coast size-distribution curves shown in figure 46*

Source and month	1933	1934	1935	Total
South Carolina:				
January	----	800	553	1,353
February	----	800	396	1,196
March	----	800	297	1,097
April	----	50	365	415
May	786	----	170	956
June	842	----	371	1,213
July	731	----	416	1,147
August	805	76	----	881
September	800	1,200	----	2,000
October	800	800	----	1,600
November	800	1,200	----	2,000
December	800	1,200	----	2,000
Total	6,364	6,926	2,568	15,858
Georgia and northern Florida:				
January	----	1,600	1,143	2,743
Feburary	----	1,525	714	2,239
March	----	43	287	330
April	----	422	679	1,101
May	1,753	----	650	2,403
June	1,679	----	227	1,906
July	1,747	----	305	2,052
August	1,244	1,040	----	2,284
September	1,600	1,240	----	2,840
October	1,600	1,200	----	2,800
November	1,600	957	----	2,557
December	1,600	1,200	----	2,800
Total	12,823	9,227	4,005	26,055
Central Florida:				
January	----	947	1,145	2,092
February	----	1,200	844	2,044
March	----	819	217	1,036
April	----	1,189	193	1,382
May	599	----	----	599
June	256	----	----	256
July	705	----	----	705
August	540	252	----	792
September	1,001	1,200	----	2,201
October	1,199	1,200	----	2,399
November	1,200	1,050	----	2,250
December	1,200	1,200	----	2,400
Total	6,700	9,057	2,399	18,156

In Louisiana our samples were of two types: Those from our own boat in which we occupied the same stations month after month, and those from the offshore commercial fishery. When we used our own boat we attempted to occupy 3 inside and 3 outside stations twice each half month, but we were not always successful in occupying all stations each month. Also, since we are certain that our trawl did not always function properly at our outermost station which was 9 to 12 miles southeast of Fort Livingston Light, we have omitted the records of this station from our size-distribution data. Consequently, what we call "5-stations data" include 3 stations within Barataria Bay and 2 offshore from this bay, the outermost one 3 to 6 miles southeast of Barataria Pass. Gunter (1938, fig. 1) shows the location of these stations. The months in which we occupied them can be determined from table 49. As on the Atlantic coast, we measured only a random sample of 200 shrimp from each haul, even though we often caught more specimens.

In the Louisiana offshore fishery there was a definite tendency for the fleet to seek areas where shrimp were most abundant, and this may have affected the size distributions to some extent. However, the fishermen in Louisiana rarely discarded any of the shrimp (as they often did in Texas) since they seldom caught more than a few small ones.

For our Louisiana offshore-fleet size distributions we took a random sample of 50 shrimp from the last haul made by each boat we sampled. The boats were always away from port for more than 1 day, but they always knew where they had made their last haul.

Our samples contain shrimp from various depths as follows:

1. Under 5 fathoms: March through December, but heaviest in September and October.
2. In 5 to 8½ fathoms: Every month, but heaviest from May through January,
3. In 9 to 12½ fathoms: Every month, but heaviest from January through September.
4. In 13 to 16½ fathoms: November through August, but heaviest during March, April, and December.
5. In 17 or more fathoms: November through May, but heaviest during March and April.

In the Louisiana offshore fishery we attempted to collect the samples on a semimonthly basis from April 1941 through November 1942; thereafter they were taken only periodically. The months of our sampling can be seen in table 50.

In samples from the commercial fishery at Aransas Pass, Tex., several factors enter which appreciably affect our size distributions. There the commercial trawlers tended to do selective fishing for the larger shrimp (greater than about 100 mm. in length), since these shrimp commanded a higher price. The fishermen also resorted to culling the small shrimp and discarding them. The distortion of the data based on samples of shrimp from a commercial catch treated in this way is probably as great as any which would characterize those based on 1-boat samples, as has previously been mentioned.

TABLE 49.—*Numbers of shrimp in random samples used for determining Louisiana 5-stations size-distribution curves shown in figure 40*

Source and month	1931	1932	1933	1934	Total
Inside waters:					
January	------	618	335	837	1,790
February	------	------	977	403	1,380
March	------	1,538	912	------	2,450
April	------	726	1,484	500	2,710
May	------	503	869	115	1,487
June	------	232	580	418	1,230
July	345	320	1,200	------	1,865
August	2,222	689	628	------	3,539
September	------	1,039	571	------	1,610
October	788	2,394	1,200	------	4,382
November	623	820	1,200	------	2,643
December	600	948	1,139	------	2,687
Total	4,578	9,827	11,095	2,273	27,773
Outside waters:					
January	------	------	1,002	611	1,613
February	------	------	1,197	300	1,497
March	------	300	562	------	862
April	------	------	611	255	866
May	------	584	200	201	985
June	------	417	378	------	795
July	140	718	565	------	1,423
August	442	233	848	------	1,523
September	------	800	401	------	1,201
October	------	1,780	249	------	2,029
November	------	682	600	------	1,282
December	------	600	600	------	1,200
Total	582	6,114	7,213	1,367	15,276

Our samples at Aransas Pass, Tex., were all from the commercial fishery. Here the boats went out early in the morning and returned with their catch early in the afternoon of the same day. We took 100 shrimp from each boat sampled. An attempt was made each week to equalize the number of samples from the inside and outside fishery. The numbers of shrimp we obtained are shown in table 51.

At Galveston, Tex., although fishing was permitted only in outside waters, the boats operated on a daily basis as did those at Aransas Pass. Our samples here consisted of 100 shrimp per boat,

TABLE 50.—*Numbers of shrimp in random samples from commercial boats, used for determining Louisiana size-distribution curves shown in figure 39*

Source and month	1931	1932	1933	1934	Total
Five stations:					
January		618	1,337	1,448	3,403
February			2,174	703	2,877
March		1,838	1,474		3,312
April		735	2,095	755	3,585
May		1,087	1,069	316	2,472
June		649	958	420	2,027
July	485	1,038	1,765		3,288
August	2,664	922	1,476		5,062
September		1,839	972		2,811
October	788	4,174	1,449		6,411
November	623	1,502	1,800		3,925
December	600	1,548	1,739		3,887
Total	5,160	15,950	18,308	3,642	43,060

Source and month	1941	1942	1943	1944	Total
Offshore fleet:					
January		5,899		1,800	7,699
February		2,150	1,346		3,496
March		6,050	200	400	6,650
April	2,099	2,900	700		5,699
May	4,900	1,900			6,800
June	4,850	792	599		6,241
July	800	3,092	400	1,000	5,292
August	1,100	2,658			3,758
September	850	3,550			4,400
October	2,700	4,385	1,200		8,285
November	3,200	600			3,800
December	2,050		2,199	699	4,948
Total	22,549	33,976	6,644	3,899	67,068

TABLE 51.—*Numbers of shrimp in random samples used for determining Aransas Pass, Tex., size-distribution curves shown in figure 42*

Source and month	1931	1932	1933	1934	1935	1936	1937	Total
Inside waters:								
January				300				300
February			400					400
March			2,000	300				2,300
April		100	1,200					1,300
May	582		1,200	300		300		2,382
June	100		600					700
July		200	300		300		300	1,100
August		1,800	600	500	400	400	600	4,300
September	1,025	1,000	1,200	1,100	800	400	600	6,125
October	1,600	1,200	1,200	1,000	400	300	300	6,000
November	1,800	1,400	1,200	1,000	600	200	600	6,800
December	1,200	400	600	500		300		3,000
Total	6,307	6,100	10,500	5,000	2,500	1,900	2,400	34,707
Outside waters:								
January		800		300	500	300		1,900
February		1,000	400	500	800		400	3,100
March		1,000	600	600	200	200		2,600
April		1,000	1,200	900	100	200		3,400
May	449	1,200	1,700	1,200				4,549
June	1,600	600	900	400	200	700		4,400
July	1,200	1,000	1,200	800	200	300		4,700
August	1,200	400	900			200		2,700
September	600	200						800
October	800	1,400			400			2,600
November		1,000	300			200		1,500
December	600	200		600	500	400	200	2,500
Total	6,449	9,800	7,200	5,300	2,900	2,500	600	34,749

TABLE 52.—*Numbers of shrimp in random samples used for determining Galveston, Tex., size-distribution curves shown in figure 44*

Source and month	1933	1934	1935	1936	Total
Outside waters:					
January		500	500	500	1,500
February		1,000	200	400	1,600
March		800	500		1,300
April		1,000	400	400	1,800
May		1,000	500	400	1,900
June		1,000	200		1,200
July		600	400		1,000
August		400	500		900
September		500			500
October	1,000	500	500		2,000
November	1,000	400			1,400
December	1,000	500			1,500
Total	3,000	8,200	3,700	1,700	16,600

and we attempted to sample on a monthly basis. The numbers of shrimp comprising the size-distribution curves for Galveston are shown in table 52.

We are still not certain how adequate or representative our sampling was or how truly our curves represent the shrimp population. We considered various methods of weighting our samples, but after giving consideration to each we arrived at the conclusion that no method we could devise would give a true representation of the entire shrimp population at any one moment. The principal difficulty arises from the fact that as the shrimp increase in size they change their habitat. This change of habitat is not correlated with size alone; it is also dictated by winter temperatures and influenced by spawning. As a consequence, we generally find that in any one locality there is almost always an immigration and emigration of shrimp. For these reasons we have used rough methods in arriving at our size-distribution curves; we believe that any attempt at refinement would add nothing to their accuracy.

In arriving at the size-distribution curves which we present, we have followed the same procedure in each instance. The shrimp in all hauls of each month from a similar source were combined, with each year treated separately. Then the particular months from the various years were combined by percentages of shrimp in each size group. Each month for any one year has the same weight in determining the shape of the curve for that month as does the same month in any other year. For example, in figure 39 for the 5-stations data (table 50), January 1932 with 618 shrimp has as much influence in determining the shape of the curve for January as does January 1934 with 1,448 shrimp.

Furthermore, although Weymouth, Lindner, and Anderson (1933) have shown that, after approaching maturity there is considerable difference in size between adult male and female shrimp for Georgia, and we have found no startling variation

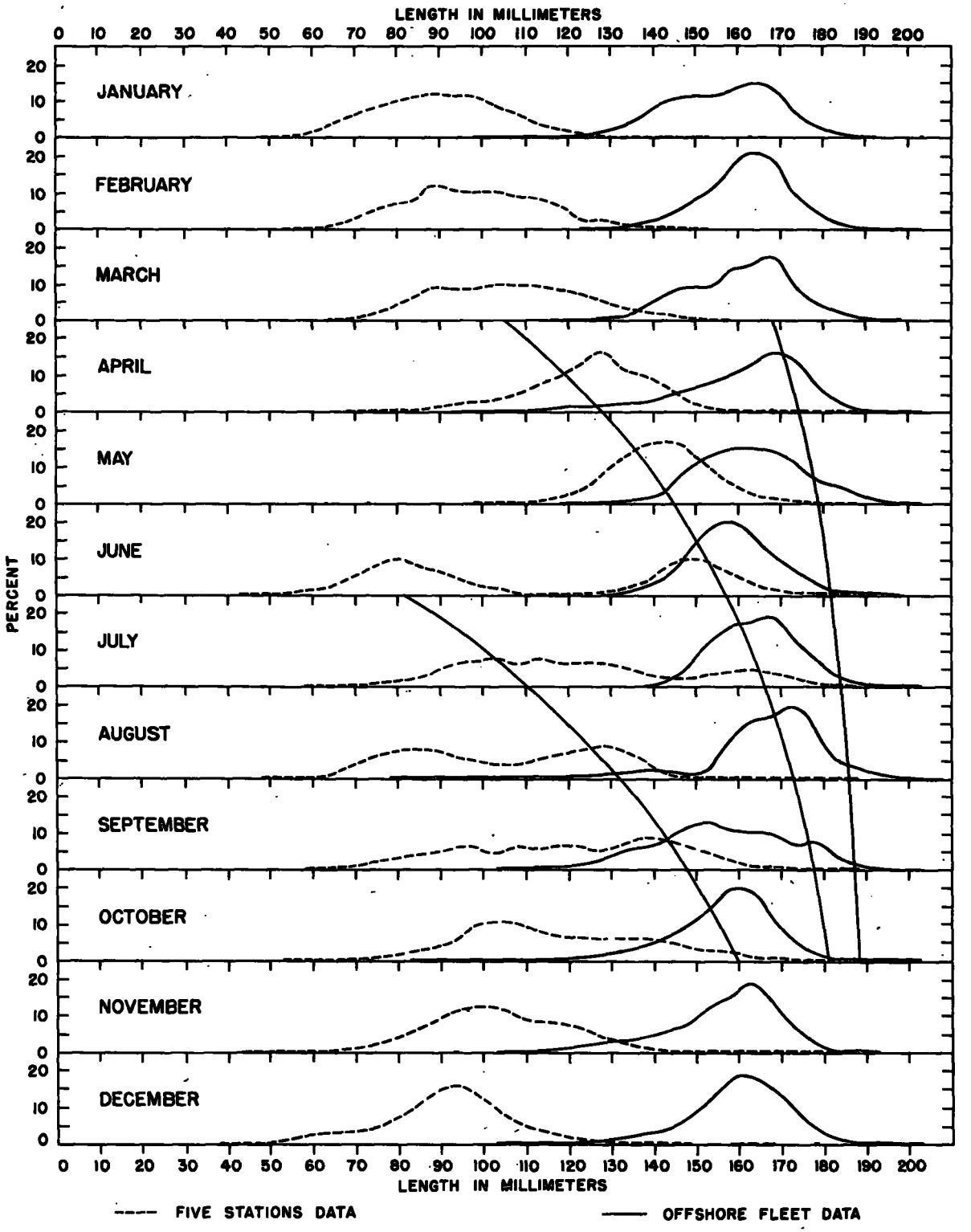

FIGURE 39.—Average monthly size distributions for Louisiana, separated into 5-stations data and offshore-fleet data.

from this in any of the other localities studied, we have grouped male and female shrimp together, for two reasons. First, the industry does not separate the sexes in commercial fishing and second, we suspect the variations in the data generally are sufficient to obscure most variations between sexes. Our method of treating the data tends to broaden the curves.

CATCH RECORDS

For the Louisiana total catch curve we have used the New Orleans Fishery Market News Service records (table 53), though they are not complete. We did not use the State records because they are based on tax receipts which were credited to the month in which the taxes were paid rather than the month in which the shrimp were caught. Our records for the Louisiana offshore fleet (table 54) were copied from the books of almost all of the companies engaged in this fishery. We are indeed grateful to these companies for their splendid cooperation. We think that our catch records for the Louisiana offshore fleet include between 90 and 100 percent of the catch of the entire fleet, and that the average monthly trend of production as shown by the Market News Service represents the total Louisiana production trend fairly accurately.

TABLE 53.—*Total Louisiana landings of shrimp, by months, 1940 to 1946*

[In thousands of barrels. A barrel is equivalent to 210 pounds of whole shrimp. Figures do not include shrimp used for drying. Data from Fishery Market News Office, New Orleans]

Month	1940	1941	1942	1943	1944	1945	1946
January	5.1	19.0	15.4	9.4	12.4	14.7	8.4
February	7.4	10.6	5.5	11.8	8.4	4.0	6.5
March	10.7	2.1	6.0	3.6	5.0	3.9	3.5
April	18.7	5.8	15.4	6.4	4.7	5.7	7.4
May	28.8	16.3	16.9	24.8	10.5	14.4	12.8
June	15.4	13.4	18.7	15.9	14.8	9.9	13.8
July	10.4	1.8	7.1	9.9	5.1	3.8	4.2
August	32.5	30.5	30.3	51.1	41.3	27.2	30.2
September	53.0	27.7	40.8	48.3	51.0	28.6	36.2
October	54.7	56.1	54.6	37.3	53.9	29.2	33.2
November	12.7	36.3	27.3	26.8	25.0	17.2	21.3
December	14.6	18.0	21.1	17.9	13.2	9.2	16.6
Total	264.0	237.6	259.1	263.2	245.3	167.8	194.1

TABLE 54.—*Louisiana offshore-fishery landings of shrimp, by months, 1938 to 1946*

[In thousands of barrels; a barrel is equivalent to 210 pounds of whole shrimp]

Month	1938	1939	1940	1941	1942	1943	1944	1945	1946
January	0.7	3.3	2.9	9.7	8.0	4.4	8.0	6.7	5.8
February	2.5	2.0	6.7	7.5	2.8	9.5	6.8	1.7	5.5
March	2.2	2.9	7.5	1.8	7.6	1.4	2.2	4.2	2.1
April	1.3	3.4	6.2	4.2	13.7	4.8	4.3	6.9	7.4
May	4.9	6.1	12.7	11.2	10.8	15.5	7.4	11.6	10.5
June	4.5	5.1	10.2	13.0	13.7	9.3	12.2	7.2	10.7
July	3.4	6.1	9.1	.3	9.0	6.6	7.7	6.0	7.1
August	2.8	5.5	4.0	3.2	5.3	5.7	7.2	5.5	1.7
September	3.2	4.1	3.0	2.5	7.1	7.1	12.9	7.8	2.0
October	4.7	4.4	12.4	11.7	16.2	12.4	23.1	13.4	10.0
November	4.6	5.6	6.0	15.2	8.4	13.4	13.8	10.1	8.1
December	5.7	7.4	8.4	8.5	6.8	9.1	10.3	6.9	8.4
Total	40.5	55.9	89.1	88.8	109.4	99.2	115.9	88.0	79.3

LOUISIANA

In our discussion of the size distributions we treat the Louisiana curves first, as we believe them to be easier to interpret since they are complete in that they follow the fishable shrimp population throughout the year, and they are less distorted by migrations than are the curves of the other localities. In each instance, we have superimposed growth curves on the size-distribution illustrations to facilitate their interpretation. The growth curves were calculated from the formula $Y=51.00+0.7322X$.

In figure 39 we show curves derived from two distinct fishing localities in Louisiana. In June, about 2 months after spawning begins, young shrimp with a mode at about 80 mm. make their appearance on the inside fishing grounds (fig. 40). The larger of these shrimp begin moving to outside waters by July, and offshore by August. By October (fig. 39) they completely dominate the offshore fishery. This group can be followed as a distinct mode from the time of its appearance inland in June, through its dominance offshore in October, and until in May it becomes fused with, and in June dominated by, another oncoming group. Our calculated growth curve appears to fit the first group almost perfectly (fig. 39), both with respect to the midpoint and the upper and lower limits of the distribution.

By December (fig. 39), the shrimp have separated into two different size groups. The earlier-spawned shrimp are offshore, and the later-spawned shrimp are inshore. There is little growth in the offshore shrimp from November through February, and rapid growth apparently is not resumed until about mid-March. The small inshore shrimp do not appear to have reached their full recruitment until January, and although some growth seems to have taken place in February, rapid growth apparently does not occur until March.

Although we do not have seining data for this time of year from Louisiana, Gunter (1950) has shown quite clearly that in Texas this second group

comes from very late spawning. We have no reason to suspect Louisiana shrimp to behave differently.

By April the small shrimp which wintered inshore start moving offshore. They dominate the offshore fishery by June and can be traced readily until they themselves become dominated in October by the oncoming young. The slight indication of bimodality in our offshore curves during summer, with the dip in July at 163 mm. and in August at 168 mm., results from sexual dimorphism (see figs. 8 and 9).

The curves suggest the entrance of a second wave in August, followed by more or less constant influxes thereafter until March. A false impression results from our technique of combining the data of several years, and actually the entrances were quite different from those indicated by figure 39. They occurred at irregular intervals. During the two years for which our data are complete, the entrances took place in June, August, October, and December 1932, and in June, September, and November 1933. There appears to be but little growth of the last arrivals between November and February. Recruitment into the lower end of this group seems to occur until January.

The entrance of the young into the Louisiana estuarine fishing grounds is most interesting. They appear in waves with distinct modes that can readily be followed. Apparently the only regularity of appearance is shown by those entering in June. They appeared for three consecutive years, and judging from our July 1931 records they had appeared in June of that year also. In both 1932 and 1933 this group could be detected in Barataria Bay until October.

In 1933 the first wave appeared in June at the head of Barataria Bay (Bayou St. Denis and St. Marys Point) with a mode between 78 and 83 mm. In July, it was found at all 5 stations with a mode that ranged between 113 and 123 mm. In August the mode was between 123 and 133 mm., in September between 133 and 148 mm., and in October it was easily distinguishable only near the mouth of the bay and in outside waters, where it ranged between 148 and 158 mm. The second wave appeared in September with a mode between 83 and 98 mm. and disappeared from the bay after November. In November its mode was between 118 and 123 mm. The third wave appeared in November at the head of the bay with a mode between 88 and 98 mm. This mode receded until January, which we suspect was caused by emigration of the larger shrimp and immigration of smaller ones. The variations each month in lengths of the modes represent variations between stations since the smallest shrimp were generally at the head of the bay and the largest in the Gulf.

Our 5-stations data are not suited for estimating the relative importance of the various waves entering the fishery, but our offshore-fleet curves reflect the relative importance of the individual influxes. We think it probable from figures 39 and 41 that the first and last successful spawnings are the most important. Since the Louisiana offshore fishery had no serious legislative restrictions and not too much seasonal fluctuation in fishing effort, it is probable that the offshore catch curve (fig. 41) closely follows the abundance trend. This curve reaches a low in August, rises in September and sharply in October, drops slowly until March, then rises to another peak in May. The October peak we can trace (fig. 39) to young shrimp appearing in inside waters in June, and the May peak to small shrimp wintering inshore.[16]

Since the data are not adequate, we cannot be certain from the 5-stations curves whether or not the first wave of young shrimp completely dominates the succeeding waves during the summer, and likewise the inshore fall fishery. It is possible that this group is important to the offshore fishery only because it largely escapes the inshore fishery. Nevertheless, the first wave certainly must contribute heavily to the inshore fishery during August and September, and from this it would seem likely that it completely dominates the other waves.

In spite of the shortcomings of our sampling technique and treatment of the data, and in spite of the rapid growth of the shrimp, the sharpness of the two December modes in figure 39 is apparent and hence indicates two relatively short periods of

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[16] We realize the insecurity of our position in using, in combination, size-distribution data collected 10 years apart, but if, as we think, our data represent average conditions (and we have treated them to make them as nearly average as possible) then we are justified in using them. The displacement to the left of the offshore modes in exactly those months (May and June, and August and September) in which the 5-stations curves display a marked skewness or decline at their right extremities (indicating migration of the large individuals) certainly suggests that our method is valid.

The trend of the All Louisiana catch curve (fig. 41) is affected by changing fishing intensity caused both by closed seasons and by changing effort during the open season. July, for example, is low because of closed season while actually, with unrestricted fishing, we would expect it to be greater than June.

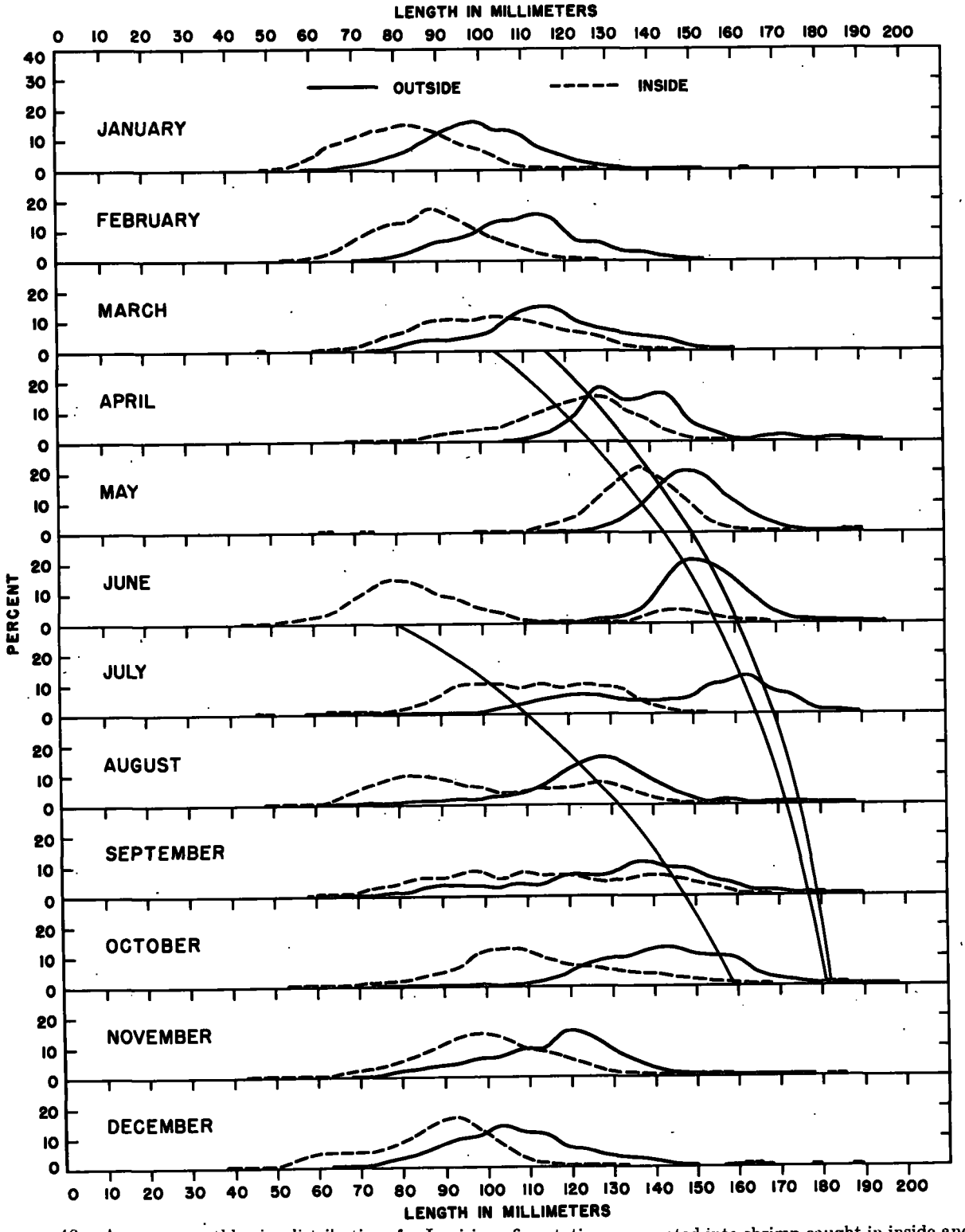

FIGURE 40.—Average monthly size distributions for Louisiana five stations, separated into shrimp caught in inside and in outside waters.

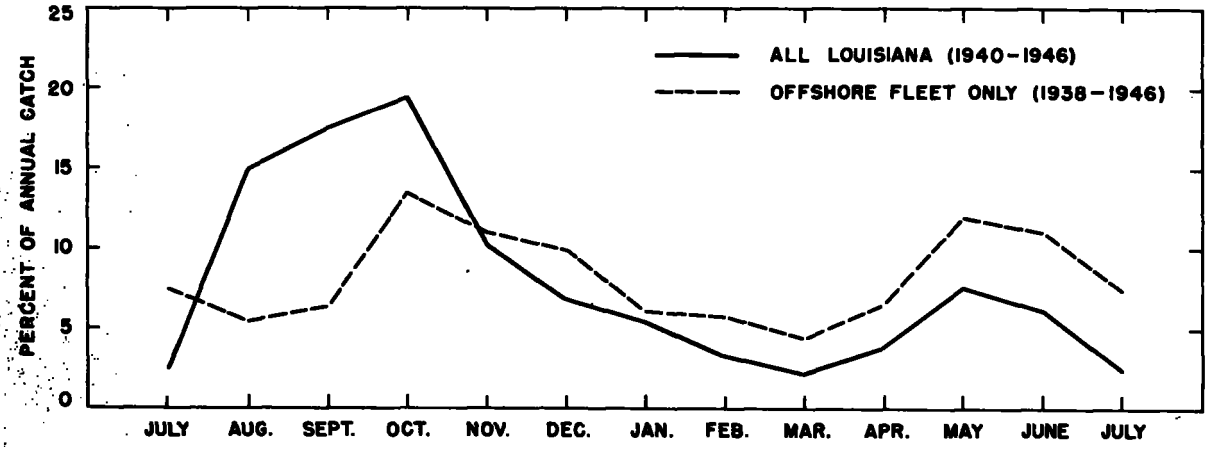

FIGURE 41.—Monthly percentage of average annual shrimp catch for all Louisiana (less shrimp used for drying) and for the Louisiana offshore fleet. See tables for further data.

successful spawning. This, supported by the evidence from the catch records (fig. 41) leads us to conclude that only the first and last waves of recently spawned shrimp are dominant, and that the intermediate waves are relatively insignificant.

If the progression of the modes which represent the shrimp entering the 5-stations area in June is considered together with the superimposed growth line, it will be seen that during the period June to September (when this population is comparatively free from shrimp of different spawnings) the midpoint of each mode coincides rather closely with the upper limit of the mode in the previous month and the lower limit of the mode in the succeeding month. In other words, the mode in each instance is well bracketed by allowing for 1 month's growth before and 1 month's growth after that represented by the midpoint. This would indicate that there is no more than 2 months' difference in the ages of the shrimp represented by the mode and that the spawning success extends over a 2-month period. However, since the curves represent samples taken over the entire month (during which growth had been taking place) rather than only at the midmonth, we can compensate for this growth by eliminating 2 weeks from either side, thereby restricting the period of spawning success for each mode to 1 month. Because of this and our spawning data, we believe that the shrimp producing the mode in inside waters in June at about 80 mm. come from shrimp spawned in April. Although this group can clearly be traced to the offshore mode at about 160 mm. in October, the marked spread at its lower end in this and subsequent winter months indicates that by this time the curve encloses some shrimp spawned in May, while those shrimp at its upper end, larger than 170 mm., were probably contributed by stock of previous years.

The range shown by the mode at about 90 mm. in December also represents about 1 month's spawning. During the spring this group can be traced in a manner similar to that previously described.

It appears then that about 6 months of growth are required for a shrimp to reach 160 mm. in length. The second mode, which appears in the 5-stations curves during winter, and which can readily be traced to its appearance offshore in June (fig. 39), could therefore be attributed to shrimp which in June had just slightly less than 6 months of growth. If we assume that no growth occurred from mid-October to mid-March it would place this group as having been spawned the previous July. However, if there was one month or more of growth during this 5-month period between October and March (which seems entirely within reason from our data) then most of these shrimp must have been spawned in August or later. Furthermore, as suggested by the data of Anderson, King, and Lindner (1949, fig. 1) and of Gunter (1950, fig. 1), if the very young are not slowed in growth during winter as much as the slightly larger sizes, most could have come from September, or possibly October spawning.

Apparently in Louisiana there are two important periods of spawning success, one at the beginning and the other at the end of the spawning season.

TEXAS

Aransas Pass

The curves for the shrimp at Aransas Pass, Tex., differ from those in Louisiana in that at Aransas Pass there appear to be three successful spawning groups instead of two. However, the second and third of these evidently contribute more to the fishery than does the first, so that actually there are only two successful spawning periods.

In figure 42 the young appearing in inside waters in July with a mode at about 115 mm. can, from our growth curve, be attributed to April spawning. A second group, which can be traced to late May or June spawning, enters the fishery in September with a mode at about 120 mm. The lower ends of the curves for September seem to show the effect of selective fishing and culling, and the modes shown in our curves for this month, therefore, probably are a few millimeters longer than the true mode for this group. The second group dominates the fall and winter fishery. We do not think the first group could have been fished out, as generally there was little fishing in inside waters during July and August. Furthermore, since this first group made but slight impression on the curves in outside waters in August and September we do not believe the shrimp comprising it to have been very abundant.

Because of selective sampling by the fishing fleet, the third group, which is comparable to the second or late-spawned group in Louisiana, does not appear continuously in our curves until February, although Gunter (1950, fig. 1) shows this group throughout the winter.[17] This third group, which produces the June peak in the catch (fig. 43), we can follow in the outside waters until September. The relation between the growth lines and the modes for this group of shrimp after June suggests that either this group grows much less rapidly than the comparable group in Louisiana or else the fishery was not operating on the entire spawning stock. From the skewness of the curves we suspect the latter explanation to be the more likely. The commercial fleet at Aransas Pass during the years we were sampling never operated far from land and if the shrimp spawn offshore (which we think they do) then our samples would be heavily weighted by the smaller sizes, because the larger shrimp tend to spawn first.

This same phenomenon occurs in our Atlantic-coast curves (figs. 45 and 46) and probably for the same reason, since most of our outside samples were taken close to shore. Our 5-stations curves (fig. 40) also show this for the immature shrimp from August through October. In this instance we can demonstrate that the slow advance in the upper mode results from the large shrimp moving offshore (fig. 39).

As we have mentioned, the first-spawned group, which appears in July with a mode at about 113 mm. (fig. 42) and which we attribute to April spawning, does not appear to be particularly abundant. This could be caused either by the lack of sufficient spawners or by some environmental phenomenon, which we do not know. If, as we believe, spawning is continuous once it begins, then the sharpness of the mode and its advance from July to August suggests some external cause rather than the lack of spawners.

On the other hand, apparently the bulk of the fall and winter catch in this region comes from shrimp spawned in late May or early June. This coincides with the beginning of spawning of the group which we show in February in inside waters with a mode at about 98 mm. If, as it appears from our curves, there are few early-spawning shrimp, then perhaps there may be a relation between the number of spawners and the resultant crop. However, such a relation would not account for the scarcity of very small shrimp during summer, as shown by Gunter (1950), nor would it account for the obviously very late-spawned shrimp which, as we demonstrate, cause the June peak in the catch.

Galveston

Our Galveston, Tex., curves (fig. 44) during part of the year (October to January) appear to be

[17] Gunter (1950) has shown the scarcity of small shrimp in central Texas during midsummer, which he interprets to mean (as do we) two separated periods of successful spawning. We suspect that the mode which Gunter shows in June 1941 at 28 mm. accounts for the July mode at 83 mm. and the small September mode at about 133 mm. Attributing the shrimp appearing in July 1941 at 83 mm. to the group producing the prominent mode at 113 mm. in September would require either a slower growth rate for young Texas shrimp during summer than in spring (which does not appear to be true from our data, and the spring growth shown by Gunter's data from February to April 1942 is in complete accord with our growth rate), or a growth rate different from that in Louisiana, which does not appear probable. The mode he shows in July at 38 mm. could account for the mode he shows in September at about 113 mm. and in October at about 133 mm. This is according to our growth formula which may be entirely unreliable below 80 mm. If we assume that about one month is required from the time the eggs are laid until the young appear in his seine catches with modes between about 28 and 48 mm., then the mode Gunter shows in May 1942 could be attributed to April spawning and would also account for the shrimp about 133 mm. long he shows in August of both 1941 and 1942.

It must be remembered that Gunter's data, like much of ours, are not adequate.

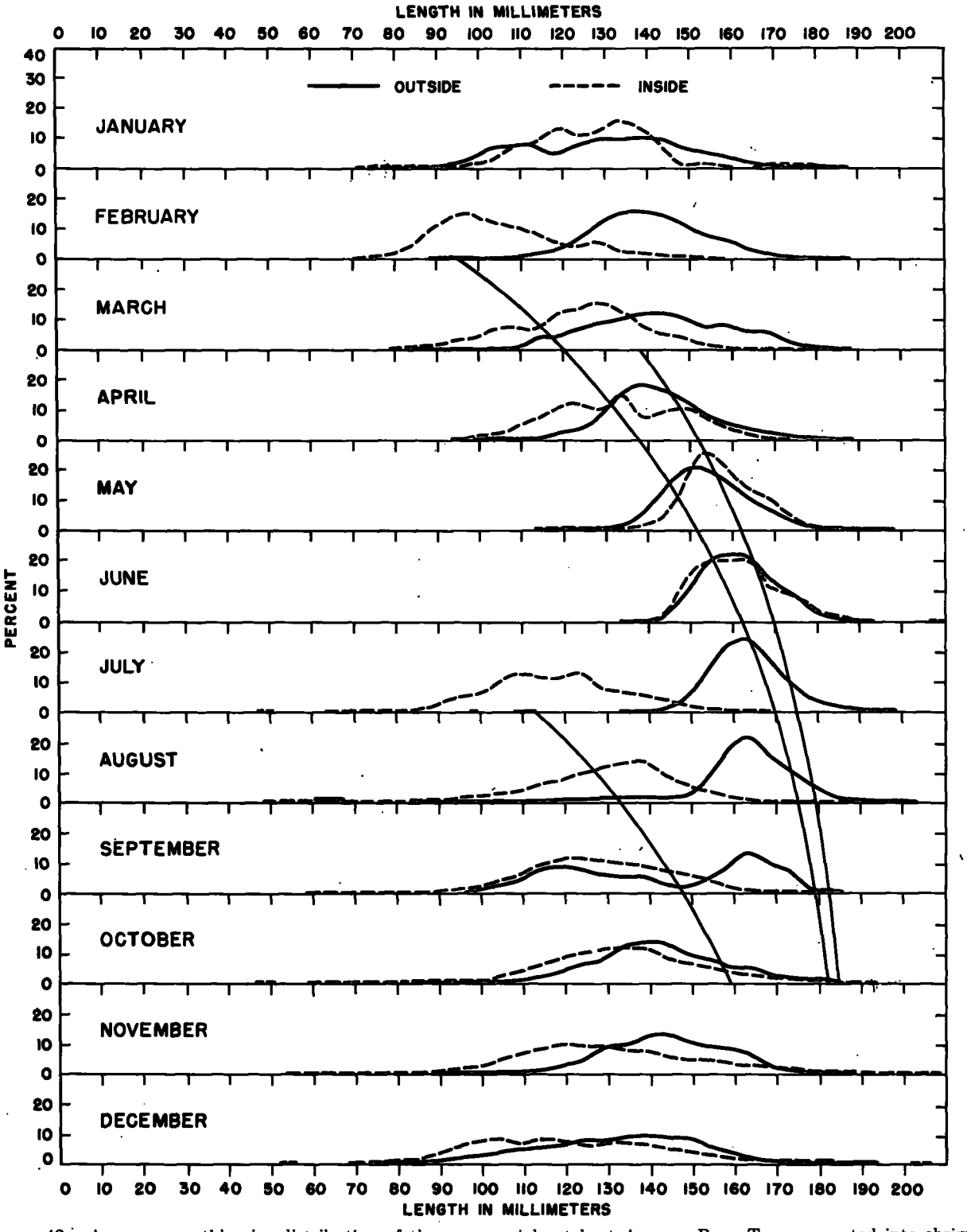

FIGURE 42.—Average monthly size distribution of the commercial catch at Aransas Pass, Tex., separated into shrimp caught in inside and outside waters.

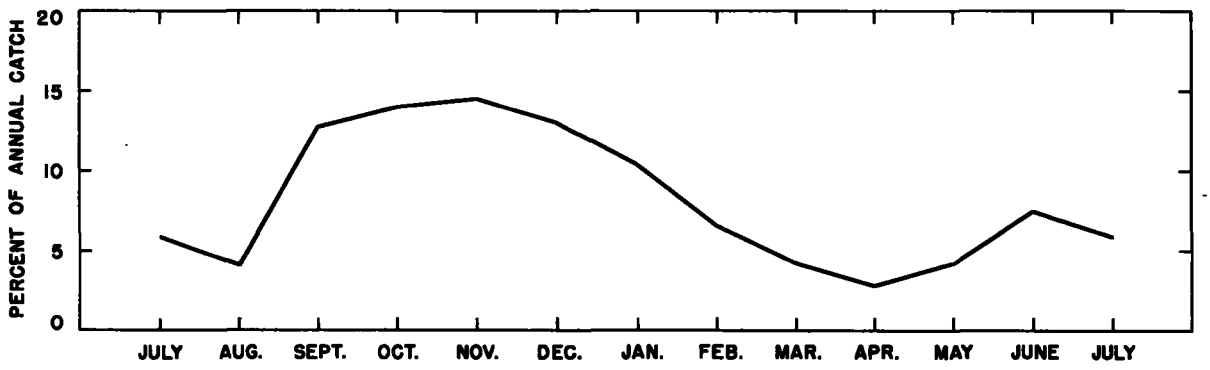

FIGURE 43.—Monthly percentages of average annual shrimp catch for Texas. This figure is derived from Anderson, Lindner, and King (1949, table 1).

intermediate between those for Louisiana and those for Aransas Pass, and during another part of the year (February to September) they appear comparable to the Louisiana offshore fleet curves. We think that actually the shrimp population at Galveston behaves in a manner comparable to the Louisiana population and that the anomalies in our curves result from inadequate sampling of the population by the fishing fleet and by ourselves. Throughout the year, the Galveston fleet fished relatively close to shore. In the fall and early winter this tended to deemphasize the proportion of April-spawned shrimp and overemphasize those spawned later. Nevertheless, the mode in March at about 160 mm. can be attributed to shrimp spawned the previous April, and that appearing in May at about 150 mm. can be attributed to shrimp spawned the preceding August or later.

The curve for September appears misplaced, but this is the result of sampling. It represents only 1 year, but is quite comparable to the September curve for the Louisiana offshore fleet. Most of the shrimp larger than 153 mm. were adults and are representative of the summer spawners.

ATLANTIC COAST

Our curves for the Atlantic coast (figs. 45 and 46) are difficult to interpret for two reasons. First, since the samples are from a single boat the data are inadequate, and the curves cannot be construed to represent the real abundance of shrimp by lengths. Second, coastwise migrations confuse their interpretation.

The curves can be interpreted in several ways. Their broadness and flatness suggest a more continuous spawning than occurs in the other localities. This may merely be a reflection of our sampling technique and treatment of the data. Both our curves and those of Weymouth, Lindner, and Anderson (1933, fig. 10) suggest three periods of spawning success: April, June, and August or later. The young from the first of these spawnings appear on the Georgia and northern Florida fishing grounds in July (fig. 45) with a mode at about 100 mm. (Apparently initial spawning success averages about 2 weeks later in this region than it does in Louisiana.) The young from the second spawning success appear in September with a mode at about 110 mm., and those from the third first form a mode in figure 46 at about 100 mm. in March.

Evidently all of the first group, and perhaps most of the second, migrate south into central Florida during late fall and early winter. All of the third group and the smaller shrimp of the second group remain. In our curves (fig. 46) the three groups are represented by modes at about 155 mm., 130 mm., and 100 mm., in February. In those of Weymouth and others (*loc. cit.*), the second and third groups demonstrate modes in February 1931 at about 140 mm. and at 100 mm.; and during the winter of 1931–32 they appear again, but at about 130 mm. and 100 mm., respectively. Of course, differential migration according to size and year can cause considerable shifting in the mode of the second group during winter. Also the imperfections of our sampling technique can result in shifts in all the modes.

If we accept the foregoing interpretation, then the young from the first and second successful spawnings produce the fall peak in the catch (fig. 15) in the northern and central sections, and the winter peak in central Florida. All three, but most likely those principally from the third, form the spring run with peak catches in June.

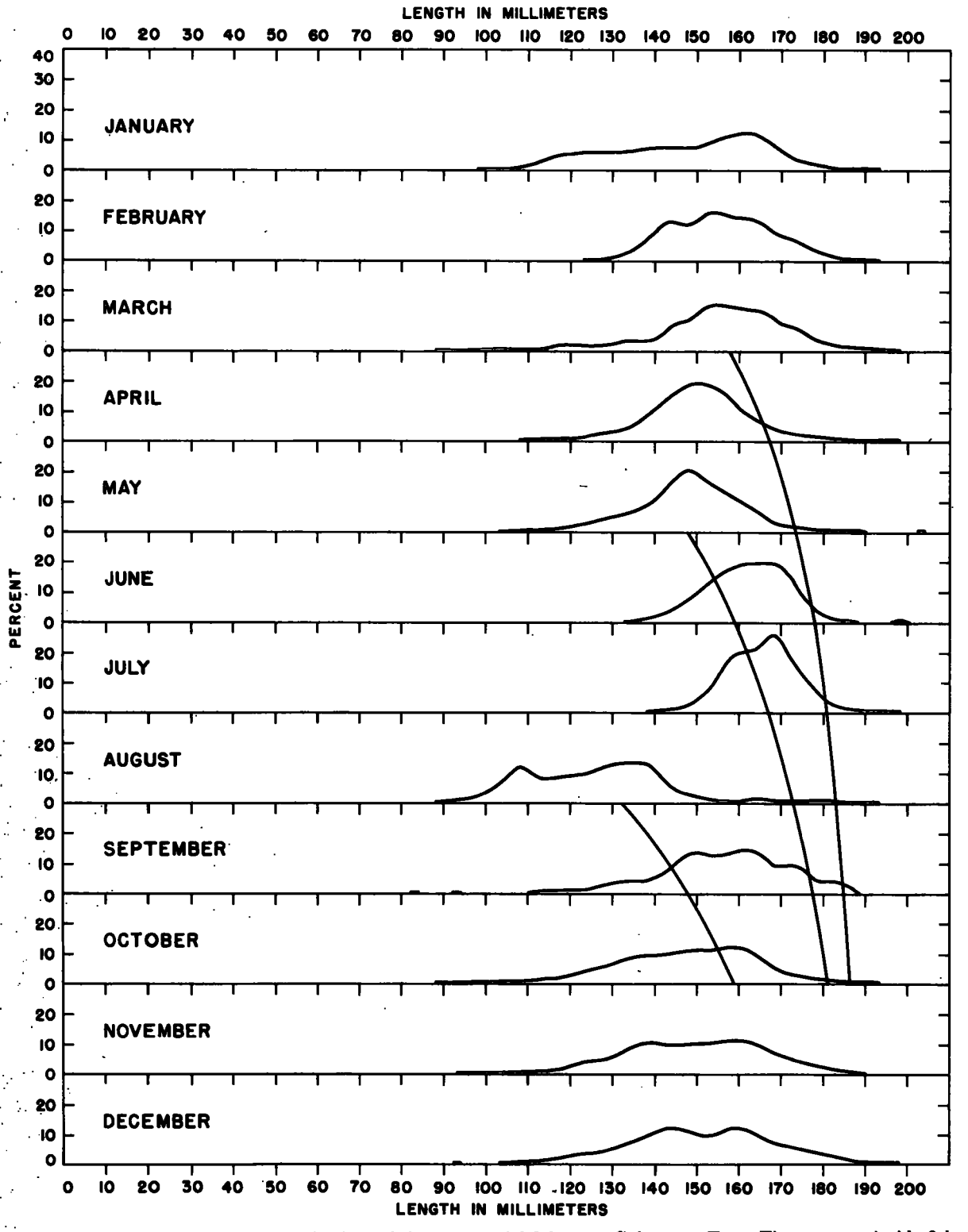

FIGURE 44.—Average monthly size distributions of the commercial fishery at Galveston, Tex. There was no inside fishery at Galveston.

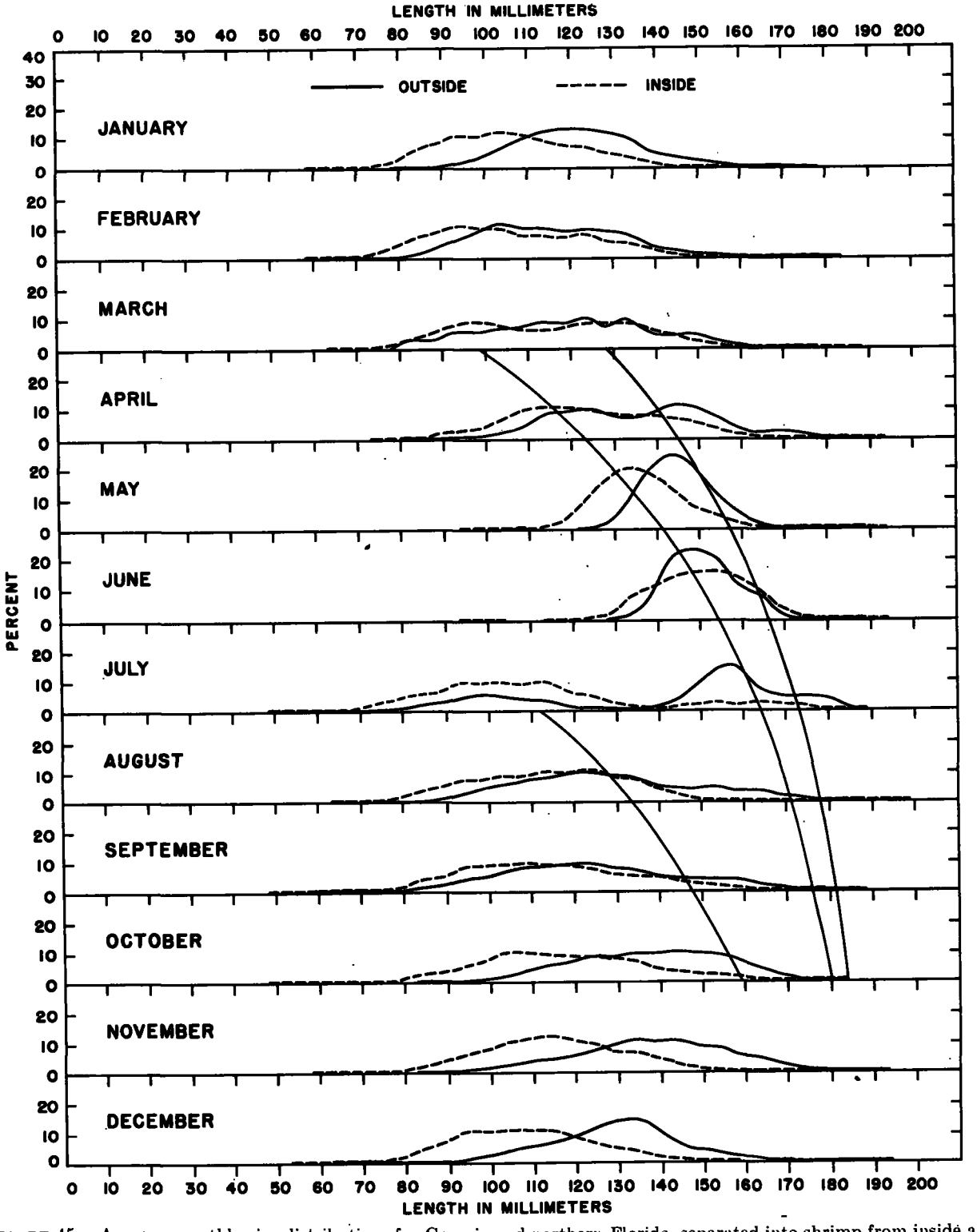

FIGURE 45.—Average monthly size distributions for Georgia and northern Florida, separated into shrimp from inside and outside waters.

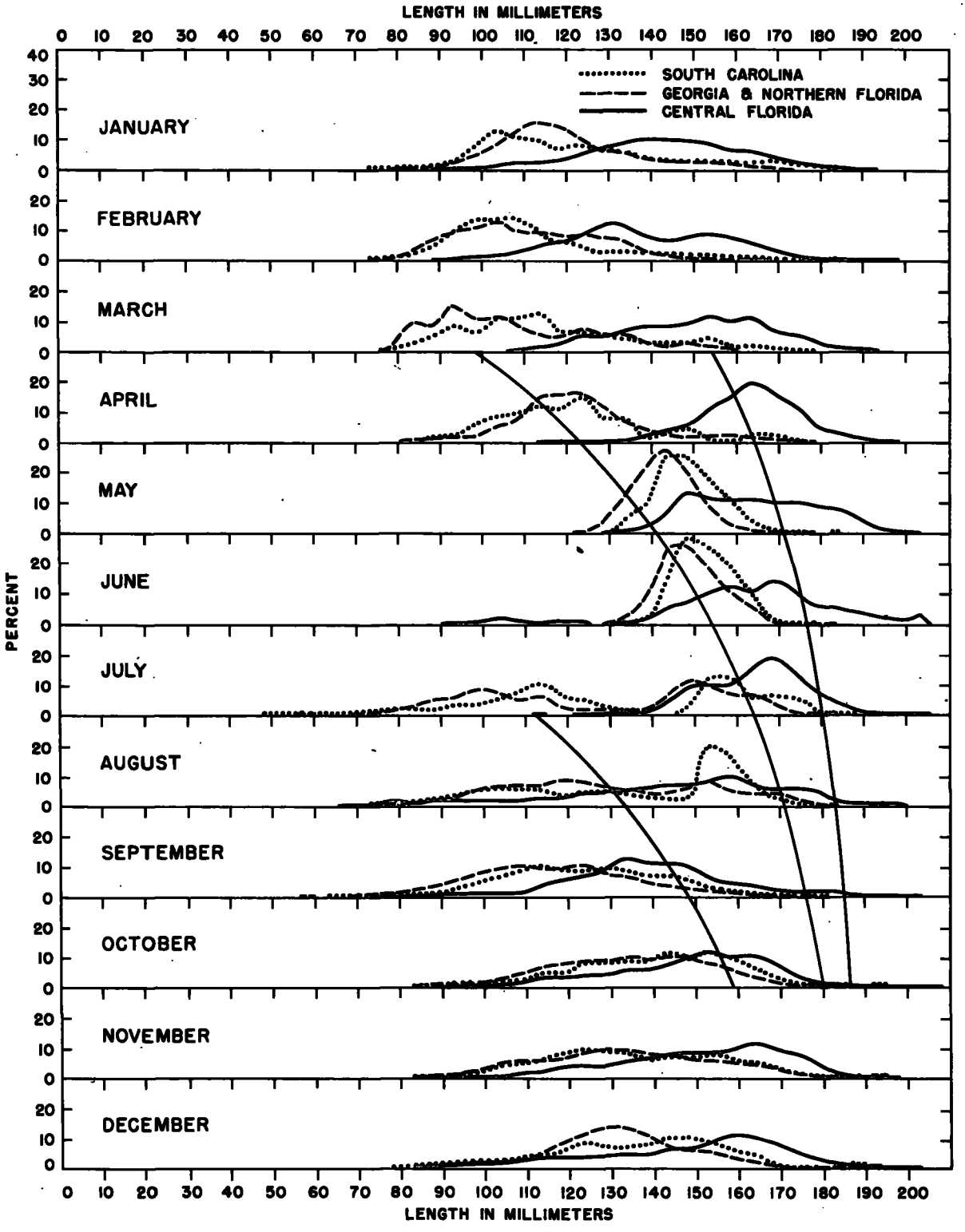

FIGURE 46.—Average monthly size distributions from outside waters of South Carolina, Georgia and northern Florida, and central Florida.

Our data are inadequate for differentiating between the relative importance of the three successful spawnings.

Except, perhaps, for the indication of a slightly earlier spawning success, the South Carolina curves are comparable to those for Georgia and northern Florida.

The appearance in central Florida of young shrimp with an average length of about 110 mm. in June suggests an occasional spawning in this section as early as mid-March.

SUMMARY

GROWTH

Tagged shrimp were measured both at release and after recapture. The increments thus observed were described with reference to the size at release. The increment was greater for the smaller shrimp. This relation of increment as a function of initial total length was described as linear. At 10 cm. total length, the 1-month increment is nearly 3 cm., while at 17 cm. total length, it is less than 1 cm.

From November to April, very little growth was observed. During the rest of the year, growth was rapid: After 12 months of growing season, these shrimp would have completed nearly all of their lifetime increase in length.

MIGRATION

From tagged shrimp released in various areas of the entire fishery and at various seasons, the location of recoveries demonstrated what movement, if any, occurred.

Releases during the fall months on the south Atlantic coast were recovered consistently south of the area of release, while those released during winter and early spring were recovered largely to the north.

Shrimp released along the major portion of the Gulf coast showed no indication of coastwise migration. They were recovered in all directions from the point of release, and they had not moved far; none had crossed the Mississippi-delta region. Only in the region of southern Texas may there be a coastal migration, but the evidence from this area is not adequate to prove or disprove it.

In all areas the small shrimp found in inside waters were eventually recovered from outside waters.

SPAWNING

The evidence from which inferences on spawning are derived consists in observations on the degree of maturity of the ovaries of female shrimp. Ripe ovaries were taken in most areas from April through September. The size composition of the ripening populations changed during this time, however, and there may be two or more groups of spawners, possibly spawning at different times of this season. Judging from size at maturity, shrimp spawned in the spring or summer probably spawn in the corresponding season of the following year.

DISCUSSION AND RECOMMENDATIONS

In all the localities we studied there appear to be 2 or 3 separated periods of spawning success. All localities are consistent in that the first appears to be associated with the beginning of the spawning period, and the last with the end of spawning. In those localities where there appear to be three periods, the middle one seems to be associated with the beginning of the spawning of the last group from the previous year. If spawning were rhythmic, with a beat in April, another in June, and a third in August or later, we could postulate a direct relation between the numbers of shrimp spawning and the crop produced. However, our spawning data indicate more or less continuous spawning from the beginning of the season until the end, with the peak of spawning in June or July. Consequently, it appears that some factor other than the number of spawners causes the interruptions in spawning success.

We do not know where the answer lies. Perhaps mass mortality of very small shrimp on either the spawning or nursery grounds is the cause of the fluctuations. This could result from any one or more of a combination of factors, such as unfavorable currents preventing the young from reaching the nursery grounds, periodic disease in epidemic form wiping out vast numbers of young, food scarcity caused by the first arrivals consuming all available food, and predation including cannibalism.

Perhaps the shrimp is its own worst enemy. The Louisiana data are certainly suggestive of this. Despite apparent continuous spawning throughout the season, evidently only the earliest and latest spawnings are really successful, and the

latest is concomitant with the earliest-spawned shrimp moving offshore from the inland nursery grounds. The second successful spawning in Louisiana (and the last in all other localities) does not seem to occur until vast numbers of shrimp have departed from the nursery grounds. Also in Louisiana, waves of oncoming young shrimp appear to be spaced about 2 months apart, which suggests spawning successes coinciding with mass departures of the preceding wave from the inner to the outer nursery areas.

Preliminary analyses of some of our data, including those derived from tagging, suggest that the ratio between loss from natural mortality and gain in weight through the rapid growth of individual animals is such that the total poundage of shrimp available to the fishermen would be increased if the shrimp were protected from the time they appear on the inside fishing grounds in summer until they move to outside waters in fall. Likewise, on this same basis, it might be advantageous to afford protection to the small shrimp while they are growing rapidly during early spring, or possibly to this same group during winter.

Viosca (1920) noted that in the estuarine waters of Louisiana (and most recent workers including ourselves seem to be in agreement for many other areas) the shrimp is probably the most important animal with respect both to species-mass and to food conversion. When we consider this point it is unfortunate that we do not know enough about the shrimp to be able to predict with any assurance what will happen to the population provided man does this or that. For example, while we have suggested that it may be advisable to limit fishing for small shrimp, on the other hand, heavy exploitation from inside waters may result in a more extended spawning success owing to reduced cannibalistic predation, with the obvious consequence of greater production.

We therefore arrive at the conclusion that well-controlled fishing experiments, together with additional research, are required before we can determine with any degree of accuracy how the shrimp population will respond to changes in fishing effort or in fishing seasons. We have recognized the importance of the experimental fishing approach for some time (Lindner 1936a), and more recently Burkenroad (1951) also has recommended it. Because the growth of the shrimp is so rapid, we think the experiments, if followed by competent observers, need not be drastic in their approach. Perhaps even as short a period as a month's difference in open and closed seasons in alternate years might indicate whether the particular approach was profitable. On the basis of our present information, experimental fishing of small shrimp during the periods when they are growing rapidly seems most promising.

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