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FISH AND WILDLIFE SERVICE

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

NATURAL MORTALITY RATE OF GEORGES BANK HADDOCK

BY CLYDE C. TAYLOR

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ABSTRACT

Data on the catch per day at each age and the annual fishing effort for Georges Bank haddock are available for the period 1932 to 1951. These data provide five estimates of the natural mortality rate. The estimates indicate that sampling for the older ages in the catch has been inadequate for the purpose of computing natural mortalities. Between ages 3 and 4, a negative natural mortality coefficient is obtained, indicating the possibility of incomplete recruitment at age 3.

The data between ages 4 and 6 provide two estimates of natural mortality, both near zero. It is concluded that an upper limit of the natural mortality coefficient of 0.2, corresponding to an annual expectation of death of 15 percent, is sufficiently conservative for predicting the effect of increases in mesh size on yield.

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NATURAL MORTALITY RATE OF THE GEORGES BANK HADDOCK

By Clyde C. Taylor, *Fishery Research Biologist*, Bureau of Commercial Fisheries

When a regulation to increase the mesh size of nets used by trawlers engaged in the Georges Bank haddock fishery was first considered, the importance of an accurate estimate of the rate of natural mortality of haddock was fully realized (Graham 1952). The average annual-total mortality rate over the period 1931 to 1948 was known to be 45 percent, but the proper partition of this rate into fishing and natural mortality was unknown.

To assess the changes resulting from increases in mesh size which, in effect, increase the age at which the fish are first subject to capture by the gear, yield curves were calculated using the following annual expectations of death from natural causes: 0, 7.5, 15.0, 22.5, and 30.0 percent. Experiments with nets had shown that the small-mesh net had a 50 percent selection point for haddock at 25 centimeters, corresponding to an age for haddock of about 1½ years. Yield computations showed that substantial increases in yield could be expected with larger-meshed nets at the lower natural mortality rates and that even if the natural mortality were as high as 30 percent, no decrease in yield would result from an increase in mesh size designed to raise the age of haddock at first capture to 2½ years (Graham 1952).

Before recommending an increase in mesh size to the International Commission for the Northwest Atlantic Fisheries, the Scientific Advisors to Panel 5 of that Commission reviewed the available data bearing on the haddock fishery. It was the considered opinion of that group that the natural mortality rate probably did not exceed 15 percent annually. In the course of these deliberations, it appeared that an objective estimate could not be obtained from the available data. Efforts to apply a method for estimating natural mortality from information on the catch per day and the annual fishing intensity had produced meaningless results.

I have reviewed these early attempts to estimate natural mortality of the Georges Bank haddock. The reason for their failure is apparent. Using the same data and a method of analysis differing in treatment but not in principle, estimates of the magnitude of natural mortality were obtainable and are presented here. This additional information is necessary to refine the criteria establishing the age and size at which haddock should be harvested to obtain the maximum yield.

Calculation of *M*, Natural Mortality Coefficient

Beverton and Holt (1956, Appendix D) show the derivation of an equation relating the log ratio of the annual mean abundance in pairs of successive years to the fishing intensity:

$$\log_e\left(\frac{{}_vN_x}{{}_{v+1}N_{x+1}}\right)+\log_e\left\{\frac{(cf_x+M)\,(1-e^{-(cf_{x+1}+M)})}{(cf_{x+1}+M)\,(1-e^{-(cf_x+M)})}\right\}$$
$$=cf_x+M \qquad (1)$$

where:

${}_vN_x$ = mean abundance of age group v in year x,
${}_{v+1}N_{x+1}$ = mean abundance a year later,
f_x = fishing intensity in year x,
f_{x+1} = fishing intensity in year x+1,
c = constant relating fishing intensity to the instantaneous fishing mortality rate, and
M = natural mortality coefficient.[1]

The magnitude of the second term on the left side of equation (1) departs from zero with the magnitude of the change in fishing intensity between each year in a pair. Thus, given a series of pairs of years with fishing intensities and corresponding indices of abundance of the age groups, a linear relation between fishing intensity and the total mortality coefficient should be obtained. The slope of the best fitting regression line provides an estimate of c, and the y-intercept an estimate of M.

We note from (1) that a direct solution for c and M cannot be found because of the second

[1] M is an instantaneous rate. The annual natural mortality rate is equal to $1-e^{-M}$. If $M=0.1$, for example, the annual natural mortality is $1-e^{-0.1}$, or 0.0952, or 9.52 percent.

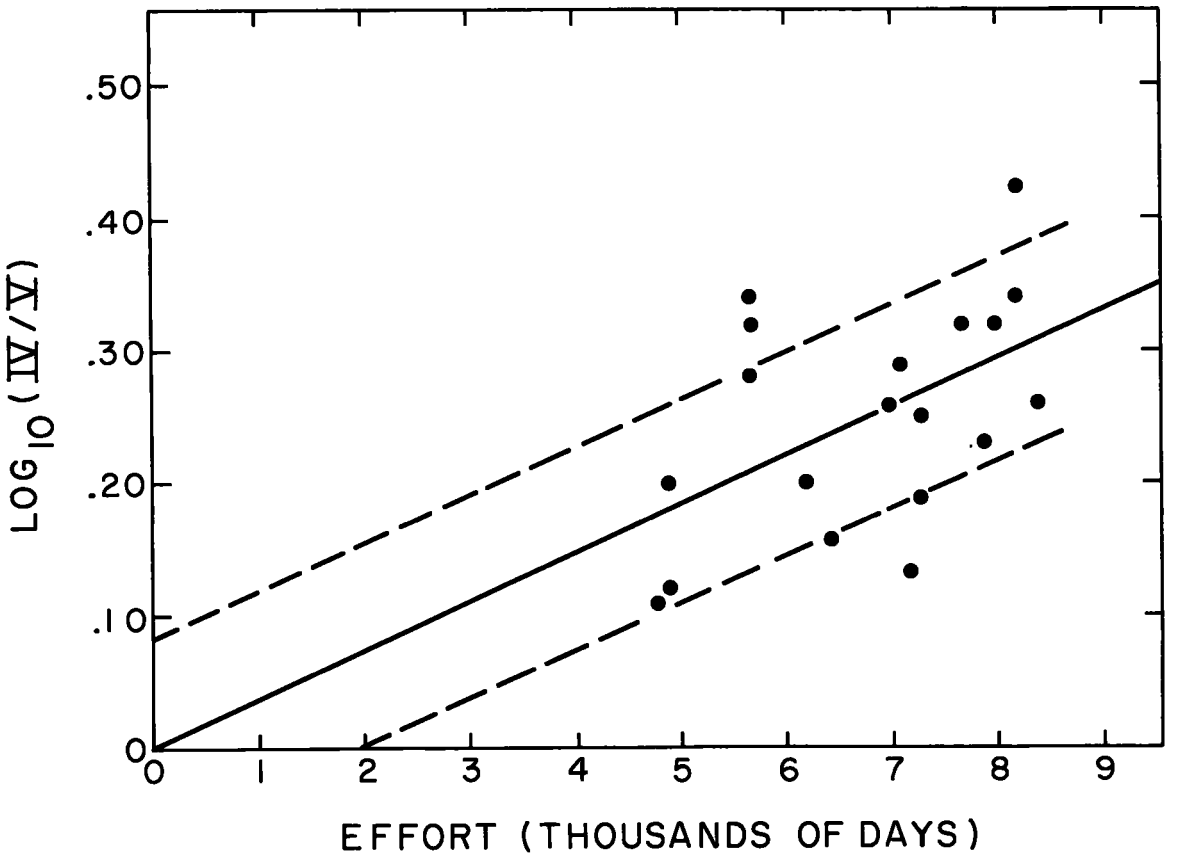

FIGURE 1.—Regression of the log-ratio of abundance, ages 4 and 5, on effort.

term on the left side of the equation, which also contains c and M. We may, however, solve for these values by an iterative process, first considering the second term to be zero and computing the line of best fit for the logs of the abundance ratios for each pair of years plotted against the effort in the first year of each pair (fig. 1). The estimates of c and M thus obtained are used to evaluate the second term of equation (1) to obtain more exact estimates. The procedure is repeated until successive estimates of c and M do not differ significantly. An illustrative example of the computational procedure is shown in Appendix A, p. 6.

Table 1 shows the catch per day in numbers of Georges Bank haddock, ages 3 to 8, for the years 1932 to 1951, together with the fishing intensity expressed as thousands of days fished within the Georges Bank area. The effort is a "calculated" effort based on the effort, catch, and catch per day of a standard study group of large otter trawlers fishing on Georges Bank. The total effort within the Georges Bank area is estimated by dividing the total catch from the area by the catch per day of the standard study group.

From the data of table 1, we may attempt five estimates of the natural mortality rate (for age groups III and IV, IV and V, etc.). The values of c and M obtained by applying equation (1) to table 1 are summarized in table 2 together with the standard error of the regression line, (S_c), the standard error of M, (S_m), the standard error of estimate, ($S_{y.x}$) and the confidence limits. A plot of the data for ages 4 and 5 is shown in figure 1. Note that the log ratio of abundance is plotted to base 10 and not base e. The value of the slope and intercept are multiplied by 2.3026 to satisfy the requirements of equation (1).

DISCUSSION

Examination of the 1951 worksheets used to compute natural mortality shows that the attempt was abandoned when a negative value of c, the

slope of the regression line, was obtained. Fishing mortality is related to fishing intensity as follows:

$$F=cf \qquad (2)$$

where F is the instantaneous fishing mortality rate. A negative value of c means that increases in fishing result in decreases in fishing mortality. This meaningless result might come about from various errors or bias in the data, such as inadequate sampling resulting in unreliable age composition data, bias in the effort data, variations in the availability of fish from year to year, or great variability in M. One might also suspect that variations in the fishing intensity, f, during the period covered by the data had not been sufficiently large to cause measurable variations in the second term of equation (1).

On examining the computations, I find that the procedure adopted was to calculate the log-ratio of the catch per day of ages 3 to 9+ in one year to the catch per day of ages 4 to 9+ in the following year.[2] This procedure is theoretically correct if the following assumptions can be safely made: (1) the fish are fully recruited to the fishery at age 3, (2) the natural mortality rate is constant over the range of ages, and (3) the sampling and age composition data are equally reliable throughout the age range.

Table 2 sheds some light on the validity of the foregoing assumptions. Between ages 3 and 4 the natural mortality estimate has a high negative value. This result raises some doubt that we are safe in concluding that recruitment is complete at age 3. Possibly the losses through natural mortality between ages 3 and 4 may be more than compensated by additional recruitment at age 4.

It has been generally assumed in the work with haddock that 3-year olds were fully available and therefore mortality rates have been computed onwards from this age. Indeed, we find that if we compute the average mortality rate from age 4, the total mortality coefficient does not differ significantly from that calculated from age 3. Earlier estimates of total mortality are not, then, invalidated. Nevertheless, the data of table 1 suggest that the mortality rate from age 3 to 4 is somewhat less than from age 4 to 5, as we might expect if recruitment is not entirely complete at age 3.

Before considering assumption (2), we need to examine assumption (3), that the data are equally reliable throughout the age range. In evaluating the reliability of these results, we find that on the average over the period in question, 87.9 percent by numbers of a year class are taken during their first 5 years in the fishery; that 6.1 percent consist of 6-year old fish; 3.0 percent are 7-year olds; and only 1.3 percent are 8-year olds. The numbers of these ages taken in the samples from the catch are of corresponding relative magnitude, so that age composition of the larger fish is determined from considerably smaller samples than are available for determining the proportions of ages among the smaller fish. Thus, while the number of ratios used in computing the regression of equation (1) may be the same, the reliability of the ratios themselves differ.

A further consideration affecting estimates derived from the older ages is evidence that, during certain periods of the year, the older fish tend to be found in deeper water not so heavily fished (Colton 1955).

Between ages 6 and 7, we obtain on the first iteration, from the data of table 1, a negative value of c (−.1264) and a high positive value of M (1.575). Again, between ages 7 and 8, we obtain a high value of M (0.491) but this time the slope of the regression line is positive (c=0.0657). Since these estimates of natural mortality are as high or considerably higher than observed total mortalities in some year classes during their lifetime in the fishery, we conclude that the data for haddock older than 6 years are not sufficiently accurate for use in estimating the magnitude of natural mortality.

Since we must question the reliability of data from age 6 onwards which are based on relatively smaller numbers of fish than for the younger ages, we are not able to decide whether the natural mortality rate is constant from ages 3 to 9 (assumption 2).

We see, then, that the three assumptions necessary for making a gross comparison of ages 3 to 9+ and 4 to 9+ are either invalid or in doubt. It is not, therefore, surprising that the attempt to use this procedure met with failure.

Considering now the estimates of natural mortality derived from the data for ages 4 and 5,

[2] Age determinations are not made for haddock older than 9 years. All fish 9 years or older are grouped as 9+ and comprise less than 1 percent by numbers of the landings.

and 5 and 6, we obtain two estimates of M which do not differ significantly (table 2). These estimates are close to zero but the confidence limits indicate the estimates are not precise.

In estimating M, which is the value of the Y-intercept of the regression line, one is extrapolating considerably beyond the range of the data. In these circumstances it is statistically sound to use an estimate of the error which depends both on the standard error, and the standard error of the slope of the regression line (Snedecor 1946, p. 120). Interpreted biologically and in the light of what is known about the Georges Bank haddock fishery, these confidence limits merely indicate the precision of the data and not the probability of the natural mortality actually exceeding these limits.

The average total mortality rate of Georges Bank haddock over the period 1931 to 1948 was 0.6 (45 percent annually) (Graham 1952). The upper 95 percent confidence limits for the estimates between ages 4 and 6 are close to this value (table 2). More than 90 million pounds of haddock, on the average, were annually removed from the fishery between 1931 and 1950. Information on the relative abundance of ages made possible accurate predictions of the catch (e. g., Schuck, 1952). The probability of the natural mortality being equal to the total mortality is far more remote than the confidence limits indicate.

Assessment of the effect of mesh regulation on the haddock fishery is an operational problem requiring a likely working value of M. Examining table 2, we note that the values of c, the slope of the regression of mortality on effort, are quite consistent from ages 3 to 6, the ages for which the abundance ratios are most accurately determined. This consistency suggests that the standard error of the regression line, $S_{y.x}$, indicates the likely limits of M. On this basis, we note from table 2 that there is one chance in three that the natural mortality coefficient exceeds 0.196 for ages 4 and 5, and only five chances out of a hundred that it exceeds 0.380. For ages 5 and 6, we obtain similar estimates at somewhat lower levels of confidence.

In view of the rather low estimates of M obtained from the abundance and effort data, it is concluded that a working value of about 0.2 is sufficiently high for a conservative prediction of the effect of mesh regulation but that models must be explored with values of M ranging up to 0.4.

On the basis of a 45 percent total-annual mortality, a natural mortality coefficient of 0.2 is equivalent to an annual expectation of death from natural causes of 15 percent, while a coefficient of 0.4 is equivalent to 30 percent.

SUMMARY

A review of an early and unsuccessful attempt to establish a natural mortality estimate for Georges Bank haddock shows that while the method applied was correct in principle, it failed to produce a meaningful result because three basic assumptions were either not fulfilled or were in doubt. These assumptions are: (1) haddock are fully recruited at age 3, (2) the natural mortality rate is constant over the range of ages, and (3) the sampling and age-composition data are equally reliable throughout the age range.

Using the same data and method, but treating the age groups individually rather than grouped, five estimates of the natural mortality coefficient are obtained. These estimates indicate that sampling for the older ages in the catch has been inadequate for the present purpose. Between ages 3 and 4, a negative natural mortality coefficient is obtained, indicating the possibility of incomplete recruitment at age 3. The data between ages 4 and 6 provide two estimates of natural mortality, both near zero.

The standard error of the regression line indicates that it is unlikely the natural mortality coefficient exceeds a value of about 0.3. Although a value of 0.2, which is equivalent to an annual mortality of 15 percent from natural causes, is sufficiently conservative for analytical purposes at the present time, other yield models with values of M ranging up to 0.4 must be explored.

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TABLE 1.—*Statistics of the Georges Bank Haddock Fishery* [1]

Year	Catch per day at Age—						
	III	IV	V	VI	VII	VIII	Effort
1932	2, 849						9. 11
1933	722	1, 144					8. 41
1934	1, 073	711	683				4. 84
1935	1, 284	583	520	438			6. 45
1936	1, 796	931	408	244	231		6. 22
1937	1, 309	704	542	256	121	65	8. 19
1938	966	482	267	207	120	44	7. 87
1939	2, 378	654	282	126	114	43	8. 02
1940	1, 658	1, 021	312	186	94	28	7. 22
1941	1, 280	1, 046	752	231	122	38	7. 33
1942	2, 566	1, 038	624	363	158	34	5. 73
1943	3, 608	1, 591	536	504	155	64	4. 88
1944	1, 414	2, 610	949	416	96	90	5. 66
1945	419	1, 246	1, 219	486	193	62	4. 89
1946	1, 997	398	854	562	218	48	7. 28
1947	1, 190	862	250	314	179	88	8. 22
1948	2, 406	704	400	174	120	68	7. 71
1949	1, 669	1, 307	330	149	88	56	7. 14
1950	708	831	680	240	114	53	5. 72
1951	3, 886	344	416	374	133	52	6. 49

[1] Catch per day is expressed in numbers and effort in thousands of days.

TABLE 2.—*Estimated values of c and M, together with errors and confidence limits*

Ages	c	S_c	M	S_M	95 percent confidence limits of M	$S_{y.x}$	Upper confidence limits of M based on $S_{y.x}$	
							67 percent	95 percent
III to IV	0. 1022	±0. 021	−0. 170	±0. 341	−0. 886 to 0. 546	±0. 272	0. 102	0. 374
IV to V	. 0845	±. 016	. 012	±. 240	−. 495 to . 514	±. 184	. 196	. 380
V to VI	. 0823	±. 022	. 004	±. 337	−. 675 to . 519	±. 239	. 243	. 482
VI to VII	*−. 1264		*1. 575					
VII to VIII	. 0657	±. 029	. 491	±. 457	−. 489 to 1. 472	±. 292	. 783	1. 075

* Based on first iteration only.

APPENDIX A

COMPUTATIONAL PROCEDURE FOR SOLVING EQUATION (1) FOR c AND M

The procedure for solving equation (1), page 1 may be outlined as follows (Beverton 1954):

1. Let $f_x=f_{x+1}$ in the second term on the left hand side of equation (1). This reduces the term to zero.

2. Plot the logs of the abundance ratios for each pair of years against the effort in the first year of each pair. Compute the regression coefficients, which are the first estimates of c and M. Call them c_1 and M_1.

3. Replot the data, computing a value of the log correction term, using c_1 and M_1 for each pair of years, and adding it to the log ratios previously plotted. Again compute regression coefficients, calling these more exact values c_2 and M_2.

4. Do a third iteration using c_2 and M_2 to estimate c_3 and M_3. Repeat the procedure until successive iterations do not differ significantly. These are the best estimates of c and M.

Work sheet for first iteration

Year class	A_x $III^N x$	B_x $IV^N x+1$	C_x A_x/B_x	D_x $\text{Log}_{10}C_x$	E_x effort
1929	2849	1144	2. 49	0. 396	9. 11
1930	722	711	1. 02	. 009	8. 41
1931	1073	583	1. 84	. 265	4. 84
1932	1284	931	1. 38	. 140	6. 45
1933	1796	704	2. 55	. 406	6. 22
1934	1309	482	2. 72	. 434	8. 19
1935	966	654	1. 48	. 170	7. 87
1936	2378	1021	2. 33	. 367	8. 02
1937	1658	1046	1. 58	. 199	7. 22
1938	1280	1038	1. 23	. 090	7. 33
1939	2566	1591	1. 61	. 207	5. 73
1940	3608	2610	1. 38	. 140	4. 88
1941	1414	1246	1. 13	. 053	5. 66
1942	419	398	1. 05	. 021	4. 89
1943	1997	862	2. 32	. 365	7. 28
1944	1190	704	1. 69	. 228	8. 22
1945	2406	1307	1. 84	. 265	7. 71
1946	1669	831	2. 01	. 303	7. 14
1947	708	344	2. 06	. 314	5. 72
1948	(3886)				(6. 49)

$$\text{Column } D_x=\log_{10}\left(\frac{v^N x}{v+1^N x+1}\right)=\log_{10}\left(\frac{III^N x}{IV^N x+1}\right)=\log_{10} 2.49=0.396$$

$N=19$ $\quad \Sigma E^2_x=932.9313$

$\Sigma D_x=4.372$ $\quad \Sigma D_x E_x=31.13234$

$\Sigma E_x=130.89$

	Base 10	*Base e*
c_1	0. 0325	0. 0748
M_1	. 0065	. 015

Work sheet for second iteration

Year class	D_x	E_x	$\frac{F_x}{E_x}$ (.0748)	$\frac{G_x}{F_x+.0150}$	$\frac{H_x}{1-e^{-a_x}}$	$\frac{I_x}{\frac{G_x H_{x+1}}{G_{x+1} H_x}}$	$\frac{J_x}{\log_{10} I_x}$	$\frac{K_x}{J_x+D_x}$
1929	0. 396	9. 11	0. 681	0. 696	0. 5014	1. 02	0. 009	0. 405
1930	. 009	8. 41	. 629	. 644	. 4748	1. 13	. 053	. 062
1931	. 265	4. 84	. 362	. 377	. 3141	. 95	−. 023	. 242
1932	. 140	6. 45	. 482	. 497	. 3917	1. 00	000	. 140
1933	. 406	6. 22	. 465	. 480	. 3812	. 94	−. 027	. 379
1934	. 434	8. 19	. 613	. 628	. 4664	1. 01	. 004	. 438
1935	. 170	7. 87	. 589	. 604	. 4534	. 99	−. 004	. 166
1936	. 367	8. 02	. 600	. 615	. 4593	1. 03	. 013	. 380
1937	. 199	7. 22	. 540	. 555	. 4260	1. 00	000	. 199
1938	. 090	7. 33	. 548	. 563	. 4305	1. 06	. 025	. 115
1939	. 207	5. 73	. 429	. 444	. 3586	1. 03	. 013	. 220
1940	. 140	4. 88	. 365	. 380	. 3161	. 98	−. 009	. 131
1941	. 053	5. 66	. 423	. 438	. 3547	1. 03	. 013	. 066
1942	. 021	4. 89	. 366	. 381	. 3168	. 92	−. 036	−. 015
1943	. 365	7. 28	. 544	. 559	. 4283	. 97	−. 013	. 352
1944	. 228	8. 22	. 615	. 630	. 4674	1. 01	. 004	. 232
1945	. 265	7. 71	. 577	. 592	. 4468	1. 02	. 009	. 274
1946	. 303	7. 14	. 534	. 549	. 4225	1. 05	. 021	. 324
1947	. 314	5. 72	. 428	. 443	. 3579	. 98	−. 009	. 305
1948	----------	(6. 49)	. 485	. 500	. 3944	----------	----------	----------

Column $F_x = c_1 f_x$

Column $G_x = c_1 f_x + M_1$

Column $J_x = \log_{10}\left\{\frac{c_1 f_x + M}{c_1 f_{x+1}} + M\left[\frac{1-e^{-(c_1 f_{x+1}+M)}}{1-e^{-(c_1 f_x+M)}}\right]\right\}$

$N = 19$ $\quad \Sigma E_x^2 = 932.9313$

$\Sigma E_x = 130.89$ $\quad \Sigma E_x K_x = 31.70379$

$\Sigma K_x = 4.415$

	Base 10	*Base e*
c_2	.0413	.0951
M_2	−.0525	−.121

The fourth iteration yields the following values for c_4 and M_4:

	Base 10	*Base e*
c_4	0. 0444	0. 1022
M_4	−0. 0740	−0. 170

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ACCELERATED DEVELOPMENT OF TESTIS AFTER UNILATERAL GONADECTOMY, WITH OBSERVATIONS ON NORMAL TESTIS OF RAINBOW TROUT

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ABSTRACT

An experimental study was made of the growth and development of the testes in rainbow trout employing unilateral gonadectomy to stimulate spermatogenesis in the infantile gonad. It was found that the remaining testis of trout more than a year old increased rapidly in weight and within a period of 6 weeks had grown to 3 or 4 times the size of a single testis in the control fish. Histological studies showed that the cellular changes occurring in these experimentally stimulated testes were identical with those found in the testes of trout maturing normally. These are described in detail. Failure of young trout to exhibit growth of the testis remaining after unilateral gonadectomy was found to be due not to lack of stimulability of the juvenile testis but most probably to the nonreactivity of the pituitary at this age. Good nutrition was observed to favor, while starvation suppressed, testis growth.

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By O. H. ROBERTSON, M. D., *Department of Biological Sciences, Stanford University, Stanford, Calif.*

While much has been learned about the process of fertilization of the egg, formation of the embryo and the hatching of fishes, relatively little study has been given to the development of the fish's sex glands and the factors which influence their growth and maturation. This is especially true of salmon and trout and is in marked contrast to the wealth of information available on the reproductive cycles in mammals, birds, and amphibians. Precise knowledge concerning the sequence of developmental stages of the gonads in the salmonid fishes is needed, not only for a clearer understanding of the mode of formation of sperm and ova, but is essential for the valid interpretation of experimental procedures directed toward influencing the rate of sexual maturation.

Fishery biologists in various parts of the world have been experimenting on speeding up development of sex products with the purpose of increasing the production of certain fishes. The method usually employed has been injections of pituitary glands. Results have varied with the species of fish tested and the criteria used for judging the effect. Such procedures have been only moderately promising in salmon and trout thus far, but would seem to be worth pursuing further in view of the urgent need in certain regions of this country to maintain the populations of Pacific salmons and sea-run trout. That more knowledge of the normally developing salmonid is necessary before studies of this nature can be successfully undertaken was discovered by the author and A. P. Rinfret when initiating an investigation of the effect of pituitary substances administered to juvenile rainbow trout, *Salmo gairdnerii* (1957).

Our observations soon showed that an appreciable percentage of young male trout exhibited spontaneous enlargement of the testes at an early age. To be certain of the gonad-stimulating action of any procedure in individual trout, it was obviously necessary to determine the size of their testes beforehand. Unilateral gonadectomy undertaken for this purpose revealed the unexpected finding of well marked ensuing increase in the size of the remaining testis in the control (uninjected) fish. This stimulation of testicular growth presented a further complication in estimating the effect of pituitary hormones on the trout's gonads but at the same time it provided another means of studying the process of gonadal development.

The present investigation was undertaken with the purpose of learning more about the natural course of sexual maturation in male rainbow trout and determining some of the factors which influence the inception and rate of spermatogenesis.

This work was aided by grants from the American Academy of Arts and Sciences and the U. S. Fish and Wildlife Service.

Especial appreciation for his invaluable aid is due my good friend and neighbor, John McCarthy, who installed the water supply to the laboratory, acts as engineer, and takes care of the experimental fish during my absences. It is a pleasure to record my indebtedness to George Dufour of Santa Cruz, Calif., for his generous cooperation in supplying trout of desired size and age throughout the past 3 years. The fact that his trout were free from disease and in excellent condition greatly facilitated the present investigation. He also provided ground liver. To Dr. Clifford Sweet of Oakland, Calif., I want to express my appreciation for suggesting the type of suture employed in the operative wound closure and for instructing me in its use.

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Thanks are due to the Upjohn Company of Kalamazoo, Mich., for the penicillin which was provided through the kindness of Dr. Jaret H. Ford. Finally, I wish to acknowledge my obligation to John Daniels of the Department of Medicine, University of Chicago, for the large number of excellent histological preparations employed in this study.

METHODS OF STUDY

Experimental Trout

The trout were obtained from the private hatchery of George Dufour, located near Camp Evers in the Santa Cruz mountains, Calif. They were hatched from eggs obtained from the brood stock maintained at Logan, Utah.

Environmental Conditions

The experiments were conducted in the author's laboratory in the Santa Cruz mountains, where an adequate supply of spring water was fed into glass-walled aquaria ranging from 10 to 18 gallons capacity. Partitions separating individual trout were found to be necessary to prevent trout from injuring each other. These consisted of ⅝-inch mesh galvanized screen held in place on the bottom by steel bars—all coated with aluminum paint. The small space allotted to each fish did not appear to be detrimental to their well being since the trout grew at the rate of 0.2 to 0.3 inch per week and remained free from fungus infection. The water temperatures ranged from 48° to 50° F. in winter to 58° to 60° F. in summer with infrequent brief rises to 65° F. A flow of water was maintained which gave a complete exchange every 30 minutes. In late summer and fall this was reduced somewhat and aeration of the water was instituted with small air pumps. Uneaten food and excreta were removed daily by means of a suction tube emptying into the outflow trough under the aquaria. A complete change of water was made following a thorough weekly cleaning.

Food

The trout were fed 6 days of the week on dried pellets provided by the U. S. Fish and Wildlife Service through the kindness of Dr. Arthur M. Phillips, Jr., Cortland, N. Y. (1953). On the seventh day ground liver was fed.

Length and Weight Measurement

The trout were measured to the nearest 0.1 inch, total length,[1] and weighed to the nearest 0.5 gram, once a week under anesthesia produced by immersion in water containing a 1:20,000 dilution of tricaine methanesulphonate, M. S. 222. A sufficient degree of anesthesia occurs usually in 2 to 3 minutes. Recovery after returning to the aquarium takes place equally rapidly. No harmful effects from this anesthetic have been observed even after daily use for a number of weeks.

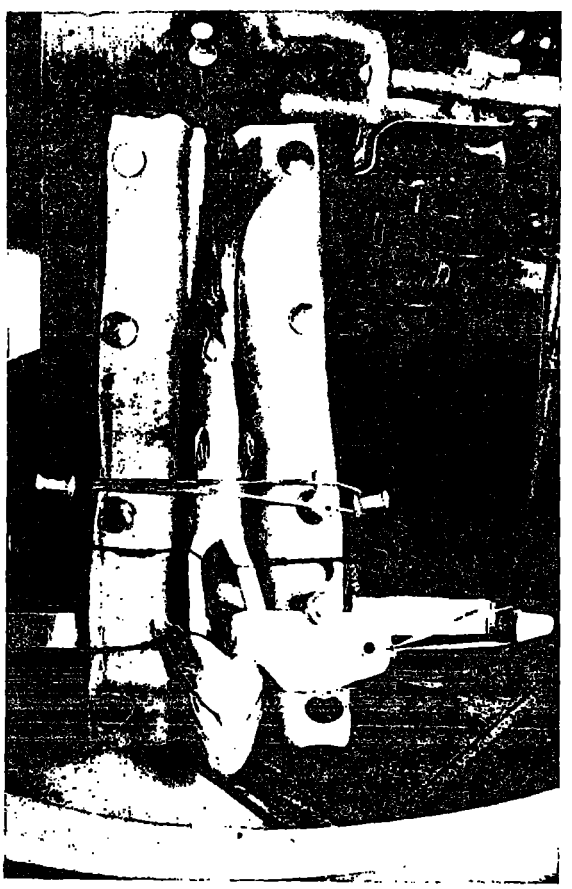

FIGURE 1.—Trout on operating board with head submersed in anesthetic solution to a level just above gills. Retractor in place.

[1] Fork length measurement was also made but total length in trout of this age and size was more satisfactory.

FIGURE 2.—Retractors for use on right and left sides.

Operative Technique

The trout having been starved 48 hours was anesthetized in a 1:20,000 dilution of M. S. 222 then placed on the operating board that dipped into a solution of 1:25,000 solution of the same anesthetic. To hold the fish on a tilting board (fig. 1) a No. 10 fishhook, with barb removed, was inserted through the skin near the anal fin and by means of an attached rubber band was pegged to the board in the desired position. The sides of the trough were placed sufficiently far apart so as not to interfere with the gills which should be completely submerged. In order to operate in the peritoneal cavity without assistance, somewhat special arrangements had to be provided: these consisted principally in the construction of retractors made of stainless steel (fig. 2), which could be held in place by means of an attached rubber band stretched over a stainless steel arm fastened to the operating board as shown in figure 1. An aluminum push pin helps hold the tractor in place. A single rubber band over the pelvic region of the trout suffices to hold the fish on the board. The instruments were sterilized in 70 percent alcohol.

Incision circa 3 cm. long in a 7- to 8-inch fish was made in the mid-line which resulted in little or no bleeding, if terminated at a point just posterior to the insertion of the pectoral fins. Four barbless fishhooks attached to small lead sinkers served to hold the body walls apart. A focusing head mirror was used to illuminate the abdominal cavity. The shaped retractor made it possible to hold the liver away from the cephalic attachment of the testis. A clearly visualized field in this area is essential since complete excision is necessary to prevent regeneration. The only important precaution to be observed at this stage is to avoid injury of the swim bladder against which the testis lies. The greater portion of the gland can be removed through this relatively small opening by pulling the gonad as far forward as possible then slipping the scissors into the abdominal cavity along its stretched caudal end. No regeneration of the remaining portion, principally spermatic duct, has been observed within the experimental period. Before closing the wound a capsule containing 5 to 10 mg. of penicillin powder was emptied into the peritoneal cavity.

The incision was sewed up with No. 5–0 chromic gut and a six-eighths of an inch or seven-eighths of

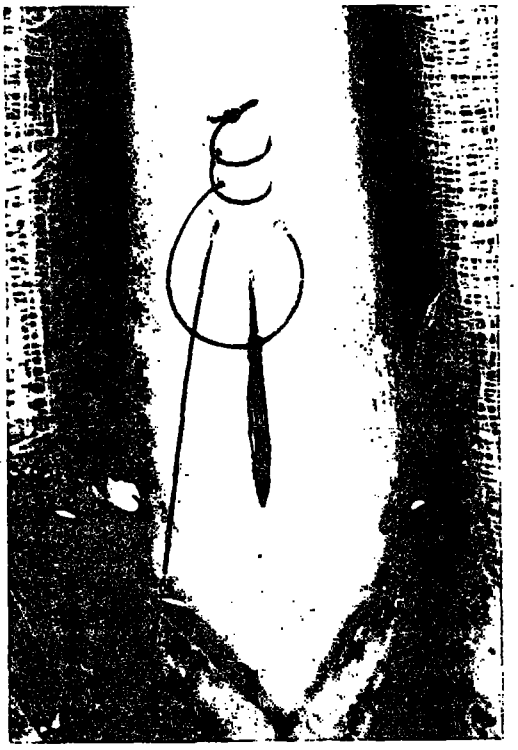

FIGURE 3.—Procedure of beginning lock stitch.

an inch straight cleft palate needle. The type of suture used known as lock stitch produced a close and even approximation of the two edges. After trying the first stitch the next was made on the right side of the incision (operator's right) passing the needle completely through the body wall about one-sixteenth of an inch from the edge, then up through the wall of the opposite side. The needle was then passed inside the diagonal loop of the preceding stitch before making the next one. Figure 3 illustrates this part of the technique. Eleven to 13 stitches were used to close a 3-centimeter incision, each one pulled snug before the next was made. It was found that stitches thus placed resulted in more rapid and even healing than when spaced further apart. The final tie was made with the short end of the suture and the needle or double end as in figure 4.

Chromic gut will begin to absorb in 2 to 3 weeks and has usually disappeared by the end of the fourth week. No post-operative care was found necessary other than withholding food for 48 hours. The mortality attributable to the operative procedure was no more than 1 or 2 percent.

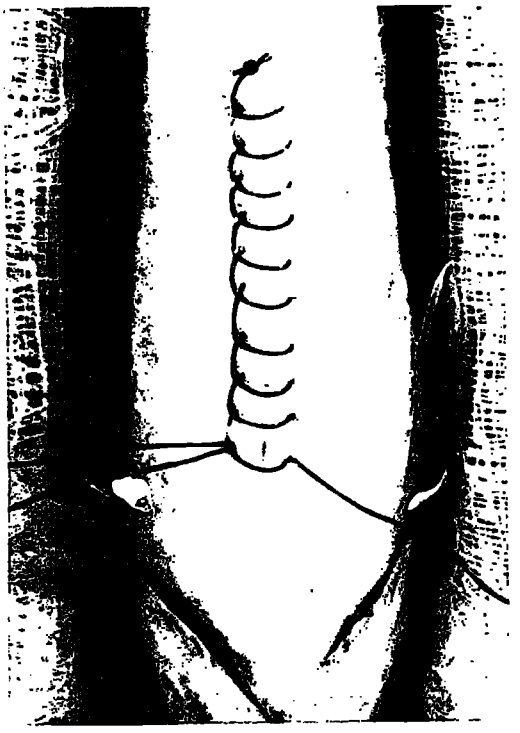

FIGURE 4.—Procedure for finishing lock stitch. The two ends are ready to tie.

EXPERIMENTAL STUDY OF DEVELOPMENT OF TESTES

Since no quantitative data on the growth and development of the testes in juvenile rainbow trout are to be found in the literature, pertinent observations were made on a large number of normal trout of different lengths and varying ages. Then a study of unilateral gonadectomy was undertaken with the objective of describing the phenomenon of accelerated growth of the remaining testis and relating the experimentally induced spermatogenesis to the normal development of the testes in rainbow trout.

Relation of Testis Weight to Length, Weight, and Age of Trout

In relation to testes weight it was found that the length of the fish was a much more informative index than was its weight. Individual trout, especially those kept in large rearing ponds, may fluctuate in weight quite rapidly, depending on the amount of food they obtain. Examination of a consecutive series of 253 trout 7 to 16 months of age, freshly taken from the hatchery rearing ponds, revealed 240 to be sexually immature and 13 with marked testicular development. The weights of the immature testes were plotted as shown in figure 5. Since this investigation dealt largely with the results of unilateral gonadectomy, one-half the weight of each pair of testes or that of a single gonad was used in making the graph. Several features of this graph will be noted at once. First the great majority of the points are clustered closely along a median line (drawn by inspection). Second, there is a gradual increase in testis weight with increasing length of the trout until it reaches about 8 inches when the testis weight curve rises more sharply with the trout's further growth. Trout greater than 10 inches in length were not included because of space considerations in the aquaria.

The importance of length versus age immediately comes to mind in this connection. Is this curve a valid one for trout of the same size but of widely differing ages? To answer this question, the weights of immature testes in trout of two length categories 6.5 to 7.4 inches and 7.5 to 8.4

inches were plotted against age as shown in figs. 6 and 7. It is seen that between the ages of 7 and 16 months the size of the testis is essentially the same in fish of similar length, i. e., growth of the infantile testes parellels growth of the other components of the trout until the process of gonadal maturation begins to occur more generally after 16 months of age (fig. 8).

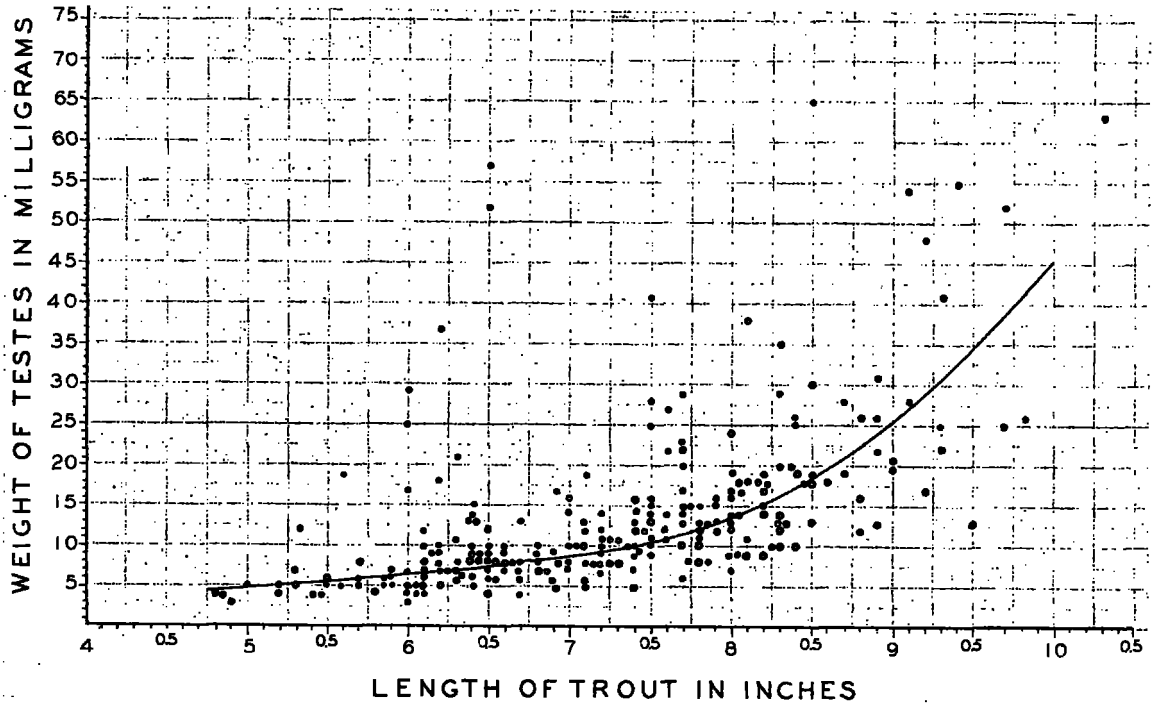

FIGURE 5.—Weight of immature testes in 240 rainbow trout ranging from 4¾ to 10 inches in length and 7 to 16 months old.

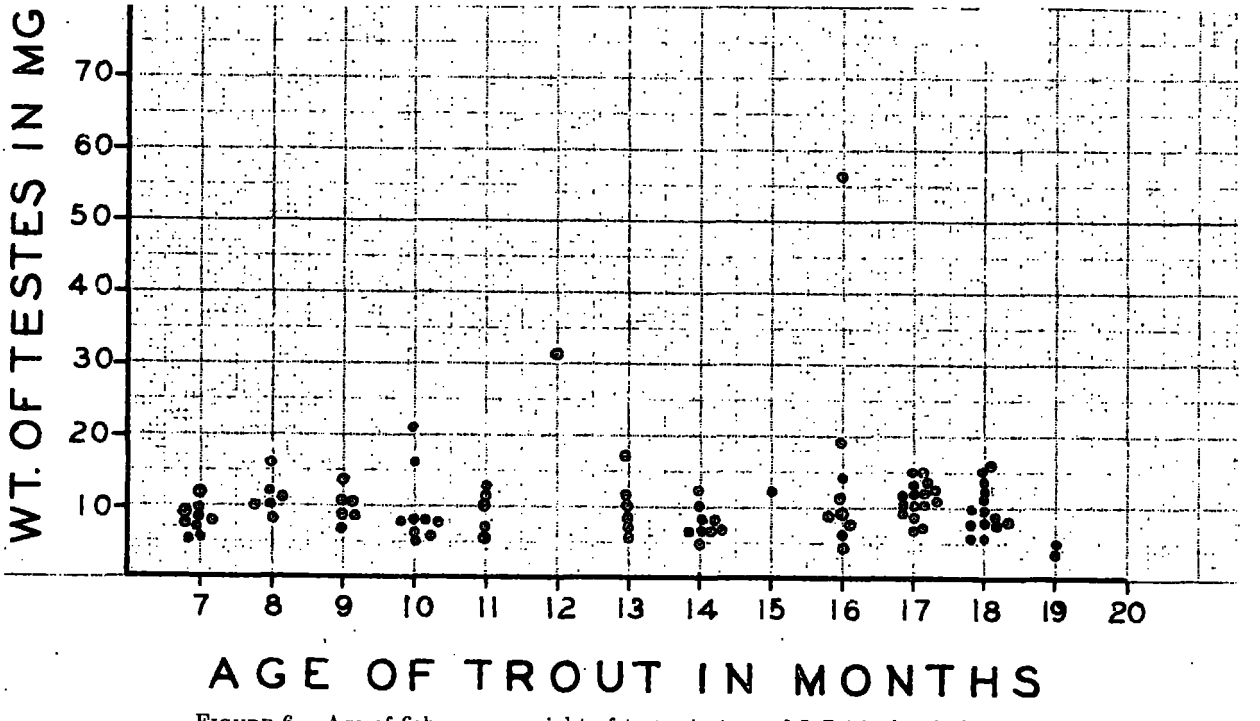

FIGURE 6.—Age of fish versus weight of testes in trout 6.5–7.4 inches in length.

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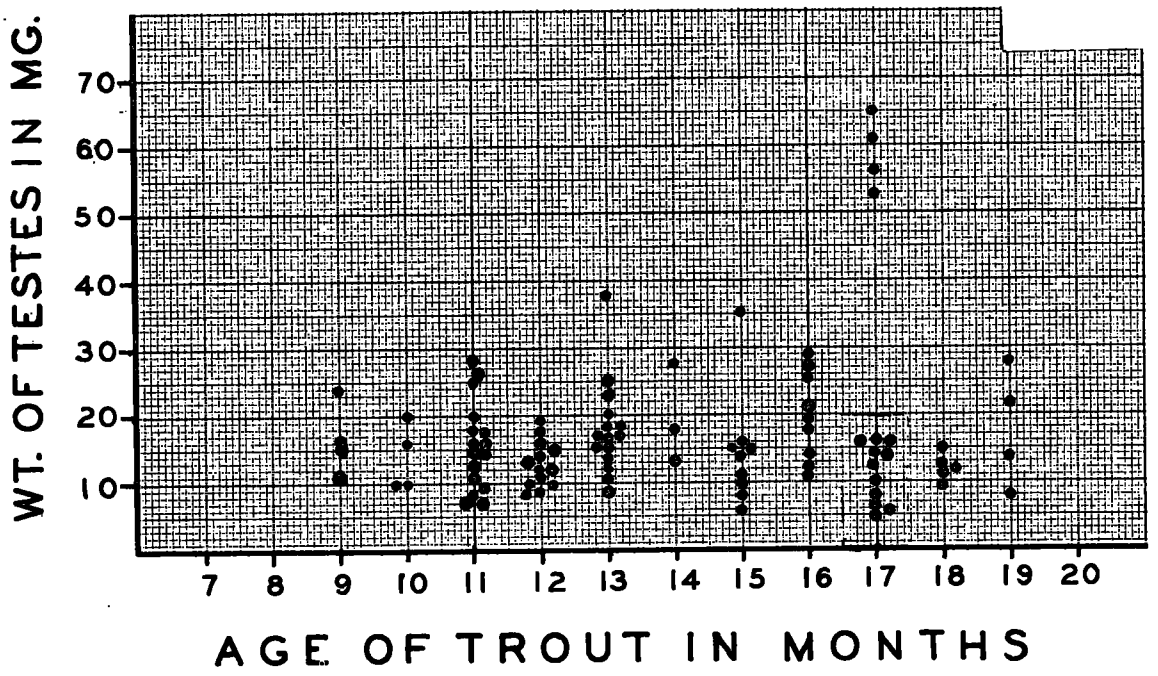

FIGURE 7.—Age of fish versus weight of testes in trout 7.5–8.4 inches in length.

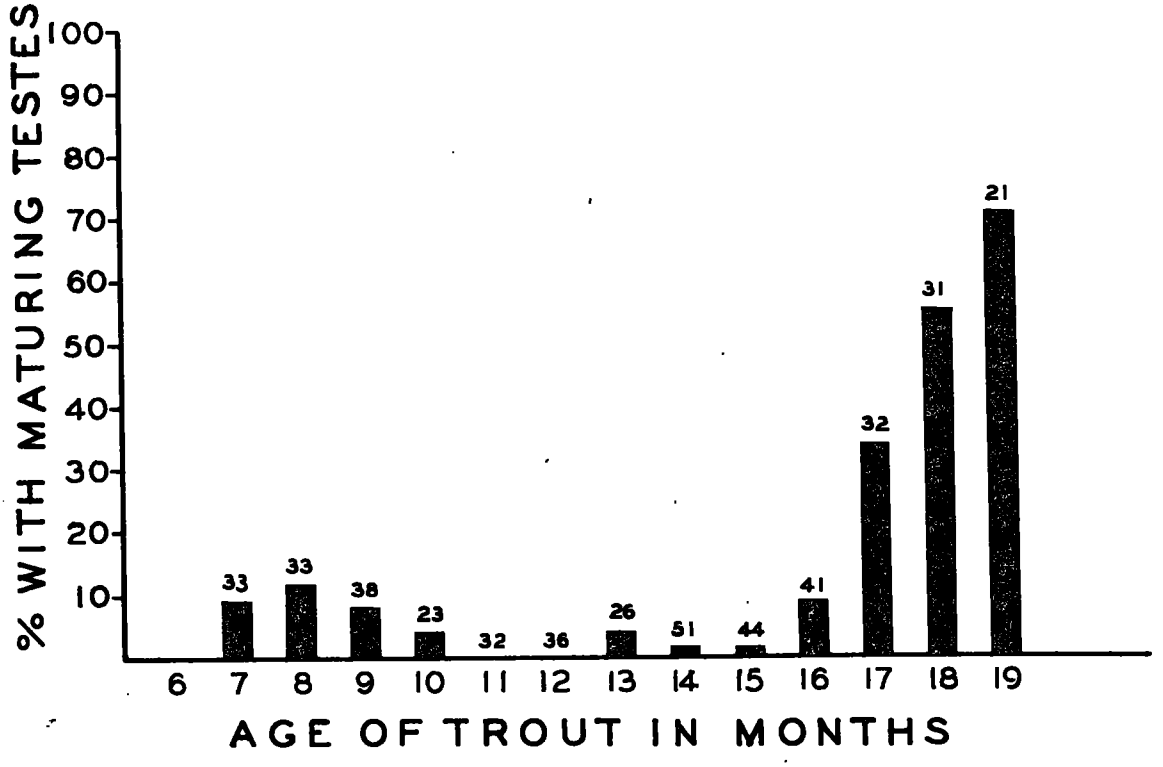

FIGURE 8.—The percentage of young rainbow trout exhibiting beginning development at successive months of age.

Occurrence of Precocious Sexual Maturity

The observed not infrequent occurrence of very large and sometimes fully mature testes in trout as young as 6 or 7 months of age indicated the importance of determining how frequently this event took place. Data on the percentage of mature trout at different ages in months based on some 350 fish hatched in 1952 and 1953 and collected over a period of 2½ years, are graphed in figure 8. The designation of "trout with developing testis" includes those fish in which single gonad weight exceeded the highest point on the curve in figure 5, namely 65 milligrams. Actually all these trout exhibited testes weights many times that of the normal growth curve. There was no essential difference between the two year classes of trout so they were combined without distinction on the graph.

It is of interest that early sexual maturity occurred more frequently in trout from 7 to 9 months of age than at later ages up to 16 months.[2] The absence of any fish showing gonadal development in the 11- to 12-month age group was observed each year. Beginning with 17 months an increasing percentage of trout exhibited testicular growth. However, a certain portion of male trout were found to have infantile gonads up to and beyond the age of two years.

Preponderance of Left Testis Weight

In order to be able to estimate the weight of the testis remaining after unilateral gonadectomy it was necessary to determine the average weight of the right and left testis. Weights of immature testes in 147 trout from 6 to 16 months of age revealed that the average weight of the left testis was approximately 15 percent (14.8) greater than that of the right. When testes weights of 35 of similar age but from another stock were added to the above group the preponderance of L/R rose to 16 percent.

The average weights of testes in varying stages of development up to full maturation (but not oozing milt) in 73 rainbow trout of ages from 6 months to 12 months showed a weight preponderance of L/R of 16.8 percent. The combined average left and right testis weights in all 255 trout gave a left preponderance of 16.3 percent.

Results of Unilateral Gonadectomy

The first series of gonadectomies were performed in January 1953 on trout 11 to 12 months old. Autopsy after 43 to 48 days revealed a striking increase in the size of the remaining testes in 3 of the 6 experimental fish and a moderate though definite increase in the others. Changes in weight from 4 mg. estimated at time of operation to 108 mg. found at autopsy, and from 15 mg. to 186 mg., occurred. For the 3 trout exhibiting the largest remaining testis, the gains in weight ranged from 1,100 to 2,450 percent. For the group of 6 fish, the percentage gain was 1,000. Controls consisting of laparotomy and inspection of testes were not run coincident with this series. However, 3 such fish operated on 6 weeks previously showed 46 days later testes of approximately the size expected from the testes growth curve (fig. 5).

A second series of unilateral gonadectomies carried out in July and August of the same year on trout of the same year class as the first series but now 17 to 18 months of age, resulted in tremendous growth of the remaining testes: e. g., from an estimated 6 mg. at the time of operation to 3,065 mg. found at autopsy 7 weeks later, more than 500-fold increase in weight, table 1. However, simultaneous controls, operated and inspected only, showed equally marked growth of testes (table 2). Whether the difference between the results of the two experiments (winter and summer) was due to the greater age of the trout in the second series and hence the likelihood of imminent spontaneous testicular maturation as indicated in figure 8, or to some other factor or factors, was not clear. The observed absence of gonadotrophin production by the infantile pituitary in some mammalian species under a certain age suggested that the age of the trout might well have an important influence on its response to unilateral gonadectomy, assuming that the underlying mechanisms is one of pituitary stimulation.

[2] Examination of thirty nine 6½- to 7-month-old trout of the 1955 hatch showed 15 percent of them to be in an advanced stage of testicular maturation. These trout were from a different source than those represented in figure 8 so were not included.

TABLE 1.—*Change in weight of remaining testes following unilateral gonadectomy in trout 18 months of age*

[Period of observation 7 weeks]

Trout No.	Length changes	Weight of excised testis	Estimated weight of remaining testis	Remaining testis at autopsy		Gain in length of trout
				Weight	Net gain [1] in weight	
	Inches	*Mg.*	*Mg.*	*Mg.*	*Percent*	*Percent*
137	5.2–6.3	R 3	L 3	[2] R 274 L 1,351	44,933	21
138	5.5–6.1	L 4	R 4	R 10	225	11
139	4.7–6.1	L 7	R 6	R 740	12,217	30
141	7.4–8.7	R 12	L 14	L 1,586	11,143	18
151	6.1–7.4	R 5	L 6	L 3,065	50,933	21
153	6.1–6.9	R 4	L 4	L 14	200	13
154	6.1–7.2	L 15	R 13	R 2,305	17,608	18
155	6.0–7.1	L 33	R 29	R 2,180	7,410	18

[1] The net percentage gain in weight of testes is calculated on the basis of the actual gain (weight at autopsy less estimated weight at operation) minus the expected gain in weight accompanying growth in length of trout as shown in fig. 5.

[2] Regenerated from tiny fragment which escaped excision.

TABLE 2.—*Change in weight of testes following laparotomy and inspection of testes in trout 19 months of age*

[Period of observation 6 weeks]

Trout No.	Length changes	Appearance of testis at operation	Estimated weight of single testis	Testes at autopsy		Gain in length of trout
				Weight	Net gain in weight of single testis [1]	
	Inches		*Mg.*	*Mg.*	*Percent*	*Percent*
156	7.3–8.4	Thread-like.	9	R–2950 L–4670	42,333	15
157	6.5–7.0	...do...	7	R–1730 L–1880	18,640	8
158	7–3–8.9	...do...	9	R–2085 L–2800	26,960	22
159	6.9–8.0	...do...	8	R–2680 L–3840	40,675	16
160	6.9–7.7	...do...	8	R–2460 L–2460	30,710	12
161	7.6–9.1	...do...	11	R–2590 L–4130	30,400	20
164	7.7–8.2	...do...	12	R–2000 L–2030	16,765	19
165	6.8–8.7	...do...	8	R–4310 L–5410	60,610	27

[1] Taken as ½ weight of the 2 testes.

In the next experimental series, observations were begun when the trout were 7 months of age and continued first at two monthly then at monthly intervals until the age of 17 months. The summarized results of 7 experiments comprising 78 trout, about equally divided between test and controls, are shown in table 3. Detailed data of one group, trout 16 months of age, are displayed in tables 4 and 5. Before the age of 13 months there appeared to be no significant difference between the test and the control trout; both showed definite though very moderate increase in testicular weight as compared with normal trout of the same length.[3] At 11 months the combined weights of the 2 testes of the controls were approximately twice that of the single testes of the unilaterally gonadectomized fish. At 13 months, however, the remaining gonad of the test fish was found to be about the same weight as the two testes of the control. This result was repeated at 14 and 15 months but at 16 months the remaining testes of the gonadectomized trout averaged twice the combined weight of the 2 glands of the controls. Figures 9 and 10 are representative of the appearance of the testes in the experimental and control trout at 16 months of age. In figure 9 a small regenerated remaining fragment of the excised right testis is shown between it and the enlarged left testis found at autopsy.

TABLE 3.—*Effect of unilateral gonadectomy at different ages on the growth of the remaining testis*

Age of trout at autopsy (months)	Number in each group	Unilateral gonadectomy		Controls		
		Remaining testis at autopsy		Number in each group	Testes at autopsy	
		Average weight	Average net gain weight		Average combined weight both testes	Estimated net gain weight single testis
		Mg.	*Percent*		*Mg.*	*Percent*
9	4	25	286	6	34	136
11	4	36	262	5	78	288
13	6	78	407	5	74	196
14	6	73	499	7	80	171
15	6	63	620	6	94	346
16	5	206	1,373	7	118	545
17	6	442	7,975	6	412	1,995

TABLE 4.—*Change in weight of remaining testis following unilateral gonadectomy in trout 16 months of age* [1]

[Period of observation 6 weeks]

Trout No.	Length changes	Weight of excised testis	Estimated weight of remaining testis	Remaining testis at autopsy			
				Weight	Gain in weight	Net gain in weight	Gain in length of trout
	Inches	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Percent*	*Percent*
328	6.3–7.3	L 22	R 19	R 292	273	1,422	16
329	6.2–6.9	L 7	R 6	R 12	6	66	11
332	6.2–7.4	R 17	L 20	L 335	315	1,560	19
333	6.0–7.1	R 5	L 6	L 104	98	1,600	18
338	7.2–8.4	R 10	L 12	L 286	274	2,217	17

[1] Trout 15 months old when operated on.

NOTE.—Average gain in length of trout, 18 percent. Average gain in weight, 87 percent.

[3] Errors arising from the estimated weight of the remaining testes in the unilaterally gonadectomized trout (see footnote to table 1) are probably not significantly different from similar errors in estimating by the same means the weight of the testes in the inspected controls. There seemed to be no better way of devising a control on the effect of the removal of one gonad.

TABLE 5.—*Change in weight of testes following laparotomy and inspection of testes in control trout at 16 months[1] of age*

[Period of observation 6 weeks]

Trout No.	Length changes inches	Appearance of testis at operation	Estimated weight of single testis	Testes at autopsy			Gain in length of trout
				Weight	Single testis		
					Gain in weight	Net gain in weight	
	Inches		*Mg.*	*Mg.*	*Mg.*	*Percent*	*Percent*
330	6.6–7.6	Stringlike	8	R 67 / L 76 / 71	63	750	15
331	6.0–7.2	do	7	R 10 / L 9 / 10	0	0	20
334	6.4–7.3	do	7	R 42 / L 45 / 43	36	471	14
336	6.2–7.1	do	7	R 112 / L 105 / 109	102	1,430	15
340	6.7–8.0	do	8	R 17 / L 23 / 20	12	75	19
341	7.3–9.0	do	10	R 59 / L 68 / 63	53	380	23
342	7.2–8.9	do	10	R 77 / L 113 / 95	85	710	24

[1] Trout 15 months old when operated on.

NOTE.—Average gain in length of trout, 19 percent. Average gain in weight, 107 percent.

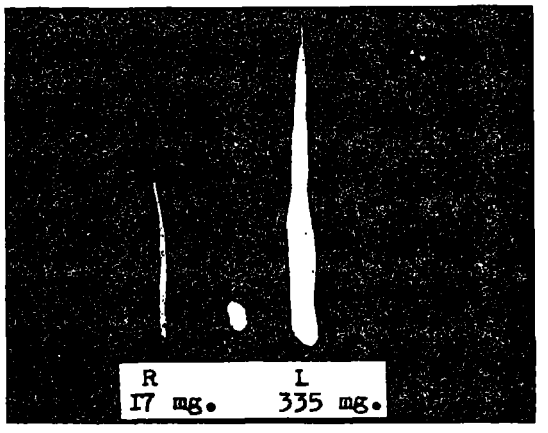

FIGURE 9.—Testes of rainbow trout No. 332, table 4. Right testis (R) excised. Left testis and regenerated fragment of right testis, weight 19 mg., found at autopsy 6 weeks later. Trout 16 months old when killed.

The percentage gain in weight gives a more accurate comparison of testicular growth on the test and control groups since this figure takes the size of the fish into account. Thus at 16 months of age the weight gain of the test-trout gonad is between 2 and 3 times that of a single testis in the control group and not 4 times as would be indicated by comparing weights alone (table 3). At 17 months of age the percentage gain in weight of the testes in the gonadectomized trout is about 4 times that of the controls but at this age a considerable percentage of the trout were manifesting spontaneous testicular maturation.

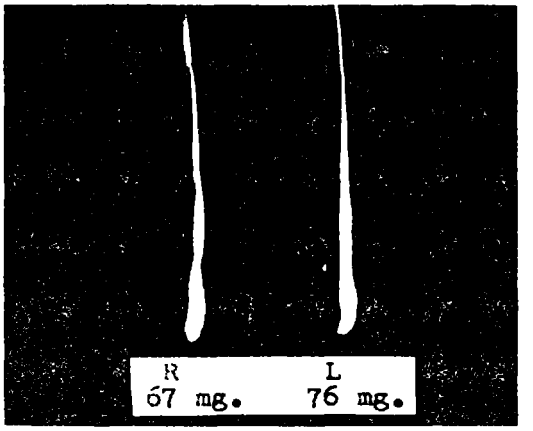

FIGURE 10.—Testis of control rainbow trout No. 330, table 5. Killed 6 weeks following simple laparotomy and inspection of testes which were seen to be infantile. Age at death 16 months.

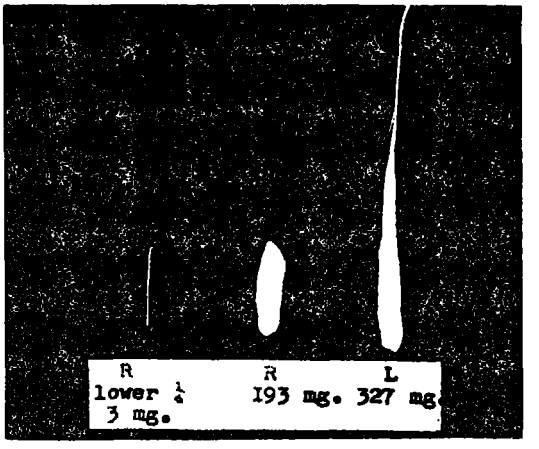

FIGURE 11.—Testes of rainbow trout No. 343 (table 6) six weeks following partial unilateral gonadectomy; caudal, one-fourth of right testis excised. Age at death 16 months.

Partial Unilateral Gonadectomy

In order to determine whether the degree of growth stimulation of the remaining testis depended on the quantity of testicular substance removed, varying portions of one testis were exercised from a series of 16 months old trout. The results of this experiment (table 6) show that the excision of as little as one-fourth (estimated) of one testis was followed by marked increase in weight of the other intact testis; as well as growth of the remaining part of the partially excised one (fig. 11). No essential difference in effect was

observed from removal of one-fourth or three-fourths of a testis. The average total testicular mass of the remaining intact testis in these 5 trout was about the same as observed in a group of the same age in which a whole testis was excised (table 4).

TABLE 6.—*Effect of partial unilateral gonadectomy on the growth of the remaining testes in trout at 16 months of age*

[Period of observation 6 weeks]

Trout No.	Length changes	Excised tests		Estimated weight of remaining testis	Remaining testis at autopsy	
		Amount estimated	Weight		Weight	Net gain in weight of intact testis
	Inches		*Mg.*	*Mg.*	*Mg.*	*Percent*
337	6.7–7.5	Caudal ¼ of left	3	8	R 33 L 17	288
343	7.1–7.7	Caudal ¼ of right	3	9	L 327 R 193	3,500
335	6.5–7.6	Caudal ½ of left	6	7	R 168 L 52	2,200
344	7.0–8.7	Caudal ½ of right	5	9	L 164 R 53	1,590
339	6.0–7.8	Caudal ¾ of left	5	7	R 111 L 23	1,414

NOTE.—Average total testicular mass=228 mg.; average percentage net gain in weight of intact remaining testis=1,738.

Growth of Testes in the Control Trout

The gain in weight of the testis in the control trout observed throughout the series of experiments summarized in table 3, suggests that laparotomy itself may have a stimulating action on testis growth. This weight gain was fairly constant, ranging from 136 percent to 288 percent until the age of 15 months when it began to increase and by 17 months, the testis, during the 6 weeks of observation increased its weight twenty-fold. There are, however, factors other than operation which undoubtedly contribute to accelerated gonadal growth in these fish. Trout taken from the hatchery rearing ponds containing large populations of fish and placed in individual compartments in the laboratory aquaria begin to grow at a greatly increased rate. The possibility that such rather sudden change in metabolism might stimulate beginning development of the male gonad was tested by placing a group of 13–16-month-old trout in the aquaria and feeding them abundantly as in the case of the experimental trout, for the same period of time, namely, 6 weeks. At autopsy, 7 of these trout were found to be males; all of them showed well-marked development of the testes (table 7). There was of course no way of knowing the varying states of maturation of the testes of these feeding controls, at the time they were taken from the rearing pond. Some information on their probable state of gonadal development was obtained by examining a number of trout taken from the same pond, of the same age, and approximately the same length as those shown in table 7. In 12 consecutively examined males of this group (6.2–7.4 inches, average 6.9 inches) only two exhibited developing testes with weights of 1554 and 1926 mg. while 10 had infantile testes with an average weight of 20 mg. (range, 12–38 mg.). So one can infer that some of the trout shown in table 7 had infantile testes at the beginning of the period of observation.

TABLE 7.—*Feeding controls*

[Trout taken from hatchery at 16 months of age, fed for 6 weeks, and killed in 17th month of age]

Trout number	Change in length	Increase in length of trout	Combined weight of both testes at autopsy
	Inches	*Percent*	*Mg.*
360	6.6–8.0	21	450
371	6.4–7.2	13	237
372	6.2–7.2	16	95
376	7.1–8–1	14	181
377	7.1–9.1	28	1,065
378	7.1–8.6	21	651
379	7.0–8.5	21	875
Average			508

OBSERVATIONS ON THE HISTOLOGY OF THE TESTIS

While significant increase in size of the infantile testes constitutes good presumptive evidence of beginning maturation, one cannot be certain without detailed comparative histological study that the actual cellular changes following experimental stimulation of testicular growth are the same as those occurring in the naturally maturing gonad. For this purpose a series of histological preparations were made of the testes of normal rainbow trout in all phases of maturation from the infantile to the spent gonad. The only detailed account of the histology of the testis of the rainbow trout the author has been able to find is that given by Weisel (1943) who described the immature and the mature trout's testes. No specimens of the intermediate or developing stages were studied, although he states that spermatogenesis in the rainbow trout and the sockeye salmon, which he described in their various developmental phases, are similar. The nomenclature employed in the present study for the early cytological elements in the process of spermatogenesis is the same as that used by Weisel.

Histology of the Testis in Normal Trout

The completely immature or infantile testis consists of small closely packed cysts or nests of primitive germ cells—spermatogonia [1]—which are separated into lobules comprising 2 or 3 to half a dozen or more cysts (fig. 12). The walls of the lobules, made up of connective tissue and blood vessels are often ill-defined. A few connective tissue cell nuclei are observed in the interstitial tissue as well as occasional clumps of small cells with oval nuclei. The first evidence of spermatogenesis is an increase in the number of cells in the cysts, due to division of the spermatogonia. Some of the enlarged cysts begin to exhibit a lumen (fig. 13). Frequent mitoses are seen. A few large ovoid nuclei with indistinct cytoplasm are observed in the interstitial tissues. The spermatogonia continue to divide and with increasing numbers the cells become smaller (fig. 14). At some point in this process these cells have been designated primary spermatocytes. These can readily be distinguished from the smaller spermatogonia when they exhibit nuclei densely packed with chromatin or a grouping of the chromatin material at one pole of the nucleus, the so-called synizesis stage (figs. 15, 16B, and 16C). Hann (1927) considers that synizesis marks the change from spermatogonium to primary spermatocyte; dispersion of chromatin throughout the nucleus follows. By this time the cysts have become dilated, many of the cyst walls have disappeared and the whole appearance of the gland is more lobulated with the lobules mostly oriented toward the surface of the testis.

With further division secondary spermatocytes are formed, considerably smaller than the primary ones (figs. 15 and 16D). These in turn give rise to spermatids which transform into spermatozoa without division (fig. 16E). This process is frequently focal and in its earlier phases all stages from cysts comprising only spermatogonia to lobules containing small numbers of spermatozoa may be seen. The mature testis exhibits lobules greatly distended with fully developed spermatozoa (fig. 17). Progressive transformation of the remaining immature elements continues until the only free cells are spermatozoa (fig. 18). Increase in size of the maturing testis is in general paralleled by progression of developmental stages. However, testes of equivalent size in different trout may not be in the same stage of spermatogenesis.

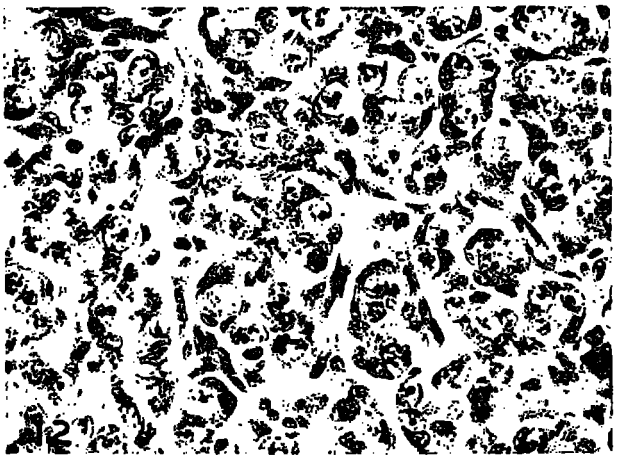

FIGURE 12.—Right testis of normal rainbow trout—length 7 to 8 inches, age 11 months. The gonad weighing 9 mg. consists of small nests of spermatogonia which in turn are grouped into lobules by septa composed of fibrous tissue and blood vessels. × 500.

[1] In a study of spermatogenesis in the Atlantic salmon parr, Jones (1940) uses the terms germ cell for the earliest stage and considers that the "germ cells" undergo a series of divisions before spermatogonia are formed. This same terminology is employed by certain other workers (Turner 1919; Bullough 1939) describing the development of the testes in other species of fish, which differs in some respects from that of the salmonids.

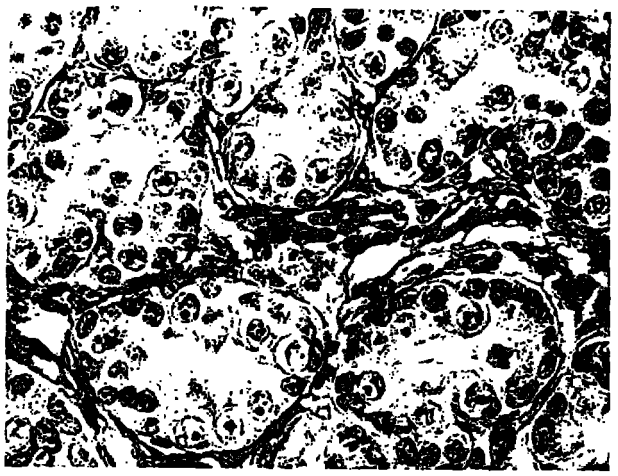

FIGURE 13.—Left testis of normal rainbow trout, length 8.4 inches, age 11 months. Testis weight 30 mg. The nests or cysts of spermatogonia show beginning enlargement with increase in the number of cells. Frequent miotic figures are evident—three occur in the photograph, two in the metaphase and one in the anaphase. × 500.

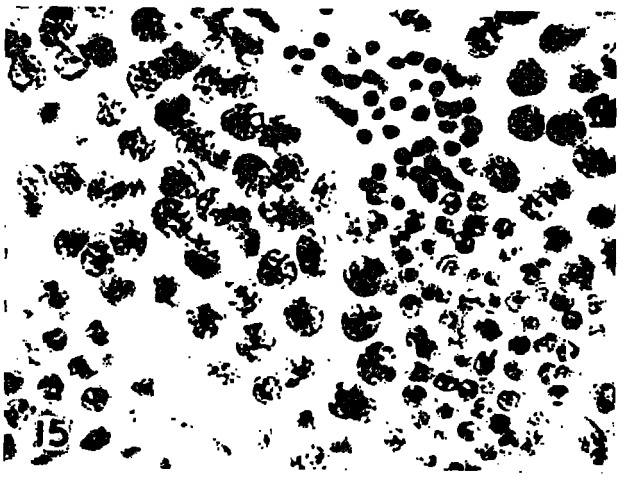

FIGURE 15.—Left testis of normal rainbow trout, length 7.9 inches, age 18 months. Spermatogenesis has proceeded further than shown in figure 14. Cells consist mostly of primary and secondary spermatocytes and small clusters of spermatids. Free spermatogonia have disappeared. × 1050.

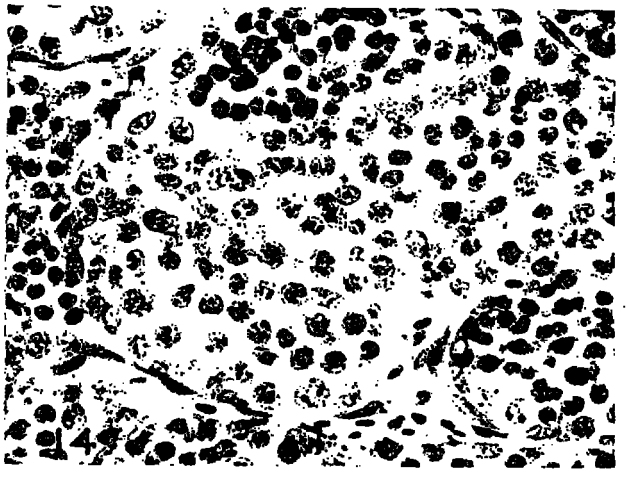

FIGURE 14.—Right testis of normal rainbow trout, length 10.4 inches, age 17 months. Testis weight 165 mg. Walls of primitive cysts have largely disappeared and cells are contained in lobules. The central lobule of the photograph consists almost entirely of spermatogonia which in the course of multiplication have diminished in size and possess little or no detectable cytoplasm. The dark staining cells in clusters above and below are primary spermatocytes. × 500.

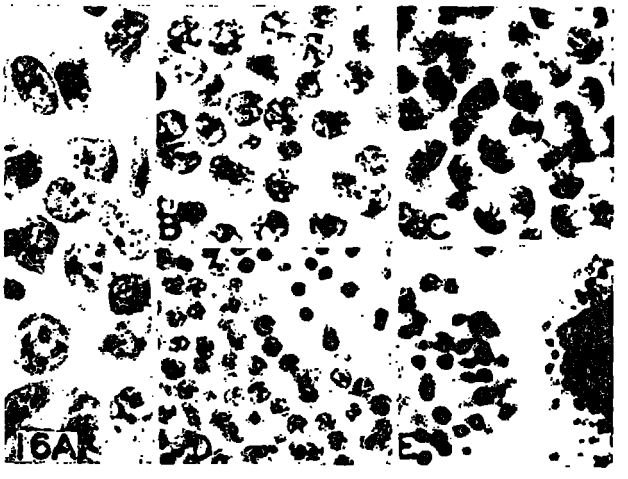

FIGURE 16.—Composite photo showing changes in size and form of cells during spermatogenesis from the free spermatogonia stage to formation of spermatozoa. (A) Spermatogonia taken from section shown in figure 14, the others from section depicted in figure 15. (B) Primary spermatocytes. (C) Primary spermatocytes in the place of synizesis. (D) Secondary spermatocytes and a few spermatids. (E) Spermatids (left) and spermatozoa (right). × 1050.

FIGURE 17.—Left testis of normal precociously mature rainbow trout; length 6.6 inches, age 8 months. Weight of testis 2,150 mg. Lobules greatly enlarged and filled with masses of fully developed spermatozoa. Cells lining walls of lobule are primary and secondary spermatocytes and spermatids. × 100.

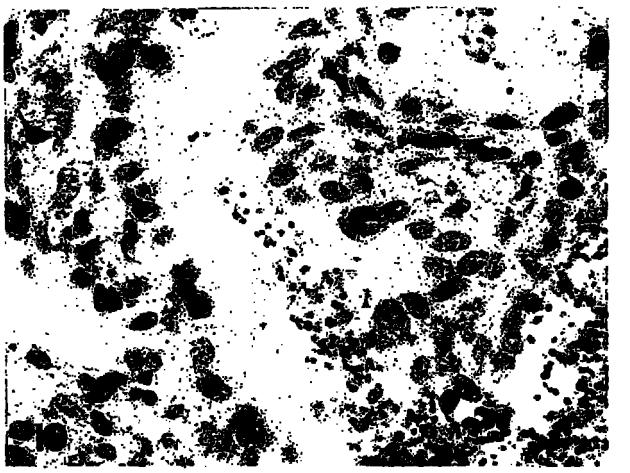

FIGURE 19.—Testis of normal spawning rainbow trout (steelhead). Testes flabby and oozing milt. Lobules much shrunken in size from fully mature state (fig. 17) and contain relatively small numbers of spermatozoa. Septa are much thickened in contrast to those in figure 18. Attached to surface of the septa are numerous lobule boundary cells—Leydig cell homologues—and an occasional spermatogonium. × 500.

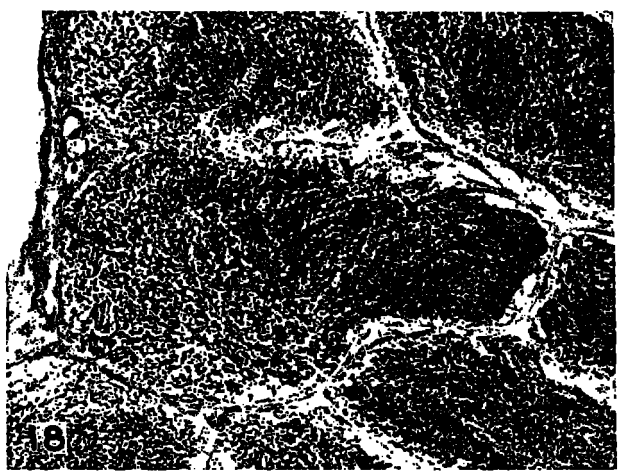

FIGURE 18.—Right testis of normal precociously mature rainbow trout; length 6.6 inches, age 11 months. Testis exuding milt partly spent, weight 453 mg. Contents of lobules consist entirely of spermatozoa; no other free cells seen. Septa thin. × 225.

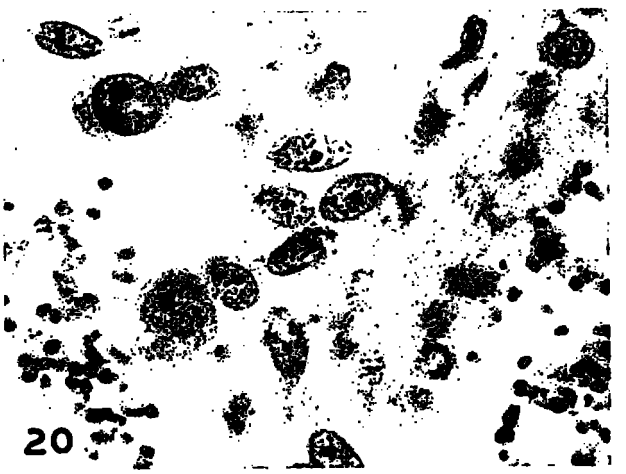

FIGURE 20.—Higher magnification of right central area of figure 19 showing several lobule boundary cells with oblong nuclei and a single nucleolus. Two spermatogonia at left of photo are easily distinguished from these cells by their larger size, rounded nucleus, which contains more heavily staining chromatin and sharply defined cell boundary. × 1050.

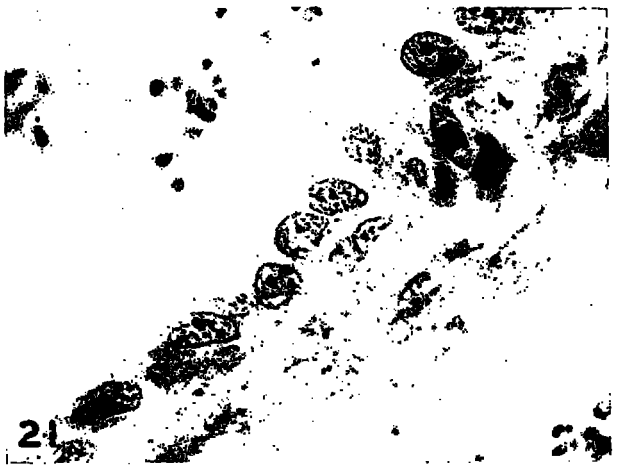

FIGURE 21.—Testis of spawning steelhead trout showing Leydig cell homologues lining the lobule. Processes of cells faintly seen. × 1050.

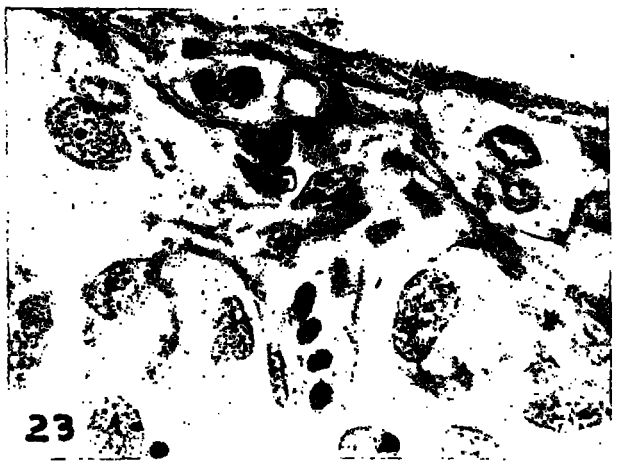

FIGURE 23.—Testis of spent steelhead trout showing Leydig-like cells in the interstitial tissues. × 1050.

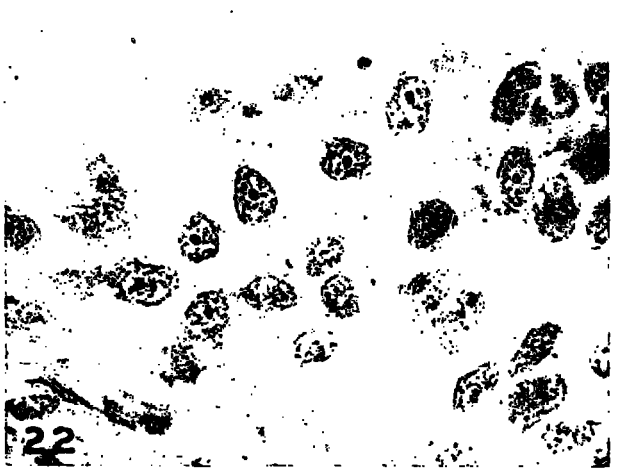

FIGURE 22.—Photo from same section as figures 19–21. In this area the lobule boundary cells are present in a syncytial-like mass. × 1050.

FIGURE 24.—Lobule boundary cells of spawning trout showing long processes extending into lumen of lobule with dark staining inclusions. × 1050.

FIGURE 25.—A group of lobule boundary cells showing inclusions. × 1050.

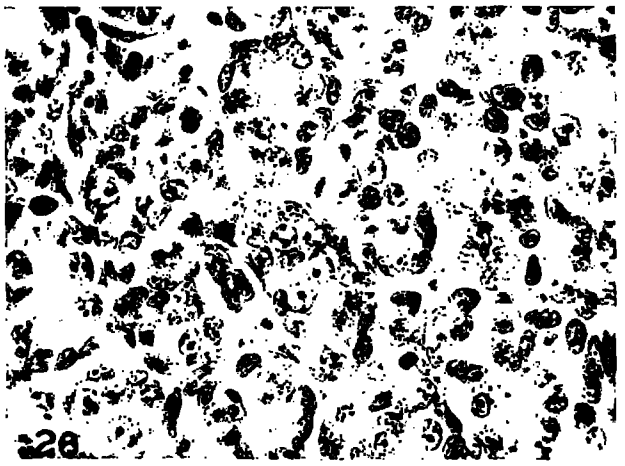

FIGURE 26.—Right testis excised from rainbow trout No. 293, length 7.2 inches, age 13 months. Weight of testis 13 mg. Histology that of infantile gonad. × 500.

With spawning, the lobules shrink and the septa become greatly thickened as shown in figure 19. Varying numbers of spermatozoa remain for some weeks. However, spermatogenesis has ceased. The lobules are lined with two quite distinct types of cell. The larger and less frequent are spermatogonia, characterized by a round nucleus containing considerable dark-staining chromatin, and a sharply defined cell boundary. The other predominant cell has an oblong nucleus with finely reticulated chromatin and a single nucleolus. Cytoplasm and cell margin is rather faint (figs. 20 and 21). They resemble the "lobule boundary cells" of Marshall and Lofts (1956) who consider them to be Leydig cell homologues. In some areas these cells are present in syncytial-like masses (fig. 22). Here and there much the same kind of cell but with a larger nucleus is present in small numbers in the interstitial tissues (fig. 23). Cytoplasmic inclusions are not uncommon in the "lobule boundary cells" and extension of the cytoplasm into tongue-like processes occurs frequently (figs. 24 and 25). Such are the chief characteristics of interstitial cells of Leydig occurring in mammals and in other groups of fishes. Failure to detect these cells in the earlier stages of the trout's spermatogenesis may be accounted for by the fact that they are probably modified connective tissue cells and quite likely do not develop until the later phase of gonadal maturation. Sertoli cells were not found.

Histology of the Testis in Trout Following Unilateral Gonadectomy

With growth in size, the remaining testes, after one was removed, exhibited the same sequence of histological changes observed in the normally maturing gonad. The only observed difference from the normal was a more focal type of early spermatogenesis occurring in many of these experimentally stimulated testes. Figure 27 shows the microscopic appearance of a remaining testis taken from a trout operated on at 13 months of age and sacrificed 6 weeks later. Primary and secondary spermatocytes as well as spermatids are present. The gonad excised at operation was found to be in the infantile state (fig. 26). With increasing size of the developing testes, the process of spermatogenesis tended to become more widespread until all the lobules were participating.

Histological examination of the testes of the control trout, i. e., those in which laparotomy and inspection only were made, revealed the finding that in fish of the same age, maturation was less advanced than in the testes remaining after unilateral gonadectomy. This was true even of the testes of control trout that showed the greatest

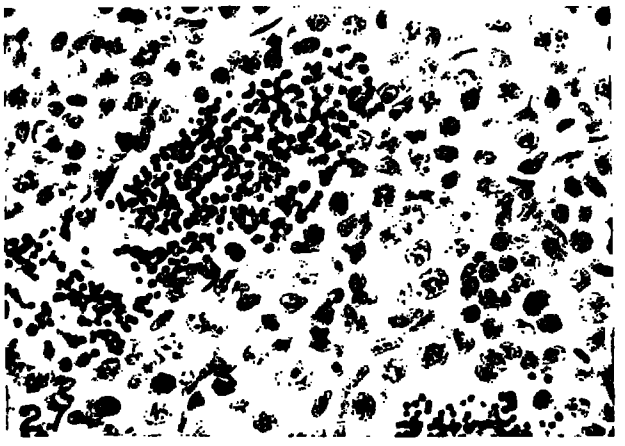

FIGURE 27.—Remaining left testis of trout No. 293 when killed weeks after unilateral gonadectomy. Testes weight 164 mg. Spermatogenesis has progressed to formation of clumps of spermatids among surrounding spermatogonia and primary spermatocytes. × 500.

growth during the experimental period. Figures 28 and 29 are photographs of the remaining testes of trout No. 332 (table 4) and of one the testis of control trout No. 336 (table 5). The percentage increase in the weight of the testis of these two fish was, as nearly as could be estimated, the same. The testis weight of the former trout, however, was 3 times that of a single testis in the latter (control) fish. In the test trout No. 332 (fig. 28), spermatogenesis is seen to be in an advanced stage with normally maturing cells (figs. 30 and 31), and although the testis of the control (fig. 29) shows all stages of development up to and including spermatozoa, these latter are present in relatively small numbers.

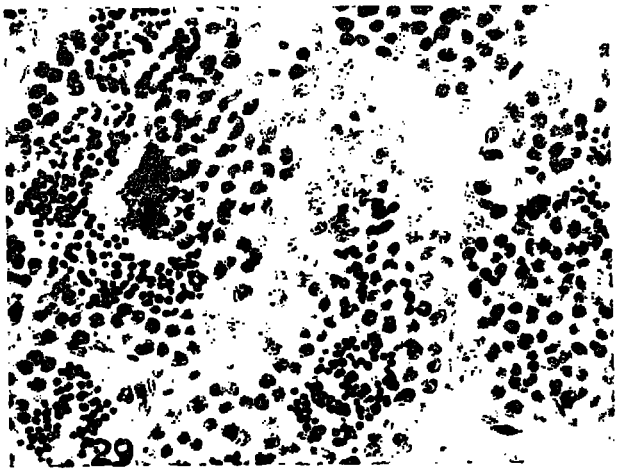

FIGURE 29.—Left testis of normal control trout, No. 336, table 5, length 7.1 inches, age 16 months, 6 weeks following laparotomy for inspection of testes which were seen to be infantile. Left testis weighed 105 mg. Histological picture that of spermatogenesis well developed to stage of spermatid formation with a few small clumps of spermatozoa as shown in photomicrograph. Process considerably less advanced than in No. 332 shown in Fig. 28. × 500.

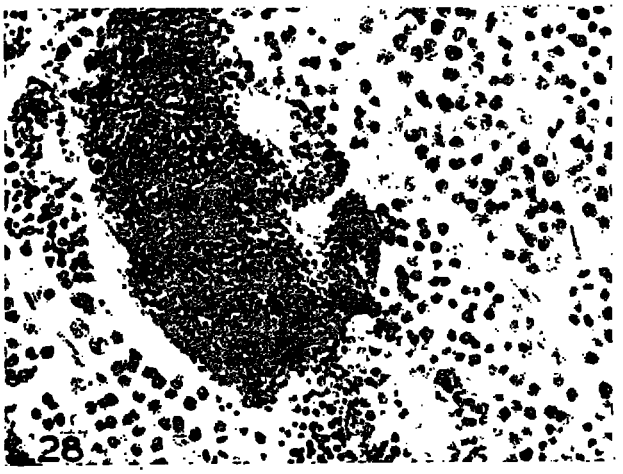

FIGURE 28.—Remaining left testis of trout No. 332, table 4, length 7.4 inches, age 16 months when killed, 6 weeks following unilateral gonadectomy. Weight of excised testis 17 mg., weight of remaining testes 335 mg. Spermatogenesis well advanced, large masses of spermatozoa present as well as spermatids, primary and secondary spermatocytes. × 500.

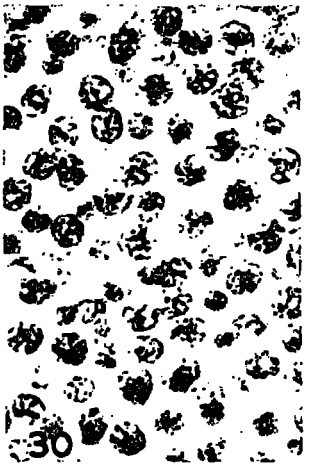

FIGURE 30.—Photographed from selected areas of section of testis of rainbow trout No. 332 shown in figure 28. Primary spermatocytes.

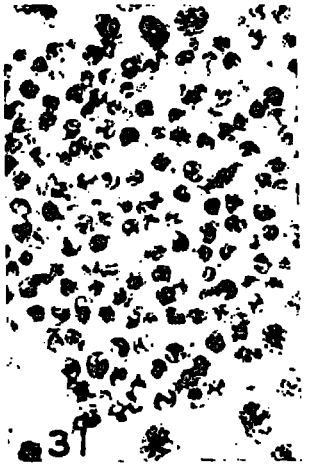

FIGURE 31.—Secondary spermatocytes. Cells appear to be developing normally as indicated by comparison with figures 16 (B) and (D). × 1050.

OTHER OBSERVATIONS ON STIMULATING TESTES DEVELOPMENT

The results of the foregoing experiments on unilateral gonadectomy leave unanswered a number of questions such as the reason for marked differences in response between trout of different ages, the influence of nutrition, the role played by the pituitary gland, and others. It was with the hope of obtaining more knowledge of the factors that control growth and development of the testes that the following experiments were carried out.

Depressing Effect of Starvation on the Growth of the Testes

Rate of growth of the individual experimental fish bore no relation to the amount of weight gain of the testes, either in the unilaterally gonadectomized trout or in the controls. While the maximum increase in the weight of the testes observed in a given experiment most often occurred in those trout exhibiting the greatest gain in length, not infrequently a moderate increase in the size of the trout was associated with a greater percentage gain in testis weight than occurred in a fish showing twice as much growth. However, in those few trout showing relatively little growth (not more than 2 or 3 percent during the period of the experiment) there was no significant increase in the weight of their testes. This led to testing the effect of starvation.

A number of trout from which one testis had been removed were starved for 25 days. The results are shown in table 8. With 4 exceptions, the remaining testes in these starved fish exhibited little or no gain in weight, despite the fact that most of the fish were in an age group and were operated on at a time of year when marked growth of the remaining testis occurred in fed fish. (See table 1.) However, the trout exhibited in table 8A cannot be compared quantitatively with those shown in table 1, since the period of observation is considerably shorter in the former group. A second similar experiment was carried out in which the fish were starved for 35 days. The results (table 8B) were essentially similar to those in the trout starved for 25 days. The average gain in weight of the remaining testes of the group was less than 60 percent, a negligible amount.

TABLE 8.—*Depressing effect of starvation on growth of remaining testis following unilateral gonadectomy*

Trout No.	Length of trout	Age at autopsy	Weight of excised testes	Estimated weight of remaining testes	Remaining testis at autopsy			Change in length of trout
					Weight	Gain in weight	Gain in weight	
A. Starvation period 25 days	*Inches*	*Month*	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Percent*	*Inches*
65	7.8	12	R 10	L 12	25	13	108	0
66	8.2	12	L 9	R 7	15	8	114	−0.1
86	7.9	12	L 12	R 10	11	1	10	−0.1
87	7.8	12	R 12	L 14	22	8	57	0
113	6.5	15	L 52	R 44	46	2	4	−0.1
118	8.1	15	R 9	L 10	22	12	120	0
124	8.0	15	L 14	R 12	45	33	275	0
181	8.0	19	L 8	R 7	6	−1	−14	−0.2
174	6.0	19	L 10	R 9	8	−1	−11	−0.2
176	7.7	19	L 13	R 11	18	7	60	−0.1
178	7.6	19	L 20	R 18	15	−3	−16	−0.1
419	8.6	19	L 18	R 15	20	5	33	0
420	8.0	19	R 10	L 12	18	6	50	+0.1
Average							59	
B. Starvation period 35 days								
464 [1]	8.0	22	L 11	R 9	10	1	10	−0.1
462	7.7	23	L 13	R 11	19	8	73	0
467	8.3	23	L 13	R 11	14	3	27	0
469	7.0	23	R 7	L 8	12	4	50	0
473	8.9	23	L 21	R 18	36	18	100	0
Average							52	

[1] 28 days' starvation.

NOTE.—The average loss in body weight of starved trout equaled 8 percent.

Stimulability of the Testes in Young Trout

The relatively small increase in weight of the remaining testes of the young unilaterally gonadectomized trout as compared with that observed in the older trout similarly treated (see table 3) could be attributed either to lack of sensitivity of the testes to gonadotrophic action or to failure of the juvenile pituitary to produce gonadotrophins in response to removal of one gonad. Test of the reactivity of the infantile male gonad in 7- to 9-month-old trout was made by implanting, intramuscularly, pituitaries taken freshly from trout with actively developing testes as well as from fish with infantile gonads. The testes of the recipient trout were inspected just before implantation of the pituitaries. The donors of the pituitaries ranged from 7 to 20 months of age. The implants were made into a pocket excavated in the muscle of the caudal peduncle. Cutting the pituitaries in 2 parts appeared to have no advantage over implanting them whole. Closure of the wound was made with closely spaced sutures. At the termination of the observation period, 35 days, the implants were examined under the dissecting microscope and if found were placed in Bouin's solution for later histological examination. The details of these experiments and the results are shown in table 9.

TABLE 9.—*Effect on testicular development in young immature trout 7 to 9 months old, of intramuscular implantation of pituitaries from male fish with developing or immature gonads*

[Period of observation 35 days]

Recipient trout No.	Donors of pituitaries			Survival of implants	Recipient's testes at autopsy		
	Age months	Weight of testes (mg.)	Degree [1] of testes development		Weight (mg.)	Percent gain in weight	Histological evidence of maturation [2]
185	[3] 20	4,800	+++	+	3,486	16,778	+
	7	2,500					
188	20	2,500	+++	+	749	4,680	+
	20	2,200					
201	20	2,590	+++	+	139	1,042	+
	20	2,500					
228	9	1,360	++	+	229	1,250	+
227	9	1,680	++	0	50	230	0
277	23	222	+	0	34	0	−
226	9	105	+	0	76	170	±
215	9	29	0	+	21	30	0
223	9	39	0	+	36	56	0
224	9	31	0	+	27	66	0

[1] Degree of testes development in pituitary donors:
+++=approaching full maturity.
++=well marked development.
+=beginning development.
0=infantile testes.

[2] Histological evidence of maturation:
+=well marked.
±=beginning.
0=none.
−=not done.

[3] When 2 pituitaries were implanted at a time 1 of them was cut in half beforehand. In single pituitary implants some were divided, others used whole.

It will be noted that 4 out of 7 trout receiving pituitaries from donors with large testes showed well-marked testicular growth. In one, R. T. 185, the testes grew from an estimated 25 mg. (observed at operation) to 3,486 mg. within 5 weeks. Figure 32 exhibits a photograph of these testes

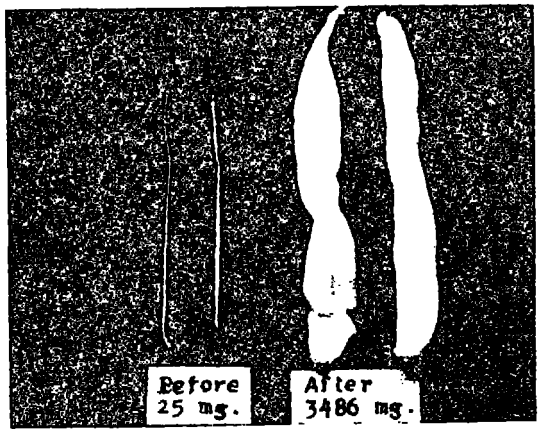

FIGURE 32.—Testes (right side of photo) of trout No. 185, table 9, 5 weeks following implantation of 2 pituitaries taken from rainbow trout with maturing testes. The testes on the left of the photo, excised from another fish, were of the same estimated size and appearance as the testes of No. 185.

removed at autopsy together with a pair of 25-mg. testes taken from another trout for comparison. In three cases Nos. 226, 227, and 277, no living pituitary tissue was found on microscopical examination of the implant, and little or no growth of the recipient's testes occurred in these fish. In trout Nos. 215, 223, and 224, implants of pituitaries taken from donors with immature testes showed well-organized and vascularized pituitary tissue but failed to produce any significant growth or maturation of the recipient's gonads.

Effects of Testis Implants in Immature Trout

In an attempt to determine what effect the implantation of immature testicular tissue would have on the growth of the remaining intact gonad, a series of experiments were undertaken in which one infantile testis was excised and immediately implanted into the spleen, or the peritoneal cavity, or into a muscle pocket in the caudal peduncle. The grafts took in all these sites. However, the relation of this procedure to increased growth of the remaining intact testis was equivocal. Of the first 4 trout thus treated, 2 showed at the end of 6 weeks moderate to very

marked accelerated growth of the remaining testis. The other 2 exhibited no change in size of the intact gonad. These trout were at an age and time of year when spontaneous gonadal development was very apt to occur. The next 5 trout treated in this way were 7 to 8 months of age when only a small percentage of male trout normally show precocious sexual development. Four of the 5 grafts were found to be living. In one of these 4, the remaining testes exhibited well-marked development with an increase in weight of 600 percent over its estimated size at the beginning of the experiment. The other 3 showed no more weight increase of the remaining gonad than one might expect from the effect of laparotomy alone. Evidence of spermatogenesis in the implanted testicular tissue was found only in those trout showing accelerated growth of the remaining testis, which suggests spontaneous increased pituitary activity in these instances. So the results of the foregoing experiments provide no evidence for either suppression or acceleration of testis growth associated with implants of the trout's own testicular tissue.

Implants of infantile or maturing testes taken from other trout failed to survive.

Rate of Growth and Development of Testes Under Experimental Stimulation

The findings of the present study indicate that the immature testes of the rainbow trout can grow with extraordinary rapidity when fish are at the appropriate age and season of the year. Table 2 displays a number of instances of this kind. In unilaterally gonadectomized fish, increases in the weight of the remaining testis of 400- to 500-fold within 6 weeks were not uncommon in trout 17 to 18 months of age. Figure 33 illustrates an instance of this kind. Whether such rapid growth occurs in rainbow trout under normal conditions is not known, since laparotomy for inspection is essential to determine the size of the testes at the beginning of the observation. And it may well be that the stress resulting from the operative procedure is responsible to a considerable degree for the intense pituitary activity. However, it seems probable from the data assembled in the present study, that when optimum conditions occur, growth and development of the infantile testis in the normal rainbow trout can take place in a relatively short space of time.

None of the considerable number of experimental fish studied had reached full gonadal maturity, even those kept under observation for as long as 10 weeks. Microscopic examination of the largest and most grossly mature appearing testes showed the predominant cell type to be spermatocytes with, however, many spermatids and spermatozoa; but the latter were not present in the great masses found in the fully ripe testes.

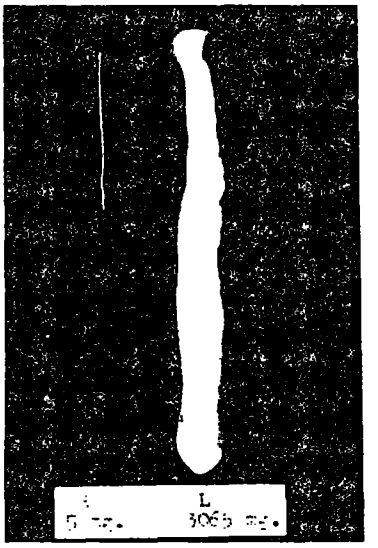

FIGURE 33.—Testes of trout No. 151, 6.1 inches long and 17 months of age when right testis was excised. Six weeks later when trout was killed, left testis weighed 3,065 mg. a 509-fold increase in weight.

DISCUSSION

The literature on unilateral gonadectomy in fishes is exceedingly sparse. Only one reference was found in which the effect of the procedure on the remaining testis was mentioned.[5] Craig-Bennet (1931) observed some hypertrophy of the remaining testis of the unilaterally gonadectomized 3-spined stickleback but gives no weights. Tozawa (1929) performed unilateral gonadectomies on the bitterling but made no mention of change in size of the testes remaining. On the other hand, a number of studies on this subject have been made with birds and mammals. Domm and Juhn (1927) found that the nonexcised testis of the chicken, when examined 32 weeks after

[5] See Addenda.

unilateral gonadectomy, weighed as much as the 2 testes of controls of similar age and size. They called this phenomenon compensatory hypertrophy. Belsky (1936) also working with chickens observed hypertrophy of the remaining testis but only some 25 to 30 percent greater than normal. Observations on the effect of unilateral gonadectomy in mammals goes back to Ribbert (1895) who employed adult rabbits and guinea pigs. He found that after an interval of 7 months the remaining testis of operated rabbits weighed almost twice as much as a single testis of the controls. The same effect was observed in guinea pigs but the weight of the nonexcised testis was only 40–50 percent greater than that of a single gland of the control. Lipschutz's (1922) results in young rabbits confirmed those of Ribbert. Likewise, Saller (1933) found that old mice responded to unilateral gonadectomy by a doubling of the weight of the remaining testis.

The results of the present study indicate that under the optimum experimental conditions, the remaining testis in the unilaterally gonadectomized trout may increase to 4 times the size of a single testis in the control during a period of 6 weeks (see table 3). This is twice the maximum growth of the remaining gonad recorded for mammals and birds observed over much longer periods of time. However, just below and above the optimum age of 16 months the weight of the remaining testis in the trout was approximately equal to the combined weights of the 2 testes in the controls.

The principal difficulty in demonstrating this phenomenon in the rainbow trout is that the operative procedure of simply opening and closing the peritoneal cavity appears to stimulate the initiation of growth and development of the testes. The effect is slight in young trout up to 14 months of age but increases progressively after this age until at 18 months the testis growth of the operated controls may be just as rapid as that of the unilaterally gonadectomized fish. It seems probable that the stress of operation constitutes the stimulating factor.

The lack of any detectable effect of unilateral gonadectomy in trout younger than 13 months of age and the significant and progressive percentage gain in weight of the remaining testis with increasing age (up to 17 months) suggests that the pituitary of the juvenile trout fails to respond to the stimulus of removing one gonad. That the infantile testis is fully responsive to pituitary gonadotrophins was shown by the very rapid growth of the testis in 7- to 9-months-old fish implanted with pituitaries taken from other trout exhibiting maturing testes. Further and equally clear evidence for stimulability of the juvenile testes is the occurrence of spontaneous precocious maturity in some 10 percent of rainbow trout at this age. These facts imply that in the great majority of fish, the ability of the pituitary to produce gonadotrophins is very limited during the first year of the rainbow trout's life. The lack of any demonstrable gonad-stimulating effect of implanted pituitaries from young trout with infantile testes (table 9, trout Nos. 215, 223, 224) supports this inference. With the beginning of the second year the gonadotrophic function develops progressively until at about a year and a half the pituitary is capable of producing large amounts of the hormone. Furthermore, with increasing age the pituitary becomes more easily stimulated, as shown by the greater effects on the testes of both unilateral gonadectomy and laparotomy alone. Most striking in this respect is the fact that just bringing trout into the laboratory and feeding them well with consequent rapid growth, caused a pronounced testicular development in all the males so treated (table 7). It should be pointed out that increased growth rate resulting from abundant food supply may not be the only factor involved in changing the habitat of the trout from outdoors to indoors. Diminished light and close confinement are possible influences in this respect, but of undetermined importance in the present experiments.

Whether the accelerated growth and development of the testis remaining after unilateral gonadectomy is due entirely to increased output of gonadotrophin from the pituitary is not clear. Weiss (1947) brought forward evidence to show that partial removal of an organ will automatically entail compensatory growth of the rest of the organ by means of reducing the concentration of certain diffusible components from the organ itself which are capable of limiting its growth. Attempts to study this possibility through reimplanting the excised testis gave equivocal results. However, improved techniques of tissue transplantation might yield more information. Evidence for this phenomenon being predomi-

nantly, if not entirely, a gonadotrophin effect is provided by the action of pituitary implants as shown in table 9. Accelerated growth of the recipient's testes occurred only when the implanted pituitaries came from donors with developing gonads and only when the implants survived. Unilateral gonadectomy in hypophysectomized trout would provide another analytical approach.

The present observations on the histological changes occurring in the testes of the rainbow trout are in agreement with those described by Weisel (1943) except for the occurrence of cells homologous with the interstitial cells of Leydig. Weisel stated that in neither the rainbow trout nor the sockeye salmon did he detect in the interstitial tissues any cells which had the appearance of secretory function. More recently, Potter and Hoar (1954) have reported the presence of interstitial cells in the testis of Pacific salmon (*O. keta*) which appear to resemble closely Leydig cells of the mammalian male gonad. Marshall and Lofts (1956) were the first to describe the occurrence of Leydig cell homologues lining the lobules in the testes of certain teleost fishes, including the char (*Salvelinus willughbii*). They have designated these as "lobule boundary cells" in contradistinction to the interstitial cells of Leydig and believe that they evolve from fibroblasts present in the lobule septa. Miller and Robbins (1954) had previously described the presence of similar cells lining the lobule of the spent testis in the salamander *Taricha torosa*. They stated that "the tissue analagous to the interstitial cells of the higher vertebrates consists of a layer of lipid containing cells of connective tissue origin together with a layer of transformed Sertoli cells." The findings of the present study, namely the occurrence of both lobule boundary cells and Leydig-like cells in the interstitial tissues would seem to place the rainbow trout in a category distinct from those fishes which exhibit only one of these two cell types. (See Marshall and Lofts.)

From accounts in the literature the process of spermatogenesis in the salmon appears to be quite similar to that observed in rainbow trout except for possible differences in the earliest stages. Jones (1940) describes migration of the germ cells in the maturing Atlantic salmon parr. Weisel makes no mention of any such phenomenon in the early maturation of the adult land-locked sockeye salmon. Certainly there was no evidence of migration of germ cells or spermatogonia in the rainbow trout of the present investigation. Further study of other species of salmonids should help clarify this subject. The reader is referred to Turner's (1919) account of spermatogenesis in the perch for the description of a special type of migration of germ cells.

The occurrence of precocious sexual maturity in the trout observed in the present work is apparently quite a common phenomenon in the Atlantic salmon. A study by Orten, Jones, and King (1938) summarizes earlier data on this subject and adds their own observations. They found that about 40 percent of the population of salmon parr captured in the fall of the year were sexually mature. They also make the statement that precocious sexual maturity occurs notably in rainbow trout.

SUMMARY

An operative procedure for unilateral gonadectomy was developed and carried out in rainbow trout with a very low resulting mortality. Removal of one gonad from male trout with infantile testes at a suitable age, stimulated the initiation of spermatogenesis in the remaining gonad which showed rapid growth and development. Control trout of the same size and age in which laparotomy only was performed, exhibited similar changes but to a much lesser extent.

Unilateral gonadectomy in trout under one year of age resulted in relatively little increase in the size of the remaining testis, while from one year on, the effect of this procedure on testes growth increased progressively. That this difference was not due to the lack of sensitivity of the young immature testis to gonadotrophic action was indicated by the marked growth and development of such testes following intramuscular implants of pituitaries taken from trout with maturing testes. Rather, it seemed probable that the pituitary of the young sexually immature fish was incapable of responding to the stimulus of unilateral gonadectomy. This inference was supported by the absence of demonstrable gonadotrophin content of the pituitaries of such fish. Starvation suppressed the growth of the testes in both unilaterally gonadectomized and control trout.

Observations were made on the histological changes occurring during the complete cycle of spermatogenesis in both normal and experimental trout. No significant differences between the two were found. Also data on the size and growth rate of the testes of normal rainbow trout and the incidence of naturally occurring precocious maturity in young males are presented.

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ADDENDA

1. Several additional references in unilateral gonadectomy in fishes have recently come to the author's attention:

Bock, Friedrich.
1928. Kastration und sekundäre geschlechtsmerkmale bei teleostiern. Ztschr. f. Wiss. Zool. 130: 455–468.

Bock noted increase in size of remaining testis in unilaterally castrated sticklebacks, but gave no weights.

Peters, Hans M.
1957. Über die regulation der gelegrösse bei fischen. Ztschr. f. Naturforsch. 12–b: 255–261.

Peters observed that after removal of one ovary or parts of both glands the remaining ovarian tissue regenerated to the point of producing the normal number of eggs and mass of egg tissue but not in excess of normal.

Wunder, Wilhelm.
1955. Das verhalten von hoden, niere und leber nach entfernung von teilstücken beim karpfen. Zool. Anz. 155: 232–239.

Wunder found an increase in the weight of the remaining testis threefold to sixfold that of the excised gland. He employed carp with well-developed testes and gives no adequate operative controls; hence his results are in no way comparable with those of the present study.

2. Fixation of the testes of spawning steelhead trout revealed an intense concentration of lipid material in the lobule boundary cells, thus providing additional evidence for their functional identification with the Zeidig interstitial cells of the mammalian testis.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

DESCRIPTION AND DISTRIBUTION OF LARVAE OF FOUR SPECIES OF TUNA IN CENTRAL PACIFIC WATERS

By WALTER M. MATSUMOTO

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ABSTRACT

The larvae of four species of tuna—yellowfin (*Neothunnus macropterus*), skipjack (*Katsuwonus pelamis*), little tunny (*Euthynnus yaito*), and frigate mackerel (*Auxis thazard*)—are described in detail. Diagnostic characters are given to aid in the identification of the species.

The geographical and seasonal distributions of tuna larvae in equatorial waters from 1950 to 1952 are described. Yellowfin and skipjack larvae, which were the most abundant of the four species, were found to occur over a wide area between 23° N. and 15° S. latitude, from 120° W. to 180° longitude, the limits of the area investigated. The distribution was generally uniform over the entire area, but a slightly heavier concentration was noticed between 140° W. and 160° W. longitude from 5° S. to about 10° N. latitude. Although the geographical range has not been completely defined, the close adult-larva relationship points to a continuous transoceanic distribution along the equatorial currents. Both species appeared to be uniformly abundant throughout the year.

Nearly all the larvae were concentrated in the top 50 meters of water, with indications of a vertical, diurnal migration.

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DESCRIPTION AND DISTRIBUTION OF LARVAE OF FOUR SPECIES OF TUNA IN CENTRAL PACIFIC WATERS

By WALTER M. MATSUMOTO, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

The distribution of tuna larvae in the central Pacific is only one of several facets of an investigation of the life history, distribution, and abundance of tuna being undertaken by the Pacific Oceanic Fishery Investigations (POFI), of the United States Fish and Wildlife Service. The purpose of the present study is to identify and describe the tuna larvae found in these waters, to gain information on the location and time of spawning, and to obtain another measure of the comparative magnitude of the adult populations of the different species.

While it would have been logical and desirable to study the early life history of the tunas, beginning with the eggs, it was not possible to do so, since there were no discernible differences between the eggs of one species of tuna and those of another. All the ripe or near-ripe eggs examined from known species appeared alike (all had an opaque yolk mass and a distinctly noticeable oil droplet), and the range of egg diameter measurements for any one species overlapped that of the others. Consequently, no detailed work was done on their identification.

This paper presents comparative descriptions, based on material from zooplankton hauls, of the larvae of four species of tuna: yellowfin, *Neothunnus macropterus* (Temminck and Schlegel); skipjack, *Katsuwonus pelamis* (Linnaeus); little tunny, *Euthynnus yaito* Kishinouye; and frigate mackerel, *Auxis thazard* (Lacépède). The collections are sufficiently complete to enable us to trace the several species from early through late larval stages. The report also contains discussions of the horizontal and vertical distribution of these larvae, the diurnal variation and species composition of the larval catches, and estimations of the spawning area and time of spawning as evidenced by the development and distribution of the larvae.

NOTE.—Approved for publication, February 26, 1957. Fishery Bulletin 128.

The zooplankton samples from which the tuna larvae were collected were obtained from two main areas, equatorial waters and Hawaiian waters, during the years 1950 to 1952 on eight cruises of the POFI research vessel *Hugh M. Smith*. General station positions are shown in figures 1 and 2 (data on larvae collections for all

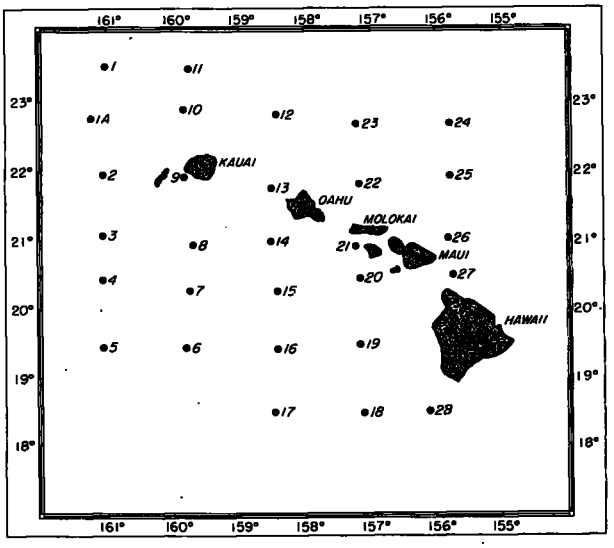

FIGURE 1.—Station locations of the *Hugh M. Smith* during cruise 6 in Hawaiian waters

the cruises are compiled in appendix tables 1 to 8, pp. 67–72). Samples were taken in 1-meter nets (*see* King and Demond, 1953, for detailed description), hauled according to two different methods. The first method was a 1-hour horizontal haul in which three nets were towed simultaneously at three different depths. The second method was a 30-minute oblique haul, a single open net being lowered to a depth of 200 meters and raised to the surface in a continuous operation.

In addition to the material collected by POFI, about 100 specimens of *E. yaito* and over 500 specimens of *A. thazard* taken in waters of the

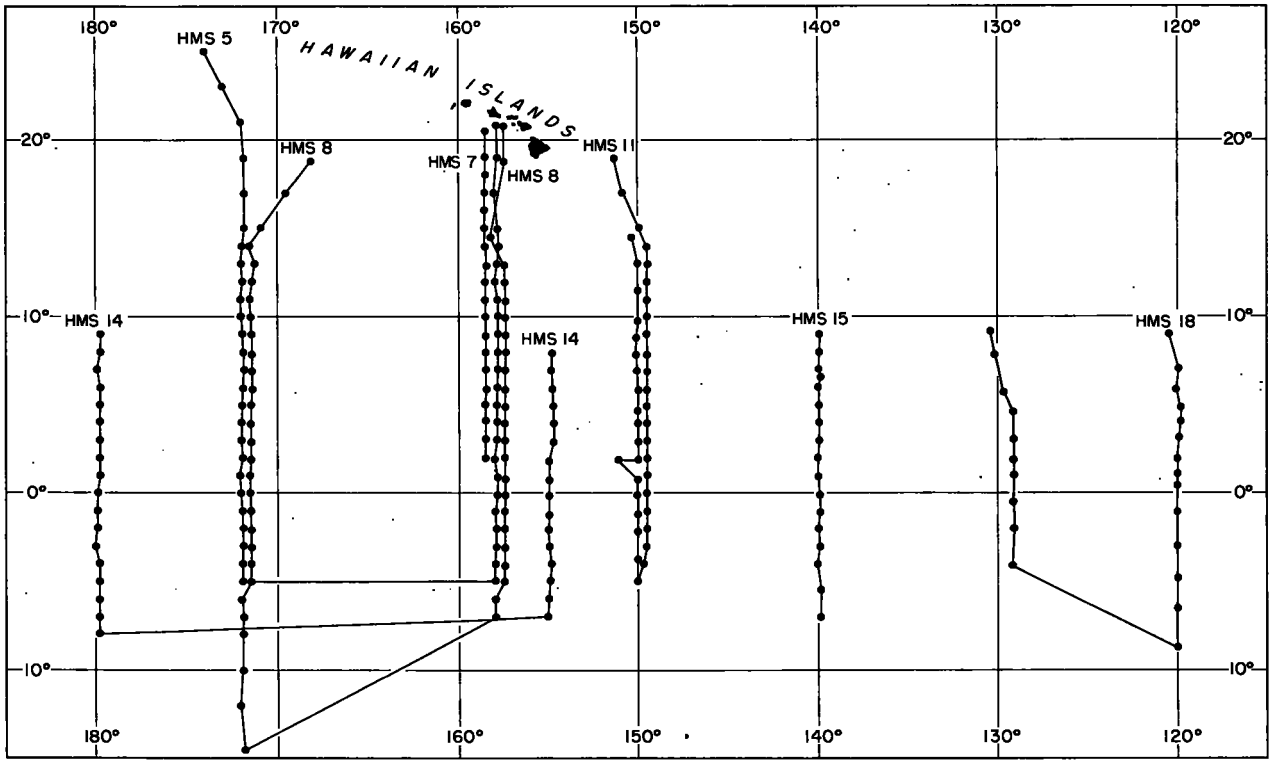

FIGURE 2.—Station locations of the *Hugh M. Smith* in equatorial waters.

East Indies during the 1928–30 *Dana* Expedition were examined.

The author wishes to thank the many POFI staff members who assisted in sorting the fish larvae from plankton samples, Wilvan Van Campen for numerous translations of literature in the Italian and Japanese languages, Tamotsu Nakata for drafting the charts in the text and for his advice on the reproduction of the drawings of tuna larvae, and the various staff members who critically reviewed the manuscript. Special thanks go to Dr. Å. Vedel Tåning, through whose kindness it was possible for us to examine the larval tunas collected during the 1928–30 *Dana* Expedition; to Dr. Milner B. Schaefer, Director of the Inter-American Tropical Tuna Commission, for the loan of juvenile *A. thazard*; to the California Division of Fish and Game for the loan of juvenile *E. lineatus*; to the Gulf Fishery Investigations for the loan of juvenile *E. alletteratus*; and to Dr. E. H. Ahlstrom, South Pacific Fishery Investigations, U. S. Fish and Wildlife Service, for his helpful criticisms and suggestions on the drawings of the larvae.

DESCRIPTION OF SPECIES

While there have been several valuable contributions to the identification of juvenile tunas, very little has been done on the identification of the larvae. The two most complete studies to date are those by Ehrenbaum (1924) and Wade (1951). Ehrenbaum examined larvae collected on the Danish oceanographical expeditions of 1908–10 to the Mediterranean and adjacent seas. The lack of juveniles in his collections did not permit him to make positive species identifications, and although his work has been cited in this paper as a general reference, for the most part his identifications have not been followed. Wade studied the larvae taken from waters around the Philippine Islands and was successful in collecting larval as well as juvenile specimens of *N. macropterus*, *K. pelamis*, and *E. yaito* (Wade 1950). His collections came from an area where adults of five species of Scombridae had previously been recorded [i. e., *Thunnus orientalis*, *T. germo* (=*Germo alalunga*), *Parathunnus mebachi* (=*P. sibi*), *Kishinoella tonggol*, and *N. macropterus*]. While there is good reason to believe that Wade's designation

of certain larvae as *N. macropterus* is valid, some doubt exists as to his identification of *E. yaito*.

Prior to Wade's work, Schaefer and Marr (1948a, 1948b) had studied larval and juvenile stages of *N. macropterus*, *K. pelamis*, *E. lineatus*, and *A. thazard* taken off the Pacific coast of Central America. They had no difficulty in identifying the last three species. Regarding the first, their material came from an area where *P. sibi* is relatively scarce and their larger specimens showed anatomical characters that distinguish *N. macropterus*. However, these authors admitted the possibility that the smaller specimens were *P. mebachi* (=*P. sibi*), since identification could not be certain until juveniles of both species were available.

Our *N. macropterus* larvae resembled those examined by Wade and fitted nicely into the series of juveniles collected by Schaefer and Marr. Since ripe or nearly ripe gonads have been taken from adult *P. sibi* in equatorial waters (Yuen 1955), there is a possibility that some of the larvae could also be the young of *P. sibi*. While all indications seem to favor their being *N. macropterus*, final identification must wait until larvae and juveniles of *G. alalunga*, *P. sibi*, and some of the other scombrids have been caught and identified.

A situation somewhat comparable to that obtaining for *Neothunnus-Parathunnus* also exists for the species of *Auxis* discussed here. As pointed out by Wade (1949), the Philippine and East Indian regions have two species of this genus, *A. thazard* and *A. tapeinosoma*, these being rather easily separated as adults but much less so as juveniles. Apparently, only *thazard* occurs in the Hawaiian area,[1] and Hawaiian *Auxis* larvae are accordingly referred to this species. Because the present study also includes East Indian material, the possibility exists that specimens from that area may represent two species even though all material examined appeared identical with the Hawaiian *thazard*. There was no great difficulty in identifying larvae of *K. pelamis* and *E. yaito*.

In this section the detailed description of the smallest recognized specimen is given first. Descriptions of larger specimens follow in size sequence, and only the more prominent characters are noted. Finally, the distinctive characters or combinations of characters by which these species can be separated are discussed. The scheme of describing each specimen in its entirety, instead of following the development of certain anatomical characters throughout the size categories, was chosen because it seemed that this method would be more convenient for the reader. All descriptions and counts of the teeth and chromatophores on the head and body, unless specified otherwise, are based on one lateral half of the body, usually the left.

The smaller specimens were still in the initial stages of development and lacked many of the characters by which the adults are identified. They were separated into species by first segregating those larvae that were similar in appearance and then arranging them in a series according to size. From each series several specimens of various sizes were stained with alizarin according to the method described by Lipman (1935). The larger specimens in these series were more than 10 millimeters fork length and already possessed sufficient adult characters to permit positive identification. The more prominent and persistent characters, other than those used in identifying the larger specimens, were examined and traced down to the smallest individual in each series. The most useful of these characters are listed in tables 4 and 5 (pp. 53, 54). The six measurements used in tables 4 and 5 are defined as follows:

1. Total length: The distance from the tip of the upper jaw to the end of the longest caudal ray when the tail is not forked, and to the end of the middle caudal ray when the tail is forked.

2. Head length: The distance from the tip of the upper jaw to the posttemporal spine when the spine is present, and to the posterior margin of the head at the level of the vertebral column when the posttemporal spine is absent.

3. Mouth length: The distance from the tip of the upper jaw to the middle of the posterior edge of the maxillary, with the mouth closed or agape, varying with the specimen.

4. Snout length: The distance from the tip of the upper jaw to the anterior edge of the orbit.

5. Diameter of orbit: The diameter of the eye socket taken parallel to the body axis.

[1] After this paper was submitted for publication, 21 specimens of long-corseletted *Auxis*, probably *A. tapeinosoma*, were taken about 1 mile offshore from the Island of Lanai in the Hawaiian Islands, November 30, 1957, by the Fish and Wildlife Service research vessel, the *John R. Manning*. This is the first record of the capture of long-corseletted *Auxis* in Hawaiian waters. Inasmuch as the waters around these islands have been subjected to rather intense tuna fishing since the turn of the century and a careful check has been kept of the local fish markets for a form of *Auxis* other than *thazard* for the past 8 or 9 years, we believe that the long-corseletted form occurs very rarely in local waters and that its recent appearance may be due to unusual oceanographic conditions. In our opinion, its discovery does not materially change the larval identification presented here.

6. Dorsal interspace: The distance between the insertion of the first dorsal fin and the origin of the second dorsal.

7. Tooth counts: Counts given for one side only.

In general, tuna larvae are characterized by a compact, triangular visceral mass with a short intestine that is directed ventrally at its posterior end. The entire visceral mass is located well forward in the body, the preanal distance being less than one-half the total body length on specimens up to about 9 mm. A continuous median fin membrane starts at the nape and extends completely around the caudal region to the anal opening. The myomeres, when distinct, number between 38 and 42. The head, mouth, teeth, and eyes are well developed, and prominent preopercular spines are noticeable. Pigmentation is rather sparse, most of it being concentrated over the abdominal sac, over the brain, and in the caudal region, depending on the species.

As an aid in comparing the differences between larvae of various species and at different stages of development, the following summary of the key characters is presented in advance of the detailed descriptions, together with a sketch of a typical tuna larva (fig. 3) in which is incorporated the nomenclature used in this paper.

Neothunnus macropterus

a. Complete lack of chromatophores on the trunk, except over visceral mass, until the larva approaches 14 mm. total length.

b. No chromatophores over the forebrain.

c. Heavy pigmentation on the first dorsal fin in specimens of more than 7 mm.

Katsuwonus pelamis

a. Presence of a distinct chromatophore on the ventral midline of the caudal region.

b. Early appearance of chromatophores over the forebrain in specimens of more than 7 mm. total length.

c. Single chromatophore on middle of mandible in specimens of more than 7 mm.

d. Chromatophores only along outer edge of first dorsal fin.

Euthynnus yaito

a. Up to 4 chromatophores along the posterior base of the anal fin and the first 2 or 3 anal finlets. No chromatophores along the dorsal margin of the caudal region.

b. Series of chromatophores along the mandible, usually extending over the anterior half.

c. Heavily pigmented first dorsal fin.

d. Chromatophore usually present at the symphysis of the pectoral girdle.

Auxis thazard

a. A short series of closely spaced chromatophores on the middorsal, midlateral, and midventral lines of the caudal region.

b. Lower jaw free from pigmentation, except at the tip.

c. First dorsal fin relatively unpigmented, with 3 or less chromatophores at about 12 mm. in total length.

d. Chromatophore usually present at the symphysis of the pectoral girdle.

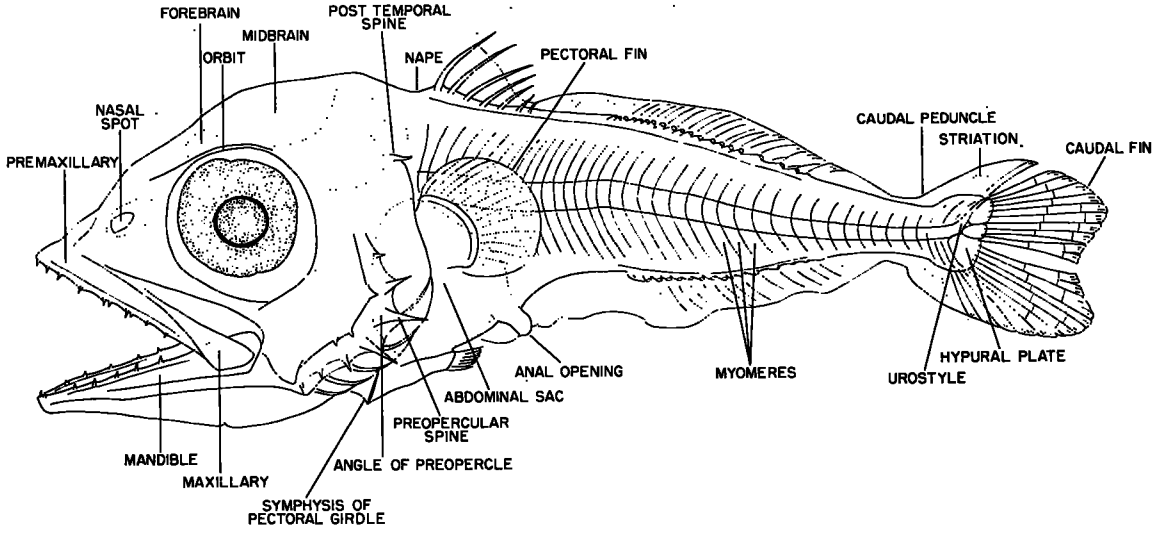

FIGURE 3.—A typical tuna larva with the nomenclature employed for various parts of the body.

YELLOWFIN (*NEOTHUNNUS MACROPTERUS*)

The description of this species is based on a study of 264 specimens, whose total lengths range from less than 3.0 mm. to 14.2 mm. (table 1). While the specimens less than 3.9 mm. in length could not be identified positively, they so closely resemble the smallest larva identified as *N. macropterus* that they are included in the total.

The smallest specimen identified as *N. macropterus* measures 3.9 mm. (fig. 4) and has about 40 myomeres. The body is evenly tapered caudally, and the abdominal sac is roundly triangular with the anal region directed sharply downward. The anal opening is well ahead of the midlength of the body. The snout on this specimen is slightly distorted, and no comparison of the head parts involving snout measurements has been attempted, although it is evident that the snout is only slightly longer than half the diameter of the orbit. No teeth are observable on this specimen, but other specimens of about the same length show up to 3 feeble teeth on each ramus of both jaws. Three spines project posteriorly along the edge of the preopercle, the middle one being the longest, and 2 minute spines are present on the surface of the preopercle just anterior to the preopercular spines.

The unpaired fins are not developed, but are represented by a continuous membrane extending from the nape completely around the caudal end of the body to the anal opening. Membranous pectoral fins are present, but ventral fins are lacking.

Head pigmentation is rather sparse, with only about 4 very small, scattered chromatophores over the membrane covering the brain and 2 internal

TABLE 1.—*Number and size range of larval* Neothunnus macropterus *collected by the* Hugh M. Smith *in Hawaiian and equatorial waters*

[See figs. 1 and 2 for location of stations]

Cruise and station	Number of larvae	Size range (mm.)
HAWAIIAN WATERS:		
Cruise 6:		
No. 1	2	5.3-6.0
No. 1A	5	4.4-6.5
No. 2	13	3.0-6.0
No. 5	2	3.5-4.5
No. 6	2	3.8-4.2
No. 7	5	5.4-8.0
No. 8	1	4.6
No. 10	12	3.3-6.1
No. 11	5	4.0-6.8
No. 13	6	4.0-5.6
No. 14	13	3.6-6.0
No. 15	7	4.0-10.2
No. 16	4	3.5-5.6
No. 18	16	3.2-7.5
No. 19	2	5.2-6.5
No. 21	8	3.6-6.5
No. 24	2	4.6-7.45
No. 25	15	3.5-5.6
No. 26	6	3.0-3.9
No. 27	6	2.5(?)-6.5
Total	132	2.5(?)-10.2

TABLE 1.—*Number and size range of larval* Neothunnus macropterus *collected by the* Hugh M. Smith *in Hawaiian and equatorial waters*—Continued

Cruise and station	Number of larvae	Size range (mm.)
EQUATORIAL WATERS:		
Cruise 5:		
No. 8	1	3.3
No. 12	1	4.9
No. 13	2	<3.0, 4.2
No. 14	1	7.0
No. 15	1	<3.0
No. 17	1	<3.0
No. 21	2	4.4, 5.2
No. 25	1	3.8
No. 26	9	3.2-4.6
No. 39	1	6.0
No. 41	1	4.9
No. 42	2	4.9, 5.5
No. 43	1	5.5
No. 45	1	3.5
No. 48	2	3.7, 4.9
No. 51	3	3.1-5.2
Cruise 8:		
No. 9	2	6.2, 7.9
No. 16	1	5.3
No. 21	1	3.0
No. 22	1	<3.0
No. 24	5	<3.0-5.6
No. 77	6	3.5-4.0
No. 78	4	<3.0-4.2
No. 79	2	4.0, 5.0
No. 82	1	14.2
No. 85	1	4.9
No. 93	1	6.2
No. 94	1	4.7
No. 97	1	5.2
No. 101	1	3.7
Cruise 11:		
No. 4	2	<3.0, 4.8
No. 6	2	5.3
No. 8	4	3.1-8.0
No. 9	4	3.2-5.6
No. 10	2	3.5, 3.7
No. 11	7	<3.0-6.6
No. 12	2	5.2, 6.6
No. 22	3	3.3-7.1
No. 23	1	3.0
No. 33	1	6.0
No. 35	1	4.0
No. 36	1	5.9
No. 37	2	4.5, 4.6
No. 40	3	<3.0-3.8
No. 42	1	3.8
No. 46	4	3.0-3.6
Cruise 14:		
No. 12	1	5.0
No. 14	1	5.0
No. 19	3	4.0-4.1
No. 20	1	7.1
No. 21	2	3.7, 4.1
No. 22	1	3.7
No. 30	4	3.8-6.4
No. 31	2	5.7, 7.8
No. 32	3	4.6-7.7
Cruise 15:		
No. 5	4	<3.0-6.0
No. 6	2	5.0, 8.1
No. 7	1	3.0
No. 14	1	4.5
No. 15	1	3.2
No. 16	1	4.1
Cruise 18:		
No. 4	2	3.0, 3.2
No. 5	2	3.1, 3.2
No. 6	1	3.2
No. 8	1	4.6
Total	132	<3.0-14.2

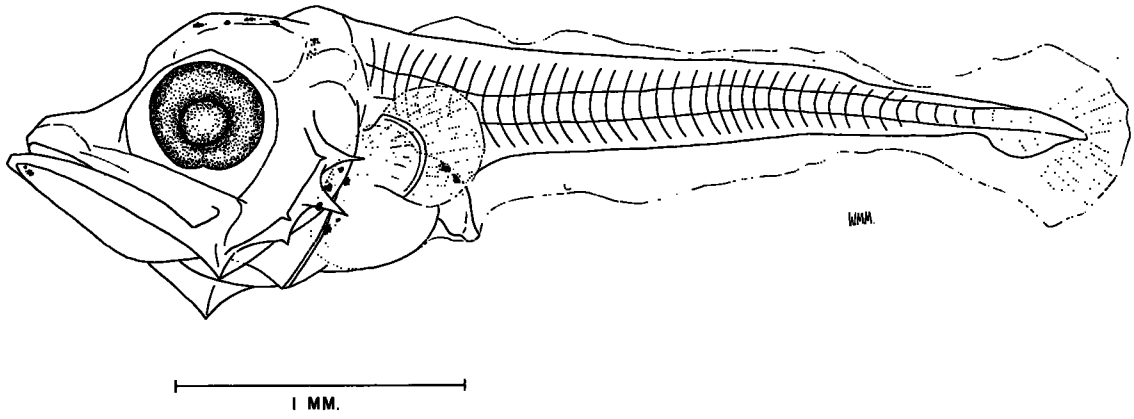

FIGURE 4.—*Neothunnus macropterus*, 3.9 mm. total length.

chromatophores along the posterior margin of the brain. Several large chromatophores are present over the anterior and posterior regions of the abdominal sac, but the rest of the body is free of pigmentation.

A specimen of 4.75 mm. has the same general appearance of the preceding stage, with 39 or 40 myomeres, but the body has deepened slightly. The teeth have increased to 5 on the upper jaw, but the 3 remain on the lower jaw. There is a slightly depressed, ovate, nasal spot on the snout which represents the future nostrils. The preopercular spines have increased to 4: 2 long spines at the angle and 2 small spines on the horizontal edge. There is no change in pigmentation, and the pelvic fins are just emerging as minute fleshy outgrowths from the ventral outline of the body beneath the abdominal sac.

Certain changes are evident in a 5.5-mm. specimen (fig. 5). The head appears slightly larger, 36.8 percent of the total length, and the snout, which is two-thirds the diameter of the orbit, is bluntly pointed. The mouth represents only 60.1 percent of the head length and all the teeth, 8 on the upper jaw and about 4 on the lower jaw, are small and feeble. Six preopercular spines are visible: 1 small spine on the vertical edge; 3 longer spines at the angle, the middle one being the longest; and 2 short spines on the horizontal edge.

The unpaired fins are still represented by a continuous membrane, which has degenerated in the region of the future first dorsal fin and appears slightly heavier there. The membrane also shows signs of degeneration in the region of the caudal peduncle, and about 10 incomplete rays are noticeable in the caudal fin. The pelvic fins are quite evident although they are still rudimentary.

The tips of both jaws bear several small chromatophores, and there are about 14 large chromatophores over the midbrain, although these

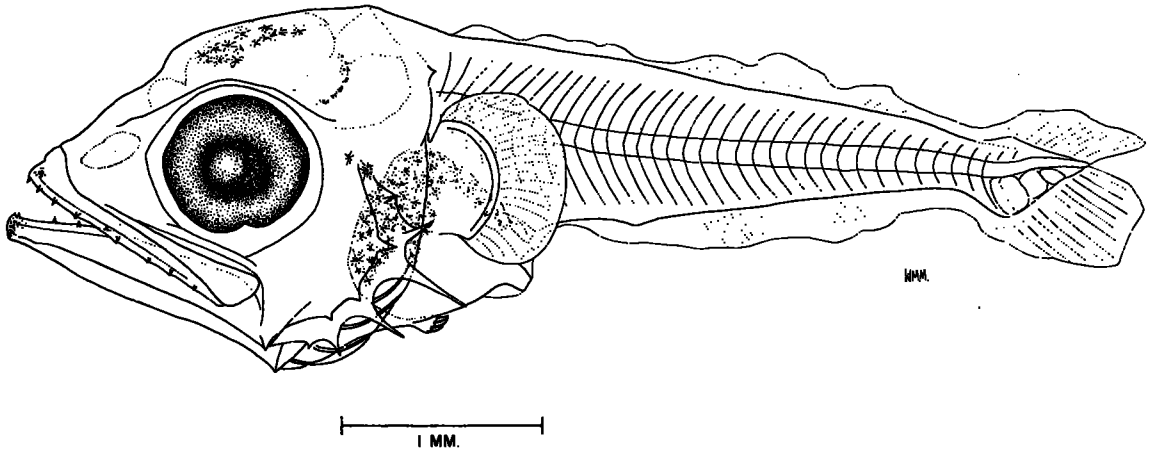

FIGURE 5.—*Neothunnus macropterus*, 5.5 mm. total length.

extend only over half of the brain area. A band of dark pigmentation lies along the posterior margin of the brain, and the 2 dermal chromatophores on the side of the head near the dorsal end of the preopercle make up the remainder of the pigmentation on the head. The dorsal half of the abdominal sac bears numerous large chromatophores, while the rest of the body is unpigmented.

Except for the appearance of 4 short spines in the first dorsal fin, about 12 rays in the caudal fin, and the formation of a very small spine near the posttemporal region, the specimen at 6.4 mm. (fig. 6) remains relatively the same in appearance as the previous one. There is a single, faint chromatophore on the third interradial membrane of the first dorsal fin, and the fin membrane here has degenerated to the height of the spines. The membrane is still high over the rest of the body.

At 7.15 mm. (fig. 7), the anal opening is closer to the midpoint of the body length. The snout is slightly longer, but is still not quite as long as the diameter of the orbit, and the nasal spot is beginning to constrict in the middle. The mouth is not very large and represents 62.1 percent of the head length. There are 10 or 11 small teeth on the maxillary and 6 or 7 similar teeth on the mandible.

The most noticeable development here is in the first dorsal fin, which bears 7 strong spines, the first 5 of them very long. About 19 rays are present in the caudal fin, which is just beginning to fork. The pelvic fins are only slightly larger than in the previous specimen.

There is an increase in the pigmentation over the brain, at the tips of both jaws, and over the abdominal sac. The band of pigment along the

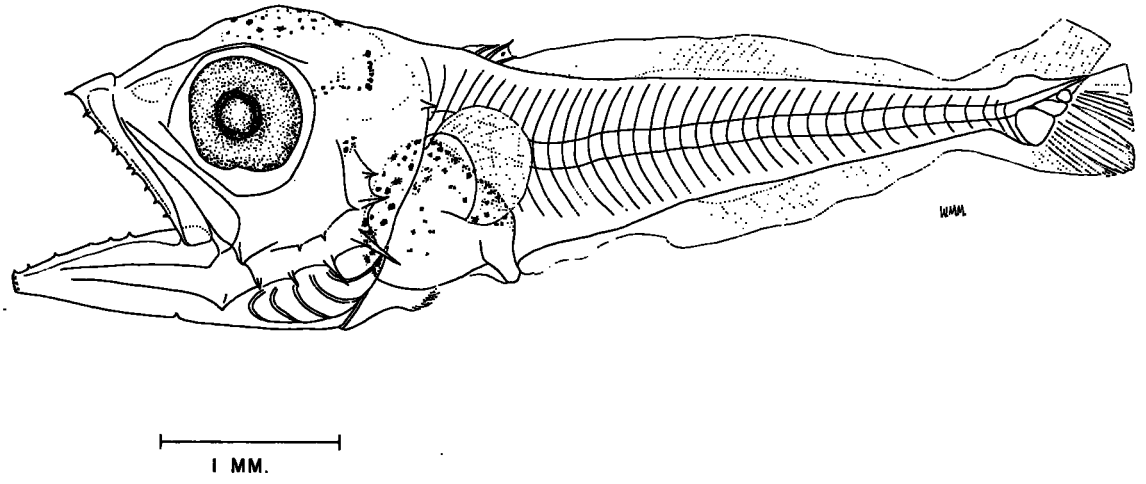

FIGURE 6.—*Neothunnus macropterus*, 6.4 mm. total length.

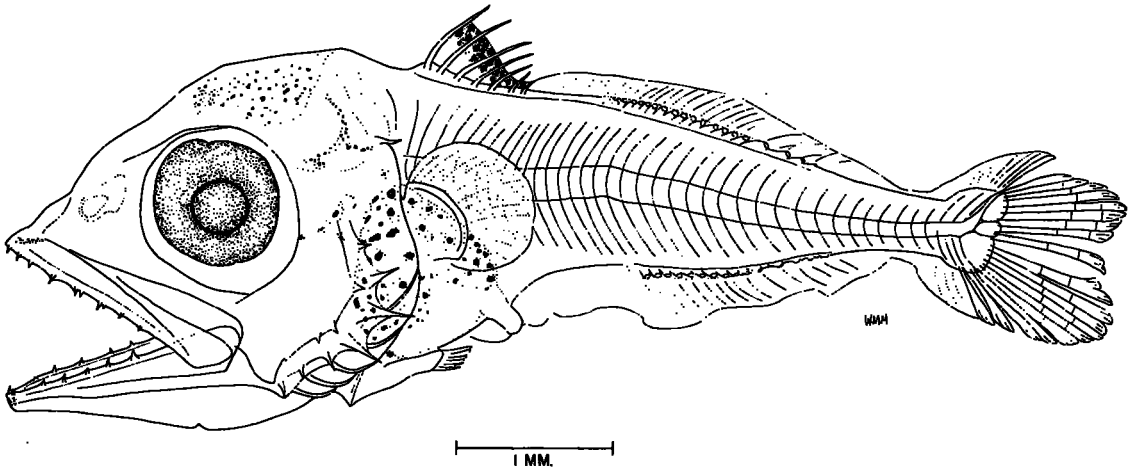

FIGURE 7.—*Neothunnus macropterus*, 7.15 mm. total length.

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posteroventral margin of the brain and the chromatophores near the dorsal end of the preopercle have increased in number and are most noticeable. Two chromatophores are present near the posterior edge of the orbit, and the darkly pigmented distal half of the interradial membrane of the first dorsal fin is rather prominent.

Some interesting development is noted in a stained specimen of 7.45 mm. While many of the dermal bony structures have ossified, the anterior vertebrae are just in the process of ossification. The first six vertebrae appear as "rings" and each of them has a very large, complete neural arch. On succeeding vertebrae the areas of ossification diminish in size until only the bases of the neural and haemal arches and their corresponding spines are evident at about the 14th vertebra. Posteriorly, only the urostyle is completely ossified and the hypural plate is just beginning to ossify.

A 7.95-mm. specimen is shown in figure 8. The general shape of the body remains the same as in the preceding specimen. The more obvious developments are the almost complete separation of the nasal openings, the deeper fork of the caudal fin, and the darker and larger area of pigmentation on the first dorsal fin, which is now almost completely pigmented, except for a narrow strip near its base. About 9 to 10 teeth are present on each jaw and 3 teeth are noticeable on the palatine bone.

While both the dorsal and anal fin rays are represented only by striations, there are 13+13 caudal rays. The pelvic fins, although complete with 1 spine and 5 rays, are very short. The rays of the pectoral fins are not distinct and appear only as striations.

In a 9.2-mm. specimen there is no apparent change in the head size, which is 37.9 percent of the total length of the body (fig. 9). The anal opening is at the midpoint of the body length, and the snout appears longer, its length being about the same as or slightly greater than the diameter of the orbit. The nares are separate, and both upper and lower jaws bear 12 teeth, while the palatine bone has about 4 very small teeth. Seven preopercular spines are discernible: 2 spines on the vertical edge, 2 spines at the angle, and 3 spines on the horizontal edge.

The first dorsal fin has 10 spines and a slightly convex outline. The rays of the second dorsal fin are not clearly defined and no accurate count could be made. There appear to be about 6 or 7 dorsal "finlets" and the anal fin has about 14 rays and 7 finlets, though the finlets are not completely formed and none of them is definitely separated from the others. The caudal fin has 14+15 rays, and the depth of the fork is about one-third the length of the longest caudal fin ray. The pelvic fins have the full adult complement of spines and rays, the longest of which are nearly as long as the longest spine of the first dorsal fin.

A stained specimen of 10.2 mm. shows 13 completely ossified vertebrae, and 13 more which are only partly ossified. The first haemapophysis appears on the 8th vertebra, and closed haemal arches are present only on the 11th, 12th, and 13th vertebrae. On the 12-mm., stained speci-

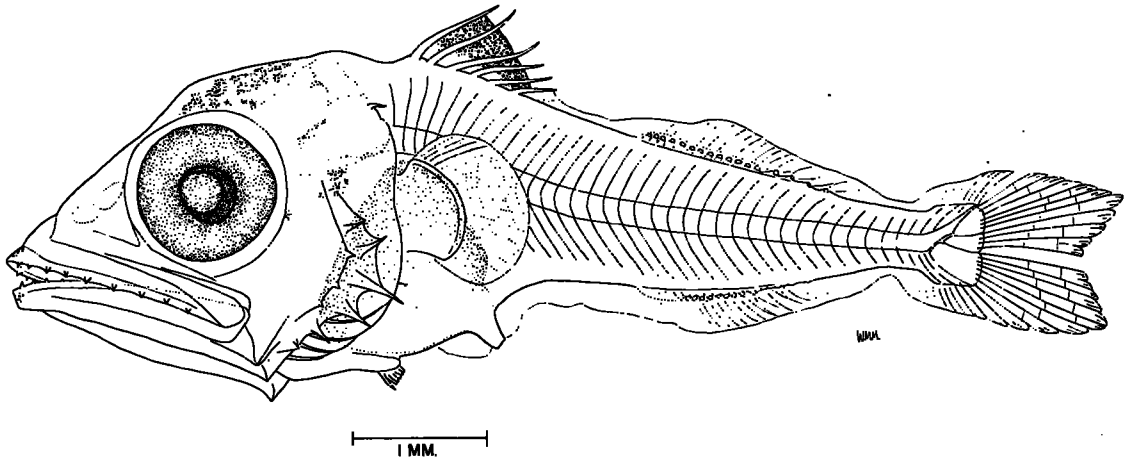

FIGURE 8.— *Neothunnus macropterus*, 7.95 mm. total length.

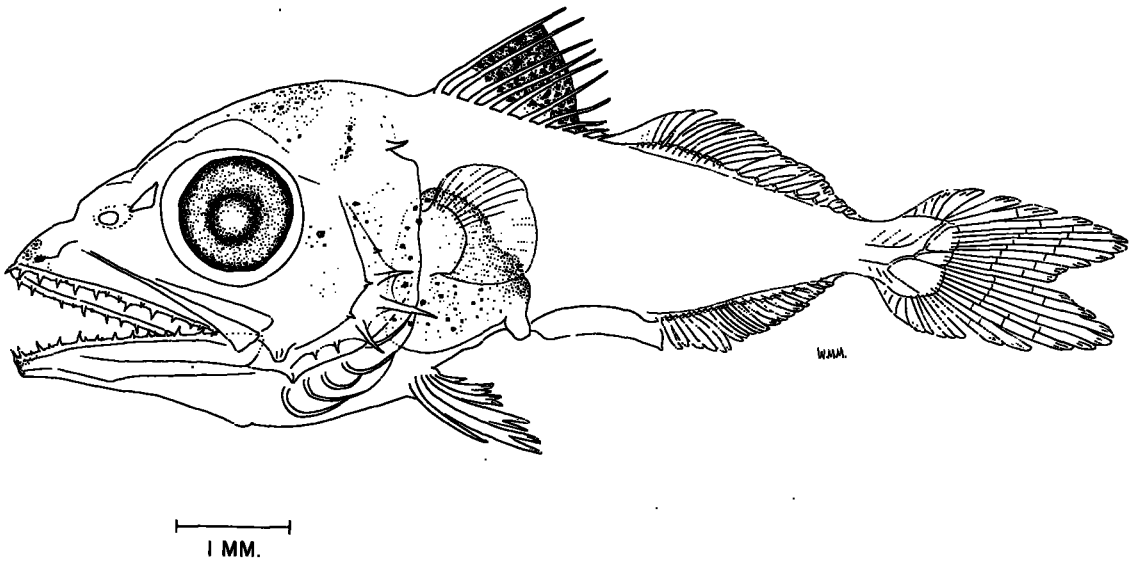

FIGURE 9.—*Neothunnus macropterus*, 9.2 mm. total length.

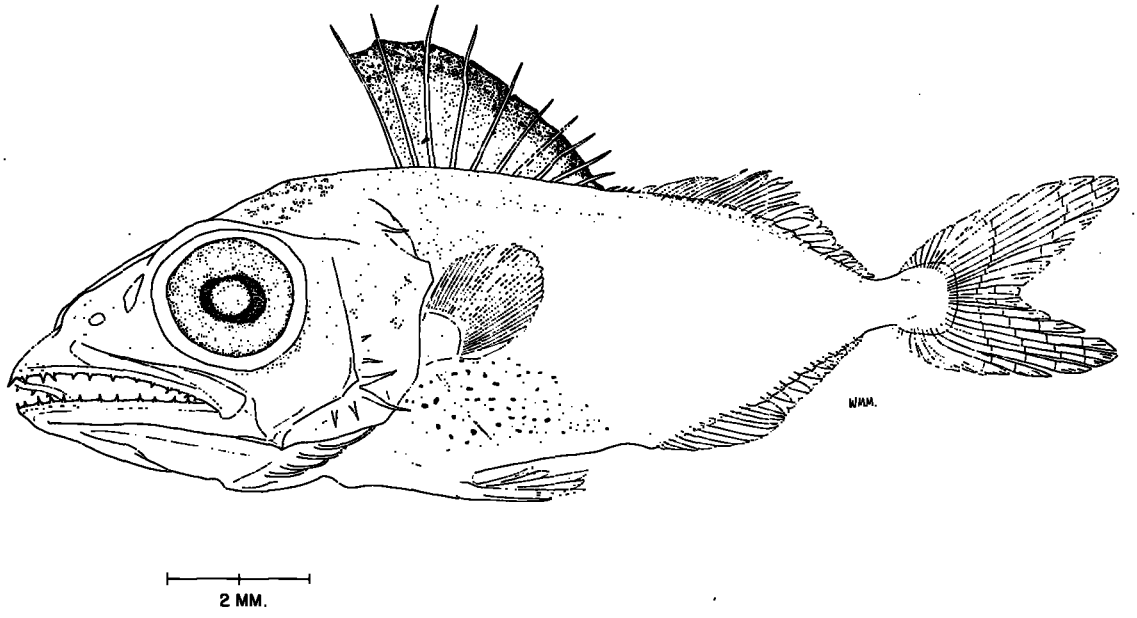

FIGURE 10.—*Neothunnus macropterus*, 14.25 mm. total length.

men all of the vertebrae are ossified, and they number 18 precaudals and 20 caudals, including the urostyle. The first few vertebrae are beginning to assume the hourglass shape of the adult centrum. The haemal arches are narrow, none of them being as wide as the diameter of the centrum at this stage of development.

At 14.25 mm. (fig. 10) the body is much deeper, especially near the insertions of the second dorsal and anal fins. The triangular abdominal sac is large and elongate, and the anal opening is just anterior to the insertion of the anal fin.

The head, which is 39.7 percent of the total body length, appears very large, and the length of the snout is equal to the diameter of the orbit. The nares are well separated, the round, anterior naris being about one-third the size of the nearly elliptical, posterior one. About 13 or 14 teeth are noticeable on both the upper and lower jaws in the unstained specimen. Six preopercular

spines are visible, but only the 2 longest ones at the angle still project free from the preopercular bone.

The first dorsal fin is composed of 14 spines and the fin outline appears slightly convex. Both the second dorsal and anal fins consist of 15 rays and 8 finlets. There are about 18+19 rays in the caudal fin, but those near the anterior edges are not clear enough to be counted accurately. The pelvic fin is very large and is almost as long as the pectoral fin, which now bears about 30 rays.

Pigmentation is beginning to resemble that of juveniles. The large chromatophores over the brain still extend over a relatively small area, but numerous, very minute chromatophores appear over the posterior part of the head and extend posteriorly in a band to a point beneath the insertion of the second dorsal fin. There is a patch of similar pigmentation immediately behind the opercle and dorsal to the pectoral-fin insertion. Small chromatophores also line the posteroventral margin of the orbit, while 5 to 6 large chromatophores are present on the surface of the opercle posterior to the eye. Pigmentation over the abdominal sac remains unchanged, while the first dorsal fin is now completely pigmented. A faint line of chromatophores is present along the bases of the first and second dorsal fins, extending posteriorly to about the second dorsal finlet. The rest of the body has no pigmentation.

SKIPJACK (*KATSUWONUS PELAMIS*)

A total of 476 specimens of *K. pelamis* measuring from 2.3 mm. to 20.1 mm. was sorted from plankton collections and examined (table 2). Also studied were 34 specimens from 20.0 mm. to 43.0 mm. collected with dip net at night-light stations in Kingman Reef lagoon in May 1951.

The smallest specimen that could be identified positively as *K. pelamis* measures 3.7 mm. in length (fig. 11); this specimen appears somewhat distorted in preservative. The body is elongate with both the dorsal and ventral outlines tapering evenly to the caudal end. The abdominal sac is roundly triangular in shape with the anal opening slightly anterior to the midpoint of the total length of the body.

Although the snouts on other specimens of comparable size are rather pointed, this is not evident here, probably because of distortion. The upper

TABLE 2.—*Number and size range of larval* Katsuwonus pelamis *collected by the* Hugh M. Smith *in Hawaiian and equatorial waters*

[See figs. 1 and 2 for locations of stations]

Cruise and station	Number of larvae	Size range (mm.)
HAWAIIAN WATERS:		
Cruise 6:		
No. 1	1	6.0
No. 1A	11	4.4–7.0
No. 2	4	4.0–6.0
No. 4	10	3.5–4.5
No. 5	14	3.6–5.5
No. 7	4	4.5–6.5
No. 8	9	3.5–8.5
No. 10	29	2.5 (?)–7.55
No. 11	9	4.1–7.65
No. 13	12	4.0–5.6
No. 15	13	3.2–6.5
No. 16	6	?–8.0
No. 18	27	3.6–8.8
No. 19	3	9.85–12.5
No. 20	2	3.6, 5.0
No. 22	2	4.0, 6.6
No. 24	3	6.2–8.8
No. 25	1	3.7
No. 27	4	3.5–3.7
Total	164	2.5–12.5
EQUATORIAL WATERS:		
Cruise 5:		
No. 2	1	4.5
No. 4	3	3.4–3.6
No. 11	3	4.6–5.0
No. 14	4	3.5–6.1
No. 16	2	9.1, 10.1
No. 19	1	3.8
No. 21	1	4.0
No. 22	8	3.5–8.8
No. 23	24	3.2–6.9
No. 25	17	2.7–4.9
No. 26	2	6.8, 10.0
No. 32	1	4.6
No. 35	1	7.0
No. 36	6	2.9–4.5
No. 37	6	3.3–8.0
No. 38	1	4.6
No. 42	1	6.5
No. 43	2	Distorted.
No. 45	4	3.1–4.0
No. 46	1	4.5
No. 51	2	3.6, 4.6
Cruise 8:		
No. 11	3	4.6–5.6
No. 20	1	7.2
No. 25	2	2.8, 3.0
No. 77	9	3.0–5.4
No. 78	2	4.0, 4.6
No. 79	5	4.1–6.1
No. 80	2	2.5, 5.0
No. 81	2	4.0, 4.2
No. 84	4	5.1–20.1
No. 85	1	3.6
No. 87	1	3.0
No. 88	1	3.0
No. 89	1	3.7
No. 90	8	5.0–6.5
No. 91	3	2.7–6.5
No. 93	1	8.1
No. 94	1	4.0
No. 95	2	5.0, 8.0
Cruise 11:		
No. 1	1	3.6
No. 6	1	5.0
No. 9	1	9.4
No. 10	1	3.1
No. 11	6	2.9–12.6
No. 12	1	6.7
No. 22	2	3.9, 8.0
No. 23	1	5.0
No. 24	2	5.5, 14.9
No. 26	2	6.5
No. 27	3	3.5–5.1
No. 29	21	3.8–6.5
No. 31	7	3.0–8.0
No. 33	1	4.1
No. 36	1	10.9
No. 37	3	3.4–6.3
No. 38	1	6.6
No. 41	1	3.9
No. 42	1	6.1
No. 43	1	4.2

TABLE 2.—*Number and size range of larval* Katsuwonus pelamis *collected by the* Hugh M. Smith *in Hawaiian and equatorial waters*—(Continued)

[See figs. 1 and 2 for location of stations]

Cruise and station	Number of larvae	Size range (mm.)
EQUATORIAL WATERS—Continued		
Cruise 14:		
No. 2	9	3.5–6.0
No. 4	1	3.1
No. 7	1	3.3
No. 8	1	3.0
No. 9	14	3.4–10.3
No. 10	2	5.0, 7.0
No. 12	4	5.0–9.4
No. 14	3	2.3–6.0
No. 17	2	4.2, 9.0
No. 18	3	3.5–5.6
No. 20	7	4.0–6.2
No. 21	8	4.0–4.6
No. 22	2	3.5, 4.5
No. 24	1	3.7
No. 25	2	3.0
No. 29	4	3.2–5.0
No. 30	4	3.5–6.5
No. 32	1	4.0
Cruise 15:		
No. 6	7	3.2–6.5
No. 7	10	3.2–7.5
No. 8	10	3.1–5.0
No. 9	8	2.7–5.9
No. 10	1	19.0
No. 14	3	3.2–4.2
No. 15	1	3.6
No. 17	1	4.5
Cruise 18:		
No. 5	1	4.5
No. 6	1	10.1
No. 21	1	5.0+(distorted).
No. 24	1	5.4
Total	312	2.3–20.1

and lower jaws contain 4 and 6 teeth, respectively, and there are 3 spines along the edge of the preopercle, the middle one being the longest. The pectoral fins are present, but are represented only by a thin membrane, while the pelvic fins are completely absent. The median fins are represented by a continuous membrane which begins at the nape and continues around the caudal end to the anal opening. No fin rays are developed, but a few faint striations can be seen in the caudal region.

Most of the pigmentation is subcutaneous. About 10 small chromatophores are scattered over a fairly large portion of the membrane covering the midbrain. The dorsal edge of the abdominal sac is pigmented with very small chromatophores, while a very large one is evident on the anterior edge. A single chromatophore is present along the midventral line at about the 34th myomere. In all specimens examined the presence of this chromatophore is extremely consistent, although sometimes 2 or 3 replace the usual 1. The only dermal pigmentation on this specimen occurs at the tip of the lower jaw, where 2 to 3 small chromatophores are noticeable.

A specimen of 5.35 mm. (fig. 12) shows some advances in development. The head, representing 38.7 percent of the total length, is very large in relation to the rest of the body, and the sharply pointed snout is slightly longer than the diameter of the orbit. The length of the mouth is equivalent to 71.6 percent of the head length, and is much larger than that of *N. macropterus* of a comparable size. The teeth, 13 on the upper and 11 on the lower jaw, are well developed, and 6 spines are present along the edge of the preopercle. The pigmentation is now more extensive and covers more than half the area of the midbrain. The pelvic fins are seen only as small buds. No vertebrae are formed as yet and myomeres are only faintly visible. They number either 41 or 42.

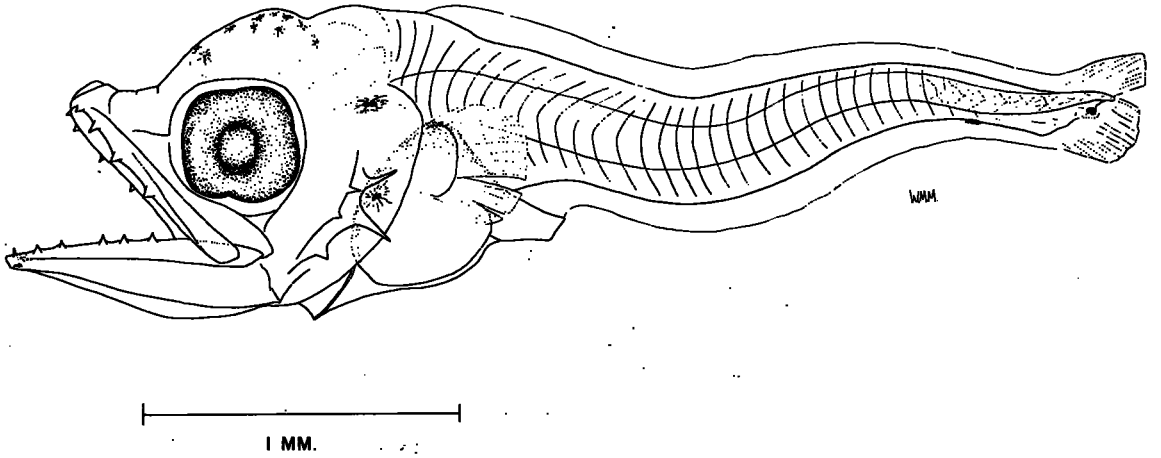

FIGURE 11.—*Katsuwonus pelamis*, 3.7 mm. total length.

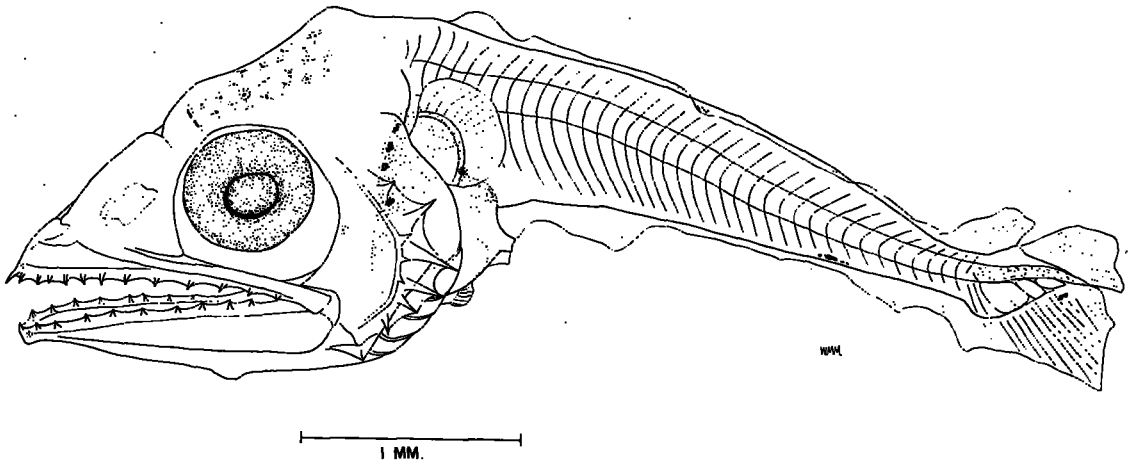

FIGURE 12.—*Katsuwonus pelamis*, 5.35 mm. total length.

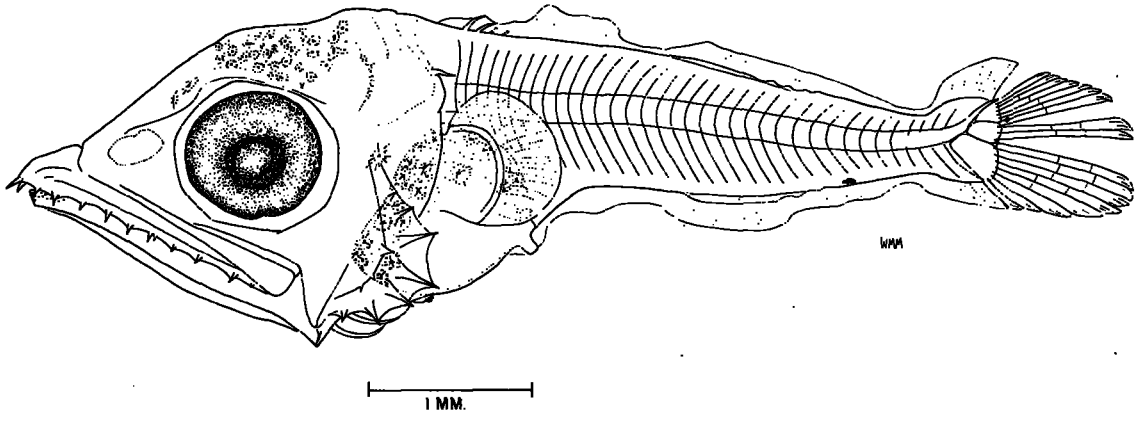

FIGURE 13.—*Katsuwonus pelamis*, 6.7 mm. total length.

The beginnings of the hypural plates are present, and the urostyle has developed and is turned upward.

The greatest change in a 6.7-mm. specimen (fig. 13) is in the first dorsal fin, where 4 spines have developed, the first 2 being very distinct. The only fin showing further development is the caudal, which now contains 18 rays. The urostyle is turned upward and the hypural plates are in a more terminal position. These bones are not yet ossified and do not take a stain.

The number of chromatophores over the midbrain has increased to about 33, and 2 closely set chromatophores are present over the forebrain, well ahead of the main, pigmented area. One or 2 large, dermal chromatophores appear on the side of the head near the dorsal end of the preopercle, while the pigmentation on the abdominal sac shows only a slight increase. No change is shown by the single chromatophore on the midventral line of the caudal region, or in the 41 myomeres.

At 7.1 mm. (fig. 14), the body is very much deeper and the head, composing 43.2 percent of the total length of the body, is still large. The snout length is almost equal to the diameter of the orbit. Eight short spines are present in the first dorsal fin, and the fin rays and finlets of the second dorsal and anal fins are beginning to develop. These appear only as striations in the membrane and cannot be counted accurately. The membrane between the first and second dorsal fins is beginning to degenerate, and there are about 12+11 rays in the caudal fin, the posterior edge of which has just begun to fork.

Pigmentation over the brain is similar to that on the previous specimen, but it extends over almost the entire midbrain area. Two additional

chromatophores appear: a small one on the lower jaw, at about one-fourth of the jaw length posterior to the tip, and another on the first dorsal fin at the outer edge of the second interradial membrane.

Several noticeable changes have taken place by the time the species has reached a length of 8.75 mm. (fig. 15). The anal opening is now slightly posterior to the midpoint of the total length of the body. The head is still large, 41.3 percent of the total length, and the snout, which is nearly equal to the diameter of the orbit, is sharply pointed. The growth across the nasal opening is complete, thus forming 2 openings. The mouth is large and represents 66.0 percent of the head length. There are 16 to 18 teeth on both jaws and about 5 on the palatine bone.

Eight or 9 spines are present in the first dorsal fin and, while their number does not differ appreciably from that in the 7.1-mm. specimen, they are nearly twice as long. There are about 10 rays and 6 or 7 finlets in both the second dorsal and anal fins. The pelvic fins are well developed, with 1 spine and 5 rays, while the pectoral fins are only striated.

Changes in pigmentation consist of the appearance of a few more chromatophores over various parts of the body. Several dark chromatophores are scattered on the tip of the snout, and the chromatophore on the lower jaw has moved back

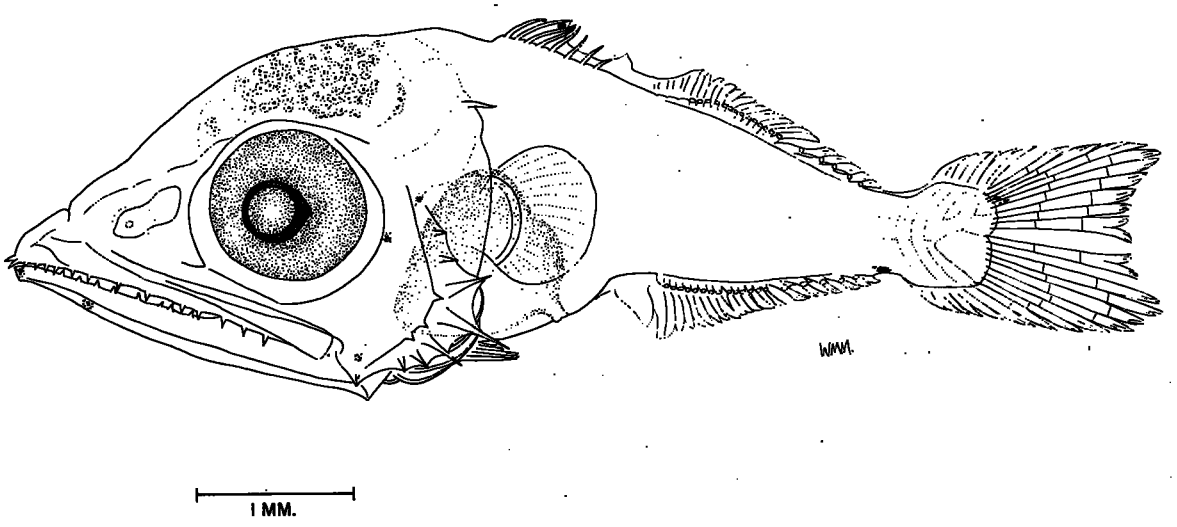

FIGURE 14.—*Katsuwonus pelamis*, 7.1 mm. total length.

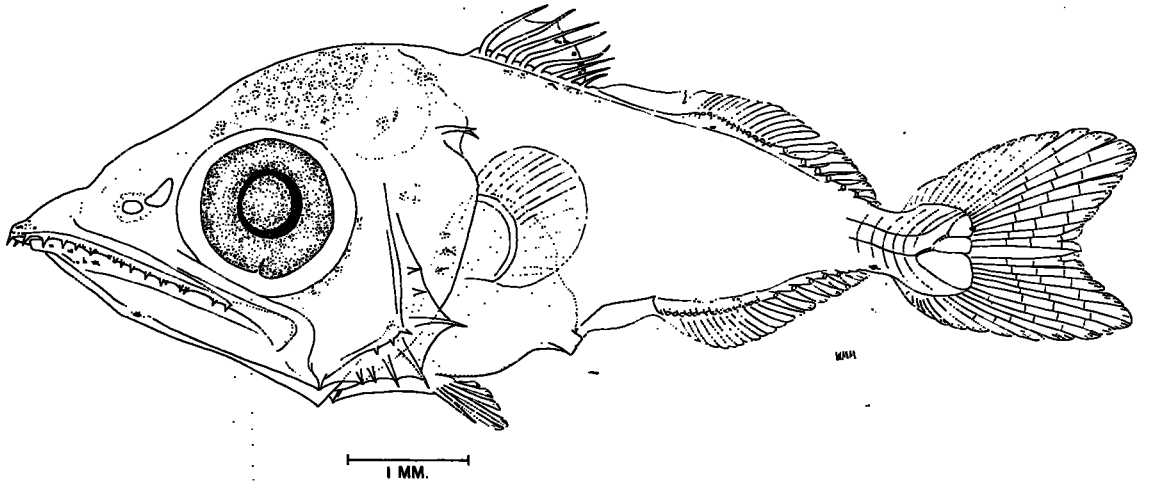

FIGURE 15.—*Katsuwonus pelamis*, 8.75 mm. total length.

to about one-half the length of the mandible. The posteroventral edge of the orbit is lined with about 10 small chromatophores, and about 6 fairly large, faint chromatophores are present on the preopercular surface posterior to the eye. Three or 4 small chromatophores also are noticeable in the posttemporal region, while 6 to 8 chromatophores appear along the base of the first dorsal fin and 1 near the second dorsal fin insertion. The outer edges of the 3d through the 6th interradial membranes of the first dorsal fin are pigmented with about 6 large chromatophores. Three chromatophores are also present along the base of the anal fin.

Rapid vertebral development has occurred between the 8.0-mm. and the 8.8-mm. specimens, both of which were stained. Only the urostyle is ossified on the smaller specimen, while the larger one shows complete ossification of the urostyle and the first 11 vertebrae. The first haemapophysis occurs on the 9th vertebra and the first closed haemal arch on the 11th.

Very definite changes are seen in a 10.9-mm. specimen (fig. 16). The abdominal sac is still roughly triangular, but the anal opening has moved back toward the anal-fin insertion. The nostrils are farther apart and, while the posterior one is still elliptical in shape, the anterior one is now smaller and more circular.

There are 9 preopercular spines: 4 small spines on the horizontal edge, 3 short spines on the vertical edge, and 2 very long spines at the angle. All of these, with the exception of the 2 long ones at the angle, are completely overgrown by the preopercular bone.

Fin development shows the greatest changes. There are 13 definite spines in the first dorsal, about 15 rays plus 8 finlets in the second dorsal, and about 14 rays plus 7 finlets in the anal fin. However, differentiation between the last fin ray and the first finlet is not clearly defined. The caudal fin rays number 16+16, and the pelvic fins show the full complement of 1 spine and 5 rays.

There is an increase in the number of chromatophores over the brain, at the tips of both jaws, and along the posteroventral margin of the orbit. The area posterior to the brain between the posttemporal spine and the dorsal edge of the body bears numerous small chromatophores, which extend backward along the dorsal margin of the body and gradually disappear near the base of the first dorsal finlet. Four small chromatophores are present along the base of the anal fin, and the single, dark chromatophore still persists on the ventral midline of the caudal peduncle. Six large chromatophores appear on the midlateral line of the body between verticals through the second dorsal insertion and the first dorsal finlet.

The vertebral count on a stained specimen of 9.85 mm. is 20 precaudal plus 21 caudal vertebrae, including the urostyle. All of the vertebrae are completely ossified, but none of the centra shows the typical hourglass shape of the adult. The first haemapophysis is on the 9th vertebra, and the first closed haemal arch is on the 11th. There are no inferior foramina along the vertebral column at this stage of development.

At 14.5 mm. (fig. 17), the body does not appear to be quite as deep as in the smaller specimens and the head is smaller in relation to the body (37.2

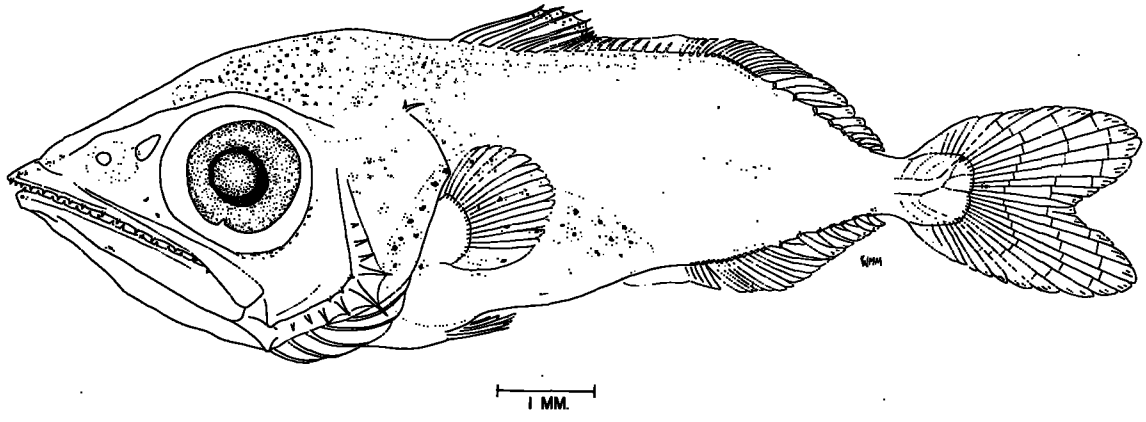

FIGURE 16.—*Katsuwonus pelamis*, 10.9 mm. total length.

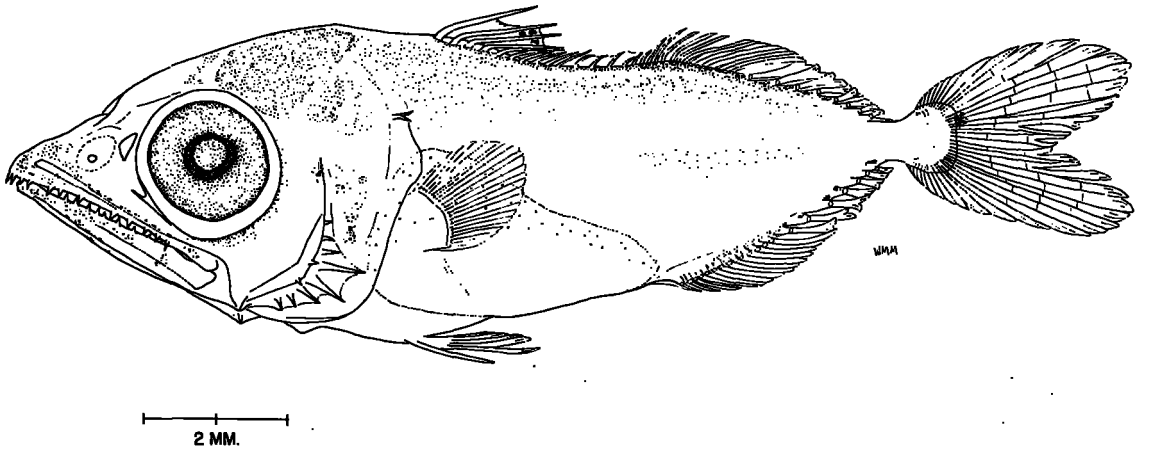

FIGURE 17.—*Katsuwonus pelamis*, 14.5 mm. total length.

percent of total length) than in the previous specimens. The abdominal sac is elongate, and the anal opening is very close to the insertion of the anal fin.

The nostrils are further differentiated, with the round, anterior nostril about one-fifth the size of the triangular, posterior one. The mouth is relatively smaller, 57.9 percent of the head length, and bears about 15 teeth on the upper jaw and about 17 teeth on the lower jaw. Six teeth are also evident on the palatine bone.

The dorsal fin has 16 spines, 15 rays, and 8 finlets, and the first dorsal has assumed the characteristic concave outline of the adult fin. The pelvic fins are very well developed and appear to be a little more posterior than on previous specimens. The pectoral fins have 20 rays, while the well-forked caudal has 22+22 rays.

There are 20 precaudal and 21 caudal vertebrae. The first haemapophysis appears on the 8th or 9th vertebra, while the first completely closed haemal arch is on the 12th. Neither the inferior foramina nor the large haemal arches, which form what Kishinouye (1923) calls the "trellis" and Godsil and Byers (1944) call a "complex basket work," are developed.

Pigmentation is more extensive in all areas described on previous specimens. The chromatophores over the snout have increased in number and line the entire length of the upper jaw. Similarly, two-thirds of the length of the lower jaw is also lined with chromatophores. The midbrain is completely covered with dark, very-closely set chromatophores, and the small patches over the forebrain and on the side of the head immediately posterior to the brain are more intense. The 7 or 8 chromatophores on the surface of the opercle, posterior to the eye, are very large and noticeable. The pigmentation along the posteroventral margin of the orbit is also more intense and extends along nearly half the circumference. Dorsally, the band of chromatophores on the caudal trunk is much wider. It tapers posteriorly and finally terminates near the base of the 5th dorsal finlet. Six or seven darkly pigmented spots are present on the outer edge of the interradial membranes of the first dorsal fin between the 2d and 6th spines. The base of the anal fin is lined with tiny chromatophores, and 3 fairly large chromatophores are present at the bases of the first 3 anal finlets. A band of small chromatophores is also present on the midlateral line beginning at a vertical through the second dorsal insertion and extending to a vertical through the base of the 4th dorsal finlet. The single, large chromatophore at the midventral line of the caudal peduncle still persists, as do the large chromatophores over the dorsal half of the abdominal sac.

A 20.0-mm. specimen, which is not illustrated, was taken at a night-light station in Kingman Reef lagoon, and this individual already shows the characteristic appearance of the juvenile form. The body is narrow and long, with the greatest depth located at a vertical through the pelvic-fin insertion and equal to about one-fourth the total length. The head length is about one-third the total length, and the snout still retains

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the rather sharply pointed profile. Except for the increase in pigmentation over the body, this specimen resembles the 14.5-mm. one very closely. A stained specimen of a similar size shows the dorsal fins with 16 spines, 15 rays, and 8 finlets, and the anal fin with 15 rays and 7 finlets. The pectoral fins consist of 20 or 21 rays and the caudal fin has 22+22 rays. The vertebrae number 20 precaudals and 21 caudals, with the first haemapophysis on the 9th and the first closed haemal arch on the 11th vertebra. The inferior foramina are just beginning to form on the 13th through the 22d vertebrae, but they are not yet completely closed.

This description agrees very closely with Schaefer and Marr's (1948b) 21-mm. specimen and also with Kishinouye's (1926) 26-mm. specimen. Examination of other stained specimens (22 mm., 27 mm., 33 mm., and 49 mm.) shows that many of the adult complement of meristic characters have appeared by the time the species has reached 27 mm. in length. The inferior foramina are completely closed on the 14th through the 33d and 34th vertebrae in the 27- and 49-mm. specimens, respectively. The foramina are slightly increased in size on the latter specimen, but the trellis is still not evident.

LITTLE TUNNY (*EUTHYNNUS YAITO*)

No specimen of *E. yaito* was recognized in our collections. The following description is based on more than 100 larvae, believed to be *Euthynnus*, which were taken in East Indian waters during the *Dana* Expedition of 1928–30. The largest specimen (12.25 mm.) has 39 vertebrae and seems identical in external appearance to the two *E. lineatus* (21 and 26 mm.) taken by the California Department of Fish and Game from the waters off Costa Rica and also to the juveniles of 20 *E. alletteratus* (25 to 55 mm.) taken by the U. S. Fish and Wildlife Service, Gulf Fisheries Investigations, from the Gulf of Mexico. That the larva is definitely not *E. lineatus* can be seen from the vertebral count, for *E. lineatus* normally has only 37 vertebrae. Positive identification, either as *E. yaito* or *E. alletteratus*, would be relatively easy if the gill rakers were fully developed. Since they are not, the larva was designated as *E. yaito* because this species occurs in the central and western Pacific Ocean, while *E. alletteratus* is found in the Atlantic Ocean and the Mediterranean Sea.

The smallest specimen identified as *E. yaito* measures 4.6 mm. in total length (fig. 18). The head length is moderate (33.9 percent of the total length) and there are 40 myomeres. The abdominal sac is nearly triangular in shape, as in the two previous species.

The mouth, representing 71.9 percent of the head length, is fairly large and contains 12 and 9 teeth on the upper and lower jaws, respectively. The snout is comparable to that of *K. pelamis* of similar size, and the distance from its tip to the anterior edge of the orbit is almost equal to the diameter of the orbit. There are 3 long spines along the posterior edges of the preopercle, the one at the angle being the longest.

Most of the median fins show very little development, there being about 4 or 5 rays in the caudal and only strong striations representing rays in the

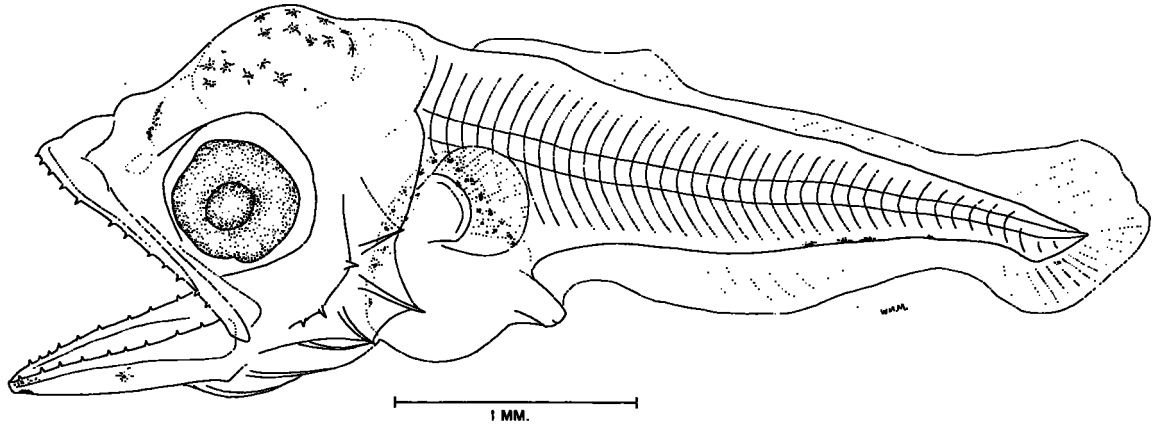

FIGURE 18.—*Euthynnus yaito*, 4.6 mm. total length.

region of the future anal and dorsal fins. The pectoral fins also show only striations, and the pelvic fins are absent.

The pigmentation on the head consists of 3 small chromatophores over the forebrain and about 15 chromatophores over the midbrain. There is a single small chromatophore at the middle of the mandible and another at the symphysis of the pectoral girdle, which is not shown in the drawing. There is no pigmentation along the dorsal edge of the trunk, but 5 chromatophores are present along the ventral margin of the trunk near the caudal region.

A 5.5-mm. specimen (fig. 19) shows marked changes. The proportions of the head, snout, and mouth closely resemble those of *K. pelamis* (see table 4, p. 53). The mouth now contains 13 and 15 teeth in the upper and lower jaws, respectively, and the preopercular spines have increased to 6.

There are 5 short spines in the first dorsal fin and about 9 rays in the caudal. The rest of the median fins and the pectorals still show only strong striations. The pelvic fins are just emerging as small buds.

Pigmentation is more extensive over the midbrain and over the abdominal sac. There is also an increase in the number of chromatophores at the tip of the snout and lower jaw, and the single chromatophore at the middle of the mandible and that at the pectoral symphysis are still evident. In addition, 2 small chromatophores are present on the ventral midline just anterior to the anus, and a single conspicuous chromatophore is present in the first dorsal fin. The dorsal midline of the trunk is still free from pigmentation, while the ventral midline shows 3 well-separated chromatophores in the region of the future anal finlets.

Some noticeable changes are present on the 7.6-mm. specimen (fig. 20), the most prominent

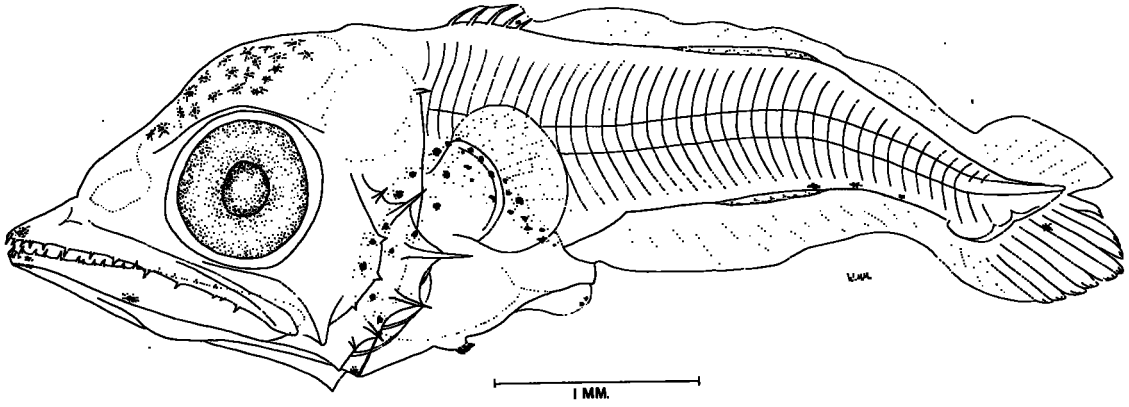

FIGURE 19.—*Euthynnus yaito*, 5.5 mm. total length.

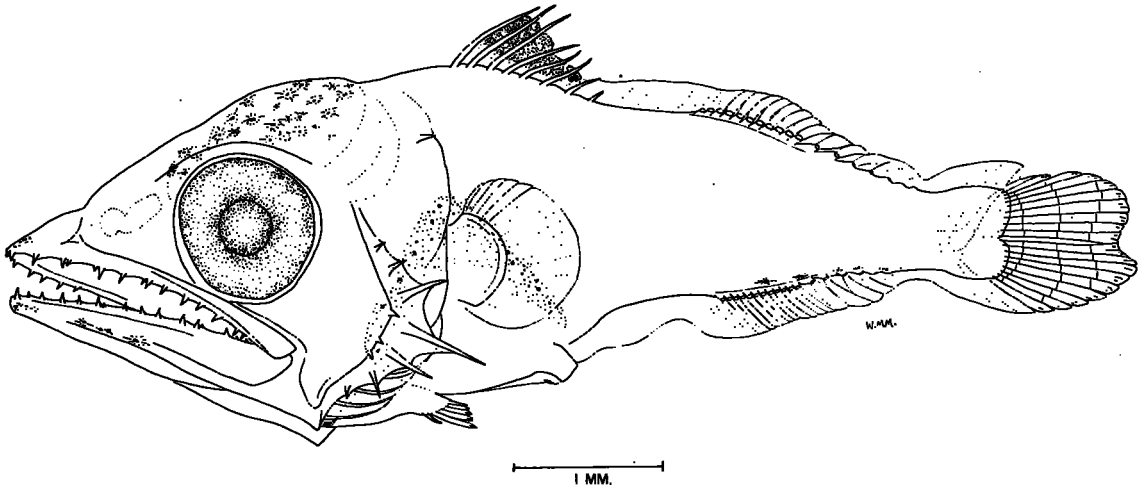

FIGURE 20.—*Euthynnus yaito*, 7.6 mm. total length.

of these being in the pigmentation. The first dorsal fin is almost completely pigmented and the anterior half of the mandible bears a series of 4 or 5 chromatophores.

The head is still large (39.8 percent of the total length) and the length of the snout is much greater than the diameter of the orbit. There are about 16 teeth on both the upper and lower jaws, and 7 spines are noticeable on the posterior edge of the preopercle.

The first dorsal fin has 8 spines, the length of the longest spine being slightly less than half the distance between the dorsal-fin insertions. The second dorsal and anal fin rays are beginning to form and, while the rays themselves are not clearly evident, there appear to be about 11 radials in the second dorsal and 12 in the anal. The radials of the first 7 dorsal finlets and first 6 anal finlets are also evident. The caudal fin shows 9+9 rays, and the pelvic fins, although very small, are complete with 1 spine and 5 rays. Only about 5 rays are noticeable in the pectoral fins. The myomeres remain the same (40 or 41) as in the previous specimen.

A 9.6-mm. specimen (fig. 21) already shows a close resemblance to the juveniles of *E. lineatus* (21 mm.) and *E. alletteratus* (25 mm.), insofar as pigmentation is concerned. The first dorsal fin is heavily pigmented, and the pigmentation at the tip of the snout is more extensive. The number of chromatophores along the lower jaw has increased and chromatophores now extend over two-thirds of the length of the mandible. The chromatophore at the symphysis of the pectoral girdle still persists, and the pigmentation over the rest of the body remains unchanged.

The relative sizes of the head, snout, and mouth are somewhat smaller than those of *K. pelamis* and *N. macropterus*, and only 6 spines are evident along the preopercular edges.

There are 13 spines in the first dorsal fin, the length of the longest spine being greater than half the distance between the dorsal-fin insertions. The second dorsal and anal fins each contains 13 rays. The finlets are poorly developed, but 8 and 7 finlet radials are clearly evident in the dorsal and anal, respectively. The rest of the fins also show an increase in the number of rays.

The largest specimen (not figured) in the series measures 12.25 mm. (tables 4 and 5). Its head is large (40 percent of the total length) and the length of the snout is greater than the diameter of the orbit. The mouth is also large, much more so than in *K. pelamis* and *N. macropterus*, and contains 25 and 28 teeth in the upper and lower jaws, respectively. Staining with alizarin revealed 39 (20+19) vertebrae.

The unpaired fins now have their full complement of spines and rays, with 15 spines in the first dorsal and 14 rays in the second dorsal, and 8 dorsal finlets. The anal fin contains 14 rays and 7 finlets. The longest spine in the first dorsal fin measures about half the distance between the first and second dorsal-fin insertions.

The entire first dorsal fin from the first to the tenth spine is completely pigmented. Small chromatophores are present along the base of the first dorsal fin and over the nape. A series of 4 widely

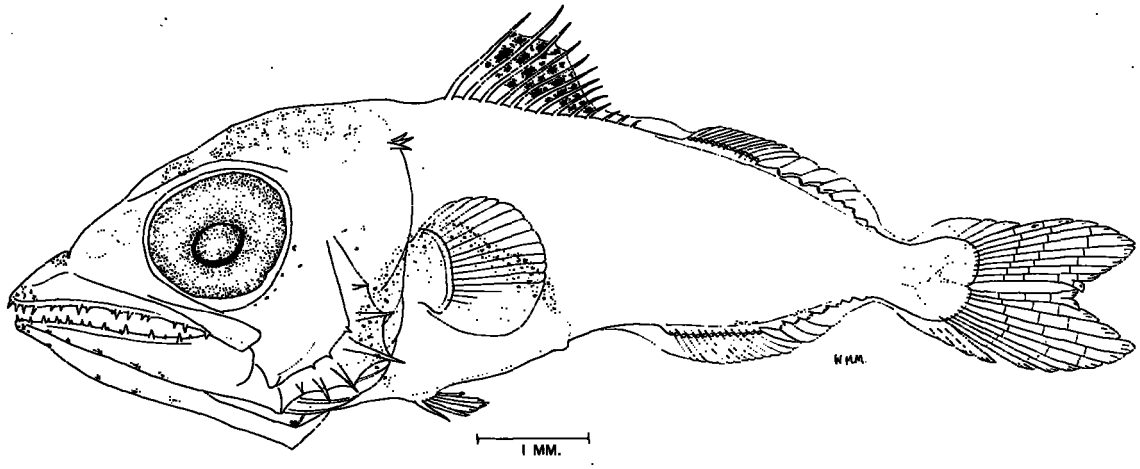

FIGURE 21.—*Euthynnus yaito*, 9.6 mm. total length.

spaced chromatophores is seen along the posterior base of the second dorsal fin and the bases of the first 3 finlets. Similar pigmentation is also present at the bases of the last 3 anal rays and the first 3 finlets. The lower jaw contains 8 well-spaced chromatophores distributed over its entire length, while the rest of the pigmented areas remain as in the 9.6-mm. specimen.

This last specimen has the same pigmentation as the 21-mm. and 26-mm. specimens of *E. lineatus* taken from the waters off Costa Rica by the California Department of Fish and Game. The only major difference is in the number of vertebrae, 37 (20+17), for the 21-mm. Costa Rican specimen as compared with 39 (20+19) for the 12.25-mm. specimen just described.

FRIGATE MACKEREL (*AUXIS THAZARD*)

Of the 38 specimens of *A. thazard* taken by the *Hugh M. Smith* (table 3), only a few specimens were in suitable condition to permit accurate reproduction. Consequently, specimens from the *Dana* collection from the East and West Indies and the Gulf of Panama were used to complete the series.

The 3.7-mm. specimen (fig. 22) described here as probably *A. thazard* is typical of the other specimens in the group ranging from 2.5 to 4.0 mm. in table 3. It has a short head with a very elongate body containing 39 myomeres and tapering very gradually toward the caudal end. The abdominal sac is triangular in shape with the anus located well forward of the middle of the total body length. The greatest depth of the body is at the symphysis of the pectoral girdle, where it is about one-fourth of the total body length.

TABLE 3.—*Number and size range of larval* Auxis thazard *collected by the* Hugh M. Smith *in Hawaiian and equatorial waters*

[See figs. 1 and 2 for location of stations]

Cruise and station	Number of larvae	Size range (mm.)
HAWAIIAN WATERS:		
Cruise 6:		
No. 1A	1	3.6
No. 7	1	6.2
No. 8	4	2.5–8.2
No. 10	10	2.7–3.7
No. 11	2	7.02, 8.1
No. 13	12	3.0–5.2
Total	30	2.5–8.2
EQUATORIAL WATERS:		
Cruise 5:		
No. 21	2	2.6
No. 51	2	4.2, 5.5
Cruise 14:		
No. 26	1	3.6
No. 29	1	3.1
Cruise 15: No. 3	1	7.2
Cruise 18: No. 31	1	4.0
Total	8	2.6–7.2

Since the snout is distorted, no comparisons of the head parts can be made. However, the snout appears very short and blunt and the mouth contains only 5 teeth, 3 on the upper jaw and 2 on the lower. Only 3 preopercular spines are noticeable, the middle one at the angle being the longest. Two small spines are also present on the preopercular surface.

The median fins are represented by a continuous fin membrane which starts at the nape and goes completely around the caudal end to a point slightly anterior to the anal opening. The pectoral fins are also membranous.

The pigmentation is most striking along the ventral midline of the caudal trunk, where 9 small, dark chromatophores are present. While the figured specimen shows a dark chromatophore on the dorsal midline of the caudal peduncle and 2

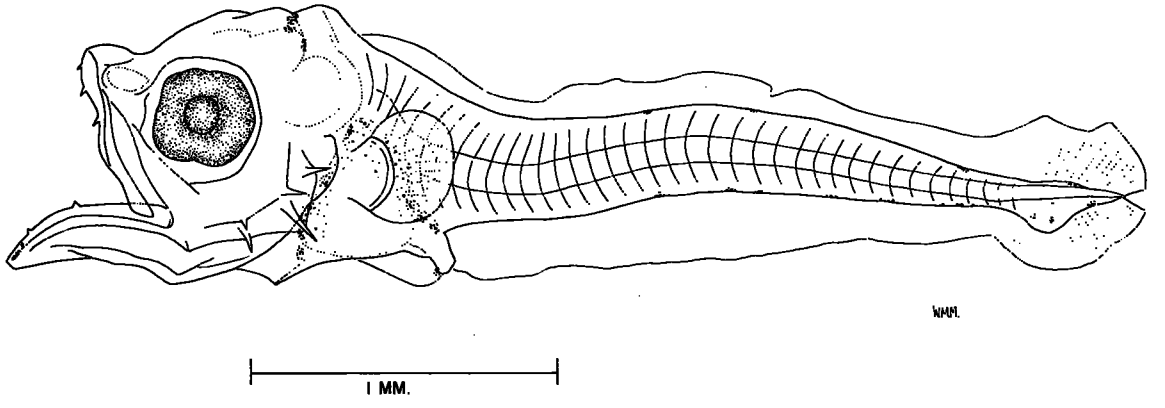

FIGURE 22.—*Auxis thazard* (?), 3.7 mm. total length.

more well-spaced and very light chromatophores near the middle of the body on the dorsal edge, other specimens show only the one on the caudal peduncle. On some specimens even this single chromatophore is absent. Several dark chromatophores are present along the posterior margin of the midbrain, and the very small chromatophores at the tip of the lower jaw are barely noticeable. The abdominal sac is pigmented regularly as in the other species, with most of the pigmentation concentrated along the anterior and dorsal surfaces. A single conspicuous chromatophore is present just anterior to the anal opening, and in this specimen the symphysis of the pectoral girdle does not show any pigmentation.

The smallest specimen identified confidently as *A. thazard* measures 4.5 mm. (fig. 23). The head is moderate (34.2 percent of the total body length) and the body contains 40 myomeres. The snout is short, slightly over three-fourths of the diameter of the orbit, and the mouth is moderately large and measures almost two-thirds of the head length. There are 5 small teeth on the upper jaw and 4 on the lower. The posterior edge of the preopercle bears 3 spines, the longest one located at the angle.

The pigmentation on the head consists of 6 large chromatophores over a small area of the midbrain and a faint tinge of pigment at the tip of the lower jaw. A single chromatophore is present at the symphysis of the pectoral girdle and another just anterior to the anus. The triangular abdominal sac is pigmented regularly, similarly to the three preceding species. A series of 2 to 3 chromatophores is present along the middorsal, midlateral, and midventral lines of the caudal region. In addition, 7 well-spaced chromatophores are present on the posterior half of the trunk along the midventral line.

The unpaired fins are represented by a continuous membrane and except for the caudal fin, where 10 rays are evident, none of the others shows any fin rays. The pectoral fins are also membranous and the pelvic fins are absent.

Only a few changes are noticeable on a 5.5-mm. specimen (fig. 24). The head is small and the moderate mouth, representing 60.3 percent of the head length, contains 12 teeth on each jaw. The snout is somewhat pointed and the distance from its tip to the anterior edge of the orbit is about four-fifths the diameter of the orbit. There are 6 spines along the edge of the preopercle and a small spine is visible in the posttemporal region.

The fins, except for the pelvics, which appear as small buds, show relatively little change from the specimen described above.

The pigmentation on the head consists of about 13 chromatophores which are closely grouped over the midbrain, the rest of the head being unpigmented. The abdominal sac remains the same as in the previous specimen. A series of 2 to 4 chromatophores is present along the middorsal, midlateral, and midventral lines of the caudal region. In addition, 2 widely spaced chromatophores are present along the ventral midline anterior to the caudal peduncle.

Further changes are apparent on a 7.05-mm. specimen (fig. 25). The head is slightly larger and the anus is at the middle of the total length of the body. The snout is pointed and is almost equal in length to the diameter of the orbit. The mouth is large and represents 61.4 percent

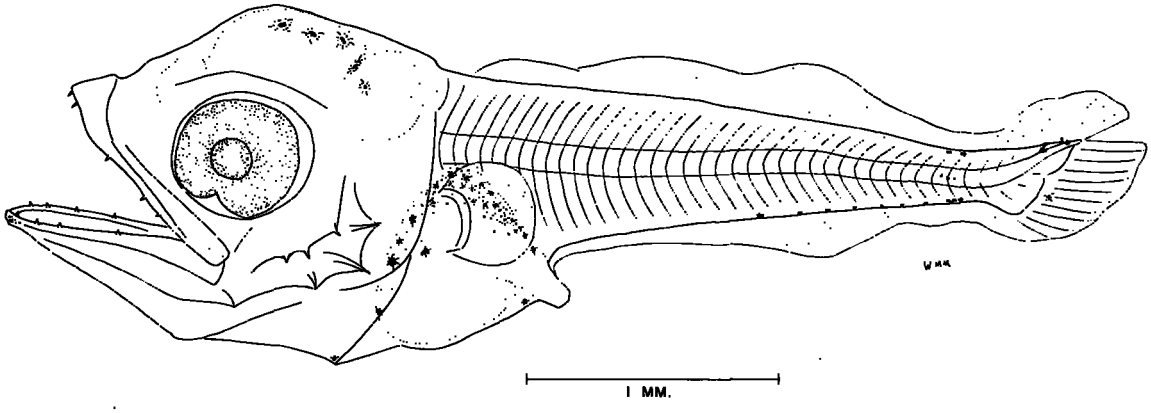

FIGURE 23.—*Auxis thazard*, 4.5 mm. total length.

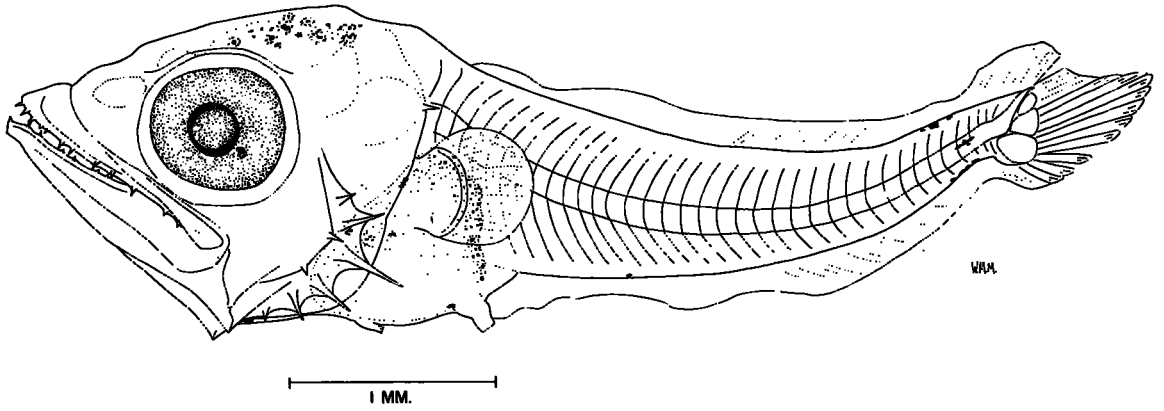

FIGURE 24.—*Auxis thazard*, 5.5 mm. total length.

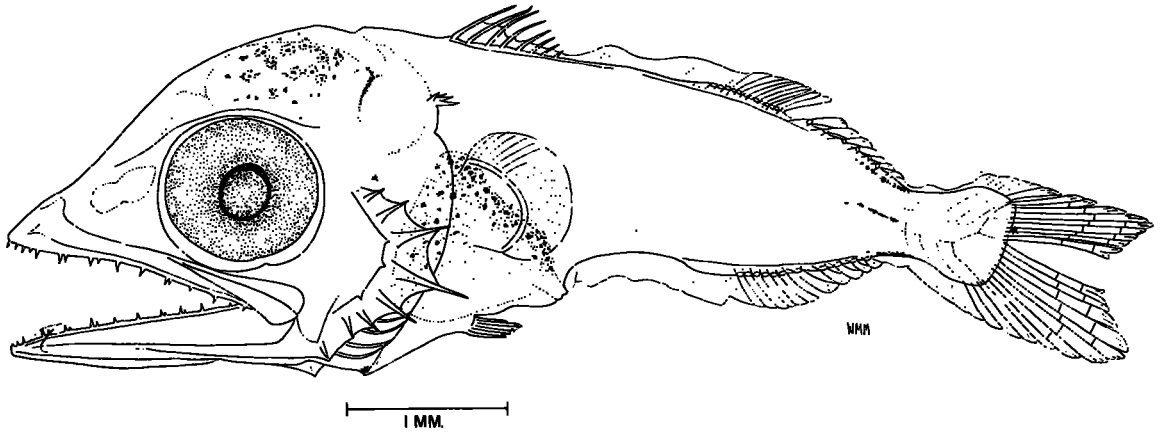

FIGURE 25.—*Auxis thazard*, 7.05 mm. total length.

of the head length. Sixteen to seventeen prominent teeth are present on each ramus of the upper and lower jaws, and 1 tooth is evident on the palatine bone. There are 7 preopercular spines: 2 spines on both the vertical and horizontal edges and 3 long spines at the angle, the middle one being the longest. The single posttemporal spine now has 4 prongs.

The first dorsal fin has 8 spines, the second through the fourth spines being longer than the first. The length of the longest spine is less than one-third the distance between the insertions of the first and second dorsal fins. About 10 rays are present in the second dorsal fin, followed by 6 or 7 dorsal finlets. The anal fin contains about 6 rays and 4 to 5 finlets, while the caudal fin with 10+11 rays is just beginning to fork. The pectoral fins have 7 rays, and the well-developed pelvic fins have 1 spine and 3 to 4 rays.

The pigmentation over the head and the abdominal sac is more extensive than on the previous specimen, and the chromatophores on the caudal region now number 6, 5, and 4 along the middorsal, midlateral, and midventral lines, respectively. The chromatophore at the symphysis of the pectoral girdle is still present, but the single chromatophore anterior to the anal opening is absent. In addition to these, only 1 very faint chromatophore is present on the side of the head near the dorsal origin of the preopercle.

After staining, the 7.05-mm. specimen shows 11 completely ossified vertebrae. From the 12th through the 15th vertebrae only the bases of the neural and haemal arches are ossified. The urostyle is completely ossified, while the 2 preceding vertebrae are only partially so. There are 40 myomeres on this specimen.

Except for a slight increase in pigmentation, an 8.20-mm. specimen (not figured) shows development similar to that of the 7.05-mm. specimen

just described. The most noticeable differences are the absence of the chromatophore at the symphysis of the pectoral girdle and the presence of a few small chromatophores on the first dorsal fin.

A 9.7-mm. specimen (fig. 26) has the same general appearance as the preceding specimen. The head (34.7 percent of the total length) appears small, while the anus is now located in the posterior half of the body.

There are 9 spines in the first dorsal fin, the length of the longest one being less than one-fourth the distance between the insertions of the first and second dorsal fins. There are 12 rays in the second dorsal followed by 8 dorsal finlets. The anal consists of 10 rays and 7 finlets. Each pectoral fin contains 15 rays, while the pelvics are complete with 1 spine and 5 rays. The caudal fin consists of 12 dorsal and 13 ventral rays.

Only slight changes are noted in the pigmentation, with 3 chromatophores present over the forebrain, 1 over the tip of the snout, and a few scattered chromatophores over the preopercle. The series of chromatophores along the middorsal line has increased to 16 and extends almost to the insertion of the second dorsal fin. Similarly, the chromatophores along the midventral line also have extended forward to the middle of the anal fin. The midlateral series contains 7 chromatophores.

The 11.2-mm. specimen (fig. 27) differs in several ways from the 9.7-mm. specimen. The head and snout appear much smaller than those of the three previous species. The mouth, however, is moderate (representing 58.6 percent of the head length) and contains 21 and 18 teeth on the upper and lower jaws, respectively. The anus has moved back still further, and the abdominal sac has become more elongate. The nasal depression has completely divided into two separate nostrils, the anterior one being associated with the nasal rosette.

The dorsal and anal fins and finlets have the full complement of spines and rays, and the

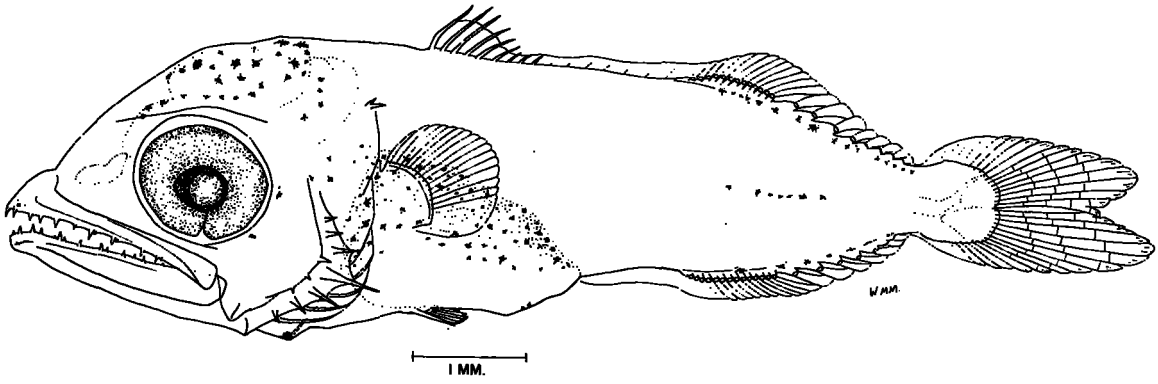

FIGURE 26.—*Auxis thazard*, 9.7 mm. total length

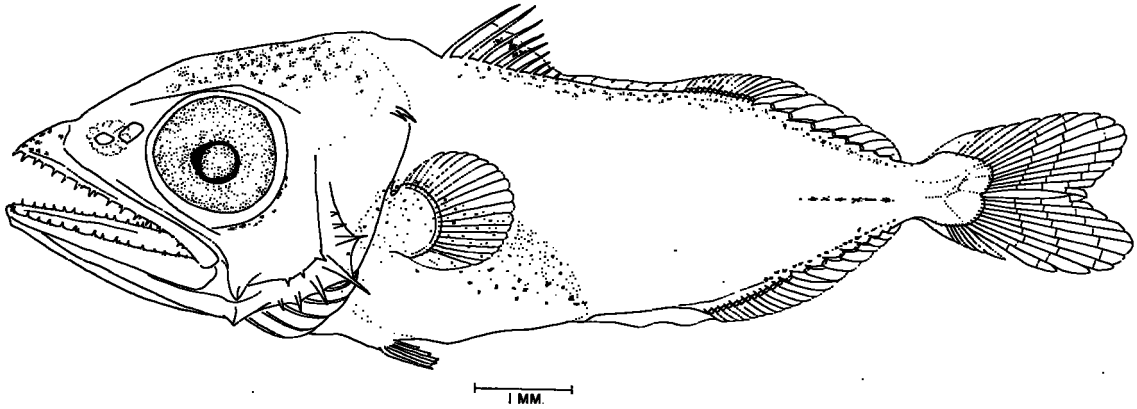

FIGURE 27.—*Auxis thazard*, 11.2 mm. total length.

length of the longest spine of the first dorsal fin is slightly less than one-third the distance between the first and second dorsal-fin insertions. The pectoral fins have 19 or 20 rays, while the caudal fin consists of 14+14 rays.

There are quite a few changes in the pigmentation at this size. The first dorsal fin contains 3 large chromatophores, and the pigmentation over the dorsal edge of the body now extends to the origin of the first dorsal fin. Other areas showing increased pigmentation are the snout, midbrain, and posteroventral margin of the orbit.

The 11.2-mm. specimen has 7 rather weak spines representing the future subcutaneous spines of the dorsal interspace (Schaefer and Marr, 1948a). The specimens of juvenile *A. thazard* measuring between 11 and 50 mm. from Costa Rica, Colombia, and the Galapagos Islands also have weak spines in the dorsal interspace. In many instances these spines project freely and are easily seen. On the basis of all characters considered, the larvae described here are identical with the juveniles of *A. thazard* from the coastal waters of Central America.

COMPARISON OF SPECIES

It is extremely difficult, if not impossible, to differentiate the larvae of various species of tuna by using the methods employed in identifying the adults. Measurements and meristic counts are not applicable because the larvae are undergoing rapid growth and differentiation. Development is apparently so rapid that even specimens of comparable sizes show marked differences in many characters.

During this study it was found that certain chromatophores and patterns of pigmentation persisted throughout the size ranges examined, and these markings seemed much more reliable than the other characters. Consequently, identification and description of the various species were based primarily on pigmentation, and the other characters were used only supplementally (tables 4 and 5).

Among the four species described, *E. yaito* and *A. thazard* can be separated from *N. macropterus* and *K. pelamis* quite readily by the pigmentation of the body. Larvae of both species bear a single chromatophore at the symphysis of the pectoral girdle and another on the midline of the body just anterior to the anal opening. The occurrence of these chromatophores is somewhat variable, and in some instances either one of the two may be absent. Nevertheless, the presence of either one is quite conclusive evidence that the specimen is either *E. yaito* or *A. thazard*, since no other species examined has these chromatophores. Mead (1951), in his descriptions of *A. thazard* and *E. lineatus* from the Pacific coast of Central America, found that the chromatophore at the symphysis of the pectoral girdle was present in the majority of his specimens. Wade (1951) did not mention this chromatophore, but our examination of the larvae collected by him from Philippine waters showed it to be regularly present on specimens which he designated as *E. yaito* and *Auxis* sp.(?), and absent from *K. pelamis* and *N. macropterus*. Besides this character, *E. yaito* and *A. thazard*

TABLE 4.—*Comparison of body proportions among larvae of four species of tuna, by total length*

[Asterisk (*) indicates measurements not accurate; snout distorted in preservation]

Size group	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Euthynnus yaito*	*Auxis thazard*
Head length/ total length:	*Percent*	*Percent*	*Percent*	*Percent*
3 mm	*31.2	*28.3		*25.3
4 mm			33.9	34.2
5 mm	36.8	38.7	37.7	35.8
6 mm	32.4	38.5	41.7	33.0
7 mm	35.2	43.2	39.8	39.4
8 mm	36.4	41.3	38.8	
9 mm	37.9		33.5	34.7
10 mm		38.4		36.2
11 mm				36.3
12 mm			40.0	
14 mm	39.7	37.2		
Mouth length/head length:				
3 mm	*57.8	*69.7		*59.4
4 mm			71.9	65.4
5 mm	60.1	71.6	72.0	60.3
6 mm	57.0	68.2	66.0	63.1
7 mm	62.1	68.6	67.1	61.4
8 mm	60.5	66.0	61.3	
9 mm	61.9		59.1	56.9
10 mm		67.9		55.7
11 mm				58.6
12 mm			65.3	
14 mm	56.9	57.9		
Snout length/orbit diameter:				
3 mm	*65.0	*75.0		*66.7
4 mm			99.9	85.0
5 mm	68.9	103.6	103.6	81.5
6 mm	70.5	98.2	105.8	88.2
7 mm	86.2	94.1	117.4	90.7
8 mm	82.7	93.9	91.3	
9 mm	104.3		91.6	86.4
10 mm		103.4		78.6
11 mm				88.4
12 mm			112.9	
14 mm	100.6	87.5		
Total length of specimen:	*Mm.*	*Mm.*	*Mm.*	*Mm.*
3 mm	*3.90	*3.70		*3.70
4 mm			4.60	4.50
5 mm	5.50	5.35	5.50	5.50
6 mm	6.40	6.70	6.00	6.25
7 mm	7.15	7.10	7.60	7.05
8 mm	7.95	8.75	8.00	
9 mm	9.20		9.60	9.70
10 mm		10.90		10.90
11 mm				11.20
12 mm			12.25	
14 mm	14.25	14.50		

bear a series of chromatophores (3 or more) along the ventral midline of the caudal trunk.

Three, or possibly four, distinctive patterns of pigmentation permit the separation of *E. yaito* from *A. thazard*. The first dorsal fin is generally more heavily pigmented in *E. yaito*. The first sign of this pigmentation is seen on a 5.5-mm. specimen with the appearance of 1 faint chromatophore. When the species is about 7 mm. in length the distal half of the first dorsal fin appears black. The pigmented area increases with growth of the larva and the entire fin is almost completely pigmented at about 12 mm. In *A. thazard* this pigmentation does not start to appear until the species has attained a length of about 10 mm. An 11.2-mm. specimen has only 2 or 3 faint chromatophores near the distal edge of the fin membrane.

TABLE 5.—*Summary of the more prominent diagnostic characters of tuna larvae at various sizes, by species*

Character	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Euthynnus yaito*	*Auxis thazard*
	3.9 mm.	**3.7 mm.**	**4.6 mm.**[1]	**4.5 mm.**[1]
Teeth	Not clearly seen	4 upper; 6 lower	12 upper; 9 lower	5 upper; 4 lower.
Preopercular spines	3	3	3	3.
Myomeres	About 40	Incomplete	40	40.
1st dorsal spines				
1st dorsal fin outline				
Pigmentation:				
1st dorsal fin				
Middorsal line	No chromatophores	No chromatophores	No chromatophores	2 chromatophores on caudal peduncle.
Midlateral line	do	do	do	3 chromatophores on caudal peduncle.
Midventral line	do	1 chromatophore on caudal peduncle.	5 chromatophores on posterior half of body.	3 chromatophores on caudal peduncle; 7 to middle of body.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	No chromatophores	Do.
Midbrain	4 chromatophores over small area.	10 chromatophores over large area.	15 chromatophores over large area.	6 chromatophores over small area.
Forebrain	No chromatophores	No chromatophores	3 chromatophores	No chromatophores.
Mandible (other than at tip)	do	do	1 chromatophore at middle	Do.
	5.5 mm.	**5.35 mm.**	**5.5 mm.**[1]	**5.5 mm.**
Teeth	8 upper; 4 lower	13 upper; 11 lower	13 upper; 15 lower	12 each jaw.
Preopercular spines	6	6	6	6.
Myomeres	38	41 or 42	40 or 41	About 39.
1st dorsal spines			5; longest spine <½ dorsal interspace.[2]	
1st dorsal fin outline				
Pigmentation:				
1st dorsal fin			1 chromatophore	
Middorsal line	No chromatophores	No chromatophores	No chromatophores	3 chromatophores on caudal peduncle.
Midlateral line	do	do	do	2–3 chromatophores on caudal peduncle.
Midventral line	do	1 chromatophore on caudal peduncle.	3 chromatophores at bases anal and finlets.	4 chromatophores on caudal peduncle; 2 near middle of body.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	2 chromatophores	Do.
Midbrain	14 chromatophores over small area.	24 chromatophores over large area.	18 chromatophores over wide area.	13 chromatophores over moderate area.
Forebrain	No chromatophores	No chromatophores	3 chromatophores	No chromatophores.
Mandible (other than at tip)	do	do	1 chromatophore at middle	Do.
	7.15 mm.	**7.1 mm.**	**7.6 mm.**[1]	**7.05 mm.**
Teeth	10–11 upper; 6–7 lower	15 each jaw	16 each jaw	16–17 each jaw.
Preopercular spines	6	7	7	7.
Myomeres	40	41	40 or 41	40.
1st dorsal spines	7; longest spine <½ dorsal interspace.[2]	8; longest spine <⅓ dorsal interspace.[3]	8; longest spine <½ dorsal interspace.[2]	8; longest spine <⅓ dorsal interspace.[3]
1st dorsal fin outline				
Pigmentation:				
1st dorsal fin	6 chromatophores	1 chromatophore	Almost completely pigmented.	No chromatophores.
Middorsal line	No chromatophores	No chromatophores	No chromatophores	6 chromatophores on caudal peduncle.
Midlateral line	do	do	do	5 chromatophores on caudal peduncle.
Midventral line	do	1 chromatophore on caudal peduncle.	2 chromatophores—well separated.	4 chromatophores on caudal peduncle.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	do	No chromatophores.
Midbrain	50+ chromatophores over small area.	50 chromatophores over large area.	45 chromatophores over entire area.	25 chromatophores over moderate area.
Forebrain	No chromatophores	2 chromatophores	3 chromatophores	No chromatophores.
Mandible (other than at tip)	do	1 chromatophore ¼ distance from tip.	4–5 chromatophores over anterior half.	Do.

See footnotes at end of table.

TABLE 5.—*Summary of the more prominent diagnostic characters of tuna larvae at various sizes, by species*—Continued

Character	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Euthynnus yaito*	*Auxis thazard*
	7.95 mm.	**8.75 mm.**	**8.0 mm.**[1]	**7.7 mm.**[1]
Teeth	9–10 each jaw	16–18 each jaw	18 upper; 19 lower	15 upper; 17 lower.
Preopercular spines	7	7	7	7.
Myomeres	40	41–42	40	40–41.
1st dorsal spines	7	8 or 9	10; longest spine=⅔ dorsal interspace.[2]	6; longest spine=⅓ dorsal interspace.[2]
1st dorsal fin outline				
Pigmentation:				
1st dorsal fin	Almost entire height to 6th spine.	6 chromatophores on outer fin edge.	Large chromatophores on outer ⅔ of fin.	No chromatophores.
Middorsal line	No chromatophores	6–8 chromatophores at base 1st dorsal; 1 at origin 2d dorsal.	No chromatophores	8 chromatophores on caudal peduncle.
Midlateral line	do	No chromatophores	do	4 chromatophores on caudal peduncle.
Midventral line	do	3 chromatophores at base anal; 1 on caudal peduncle.	2 chromatophores at bases anal and finlet.	6 chromatophores at bases anal and finlet.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	No chromatophores	Do.
Midbrain	22 chromatophores over small area.	45+ chromatophores over wide area.	About 46 chromatophores over entire area.	About 25 chromatophores over fairly large area.
Forebrain	No chromatophores	2–3 chromatophores	5–6 chromatophores	No chromatophores.
Mandible (other than at tip)	do	1 chromatophore ½ distance from tip.	5 chromatophores over anterior half.	Do.
	9.2 mm.	**10.9 mm.**	**9.6 mm.**[1]	**9.7 mm.**[1]
Teeth	12 each jaw	15 each jaw	17 upper; 19 lower	13 upper; 14 lower.
Preopercular spines	7	9	6	7.
Myomeres/vertebrae	13 ossified vertebrae (on 10.2-mm. specimen).	20+21 vertebrae (on 9.85-mm. specimen).	20+19 vertebrae (on 9.7-mm. stained specimen).	40 myomeres.
1st dorsal spines	10; longest spine=¾ dorsal interspace.[2]	13; longest spine <½ dorsal interspace.[2]	13; longest spine >½ dorsal interspace.[2]	9; longest spine <¼ dorsal interspace.[2]
1st dorsal fin outline	Slightly convex	Concave	Slightly concave	Convex(?).
Pigmentation:				
1st dorsal fin	Almost entire height to 8th spine.	Chromatophores on outer edge to 12th spine.	Distal ⅔ nearly completely black.	No chromatophores.
Middorsal line	No chromatophores	Chromatophores to 1st dorsal finlet.	No chromatophores	5 chromatophores on caudal peduncle; 11 chromatophores at bases 2d dorsal and finlets.
Midlateral line	do	6 chromatophores forward of caudal peduncle.	do	7 chromatophores on caudal peduncle.
Midventral line	do	4 chromatophores at bases anal and finlets; 1 on caudal peduncle.	2 chromatophores at bases anal and finlet.	3 chromatophores on caudal peduncle; 6 chromatophores at bases anal and finlets.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	No chromatophores	2 chromatophores.
Midbrain	Chromatophores (number?) over small area.	80 chromatophores over large area.	23 chromatophores over large area.	About 25 chromatophores over large area.
Forebrain	No chromatophores	4 chromatophores	5 chromatophores	3 chromatophores.
Mandible (other than at tip)	do	1 chromatophore	4 chromatophores over anterior two-thirds.	No chromatophores.
	14.25 mm.	**14.5 mm.**	**12.25 mm.**[1]	**11.2 mm.**[1]
Teeth	13–14 each jaw	15 upper; 17 lower	25 upper; 28 lower	21 upper; 18 lower.
Preopercular spines	6	8	8	7.
Vertebrae	18+20 (on 12-mm. specimen)	20+21	20+19	Not observed.
1st dorsal spines	14; longest spine=⅔ dorsal interspace.[2]	16; longest spine=½ dorsal interspace.[2]	15; longest spine about ½ dorsal interspace.[2]	9; longest spine <½ dorsal interspace.[2]
1st dorsal fin outline	Convex	Concave	Concave	Convex(?).
Pigmentation:				
1st dorsal fin	Completely black	6 or 7 chromatophores on outer edge of fin.	First 10 spines black	3 chromatophores near distal edge.
Middorsal line	Band of chromatophores to 1st finlet.	Band of chromatophores to 5th finlet.	4 chromatophores at bases 2d dorsal and finlets.	Series of chromatophores from 1st dorsal origin to caudal peduncle.
Midlateral line	No chromatophores	Band of chromatophores from 2d dorsal to 4th finlet.	No chromatophores	7 chromatophores on caudal peduncle.
Midventral line	do	Band of chromatophores at bases anal and finlets; 1 on caudal peduncle.	4 chromatophores at bases anal and finlets.	Series of chromatophores from anal insertion to caudal peduncle.
Tip of pectoral girdle	do	No chromatophores	1 chromatophore	1 chromatophore.
Anal opening	do	do	No chromatophores	No chromatophores.
Midbrain	Numerous chromatophores over small area.	Numerous chromatophores over large area.	Numerous chromatophores over large area.	About 36 chromatophores over medium-sized area.
Forebrain	No chromatophores	12 chromatophores	5 chromatophores	4 chromatophores.
Mandible (other than at tip)	do	Chromatophores on ⅔ of length.	8 chromatophores over entire length.	No chromatophores.

[1] *Dana* Expedition collection.

[2] Distance between insertions of first and second dorsal fins.

The second character that separates these two species is the series of chromatophores along the mandible in *E. yaito*. The first indication of mandibular pigmentation is seen in the 4.6-mm. specimen, where a single chromatophore appears at the middle of the lower jaw. *A. thazard* lacks this pigmentation until it reaches a length of about 15 mm. The only other species which has pig-

ment on the mandible is *K. pelamis*, but in our specimens this species showed only 1 chromatophore at about 7 mm., and this persisted unchanged until a length of 10.9 mm. had been reached. At 14.5 mm. the mandible of *K. pelamis* is well pigmented, but at this size other characters easily separated it from *E. yaito*.

Two other areas of pigmentation in *A. thazard* help to separate it from *E. yaito*. These are the dorsal and lateral edges of the body in the caudal region. The chromatophores on the middorsal line are always present in *A. thazard*, while those on the midlateral line appear indistinct among the specimens below 4.5 mm.

It should be mentioned that in *A. thazard* pigmentation of the caudal region varies considerably, especially on the midlateral line. A number of specimens measuring up to 7 or 8 mm. lacked this pigmentation (fig. 28). Whether they represent another species, *A. tapeinosoma*, is difficult to determine, since a complete series of larvae of this type could not be assembled. All other characters of these specimens lead us to believe that they belong to the genus *Auxis*.

Several excellent characters separate *N. macropterus* from *K. pelamis*. Between 8.0 and 14.25 mm., *N. macropterus* can be distinguished from *K. pelamis* by the almost completely pigmented first dorsal fin. This pigmentation is first noticeable on a 6.4-mm. specimen and is represented by a single, small chromatophore. *K. pelamis* also has some pigmentation on the first dorsal fin, which seems to develop much later than in *N. macropterus*, for only 1 or 2 very faint chromatophores are present in specimens measuring about 7 mm.

Another notable character of *N. macropterus* is the complete lack of pigmentation in the caudal region of the body until the larva approaches 14.0 mm. In the remaining three species described here, some pigmentation is present in the caudal region at all sizes.

The final character which is peculiar to *N. macropterus* is the complete absence of pigmentation over the forebrain on specimens of all sizes. In *K. pelamis* this pigmentation is present in specimens down to 7.1 mm. *N. macropterus* smaller than 7.15 mm. can be separated from *K. pelamis* by the small area of pigmentation over half or less than half the area of the midbrain, whereas in *K. pelamis* this pigmentation extends over almost the entire midbrain area. The only possible confusion in separating individuals of these two species measuring less than 7.15 mm. is in the rare cases where the chromatophore at the caudal peduncle of *K. pelamis* is absent. However, in such cases the relatively shorter snout and smaller mouth of *N. macropterus* (table 4), together with the difference in pigmentation over the midbrain, help to separate these two species.

Among *N. macropterus* larger than 9.2 mm., the outline of the first dorsal fin is definitely convex, and the longest spine of the fin is about three-fifths the distance between the first and second dorsal fin insertions (table 5). The fin outline of *K. pelamis* is concave in a 10.9-mm. specimen, and its longest spine is less than one-half the distance between the insertions of the first and second dorsal fins.

Larger specimens of *K. pelamis* can be most readily identified by staining the vertebrae. A count of 20 precaudal and 21 caudal vertebrae is

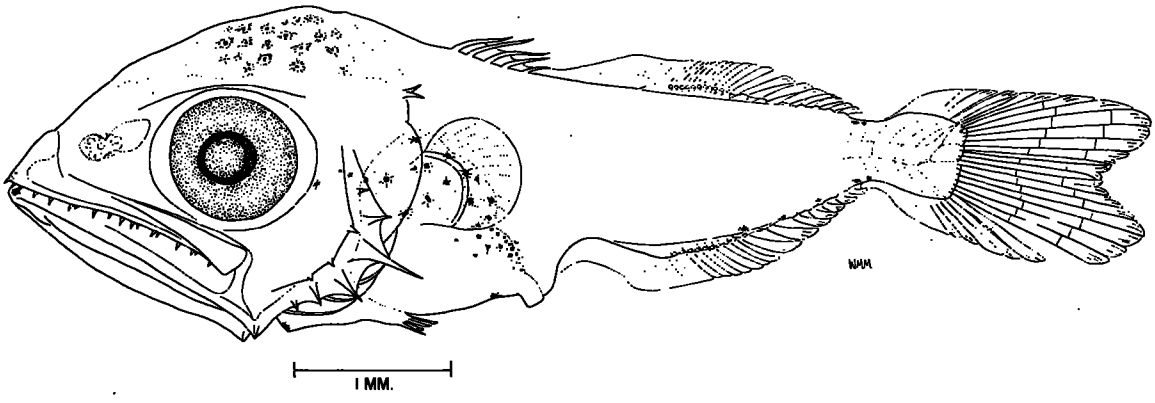

FIGURE 28.—*Auxis* sp. (?), 7.2 mm. total length.

definitive for this species, and this count can be obtained from specimens measuring only 9.85 mm. Where staining is not feasible, this species can be identified by the single distinct chromatophore at the ventral midline of the caudal peduncle throughout the entire size range. This chromatophore is absent only rarely, but at times there may be 2 instead of the usual 1. Moreover, *K. pelamis* between the sizes of 7.1 mm. and 10.9 mm. have a single chromatophore near the tip of the mandible in the smaller specimens and near the middle of the mandible in larger specimens.

K. pelamis smaller than 7.0 mm. can be distinguished from the other species by the single chromatophore at the midventral line of the caudal peduncle, by the larger mouth and longer snout, and by the large area of pigmentation over the midbrain. Forty-one or 42 myomeres can be counted on specimens of *K. pelamis* whereas other species have 41 or fewer.

DISTRIBUTION OF TUNA LARVAE IN THE CENTRAL PACIFIC

In the sections to follow we shall discuss mainly the distribution of the two species of tuna, *Neothunnus macropterus* and *Katsuwonus pelamis*, which comprise the bulk of our catch of tuna larvae, for the purpose of gaining some insight into the distribution and spawning habits of these fish. Included are discussions on horizontal and vertical distribution, species composition of the catches, and spawning areas and seasons as evidenced from the size composition of the catches. In addition to the identified larvae there is a small, unidentified group consisting in the main of small (less than 3 mm.) and damaged larvae. Since there is little reason to suppose this group contains additional species, this and the small group of *Auxis thazard* are not considered in the discussions on distribution and spawning seasons.

A vast area of the Pacific was sampled, extending from 25° N. to 15° S. latitude and from 120° W. to 180° longitude. The hydrography of this area was studied, and experimental fishing with longline gear (described in Niska 1953) also was conducted in the region between 14° N. and 9° S. latitude during the period when the plankton hauls were made.

Hydrographic observations in this region indicate a current system composed of a westerly flowing North Equatorial Current with its southern boundary varying with longitude and with season, but generally at about 10½° N. latitude; a westerly flowing South Equatorial Current with its northern edge at about 5½° N. latitude; and an easterly flowing Equatorial Countercurrent between the North and South Equatorial Currents. The width of the Countercurrent varies from 4° to 7½° and it shifts north and south over a distance of from 2° to 5° during different periods of time and at different longitudes (Cromwell 1954, table 1). These currents could have an important effect on the distribution of free-floating eggs and of newly hatched larvae, which are not yet capable of swimming about extensively.

HORIZONTAL DISTRIBUTION

Range of distribution

Approximate collecting locales for tuna larvae taken during 1950–52 are shown in figure 29. Each dot represents the occurrence of the designated species and has no quantitative connotation. Tuna larvae, both *N. macropterus* and *K. pelamis*, were taken as far north as 25° N. latitude in the vicinity of Midway Island, the most northerly area sampled during this period. Zooplankton collections presently being made in central Pacific waters up to about 45° N. latitude may show a further extension of the northern limit of larval-tuna distribution, for preliminary examination of zooplankton samples collected from this area (at 31° N. latitude along 143° W. longitude) during the winter of 1954 shows a few tuna larvae, too small for positive identification. South of the Equator, larvae have been taken at 14½° S. latitude in the vicinity of Samoa, the southernmost latitude at which a plankton station has been occupied by POFI vessels. In an east-west direction, larvae were taken at all longitudes sampled, from 120° W. to 180°. The area of larval occurrence as shown by the broken lines in figure 29 approaches 4 million square miles.

Latitudinal distribution of *Katsuwonus pelamis* and *Neothunnus macropterus*

The latitudinal distributions of the two species of tuna which comprise almost the entire larval-tuna catch in equatorial waters are plotted in figure 30, together with the corresponding adult catches on longline gear (the latter from Murphy and Shomura 1953a, 1953b). The north-south

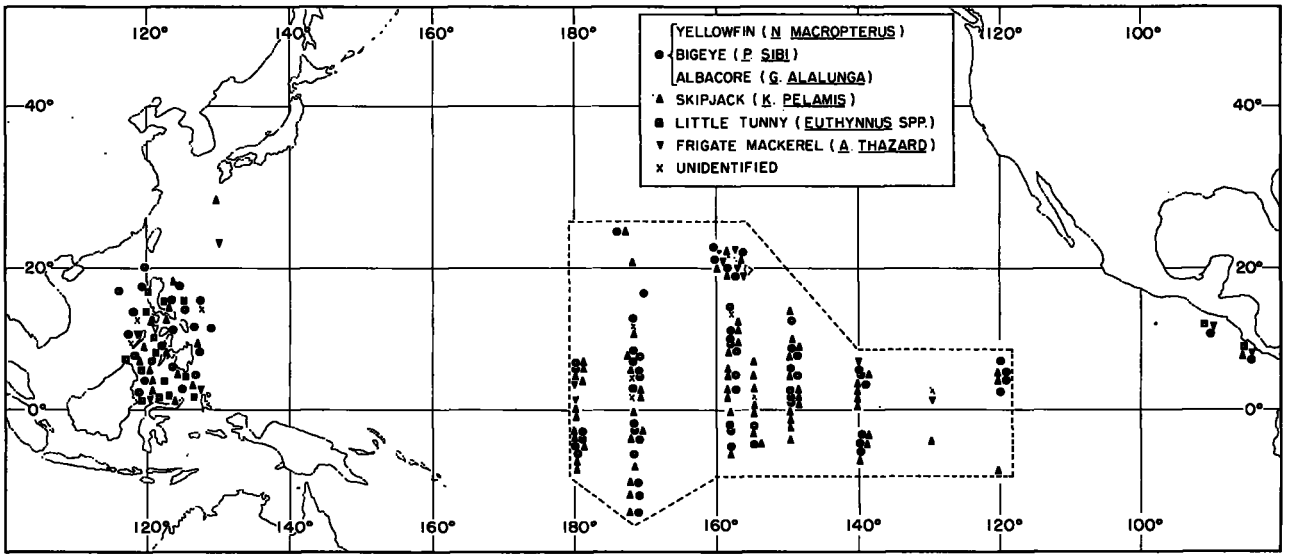

FIGURE 29.—Localities of capture of tuna larvae in the equatorial Pacific. Broken lines enclose area of POFI collections.

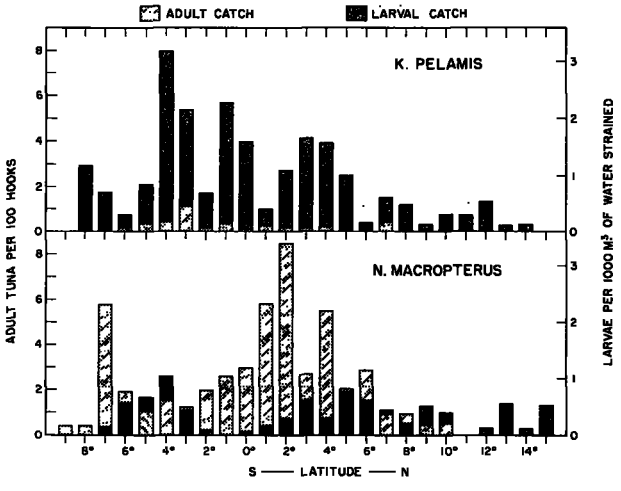

FIGURE 30.—Latitudinal distribution of the adult *Katsuwonus pelamis* and *Neothunnus macropterus*, as indicated by longline catch, and of the larvae.

range was limited by 14° N. and 9° S. latitudes in conformity with the range of fishing stations. The catch figures for both adults and larvae represent the averages of all the longitudes sampled during identical years.

Although our longline catches may not provide a true measure of the abundance of adult *K. pelamis*, they would seem to indicate that the distribution of these fish (fig. 30, upper panel) is somewhat skewed to the south, with the peak at 3° S. latitude. Larval abundance shows a similar trend, but the latitudinal range of the larvae exceeds that of the adults. This is understandable when we realize that fishing effort was reduced at the northern and southern extremities.

The adult *N. macropterus* catches (fig. 30, lower panel) present a different distribution pattern. There are two peaks, one is slightly north of the Equator and another at 7° south of the Equator. As explained by Murphy and Shomura (1953a, 1953b, and 1955) the tunas, especially *N. macropterus*, are perhaps indirectly associated with the phenomenon of upwelling that occurs along the Equator. Large catches of adult *N. macropterus* were made slightly to the north and south of the Equator where the upwelled water had aged sufficiently to allow populations of tuna forage to develop. The larval *N. macropterus* catches show a similar, but more pronounced, bimodal distribution which, although it is slightly displaced to the north, is likely related to the adult catches.

Longitudinal distribution of *Katsuwonus pelamis* and *Neothunnus macropterus*

Consideration of the larval-tuna catches (fig. 31) was limited to stations between 9° N. and 9° S. latitude, the zone in which there was the most concentrated fishing for adults, in order to compare the catches of larval and adult tuna.

It can be seen from the upper panel in figure 31 that the abundance of *K. pelamis* larvae seemed fairly uniform from 180° to 140° W. longitude and the adult abundance was uniform from 170° W.

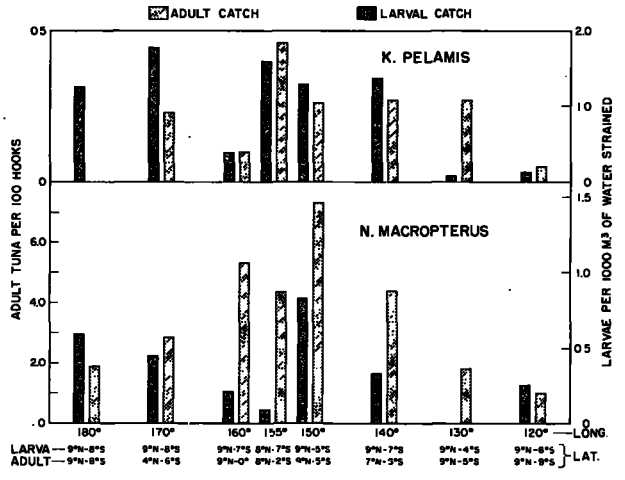

FIGURE 31.—Longitudinal distribution of the adult *Katsuwonus pelamis* and *Neothunnus macropterus*, as indicated by longline catch, and of the larvae for the area 9° N. to 9° S. latitude.

to 130° W. longitude, apart from the low catches of both larvae and adults at 160° W. longitude. The low catches of larvae at 130° W. and 120° W. longitude suggest that there is little spawning of *K. pelamis* in this region.

The adult *N. macropterus* distribution varied slightly from that of *K. pelamis* (fig. 31, lower panel), for they were found from 180° to 120° W. longitude with a peak at 150° W. longitude. The larval *N. macropterus* abundance also peaked at the 150th meridian, but aside from this there was little correspondence in the density of larvae and adults. The apparent absence of larvae at 130° W. longitude suggests that this longitude may be near the eastern limit of favorable *N. macropterus* spawning grounds. The salient feature of both *N. macropterus* and *K. pelamis* distribution is that, with the exception of *N. macropterus* along 130° W. longitude, tuna larvae were taken at all the longitudes where the adults were found.

West of 180° longitude the adults of *N. macropterus*, *K. pelamis*, and other tunas are caught all the way to the Asian coast. On the basis of the adult-larva relationship, it can be expected that tuna larvae will also be found in the region between 180° and the coast of Asia. This is not entirely supposition, for Wade (1950, 1951) has reported the capture of large numbers of these larvae from the waters surrounding the Philippine Islands. In the eastern Pacific, Schaefer and Marr (1948a, 1948b) and Mead (1951) found larval and juvenile tunas off the Pacific coast of Central America. The widely distributed records of larvae (fig. 29) together with the apparent parallels between adult and larval-tuna catch rates suggest that tuna larvae are generally distributed across the Pacific Ocean, although not necessarily with uniform abundance.

Records of larval-tuna captures in the Atlantic Ocean also seem to support the probability of a transoceanic distribution of tuna larvae. The Equatorial Current system roughly follows the same pattern in the Atlantic Ocean as in the Pacific Ocean, and tuna larvae have been taken (Ehrenbaum 1924) in a band of water between 32° N. and 7° S. latitude from the Cape Verde Islands to the coasts of Florida and Brazil (fig. 32).

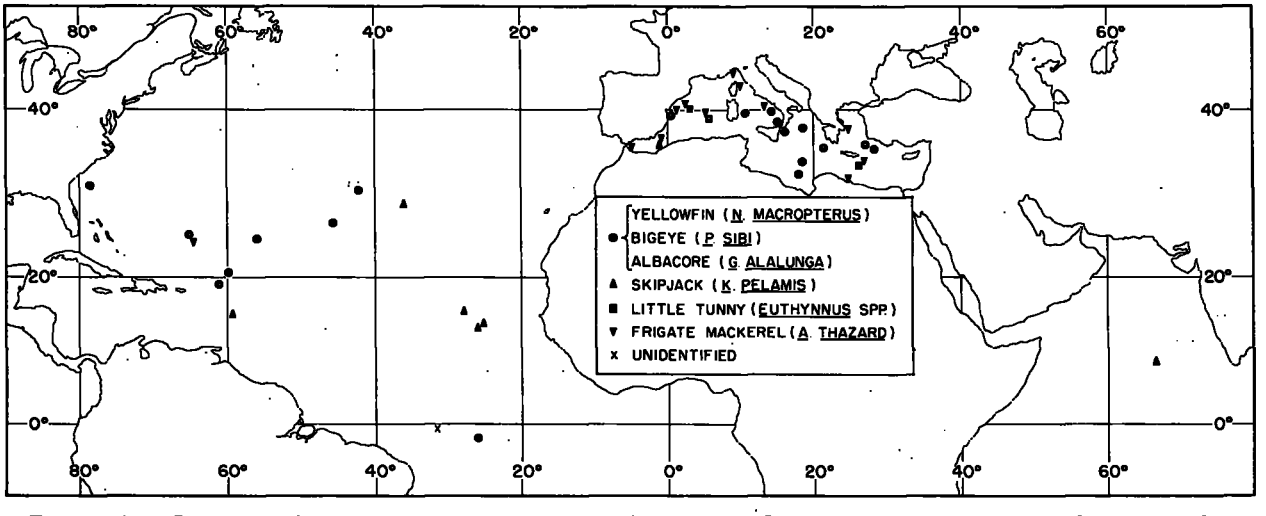

FIGURE 32.—Localities of capture of larval tunas in the Atlantic and Indian Oceans and in the Mediterranean Sea.

It is interesting to note that there are extensive records of larval tunas in the Mediterranean Sea and a record from the Indian Ocean.

VERTICAL DISTRIBUTION OF TUNA LARVAE

The data from cruise 6 of the *Hugh M. Smith* in Hawaiian waters (fig. 1) were used in studying the vertical distribution of tuna larvae. During each haul, 3 nonclosing nets, fishing at different depths, were towed simultaneously in a horizontal plane for 1 hour. At each station one of the following sets of towing depths was used: 0, 50, 150 meters; 0, 100, 150 meters; 0, 100, 200 meters; or 0, 150, 300 meters (appendix table 2, p. 68). The catches made on this cruise (table 6) show very clearly that tuna larvae are concentrated in the surface layers. Further, it is possible that all or most of the deep catches are contaminants, obtained while the nets were being raised and lowered.

TABLE 6.—*Abundance of tuna larvae in Hawaiian waters, per 1,000 cubic meters of water strained, for various depths and times of hauling*

[The figures in parentheses represent number of tows]

Time of tow	Depth in meters					
	Surface	50	100	150	200	300
Day	1.70(16)	0.42(4)	0.21(10)	0.08(8)	0.44(8)	0.36(2)
Night	8.49(9)	0.98(2)	0.55(4)	0.71(6)	1.18(3)	1.15(3)

The amount of contamination can be computed if the average concentration of larvae in the upper strata and the time spent by the net in passing through them are known.[2] It is interesting to note that, assuming the surface tows are representative of the upper 50 meters or the layer between the surface and the next shallowest net, contamination correction accounts for all of the deeper night catches and nearly all of the deeper day catches (fig. 33).

A vertical, diurnal migration of the larvae is suggested in the raw catches and is clearly shown when the surface tows are plotted according to the hour of hauling (fig. 34). (For the present, dodging is not considered; it will be shown later

[2] The following formula was used to compute contamination:

$$\text{Average number of contaminants} = \frac{\text{Average time a lower net spent in surface layer}}{\text{Average total elapsed time of tows of the surface net}} \times \text{Average surface catch.}$$

The several amounts were then subtracted from the figures in table 6 and the corrected catches plotted in figure 33.

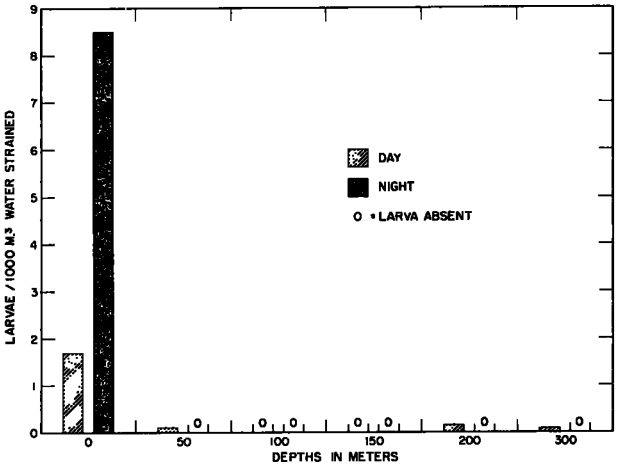

FIGURE 33.—Vertical distribution of tuna larvae from the Hawaiian area corrected for contamination, assuming that the surface hauls are representative of the upper 50 meters.

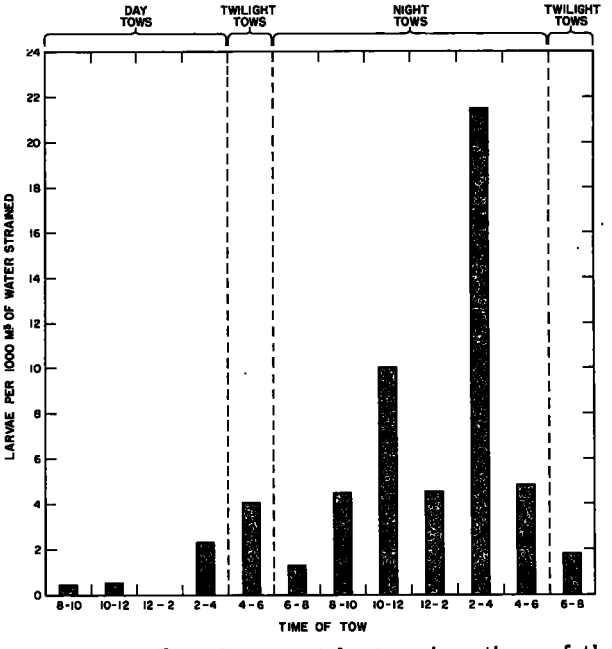

FIGURE 34.—Larval-tuna catch at various times of the day.

to be relatively unimportant.) Relatively poor catches were experienced during the day, when the larvae presumably were beyond the depth of the surface net. The catches increased after twilight as the larvae apparently migrated to the surface, the greatest catches being made between 10 p. m. and 4 a. m. The catches declined as the downward migration occurred with the approach of daylight.

The depth of the diurnal, vertical migration of

the tuna larvae cannot be specified, but its maximum can be inferred from our material. A large series of 200-meter oblique hauls in the equatorial region (table 7) shows no statistically significant diurnal variation ($t=1.421$, $P=0.14$), thus suggesting that migration may not occur down to 200 meters. That the migration is of even more limited scope is suggested by the corrected vertical distribution (fig. 33). If migration occurs down to 200 meters, then in the horizontal tows the day catches at the greater depths should be larger than the night catches and also they should be larger than the day catches at the surface. The fact that the subsurface catches are consistently less than the surface day catches suggests a migration which is probably limited to a depth of less than 50 meters, and the main concentration of larvae in the daytime occurred between the levels sampled by the surface and the 50-meter horizontal tows.

TABLE 7.—*Comparison of day and night catches of tuna larvae by 200-meter oblique tows in equatorial waters*

Time of tow	Number of tows	Larvae/1,000 m.³ of water strained
Day	49	1.50
Night	34	2.23

During the review of vertical migration and vertical distribution the problem of dodging was temporarily disregarded. It must be examined, however, and its effect considered because it can possibly bias comparisons of hauls between depths and between day and night. The presence or absence of dodging can best be examined in the 200-meter oblique tows, assuming that the net had passed through the entire vertical range of larval distribution, thus minimizing or possibly eliminating the effects of vertical migration in the catches. The night catches, although not significantly different from day catches, are about 1.5 times the latter (table 7), suggesting that dodging may have occurred. Even if the relatively greater catches in the night hauls were due to dodging, it will be noted from table 6 that the ratio of night to day catches at the surface is much greater (4.99: 1), suggesting a vertical migration, despite allowances made for the effects of dodging. Additional evidence in favor of vertical migration is provided by the relatively low night-day ratios at greater depths (table 6) as compared with the high ratio of the surface catches.

There is also little evidence in support of dodging when the frequency of captures of the larger larvae are considered, the implication here being that the larger larvae are more capable of dodging the net than are the smaller larvae. In the equatorial area, four larvae 10 mm. or larger were taken during the day and only one at night. In the Hawaiian area only two larvae over 10 mm. were obtained and these were taken at night.

Considering all the evidence, it appears that dodging may alter the catches but not enough to seriously bias our conclusions that most of the larvae live near the surface during both day and night, and that there is a vertical, diurnal migration through relatively shallow depths.

SPECIES COMPOSITION OF THE LARVAL CATCH

Our discussion of species composition is based entirely on catches from the equatorial area between 120° W. longitude and 180°, and 9° N. and 9° S. latitude so that the composition of the larval catch can be compared with that of adults from the same area. Three of the four species of tuna larvae described previously are represented in the plankton samples, while the larvae of two other species of tuna, *Parathunnus sibi* and *Germo alalunga*, either were not taken or were not recognized.

Of the three species of larvae identified (table 8), *A. thazard* constitutes an insignificant portion of the catch, 1.2 percent of the total number of tuna larvae. The *N. macropterus* and *K. pelamis* larvae comprise 22.5 and 59.2 percent, respectively. This is in contrast to the species composition of the longline catch of adults, 73.0 percent of which were *N. macropterus* and 4.4 percent *K. pelamis*. However, the longline catches probably do not provide a reliable estimate of the true abundance of *K.*

TABLE 8.—*Species composition of larval and adult tunas taken in equatorial waters*

Species	Larvae [1]		Adults [2]	
	Number taken	Percent of total catch	Number taken	Percent of total catch
Neothunnus macropterus	107	22.5	889	73.0
Katsuwonus pelamis	281	59.2	54	4.4
Auxis thazard	6	1.2		
Germo alalunga			68	5.6
Parathunnus sibi			206	16.9
Unidentified	81	17.0		
Total	475		1,217	

[1] Plankton hauls.
[2] Longline catches.

pelamis since the gear is designed and fished with the primary objective of capturing the much-larger, deep-swimming *N. macropterus*. Thus, the low catch figures for *K. pelamis* represent only a few chance catches made by the longline.

The predominance of *K. pelamis* larvae in the plankton catches presents an interesting indication of the probable adult concentration. If we assume that both species have the same fecundity and larval mortality, it would appear that the adult *K. pelamis* population is about two and one-half times that of the *N. macropterus*. However, it is known that the *K. pelamis* ovaries are smaller than the *N. macropterus* ovaries and contain fewer eggs; therefore, this estimate of the relative numerical predominance of *K. pelamis* is minimal. Thus, there is the possibility that a population of *K. pelamis* exists in this region of sufficient size to support a commercial fishery, if the schools can be located. To date, however, only a few schools, consisting mostly of small fish, have been observed and they have occurred mostly in the immediate vicinity of islands and atolls.

AREA AND LOCALITY OF SPAWNING

Most studies of spawning have been based upon observations on the condition of the gonads, and the spawning locality has been assumed to be near the site where females with running or nearly ripe eggs have been captured. This method is applicable to fishes with limited migratory movements or to those that are relatively weak swimmers. However, in the case of the tunas—fishes which possess tremendous swimming speed and range—the actual spawning site could be some distance from the locality in which adult females with nearly ripe gonads are taken. A more-nearly ideal approach to the problem of locating the spawning sites of these fishes would be to examine the less-motile stages in the life cycle, specifically the planktonic eggs and newly hatched larvae.

The present investigation was limited to the larval stages because it has not been possible to identify the eggs of the several tunas. Early larvae can be considered planktonic, and while they have limited powers of movement, it is reasonable to suspect that they do not stray very far from the actual spawning grounds. If this is so, then it can be hypothesized that the localities where tuna larvae are taken should represent the approximate spawning sites.

Three factors must be evaluated before this reasoning can be applied to our data to estimate the location of spawning grounds: (1) The size of the larvae at hatching; (2) the duration of the incubational period, throughout which the eggs are planktonic; and (3) the direction and velocity of the currents.

Determination of size of larvae at hatching.—Sanzo (1932, 1933), who observed the development of the embryo in the eggs of *Orcynus thynnus* and *Orcynus germo*,[3] reported that the larvae measured from 2.44 to 3.04 mm. in total length at hatching. The egg diameters for these two species were from 1.00 to 1.12 mm. for the former, and 0.84 to 0.94 mm. for the latter. Comparatively, the eggs from ripe gonads collected during POFI cruises measured from 0.83 to 1.08 mm. for *N. macropterus*, and from 1.00 to 1.21 mm. for *P. sibi*. *K. pelamis* eggs were from 0.55 to 0.80 mm. in diameter, but it is believed that this may represent a somewhat earlier stage of maturity. The largest egg that Brock (1954) found during his investigation of the biology of *K. pelamis* measured 1.125 mm. in diameter, and should be close to the size of the fully ripe eggs. If egg size has any bearing on size of the larvae at hatching, then newly hatched *N. macropterus* and *K. pelamis* should fall within the size ranges given by Sanzo for two species of tuna, that is, 2.44–3.04 mm.

Determination of duration of incubational period.—The embryonic development of six California fishes (Budd 1940) indicates that various pelagic species have incubational periods ranging from 90 to 264 hours, and that the eyed-embryo stage regularly appears at about the middle of the developmental period or slightly earlier. The latter observation is supported by illustrations presented by Kuntz and Radcliffe (1918) for the pelagic eggs of six species of fish. It seems that the appearance of the eyed-embryo is fixed rather definitely at about the middle of the incubational period. If this holds true for all pelagic eggs, then the incubational period for tunas could be approximated at not more than 4 days, since the eyed-embryo eggs collected by Sanzo (1932, 1933) hatched in less than 2 days.

[3] Sanzo probably followed Lütken's terminology. If so, *O. thynnus* (Linnaeus) represents "the more or less 'short-finned' genuine tunafish" and *O. germo* (Lacépède) represents the "more or less 'long-finned'" tunas (Lütken 1880). Thus, *O. thynnus* could be bluefin tuna and *O. germo* could be either yellowfin or albacore.

Direction and maximum velocities of currents in the central Pacific.—As stated previously, the North and South Equatorial Currents flow westward and the Equatorial Countercurrent flows eastward in this area. The maximum velocity of the North Equatorial Current during 1950–52 was 0.56 knots, while that of the South Equatorial Current was 1.55 knots, as measured on POFI cruises. The eastward-flowing Countercurrent showed a maximum velocity of 1.16 knots. (Current speed in knots was converted from figures in Cromwell 1951, 1954; Austin 1954; and Stroup 1954.) It is well to bear in mind that the velocity of each current varies considerably throughout the width of the current and at different longitudes (Cromwell 1954, figs. 21 and 27).

The implications in the foregoing discussions are that larvae measuring between 2.44 and 3.04 mm. would have been adrift a maximum of 4 days prior to their hatching, and that these larvae could have drifted westward a distance of about 50 or 150 miles, depending on whether they were in the North or the South Equatorial Current, or they could have drifted eastward a distance of about 100 miles if they were in the Equatorial Countercurrent. The maximum drift in terms of longitudinal distance is about 2½° westward and about 2° eastward.

In the present investigation larvae measuring between 2.50 and 3.90 mm. (which approximates the size of newly hatched larvae), presumed to be *K. pelamis* and *N. macropterus*, were taken at nearly all latitudes from 25° N. to 14½° S. (fig. 35), and also at nearly all longitudes sampled (fig. 36). They were caught at stations which generally were 5 to 10 longitudinal degrees apart and beyond the maximum drift to which these larvae could have been subjected. Thus, the presence of these newly hatched larvae along the various longitudes from 120° W. to 180° provides evidence that some spawning occurs throughout the area sampled.

TIME OF SPAWNING OF *KATSUWONUS PELAMIS* AND *NEOTHUNNUS MACROPTERUS*

Larval-catch data from equatorial waters for the years 1950–52 were segregated by months for each species, and the average catches from three bands of 10° of latitude, 5° N. to 14° N., 5° S. to 4° N., and 14° S. to 6° S. were then plotted to produce figure 37. The area was separated into such bands in order to see if there were seasonal spawning trends from north to south.

The plots show that *K. pelamis* larvae were found throughout the year and in fairly equal numbers each month between 5° N. and 14° N.

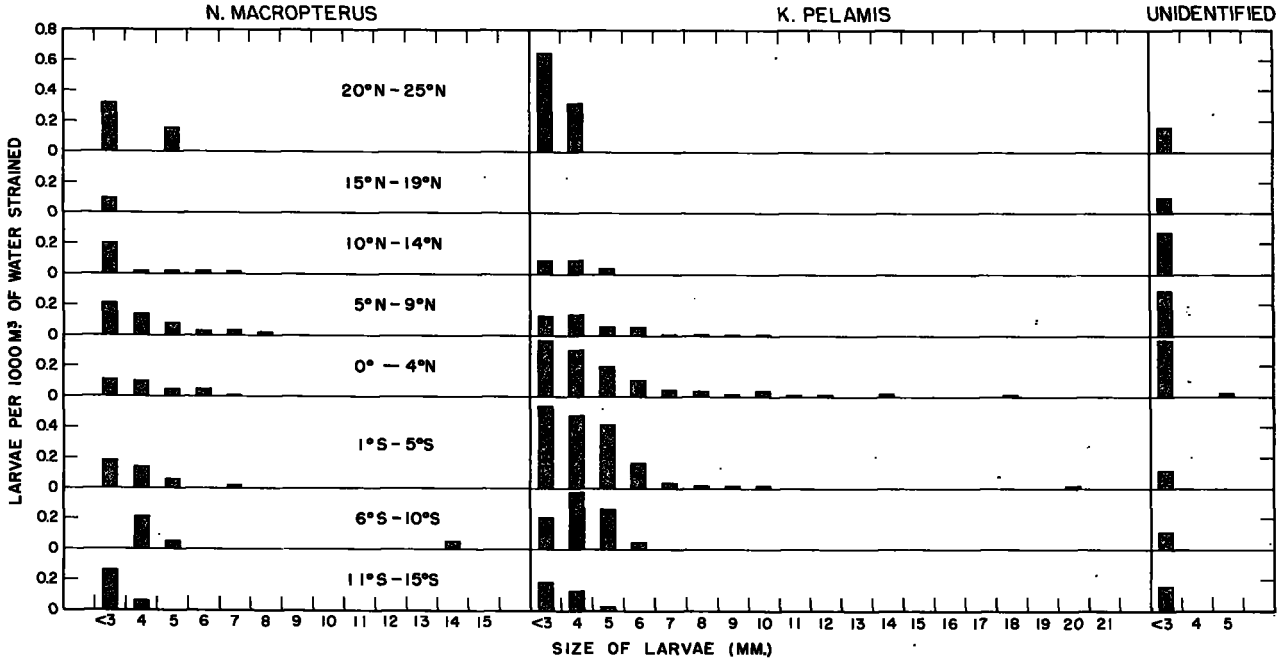

FIGURE 35.—Latitudinal variation in size composition of tuna larvae caught between 120° W. and 180° longitude.

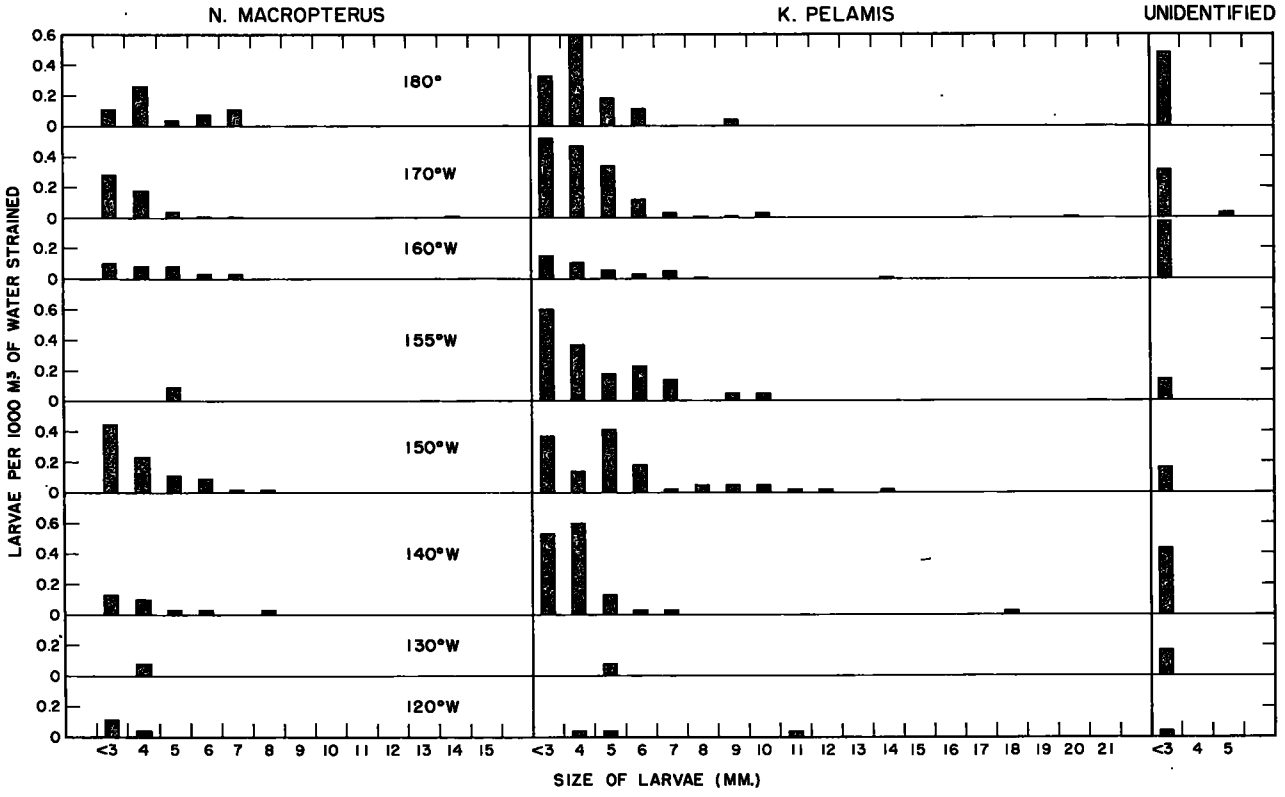

FIGURE 36.—Longitudinal variation in size composition of tuna larvae caught between 14° N. and 14° S. latitude.

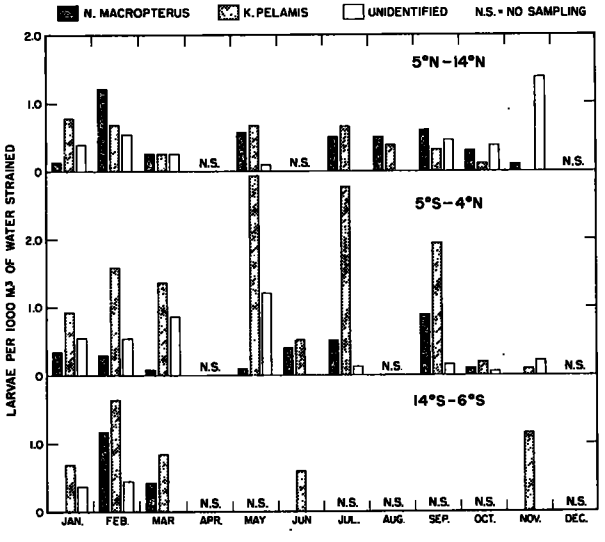

FIGURE 37.—Monthly catches of larvae in equatorial waters for three latitudinal zones, 1950 to 1952.

latitude. Substantially greater numbers of larvae occurred, however, between 4° N. and 5° S. latitude. Although this equatorial region produced *K. pelamis* larvae throughout the year, it showed a definite peak from May through September. South of 6° S. latitude larval *K. pelamis* were rather uniformly abundant; however, the catches do not represent enough months to permit a more specific interpretation. In general, it can be hypothesized that while year-round *K. pelamis* spawning occurs throughout the area between 4° N. and 5° S. latitude, the spawning activity is greatest from May through September.

There are no significant peaks of *N. macropterus* spawning between 14° N. and 5° S. latitude. However, a striking difference exists between the catches of *N. macropterus* and *K. pelamis* larvae in the area south of 5° S. latitude. Here, larvae of the former species were caught only in February and March, none being taken in January, June, and November. Seasonal spawning may occur in more southern waters, but here again data were obtained for too few months to form a definite opinion. As far as *N. macropterus* is concerned, it can be hypothesized that this

species spawns throughout the area and throughout the year at a uniform intensity.

SUMMARY

1. Four species of tuna larvae, yellowfin (*Neothunnus macropterus*), skipjack (*Katsuwonus pelamis*), little tunny (*Euthynnus yaito*), and frigate mackerel (*Auxis thazard*), are described from plankton catches taken in central Pacific waters between 23° N. and 15° S. latitude and 120° W. and 180° longitude and from the East Indies and the Gulf of Panama.

2. The most conspicuous, specific characters that distinguish the larvae are as follows:

a. *Neothunnus macropterus:* Absence of chromatophores on the trunk, except over the visceral mass, until the larvae approach 14 mm.

b. *Katsuwonus pelamis:* Presence of a distinct chromatophore on the ventral midline of the caudal region, and no chromatophore at the symphysis of the pectoral girdle.

c. *Euthynnus yaito:* A series of chromatophores along the midventral line of the trunk, from the vicinity of the anal fin base to the caudal region; presence (usually) of a chromatophore at the symphysis of the pectoral girdle.

d. *Auxis thazard:* Three short series of closely set chromatophores on the middorsal, midlateral, and midventral lines of the caudal region; presence (usually) of a chromatophore at the symphysis of the pectoral girdle.

3. Larvae of *Katsuwonus pelamis* and *Neothunnus macropterus* were found in the waters north of the Hawaiian Islands to approximately 25° N. latitude and as far south as the Samoan Islands near 15° S. latitude. The areas rich in larval *Neothunnus macropterus* coincided with the areas where the adults were frequently taken by longlining. Along the Equator, larvae were found between longitudes 120° W. and 180°, the east-west limits of the area investigated, with a decidedly rich area between 140° W. and 180°. The close adult-larva relationship suggests the possibility of a transoceanic distribution of these larvae along the Equator.

4. Larvae were found to be concentrated at or near the surface, especially at night. It seems likely that even in the daytime the bulk of the larvae occur at less than 50 meters. Diurnal migration probably occurs within this shallow zone.

5. The abundance of *Katsuwonus pelamis* larvae in the area implied that a sizeable stock of adult *Katsuwonus pelamis* occurred in equatorial waters.

6. Recently hatched larvae were found in nearly all latitudes, longitudes, and seasons, suggesting widespread, continuous spawning throughout the area sampled.

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APPENDIX

The following tables list by species the number of tuna larvae collected from the POFI research vessel *Hugh M. Smith* on 8 cruises in the equatorial Pacific in 1950–52. The tables include only those cruises or parts of cruises, from which material for this study was obtained.

APPENDIX TABLE 1.—*Tuna larvae collected on* Hugh M. Smith *cruise 5 in equatorial waters*

[All hauls were oblique from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude								
					1,000 m.³					
No. 1	27°00′ N.	175°11′ W.	6-30-50	0945	1.25					
No. 2	25°00′ N.	174°10′ W.	7- 1-50	0258	1.32	1	1			2
No. 3	22°58′ N.	173°00′ W.	7- 1-50	2315	1.34					
No. 4	21°00′ N.	172°00′ W.	7- 2-50	0415	0.74		3			3
No. 5	19°00′ N.	171°52′ W.	7- 3-50	0807	1.25					
No. 6	17°01′ N.	171°46′ W.	7- 3-50	1219	1.43					
No. 7	15°00′ N.	171°54′ W.	7- 4-50	1649	0.89				1	1
No. 8	14°00′ N.	171°57′ W.	7- 5-50	0123	0.85	1			1	2
No. 9	13°00′ N.	172°01′ W.	7- 5-50	0950	1.33					
No. 10	12°00′ N.	172°00′ W.	7- 5-50	1815	0.88					
No. 11	11°03′ N.	172°00′ W.	7- 6-50	0315	1.33		3			3
No. 12	9°54′ N.	172°02′ W.	7- 6-50	1213	1.78	1				1
No. 13	8°54′ N.	172°00′ W.	7- 6-50	2012	1.19	2				2
No. 14	7°59′ N.	171°57′ W.	7- 7-50	0350	1.62	1	4			5
No. 15	6°59′ N.	171°46′ W.	7- 7-50	1226	1.58	1				1
No. 16	6°02′ N.	171°56′ W.	7- 7-50	2130	1.38		2			2
No. 17	5°00′ N.	172°02′ W.	7- 8-50	0845	1.82	1				1
No. 18	4°00′ N.	172°03′ W.	7- 8-50	1659	1.35					
No. 19	3°00′ N.	172°01′ W.	7- 9-50	0036	1.06		1			1
No. 20	2°00′ N.	171°53′ W.	7- 9-50	0838	1.81				1	1
No. 21	0°54′ N.	172°12′ W.	7- 9-50	1746	1.59	2	1	2	2	7
No. 22	0°08′ S.	172°02′ W.	7-10-50	0143	1.94		8			8
No. 23	1°00′ S.	171°57′ W.	7-10-50	0925	1.26		24			24
No. 24	2°00′ S.	171°55′ W.	7-10-50	1740	1.41					
No. 25	2°59′ S.	171°59′ W.	7-11-50	0133	1.31	1	17			18
No. 26	4°05′ S.	171°56′ W.	7-11-50	1055	1.58	9	2			11
No. 27	5°04′ S.	171°58′ W.	7-11-50	2110	1.63					
No. 28	4°56′ S.	158°02′ W.	7-28-50	0556	1.38					
No. 29	4°00′ S.	158°03′ W.	7-28-50	1324	0.64					
No. 30	3°03′ S.	158°00′ W.	7-28-50	2137	0.87					
No. 31	2°03′ S.	158°00′ W.	7-29-50	0550	0.65					
No. 32	1°00′ S.	158°01′ W.	7-29-50	1418	1.00		1			1
No. 33	0°02′ S.	157°58′ W.	7-29-50	2221	0.77					
No. 34	0°57′ N.	157°57′ W.	7-30-50	0646	1.53					
No. 35	2°00′ N.	158°07′ W.	7-30-50	1532	0.85		1			1
No. 36	3°00′ N.	157°58′ W.	7-30-50	2302	0.97		6			6
No. 37	4°00′ N.	158°03′ W.	7-31-50	0640	1.65		6			6
No. 38	5°00′ N.	158°00′ W.	7-31-50	1750	1.18		1			1
No. 39	6°00′ N.	157°57′ W.	8- 1-50	0144	1.31	1				1
No. 40	7°00′ N.	157°57′ W.	8- 1-50	0854	0.95					
No. 41	8°00′ N.	157°50′ W.	8- 1-50	1620	3.36	1				1
No. 42	9°00′ N.	157°55′ W.	8- 2-50	0020	1.14	2	1			3
No. 43	10°00′ N.	157°53′ W.	8- 2-50	0744	1.60	1	2			3
No. 44	11°00′ N.	157°55′ W.	8- 2-50	1546	1.14					
No. 45	11°59′ N.	158°04′ W.	8- 2-50	2343	1.03	1	4			5
No. 46	13°00′ N.	157°58′ W.	8- 3-50	0800	1.46		1			1
No. 47	14°00′ N.	157°54′ W.	8- 3-50	1639	1.31					
No. 48	14°58′ N.	157°55′ W.	8- 4-50	0253	0.59	2				2
No. 49	17°00′ N.	158°08′ W.	8- 4-50	1741	0.93					
No. 50	19°02′ N.	157°59′ W.	8- 5-50	1006	1.03					
No. 51	20°53′ N.	158°02′ W.	8- 5-50	2300	0.85	3	2	2		7

[1] +11 zone time on stations 1 to 27; + 10 zone time on stations 28 to 51.

APPENDIX TABLE 2.—*Tuna larvae collected on* Hugh M. Smith *cruise 6 in Hawaiian waters*

[All hauls were 1-hour horizontal tows at depth indicated]

Station	Depth of haul	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
		North latitude	West longitude								
	Meters					*1,000 m.*[3]					
No. 1	0	23°31′	161°05.5′	8-25-50	1405	2.05	1				1
	50					1.99	1	1			2
	150					3.14				1	1
No. 1A	0	22°45′	161°15′	8-25-50	2030	2.63	5	9	1	4	19
	50					2.81		2		3	5
	150					3.32				3	3
No. 2	0	21°57′	161°05′	8-26-50	0315	2.26	12				12
	100					3.07		3		1	4
	200					4.01	1	1			2
No. 3	0	21°09.5′	161°03′	8-26-50	1042	2.15					
	50					2.07				1	1
	150					2.60					
No. 4	0	20°20′	161°05′	8-26-50	1750	2.25		8		5	13
	100					2.80		1			1
	200					3.57		1			1
No. 5	0	19°25.5′	161°05′	8-27-50	0042	2.31	2	13		10	25
	150					3.11					
	300					3.70		1		1	2
No. 6	0	19°26′	159°50′	8-27-50	0950	2.39	2				2
	100					2.48					
	200					3.98					
No. 7	0	20°16.5′	159°44′	8-27-50	1853	3.03	4		1		5
	50					3.22		3			3
	150					4.30	1	1			2
No. 8	0	20°54′	159°47′	8-28-50	0507	2.84		5	1	2	8
	100					2.66					
	200					3.68	1	4	3		8
No. 9	0	21°05.1′	159°50.5′	8-28-50	1350	2.46					
	50					2.49				1	1
	150					3.06					
No. 10	0	22°48.5′	159°51′	8-24-50	2239	2.33	10	21	2	22	55
	150					3.61		3	7		10
	300					5.80	2	5	1	1	9
No. 11	0	23°27′	159°45.7′	8-25-50	0500	2.37	5	9	2		16
	50					2.85				1	1
	150					4.21					
No. 12	0	22°43.3′	158°26′	8-24-50	1250	2.71					
	100					2.90					
	200					3.95					
No. 13	0	21°50′	158°30.6′	8-24-50	0528	2.01	4		7	3	14
	50					3.14	2	10	4	6	22
	150					3.56		2	1	2	5
No. 14	0	20°50′	158°32′	8-18-50	1720	2.29	11			2	13
	100					2.17	2				2
	200					2.25				1	1
No. 15	0	20°15′	158°24′	8-19-50	2340	2.72	5	8			13
	150					3.81		1			1
	300					5.28	2	4			6
No. 16	0	19°24′	158°23′	8-19-50	0750	3.38	3				3
	100					3.48					
	200					3.06	1	6			7
No. 17	0	18°30′	158°29′	8-19-50	1522	2.24				1	1
	100					3.31					
	150					4.09					
No. 18	0	18°22′	157°07.5′	8-20-50	0210	1.61	13	22		11	46
	100					2.43	2				2
	200					3.61	1	5		3	9
No. 19	0	19°31′	157°10′	8-20-50	2311	2.73	1				1
	100					3.93		1			1
	150					4.78	1	2			3
No. 20	0	20°23′	157°07′	8-21-50	0815	2.11				1	1
	150					3.15		1			1
	300					4.29		1			1
No. 21	0	20°55.5′	157°10.3′	8-21-50	1412	2.77	7				7
	100					2.45	1				1
	150					2.81					
No. 22	0	21°50′	157°10.5′	8-23-50	1754	2.59		1		1	2
	100					3.07				1	1
	200					4.07		1			1
No. 23	0	22°39′	157°13′	8-23-50	1020	2.84				1	1
	50					2.99					
	150					3.64					
No. 24	0	22°40′	155°47′	8-22-50	2149	2.90	1			1	2
	100					3.34					
	200					5.03	1	3			4
No. 25	0	21°56.3′	155°45.3′	8-22-50	1500	2.82	14				14
	150					3.43					
	300					3.92	1	1			2
No. 26	0	21°03.5′	155°50′	8-22-50	0711	2.11	6				6
	100					3.07				1	1
	200					4.69				2	2
No. 27	0	20°30′	155°47.2′	8-22-50	0140	2.18	6	4		2	12
	50					2.30					
	150					3.88					
No. 28	0	18°32.5′	156°07′	8-20-50	1136	2.22				3	3
	100					2.58					
	200					4.08				1	1

[1] Local civil time corresponding to +10 zone time.

APPENDIX TABLE 3.—*Tuna larvae collected on* Hugh M. Smith *cruise 7 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude			*1,000 m.*[3]					
No. 1	20°30′ N.	158°00′ W.	10-17-50	1925	0.95					
No. 2	19°10′ N.	158°02′ W.	10-18-50	0532	0.90				2	2
No. 3	18°13′ N.	158°00′ W.	10-18-50	1326	1.11					
No. 4	17°10′ N.	158°00′ W.	10-18-50	2159	0.68					
No. 5	16°11′ N.	157°57′ W.	10-19-50	0506	0.70	(2)	(2)	(2)	(2)	(2)
No. 6	15°02′ N.	157°58′ W.	10-19-50	1250	1.00					
No. 7	14°03′ N.	157°59′ W.	10-19-50	1921	1.22				3	3
No. 8	12°57′ N.	157°57′ W.	10-20-50	0330	0.73					
No. 9	12°25′ N.	158°00′ W.	10-20-50	1729	1.22					
No. 10	11°08′ N.	158°01′ W.	10-21-50	1526	1.37					
No. 11	10°01′ N.	157°55′ W.	10-22-50	0724	1.43					
No. 12	8°52′ N.	157°45′ W.	10-23-50	0742	0.96					
No. 13	8°05′ N.	157°15′ W.	10-24-50	0742	1.41				2	2
No. 14	7°17′ N.	157°04′ W.	10-25-50	0727	1.70					
No. 15	5°57′ N.	157°05′ W.	10-26-50	0737	1.57				1	1
No. 16	5°19′ N.	157°20′ W.	10-27-50	0725	2.21	1	1		3	5
No. 17	4°23′ N.	157°30′ W.	10-28-50	0912	1.87		2			2
No. 18	3°17′ N.	157°53′ W.	10-29-50	0802	1.31				1	1
No. 19	2°01′ N.	157°34′ W.	11- 1-50	0812	1.59		1			1
No. 20	6°07′ N.	162°06′ W.	11- 6-50	0950	1.93					
No. 21	6°13′ N.	163°05′ W.	11- 7-50	0810	1.57				1	1
No. 22	6°59′ N.	163°54′ W.	11- 8-50	0808	1.75				4	4
No. 23	7°24′ N.	164°25′ W.	11- 9-50	0806	1.44					
No. 24	6°31′ N.	165°45′ W.	11-10-50	0813	1.52	1			10	11

[1] +10 zone time on stations 1 to 21; +11 zone on stations 22 to 24. [2] Sample missing.

APPENDIX TABLE 4.—*Tuna larvae collected on* Hugh M. Smith *cruise 8 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude			*1,000 m.*[3]					
No. 1	20°48′ N.	157°30′ W.	1-14-51	2012	0.94				1	1
No. 2	18°47′ N.	158°01′ W.	1-15-51	1449	0.63					
No. 4	14°30′ N.	158°00′ W.	1-17-51	0925	0.43				3	3
No. 6	12°57′ N.	157°58′ W.	1-17-51	2251	0.82					
No. 7	11°59′ N.	157°50′ W.	1-18-51	0811	1.36					
No. 8	11°00′ N.	157°53′ W.	1-18-51	1633	1.40				3	3
No. 9	10°00′ N.	157°56′ W.	1-19-51	0224	1.83	2				2
No. 10	9°00′ N.	157°58′ W.	1-19-51	1154	0.99					
No. 11	8°04′ N.	157°58′ W.	1-19-51	2024	1.24		3			3
No. 12	7°08′ N.	157°58′ W.	1-20-51	0615	1.30					
No. 13	5°59′ N.	158°00′ W.	1-20-51	1505	1.81					
No. 14	5°00′ N.	158°00′ W.	1-20-51	2338	0.98					
No. 15	3°55′ N.	157°54′ W.	1-21-51	1100	0.98					
No. 16	3°02′ N.	157°57′ W.	1-21-51	2135	1.02	1				1
No. 17	2°00′ N.	158°01′ W.	1-21-51	0802	1.63				1	1
No. 18	0°58′ N.	158°07′ W.	1-22-51	1730	1.53					
No. 19	0°01′ N.	158°02′ W.	1-23-51	0328	1.93					
No. 20	0°55′ S.	157°54′ W.	1-23-51	1208	1.51		1			1
No. 21	2°00′ S.	158°00′ W.	1-23-51	2312	1.27	1				1
No. 22	3°00′ S.	158°05′ W.	1-24-51	0744	1.27	1			1	2
No. 23	4°00′ S	158°00′ W.	1-24-51	1550	1.07					
No. 24	5°00′ S.	158°00′ W.	1-24-51	2330	0.89	5				5
No. 25	6°01′ S.	158°06′ W.	1-25-51	0741	1.23		2		1	3
No. 26	7°00′ S.	158°01′ W.	1-25-51	1548	1.35					
No. 77	14°30′ S.	171°51′ W.	2-26-51	1931	1.88	6	8		4	18
No. 78	11°56′ S.	171°59′ W.	2-27-51	1129	1.92	4	2		1	7
No. 79	10°05′ S.	171°52′ W.	2-28-51	0245	1.74	2	5		1	8
No. 80	8°00′ S.	171°56′ W.	2-28-51	1821	1.45		2			2
No. 81	7°01′ S.	171°54′ W.	3- 1-51	0238	1.05		2			2
No. 82	5°59′ S.	172°00′ W.	3- 1-51	1118	1.40	1				1
No. 83	5°00′ S.	172°15′ W.	3- 1-51	1930	1.51					
No. 84	4°00′ S.	172°06′ W.	3- 2-51	0735	1.51		4			4
No. 85	3°00′ S.	171°50′ W.	3- 2-51	1537	1.51	1	1		2	4
No. 86	2°00′ S.	172°02′ W.	3- 3-51	1612	1.59					
No. 87	0°57′ S.	172°00′ W.	3- 4-51	0047	1.39		1		1	2
No. 88	0°09′ N.	171°58′ W.	3- 4-51	0926	1.07		1		1	2
No. 89	1°04′ N.	172°00′ W.	3- 4-51	1702	0.98		1		2	3
No. 90	1°54′ N.	172°02′ W.	3- 5-51	0034	1.85		8		5	13
No. 91	2°48′ N.	172°04′ W.	3- 5-51	0834	1.33		3		1	4
No. 92	3°57′ N.	172°02′ W.	3- 5-51	1816	1.22					
No. 93	4°56′ N.	171°54′ W.	3- 6-51	0249	1.62	1	1			2
No. 94	5°55′ N.	171°50′ W.	3- 6-51	1105	1.43	1	1		1	3
No. 95	6°58′ N.	171°49′ W.	3- 6-51	1939	1.91		2			2
No. 96	7°56′ N.	171°51′ W.	3- 7-51	0407	1.50					
No. 97	9°00′ N.	171°58′ W.	3- 7-51	1315	1.54	1				1
No. 98	10°02′ N.	171°56′ W.	3- 7-51	2147	1.54					
No. 99	11°02′ N.	171°52′ W.	3- 8-51	0602	1.58				1	1
No. 100	12°00′ N.	171°52′ W.	3- 8-51	1417	1.51				2	2
No. 101	13°01′ N.	171°48′ W.	3- 8-51	2236	1.72	1				1
No. 102	13°58′ N.	171°24′ W.	3- 9-51	0650	1.27					
No. 103	15°00′ N.	170°52′ W.	3- 9-51	1557	1.31					
No. 104	16°58′ N.	169°42′ W.	3-10-51	0913	1.99				1	1
No. 105	18°58′ N.	168°27′ W.	3-11-51	0207	1.94					

[1] +10 zone time on stations 1 to 26; +11 zone time on stations 77 to 105.

APPENDIX TABLE 5.—*Tuna larvae collected on* Hugh M. Smith *cruise 11 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude			*1,000 m.*[3]					
No. 1	14°37′ N.	150°12′ W.	8-24-51	0854	1.44		1			1
No. 2	13°06′ N.	149°58′ W.	8-25-51	0828	1.22					
No. 3	11°31′ N.	150°02′ W.	8-26-51	0832	1.90					
No. 4	9°41′ N.	150°01′ W.	8-27-51	0801	1.36	2				2
No. 5	8°58′ N.	150°08′ W.	8-28-51	0722	1.85					
No. 6	7°59′ N.	149°51′ W.	8-29-51	0754	2.84	2	1			3
No. 7	6°55′ N.	149°50′ W.	8-30-51	0734	1.69					
No. 8	5°59′ N.	149°55′ W.	8-31-51	0742	1.54	4				4
No. 9	4°49′ N.	150°02′ W.	9- 1-51	0743	1.95	4	1			5
No. 10	4°02′ N.	150°04′ W.	9- 2-51	0852	0.70	2	1		2	5
No. 11	2°55′ N.	150°09′ W.	9- 3-51	0739	1.70	7	6			13
No. 12	1°59′ N.	150°04′ W.	9- 4-51	0740	1.94	2	1			3
No. 22	2°00′ N.	151°18′ W.	9-19-51	0743	1.29	3	2			5
No. 23	0°55′ N.	149°54′ W.	9-20-51	0742	1.31	1	1			2
No. 24	0°01′ S.	149°56′ W.	9-21-51	0743	1.47		2			2
No. 25	1°03′ S.	150°16′ W.	9-22-51	0746	1.13					
No. 26	2°01′ S.	150°08′ W.	9-23-51	0737	1.19		2		1	3
No. 27	3°34′ S.	150°05′ W.	9-24-51	0740	1.55		3			3
No. 28	4°57′ S.	150°04′ W.	9-25-51	0906	1.34					
No. 29	4°00′ S.	150°00′ W.	9-25-51	2352	1.88		21			21
No. 30	3°00′ S.	149°57′ W.	9-26-51	0858	1.64					
No. 31	2°00′ S.	150°02′ W.	9-26-51	1719	1.39		7		1	8
No. 32	1°00′ S.	149°58′ W.	9-27-51	0210	1.51	[2]	[2]	[2]	[2]	[2]
No. 33	0°02′ N.	150°00′ W.	9-27-51	1300	1.12	1	1			2
No. 34	1°02′ N.	150°01′ W.	9-27-51	2332	1.57	[2]	[2]	[2]	[2]	[2]
No. 35	2°01′ N.	149°53′ W.	9-28-51	0840	1.54	1				1
No. 36	3°00′ N.	150°03′ W.	9-28-51	1715	1.63	1	1			2
No. 37	3°58′ N.	150°00′ W.	9-29-51	0152	1.53	2	3			5
No. 38	4°59′ N.	149°56′ W.	9-29-51	1038	1.07		1			1
No. 39	5°56′ N.	150°00′ W.	9-29-51	1919	1.66					
No. 40	6°51′ N.	149°57′ W.	9-30-51	0343	1.63	3				3
No. 41	7°51′ N.	150°57′ W.	9-30-51	1257	1.93		1		3	4
No. 42	8°57′ N.	149°58′ W.	9-30-51	2233	1.47	1	1			2
No. 43	10°00′ N.	150°13′ W.	10- 1-51	0709	1.79		1			1
No. 44	10°58′ N.	150°02′ W.	10- 1-51	1554	1.73					
No. 45	11°59′ N.	150°03′ W.	10- 2-51	0042	1.47					
No. 46	13°00′ N.	149°56′ W.	10- 2-51	0907	1.60	4				4
No. 47	14°01′ N.	150°03′ W.	10- 2-51	1733	1.78					
No. 48	15°02′ N.	150°01′ W.	10- 3-51	0144	1.60	[2]	[2]	[2]	[2]	[2]
No. 49	17°00′ N.	150°42′ W.	10- 3-51	1653	1.94					
No. 50	19°00′ N.	151°19′ W.	10- 4-51	0750	1.97					

[1] +10 zone time on all stations.
[2] No sample.

APPENDIX TABLE 6.—*Tuna larvae collected on* Hugh M. Smith *cruise 14 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude			*1,000 m.*[3]					
No. 1	7°57′ N.	154°57′ W.	1-27-52	1158	1.01					
No. 2	6°55′ N.	154°57′ W.	1-27-52	2132	1.33		9			9
No. 3	5°53′ N.	154°55′ W.	1-28-52	0813	1.13					
No. 4	4°55′ N.	154°51′ W.	1-28-52	1707	1.53		1		1	2
No. 5	3°54′ N.	154°51′ W.	1-29-52	0207	1.32					
No. 6	2°56′ N.	154°59′ W.	1-29-52	1057	1.03					
No. 7	1°54′ N.	155°03′ W.	1-29-52	2010	1.15		1		1	2
No. 8	0°54′ N.	155°11′ W.	1-30-52	0837	1.33		1			1
No. 9	0°06′ S.	155°14′ W.	1-30-52	1905	2.05		14		1	15
No. 10	1°10′ S.	155°08′ W.	1-31-52	0452	1.65		2			2
No. 11	2°00′ S.	155°03′ W.	1-31-52	1200	1.48					
No. 12	3°00′ S.	154°58′ W.	1-31-52	2124	1.51	1	4			5
No. 13	4°00′ S.	155°07′ W.	2- 1-52	0707	1.39					
No. 14	4°58′ S.	155°00′ W.	2- 1-52	1920	1.25	1	3			4
No. 15	5°53′ S.	155°03′ W.	2- 2-52	0455	1.33					
No. 16	6°50′ S.	155°05′ W.	2- 2-52	1407	1.32					
No. 17	7°56′ S.	179°53′ W.	2-15-52	0116	1.89		2			2
No. 18	7°01′ S.	179°49′ W.	2-15-52	1053	1.67		3			3
No. 19	6°05′ S.	179°58′ W.	2-15-52	1800	1.55	3				3
No. 20	5°04′ S.	179°58′ W.	2-16-52	0529	1.76	1	7			8
No. 21	4°03′ S.	179°58′ W.	2-16-52	1506	1.31	2	8			10
No. 22	2°56′ S.	180°00′	2-17-52	0040	1.39	1	2			3
No. 23	1°52′ S.	179°54′ E.	2-17-52	1107	1.34					
No. 24	0°59′ S.	179°57′ E.	2-17-52	1932	1.64		1			1
No. 25	0°52′ N.	179°59′ E.	2-18-52	0520	1.21		2		3	5
No. 26	1°03′ N.	179°58′ W.	2-18-52	1615	1.51			1	4	5
No. 27	2°07′ N.	179°57′ W.	2-19-52	0210	1.07					
No. 28	3°06′ N.	179°57′ W.	2-19-52	1105	1.74					
No. 29	4°05′ N.	179°55′ W.	2-19-52	2008	1.47		4	1	2	7
No. 30	5°06′ N.	179°50′ W.	2-20-52	0505	1.70	4	4		1	9
No. 31	6°06′ N.	179°44′ W.	2-20-52	0211	1.45	2				2
No. 32	7°04′ N.	179°59′ E.	2-20-52	1108	1.61	3	1		3	7
No. 33	8°03′ N.	179°58′ W.	2-21-52	0759	1.39					
No. 34	8°54′ N.	179°55′ W.	2-21-52	1720	1.33					

[1] +10 zone time on stations 1 to 16; +12 zone time on stations 17 to 34.

APPENDIX TABLE 7.—*Tuna larvae collected on* Hugh M. Smith *cruise 15 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude			*1,000 m.*[3]					
No. 1	8°59′ N.	139°56′ W.	5-28-52	0731	1.42					
No. 2	7°51′ N.	139°46′ W.	5-28-52	1839	1.62					
No. 3	7°00′ N.	140°00′ W.	5-29-52	0315	1.73			1		1
No. 4	6°36′ N.	139°44′ W.	5-29-52	1035	1.87					
No. 5	6°00′ N.	140°00′ W.	5-29-52	1727	2.06	4				4
No. 6	5°02′ N.	139°58′ W.	5-30-52	0208	1.90	2	7		1	10
No. 7	4°05′ N.	139°58′ W.	5-30-52	1003	2.17	1	10		2	13
No. 8	3°09′ N.	139°53′ W.	5-30-52	1838	1.51		10		10	20
No. 9	1°57′ N.	140°03′ W.	5-31-52	0344	2.46		8			8
No. 10	0°53′ N.	140°02′ W.	5-31-52	1237	1.70		1			1
No. 11	0°11′ S.	139°52′ W.	5-31-52	2138	2.06					
No. 12	1°02′ S.	139°52′ W.	6- 1-52	0515	1.95					
No. 13	2°00′ S.	139°50′ W.	6- 1-52	1257	1.57					
No. 14	3°00′ S.	139°52′ W.	6- 1-52	2026	1.52	1	3			4
No. 15	4°00′ S.	140°05′ W.	6- 2-52	0628	1.32	1	1			2
No. 16	5°30′ S.	139°57′ W.	6- 2-52	1839	1.36	1				1
No. 17	7°00′ S.	139°58′ W.	6- 3-52	0709	1.72		1			1

[1] +9 zone time on all stations.

APPENDIX TABLE 8.—*Tuna larvae collected on* Hugh M. Smith *cruise 18 in equatorial waters*

[All hauls were oblique tows from 0 to 200 meters, of 30 minutes' duration]

Station	Position		Date	Time started [1]	Water strained	*Neothunnus macropterus*	*Katsuwonus pelamis*	*Auxis thazard*	Unidentified	Total
	Latitude	Longitude								
					*1,000 m.*³					
No. 2	9°00′ N.	120°50′ W.	10–19–52	0012	1.53					
No. 4	7°06′ N.	120°00′ W.	10–21–52	0200	1.24	2			2	4
No. 5	5°50′ N.	120°16′ W.	10–22–52	0217	3.29	2	1			3
No. 6	4°53′ N.	119°59′ W.	10–22–52	2325	1.45	1	1			2
No. 7	4°01′ N.	120°06′ W.	10–23–52	1200	1.53					
No. 8	3°03′ N.	120°05′ W.	10–25–52	0004	1.54	1				1
No. 9	1°55′ N.	120°14′ W.	10–26–52	0105	3.05					
No. 10	1°02′ N.	120°17′ W.	10–27–52	0111	1.46					
No. 11	0°39′ N.	120°14′ W.	10–28–52	0115	2.62					
No. 13	1°04′ S.	120°07′ W.	10–28–52	2309	1.62					
No. 15	3°06′ S.	120°10′ W.	10–29–52	2310	1.36					
No. 17	4°50′ S.	120°21′ W.	10–31–52	1206	0.77					
No. 19	6°37′ S.	120°24′ W.	10–31–52	2307	1.37					
No. 21	8°40′ S.	120°35′ W.	11– 1–52	2308	0.88		1			1
No. 24	4°12′ S.	130°14′ W.	11– 5–52	2311	0.87		1			1
No. 26	2°15′ S.	130°11′ W.	11– 6–52	2310	1.12					
No. 28	0°27′ S.	130°09′ W.	11– 7–52	2310	1.31					
No. 30	1°10′ N.	130°08′ W.	11– 9–52	0103	2.33					
No. 31	1°42′ N.	130°22′ W.	11– 9–52	2329	1.31			1		1
No. 32	3°15′ N.	130°14′ W.	11–11–52	0005	1.40				2	2
No. 33	4°37′ N.	130°26′ W.	11–12–52	0015	0.71					
No. 34	5°42′ N.	130°50′ W.	11–12–52	2308	0.87					
No. 36	7°56′ N.	131°11′ W.	11–14–52	0002	1.18					
No. 37	9°12′ N.	131°24′ W.	11–15–52	0103	0.60					

[1] +8 zone time on all stations.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

FILTERING RATES OF THE HARD CLAM (*VENUS MERCENARIA*) DETERMINED WITH RADIOACTIVE PHYTOPLANKTON

By THEODORE R. RICE and REBECCA J. SMITH

(This report concerns work carried on as a part of a cooperative project of the United States Fish and Wildlife Service and the United States Atomic Energy Commission.)

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ABSTRACT

Filtering rates of the hard clam, *Venus mercenaria* L., were determined by ascertaining the number of radioactive phytoplankton removed from water pumped through the filtering mechanism of the clam. If the cells are not completely filtered from the water pumped, the filtering rate of the clam is less than the pumping rate. The term "filtering rate" refers to the volume of water from which the cells are removed per unit of time.

The labeling of algae with radioactive phosphorus made it possible to follow smaller initial populations than have been used in most previous investigations, yet it provided a means of accurately measuring slight changes in these populations. The number of cells present at the beginning of an experiment and the size of these cells influenced the filtering rate. The filtering rate in unialgal suspensions was different from that in mixed suspensions. The filtering rate in natural populations of phytoplankton was higher than in unialgal suspensions of green algae and lower than in unialgal suspensions of diatoms.

Silt had an adverse effect on the hard clam, since it reduced the filtering rate and stimulated the formation of pseudofeces. A similar effect was produced by the presence of *Chlorella* in the water. In relating filtering rates to size of clams, more water per gram of meat was filtered by small clams than by large clams.

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FILTERING RATES OF THE HARD CLAM (*VENUS MERCENARIA*) DETERMINED WITH RADIOACTIVE PHYTOPLANKTON

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BUREAU OF COMMERCIAL FISHESIES

Among the more-important factors affecting the efficiency of the filtering mechanism of filter-feeding animals are size and number of particles present in the water. Problems relating to nutrition may be more easily solved when the factors controlling the rate at which water is filtered and the efficiency of removal of food particles have been determined. Using either a direct or an indirect method, many measurements have been made of the rate at which water is transported through the filtering mechanism of lamellibranchs. In the direct method, the water pumped is separated and measured (Galtsoff, 1926, 1928; Nelson, 1935, 1936; Loosanoff and Engle, 1947; and Collier, Ray, Magnitzky, and Bell, 1953). Water pumped through the gills may or may not be filtered; only if the particles are removed from the water pumped can it be considered to have been filtered. In some investigations both the amount of water pumped and the efficiency of the filtering mechanism in removing particles from the water have been determined simultaneously. From the rate of removal of particles the volume of water filtered can also be determined.

With many lamellibranchs a direct measurement of the pumping rate is not practicable. As a result, indirect methods based on the rate of removal of particles from the water by the filter-feeding mechanism of the animal have been developed. The volume of water pumped can be calculated only if the filtering mechanism removes all the suspended particles from the water passing through it. If any cells escape, the filtering rate will naturally be less than the pumping rate. For this reason only the volume of water from which the cells are removed per unit of time will be referred to as the filtering rate. It is incorrect to use the terms "filtering rate" and "pumping rate" interchangeably, even though this has occurred in the literature.

In most investigations with lamellibranchs, the removal of particles by the filtering mechanism has been followed with chemical determinations and photometric techniques. Calcium carbonate, colloidal graphite, and unicellular algae were used as particles in experiments measuring the volume of water filtered by lamellibranchs (Fox, Sverdrup, and Cunningham, 1937; Jørgensen, 1943, 1949; Rao 1953; and Ballantine and Morton, 1956). Also, a neutral red solution has been employed in comparing the amount of water pumped under different environmental conditions (Cole and Hepper, 1954). Another method for determining filtering rates has been the use of radioactive phosphorus with a colonial diatom (Jørgensen and Goldberg, 1953). The labeling of unicellular algae, that is, the incorporation of radioactive phosphorus into the protoplasm for use in filter-feeding experiments, has been investigated in detail by Rice (1953). This has made possible a much more sensitive and accurate technique for determining small changes in the number of cells in a volume of water. Filtration rates based on the reduction in numbers of unicellular algae using radioactive-labeled cells were determined by Chipman and Hopkins (1954).

In a review of the literature no reference was found to the filtering rates of the hard clam, *Venus mercenaria* L. Thus, the purpose of this investigation was to determine and compare the filtering rates of this clam relative to (1) the number of algal cells present at the beginning of the experiments, (2) size of the cells used, (3) removal of a species in unialgal and in mixed suspension, (4) removal of cells in unialgal suspension and in natural populations, and (5) removal of cells in unialgal suspension before and after adding silt.

Note—Approved for publication, March 18, 1957. Fishery Bulletin 129.

MATERIALS AND METHODS

Four species of planktonic algae were fed to hard clams in both single and mixed cultures. The algae used and their sizes were as follows:

Species:	*Size:*
Chlorophyceae:	
Nannochloris atomus	2μ (in diameter)
Chlorella	4μ (in diameter)
Bacillariaceae:	
Nitzschia sp	19μ x 5μ (length and width)
Nitzschia closterium	43μ x 4μ (length and width)

Cells used in feeding experiments were first grown in sea-water culture medium to which no phosphorus was added (Rice 1953). Carrier-free radioactive phosphorus (P^{32}) placed in these cultures was rapidly taken up by the cells. All algal cells used in experiments were taken from cultures only a few days old, so that they were in a state of rapid division. Prior to starting an experiment, a portion of medium was filtered and the P^{32} in the cells was measured. Also, the number of cells in the culture was determined by cell counts made with an improved Neubauer haemocytometer. After determining the radioactivity contained in the cells and the number of cells in the culture, it was possible to dilute the proper portion of culture with enough sea water to give the desired population of cells for the feeding experiment.

Any subsequent measurement of radioactivity contained in cells from a portion of the suspension could be converted to represent the number of cells present at that particular time. By incorporating sufficient amounts of P^{32} in the cells, a small reduction in the number of cells in suspension in the water with the clam could be followed accurately. This was possible even when the population size was considerably smaller than that occurring in nature.

The clams used in this investigation were collected in the Beaufort area and kept in the laboratory in running sea water when they were not being used in experiments. They ranged from 58.6 mm. to 88.6 mm. in length and from 45.1 to 73.6 mm. in height, with the exception of smaller clams used in experiments to determine the volume of water filtered on the basis of weight of the clams. A total of 150 experiments were conducted over a period of 1 year. In each experiment, a clam was placed in a battery jar containing 2 liters of freshly collected and filtered sea water with a salinity of 30 to 35‰ and a temperature of 23°±2° C. A stirrer was used in all experiments to rapidly mix the filtered water with the nonfiltered and to prevent the cells from settling. Controls, consisting of the same number of cells suspended in an equal volume of water in which no clam was placed, showed that the stirring was sufficient to prevent the cells from settling.

Samples of the suspension of 10 cc. each were removed with a pipette from the same location in the battery jar before placing the clams in the containers and at 15-minute intervals after the clams had opened. To remove the cells from the water, each sample was filtered through a millipore filter. The filter was placed in a metal planchet and the amount of radioactivity in the cells was measured.

If the clam filters all the cells from the water that passes through the gills, it is possible to calculate the rate of water pumped by the application of Jørgensen's formula (1943):

$$m=\frac{(\log conc_o-\log conc_t)\cdot M}{\log e\cdot t}$$

In this formula, m is the quantity of water pumped in liters per hour, M is the volume of cell suspension in liters, and $conc_o$ and $conc_t$ are the cell concentrations at the initial time and after t hours of time. It is very possible that some cells pass through the gills without being removed from the water. Thus, the volume of water calculated by this formula will be referred to as the filtering rate, which no doubt is lower than the actual pumping rate.

RESULTS

To determine a representative filtering rate for the clam, it is necessary to know whether the efficiency of the gills in retaining particles is always the same in a given animal. Otherwise, it is not possible to ascertain whether a variation in the filtering rate is the result of a change in filtering efficiency or in the volume of water pumped. The animal, no doubt, changes the rate at which water is pumped through the mantle cavity. In addition to the formation of mucus on the gill surface, the animal can also change the size of the gill pores, making it very unlikely that the efficiency of removal of particles is constant.

A comparison was made of variations in filtering rates obtained at different times for an individual clam in suspensions of one species of algae. Experiments with clam F, which covered a 2½-month interval of time and population sizes of *Nannochloris* ranging from 74 million to 2,236 million cells per liter, are shown in table 1. The highest and lowest filtering rates were based on the removal of cells during a 15-minute interval of time, while the average filtering rate was based on eight 15-minute intervals. The highest filtering rate observed was about 4 liters per hour and the lowest was 0.1 liter per hour. The average filtering rates ranged from 0.8 to 2.1 liters per hour. Experiments conducted on two different days with 161 million cells per liter gave average filtering rates of 1.6 and 1.7 liters per hour. There appears to be no relation between the numbers of cells used in these experiments and the average filtering rates obtained. The experiment with 153 million cells per liter gave the largest average filtering rate, while the experiment in which 161 million and 2,236 million cells per liter were used gave about the same filtering rates.

The growth of clam F during the interval of time tested in these experiments was probably of no significance in influencing the filtering rates obtained; however, the filtering rate per gram of meat for clams of different weights was investigated. In table 2 it can be seen that the rate of filtering per gram of meat decreases as the size of the clam increases.

To compare the rates obtained when clams are filtering particles of different sizes, experiments were conducted with clams using suspensions of four species of planktonic algae (table 3). The highest and lowest filtering rates were based on the removal of cells during a 15-minute interval of time, while the average filtering rate was based on eight 15-minute intervals. The highest, lowest, and average filtering rates of the clams were consistently higher in suspensions of diatoms than of green algae.

In figure 1 are typical curves for each of the four species of algae, showing the decrease in numbers of cells due to the filtering activity of the clam. The slopes of the curves showing the removal of the two small green forms are not as steep as are those of the diatoms. The rates of removal for the two green algae were similar; also, the rates of removal of the two species of diatoms were in close agreement. It is of interest that the rates of removal of the green algae formed straight lines, while those of the diatoms gave sigmoid curves, when plotted on semilog graph paper. Even though the number of cells present in suspension was the same for the diatoms as for the green algae, the diatoms represented a larger amount of protoplasm.

A comparison was then made of the decrease in number of cells filtered when both large and small initial populations of *Nannochloris* were used (fig. 2). Regression lines were calculated and have been drawn through the points. It can

TABLE 1.—*Filtering rates of clam F in* Nannochloris *suspensions of various concentrations at different times*

[Concentration: cells/liter × 10^6]

Date	Concentration	Filtering rates (liter/hour)		
		Highest	Lowest	Average
Nov. 17, 1955	768	1.8	0.3	1.0
Nov. 19, 1955	153	4.2	.3	2.1
Nov. 30, 1955	656	2.3	.1	1.0
Dec. 12, 1955	775	2.3	.4	.8
Dec. 13, 1955	161	2.5	.9	1.6
Dec. 14, 1955	161	2.7	.9	1.7
Jan. 17, 1956	74	1.4	.4	1.0
Jan. 20, 1956	83	1.9	1.0	1.1
Jan. 27, 1956	2,125	2.2	.4	1.0
Feb. 1, 1956	2,236	2.1	1.1	1.6

TABLE 2.—*Filtering rates per gram of meat for hard clams of different weights in* Nannochloris *suspension*

Number of experiments	Wet weight of meats (gm.)	Filtering rate (l./hr./gm.)
5	6.2	0.15
5	10.9	.10
10	20.9	.07
10	28.0	.05

TABLE 3.—*Filtering rates of hard clams based on removal of four different species of algae in suspension*

[Concentration: 74 × 10^6 cells per liter]

Species	Filtering rates (liter/hour)		
	Highest	Lowest	Average
Clam F:			
Nannochloris	1.4	0.9	1.0
Chlorella	3.7	.5	1.8
Nitzschia sp.	6.9	.9	3.5
Nitzschia closterium	6.1	1.3	3.9
Clam R:			
Nannochloris	1.9	.7	1.3
Chlorella	1.0	.1	.6
Nitzschia sp.	4.8	1.7	3.1
Nitzschia closterium	5.0	1.6	3.5
Clam S:			
Nannochloris	4.2	1.0	2.2
Chlorella	1.9	.6	1.3
Nitzschia sp.	6.8	1.8	4.2
Nitzschia closterium	7.0	2.8	4.7

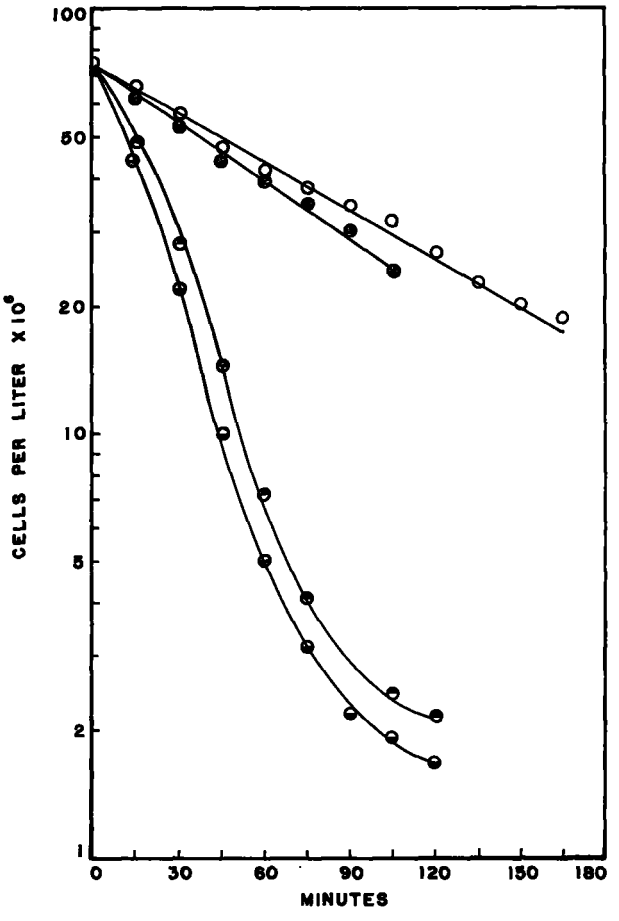

FIGURE 1.—Rates of removal of unicellular phytoplankton from suspension by the filter-feeding activity of the hard clam. (○ = *Nannochloris;* ● = *Chlorella*; ◓ = *Nitzschia* sp.; and ◒ = *Nitzschia closterium.*)

be seen that the slopes of these two lines are about the same. From this comparison it can be concluded that the filtering rate is independent of the number of cells used in these experiments.

It is also of interest to compare the effect of numbers of diatoms in suspension upon the filtering rate of the hard clam, as shown in figure 3. There is much similarity between the curves representing the removal of cells at the two intermediate population sizes. The curves representing the highest and the lowest population sizes, while being somewhat similar, are quite different from the curves for the intermediate-size populations. Obviously, the number of *Nitzschia closterium* cells in the water does affect the rate at which the clam removes these diatoms.

The rate of removal of a given species of algae by the clam differs in unialgal suspensions from that in mixed algal suspensions (fig. 4). The rate of removal of *Nitzschia closterium* cells is more rapid when this diatom is alone in a concentration of 5 million cells per liter than when 5 million *Chlorella* cells per liter are also present. The rate of removal of 74 million *Nannochloris* cells per liter, however, was more rapid when 70 million *Nitzschia closterium* cells per liter were also present than when the *Nannochloris* cells were used alone.

In many instances, data collected in the laboratory do not give a reliable index of conditions in nature. Thus, an effort was made to determine the rate of removal of particles by the clam from a natural population for comparison with data collected on unialgal suspensions in the laboratory. This is a difficult task which has not been attempted very many times and probably could not have been undertaken here without the use of radioisotopes.

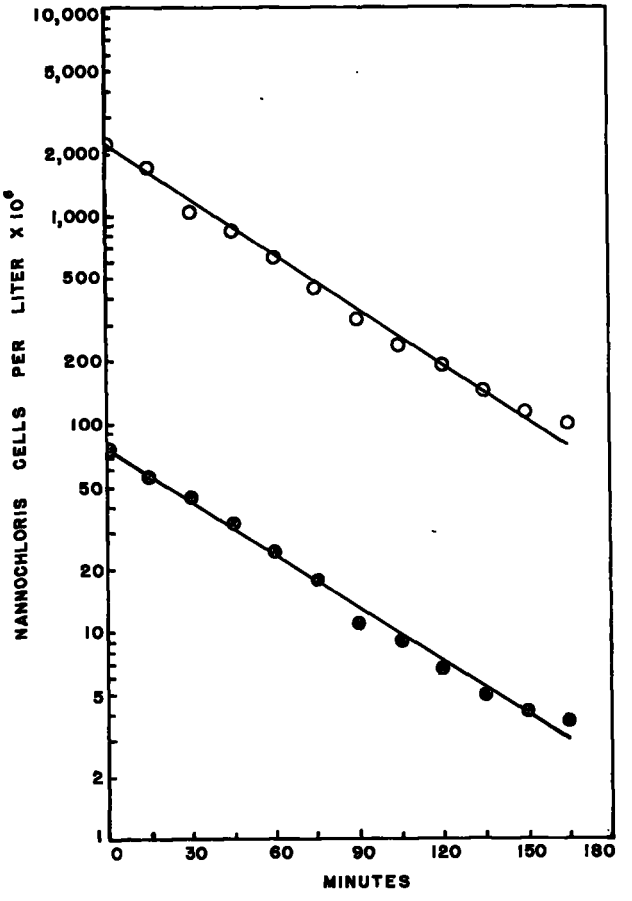

FIGURE 2.—Rates of removal by the hard clam of *Nannochloris* at two different population sizes.

From previous experiments conducted in our laboratory we knew that dividing cells take up much more radioactive phosphorus than nondividing cells. Also, it was found that the adsorption of P^{32} on the surface of the cells was small in comparison with that taken up due to metabolic activity. From this information it is probably correct to assume that the disappearance of P^{32} from solution when added to freshly collected sea water placed in the lighted culture cabinet could be attributed mostly to the metabolism of the bacteria and phytoplankton. At least it can be stated that within 24 to 48 hours after the P^{32} was added, up to 98 percent of it had been removed from the water by particles large enough to be retained on a millipore filter disc. This disc will retain particles with a diameter of at least 0.5 micron.

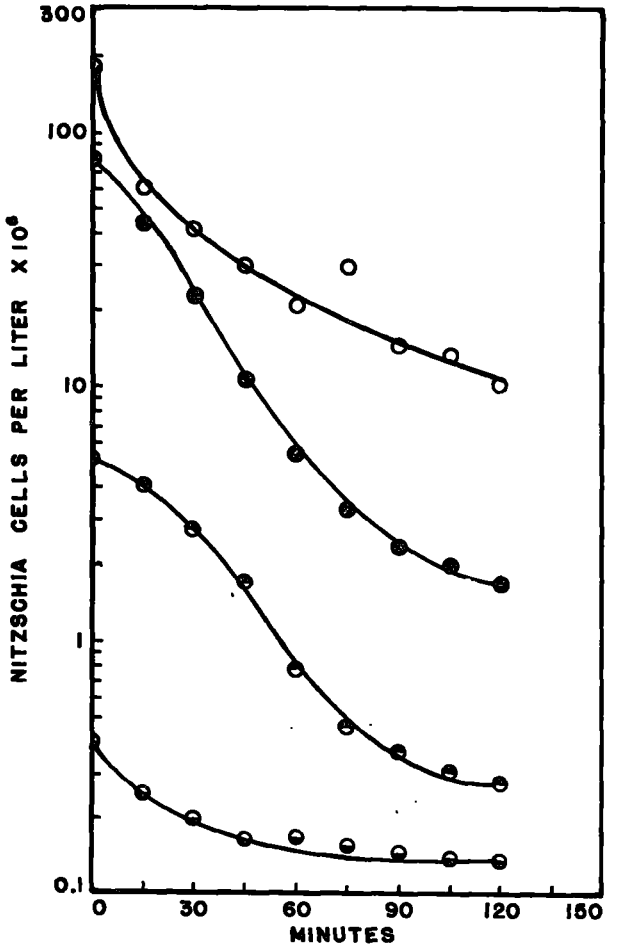

FIGURE 3.—Effect of numbers of *Nitzschia closterium* cells on their rate of removal by the hard clam.

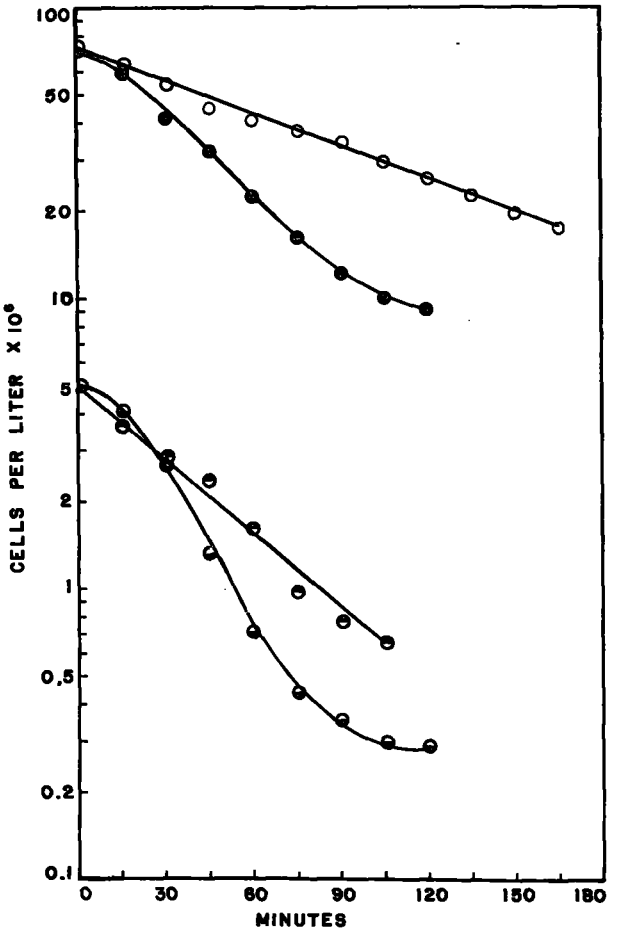

FIGURE 4.—Comparison of rates of removal of a species of phytoplankton by clams in unialgal and in mixed algal suspension. (○ = *Nannochloris* cells in unialgal suspension; ● = *Nannochloris* cells mixed with *Nitzschia closterium* cells; ◓ = *Nitzschia closterium* cells mixed with *Chlorella* cells; and ◒ = *Nitzschia closterium* cells in unialgal suspension.)

This heterogeneous assortment of particles, including bacteria, planktonic algae, and inanimate particles, was removed from the water by clams at a faster rate than *Nannochloris* cells were filtered, but not quite as rapidly as *Nitzschia closterium* cells (fig. 5). This may be representative of the rate of removal of particles under natural conditions, since a microscopic examination of a portion of the fresh sea water revealed the presence of green algae as well as diatoms. Thus, one would expect the rate of removal of the natural population to fall between the filtering rates found for green algae and for diatoms in unialgal suspensions.

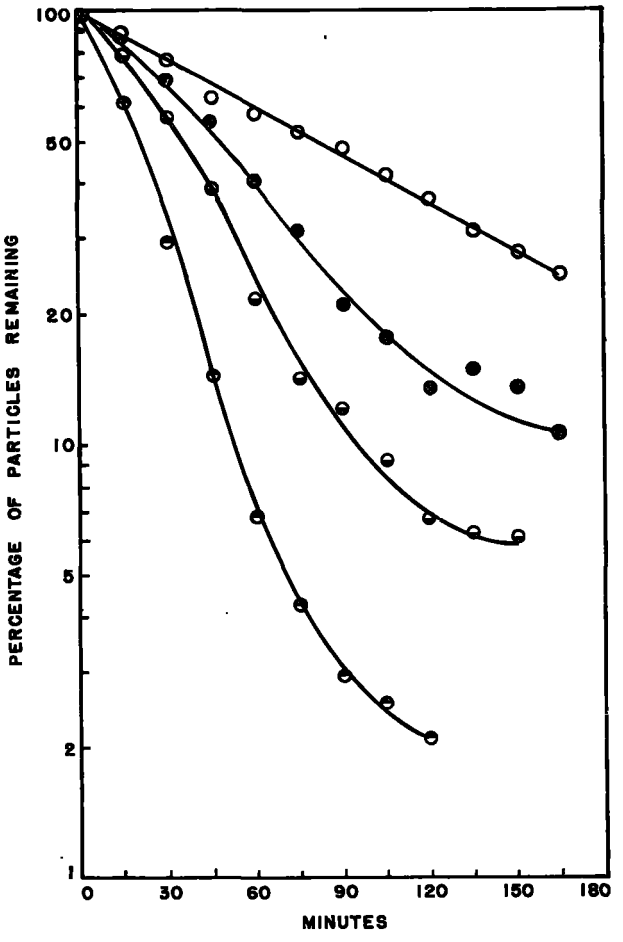

FIGURE 5.—Comparison of rates of removal of particles from freshly collected sea water with that of *Nannochloris* cells and of *Nitzschia closterium* cells. (○=*Nannochloris*; ● and ◒=Particles from freshly collected sea water; and ◓=*Nitzschia closterium*.)

The clam, a bottom-burrowing animal, may frequently be confronted with the problem of filtering cells from water that is heavily laden with silt. The silt used in these experiments was collected from an intertidal area. Care was taken to obtain silt that was as free from sand as possible. After several washings in sea water the silt was washed through cheese cloth and allowed to settle. The water was decanted from the silt, which was spread out and dried. The silt was then pulverized and stored in a glass-stoppered bottle until used.

Two approaches were used to determine the effect of silt on the rate of removal of *Nitzschia closterium* cells from the water. The first method was to add dried silt to the water in which the clam was to be placed just before the experiment. The silt would settle out of the water in a few minutes, even though the water was being vigorously stirred. A second method was to add the same amount of dried silt to sea water several days before the feeding experiment was carried out. When prepared in this manner, the silt remained in suspension a greater length of time than when added just before the experiment. The effect of 10 grams of dried silt per 2 liters of water on the rate of removal of *Nitzschia closterium* cells is shown in figure 6. For a short time following addition of the dry silt the rate of removal of cells by the clam was not as rapid as before or

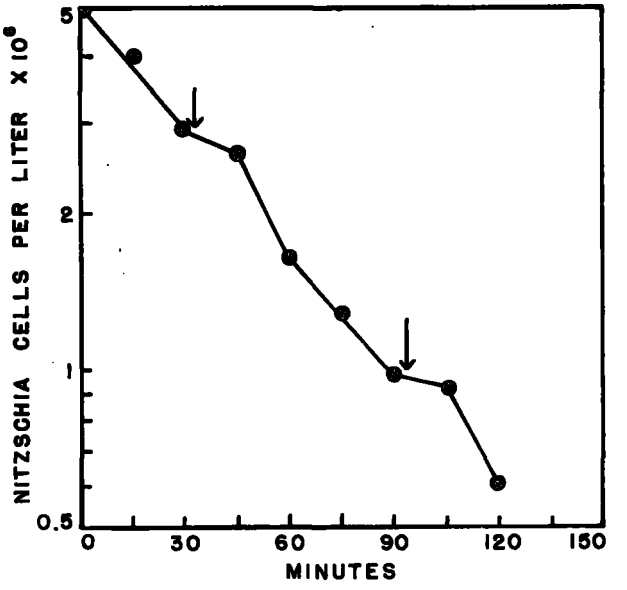

FIGURE 6.—Rate of removal of *Nitzschia closterium* cells by the clam showing effect of an addition of 10 grams of dried silt. (Arrows indicate time silt was added.)

after this time. The addition of silt that had been placed in water several days before the experiment caused the same response in the clams, but to a greater extent. A large amount of mucus was formed by the clam, apparently in an effort to remove the silt from the water. This silt-laden mucus often formed an uneven border around the edge of the shell, in addition to its floating in clumps in the water. In not one of the experiments did a clam close when silt was added to the water. We probably can assume that fewer cells were ingested by the clam during the time silt was present, since so much mucus was released in the water.

DISCUSSION

Since radioactive-labeled phytoplankton was used in these investigations, we could follow its rate of removal under various conditions. Low population sizes, such as 400,000 *Nitzschia* cells per liter used in one series of experiments, could not have been accurately measured initially, and especially throughout the experiment as the number of cells decreased, if the measurements had not been based on radioactivity. Since the amount of radioactive phosphorus per cell can be varied over a wide range, it is possible to prepare suspensions of cells with large or small populations so that a sample, regardless of the number of cells present, will give an accurate radioactivity measurement. In addition, labeled cells from small portions of suspension taken at frequent intervals will give accurate measurements. In the silt experiment, the rate of removal of the *Nitzschia* cells could not have been followed with photometric methods due to interference from the silt. Neither could photometric methods have been used to measure a reduction in the number of cells of one species of algae when another species was also present, as in mixed suspensions. Finally, the comparison made between rates of removal in natural populations and in unialgal cultures was possible when it was based on the removal of radioactive-labeled particles. These are among the many advantages associated with the use of radioisotopes in investigations similar to those presented here.

Filtering rates obtained with hard clams in unialgal suspensions of planktonic algae varied considerably with the species used. In suspensions of small cells of either *Nannochloris* or *Chlorella*, the highest filtering rate seldom exceeded 2 liters per hour, but in suspensions of diatom cells the highest average filtering rate exceeded 5 liters per hour. This difference could have been due to a greater efficiency in the retention of the diatoms by the filtering mechanism of the clam or to an increased rate of pumping water through the filtering mechanism in the presence of the diatoms. In line with present-day thinking, the clam apparently filters more water in suspensions of the larger cells because of a more efficient retention of the cells from the water pumped by the clam. However, if the clam does remove the smaller, algal cells as efficiently as the diatoms, then the higher filtering rates with the diatoms would reflect only a larger volume of water pumped by the clam in the presence of the diatoms. As far as could be determined, an increased pumping rate in the presence of a certain species of algae has not been reported in the literature, but this does not necessarily eliminate the possibility of such an increase occurring. The filtering rates obtained when *Nannochloris* cells were used in unialgal suspensions were less than when *Nitzschia* cells were also present in the water. The reason for this increased rate of removal of *Nannochloris* cells is not known. Possibly, the presence of *Nitzschia* cells stimulated the clam to pump more water, thus resulting in the removal of a greater number of *Nannochloris* cells, or the *Nitzschia* cells clogged the gills resulting in a more efficient retention of *Nannochloris*.

The filtering rate of the clam based on the removal of planktonic algae is a function of both the amount of water that is pumped per unit of time and the efficiency with which the cells are removed from this water. Since the volume of water pumped may vary from time to time when the clam is in suspensions of the same species, as well as in suspensions of more than one species, it is impossible to compare the efficiency of the clam in removing cells of different sizes. With a method for following the simultaneous removal of two species of algae from the same volume of water being pumped and filtered by the clam, the relative efficiency of removal of the cells could be measured. Even though the volume of water pumped could not be calculated any more accurately, it would be one and the same volume and could be eliminated as a factor influencing the amount of water filtered. Any differences in the filtering rates obtained by calculations from the rates of removal of two species from the same volume of water would be a reflection of the difference in the efficiency of the clam in removing the two species of algae. The simultaneous removal of two species of algae from the same volume of water can be followed with radioisotopes. This is possible, since one species of algae can be labeled with one isotope while the other species is labeled with a second isotope. Then, with radiological techniques, measurements can be obtained from which calculations can be made showing the number of cells of each species removed in a given period of time. Experiments using this approach are now being conducted in our laboratory.

It was found that the amount of water filtered per gram of meat by clams in suspensions of *Nannochloris* decreased as the weight of meats increased. Similar results were also observed for the bay scallop (Chipman and Hopkins, 1954). Whether this difference in volume of water filtered by the clam was due to a higher metabolic rate in the smaller clam or was the result of less gill surface per gram of meat in the larger clam was not investigated. The filtering rate for the adult clam, whether based on the removal of small algal cells or of diatoms, is much less than that observed for the bay scallop and the oyster. The adult bay scallop was found to filter an average of 14 liters of water per hour (Chipman and Hopkins, 1954). The oyster from New England waters has been reported to pump from 6 to 15 liters per hour (Nelson, 1935, 1936; Loosanoff and Nomejko, 1946; Loosanoff and Engle, 1947; and Loosanoff 1950).

The filtering rate of filter-feeding animals does not necessarily indicate the feeding rate, since all food particles removed from the water do not have to be ingested. According to MacGinitie (1941) feeding occurs only when a mucous sheet is present. The importance of mucus for the ingestion of food has been discussed by Jørgensen (1949) and Jørgensen and Goldberg (1953). It is believed by Ballantine and Morton (1956) that the greatest stimulus to mucous secretion is the presence of large amounts of indigestible debris in the water. In the present investigation, no observations on the formation of mucus in relation to the ingestion of food were made, but the rejection of food under certain conditions as indicated by the occurrence of pseudofeces in the water was closely followed. It can be stated that the number of cells present in the water, the presence of nonliving particles such as silt, and the particular plankton species with its associated physical and chemical characteristics influence the amount of food which will be rejected as pseudofeces.

That the number of cells present in the water could influence the feeding of lamellibranchs was suspected by Kellogg as long ago as 1915 (Kellogg 1915). Later Loosanoff and Engle (1947) showed experimentally that there are definite concentrations above which the numbers of food organisms begin to interfere with the feeding of oysters. In experiments in this investigation in which large numbers of *Nitzschia* cells were used, large amounts of pseudofeces were released to the water. When only small or intermediate populations of *Nitzschia closterium*, as well as the cells of other species, were present in the water, pseudofeces were not observed. When clams were in water containing large amounts of algal cells the formation of pseudofeces probably was due to the mechanical overloading of the gills and palps with a greater quantity of cells than could be ingested.

The influence of silt, along with several other substances, upon the rate of feeding of the oyster has been investigated by Loosanoff and Tommers (1948). They observed about a 94-percent decrease in the average rate of pumping when 3 to 4 grams of silt per liter of water were added. In our clam experiments, there was an instant and marked reduction in the filtering rate upon addition of 5 grams of silt per liter of water; however, this effect lasted for only a brief time. After about 15 minutes the clam was filtering *Nitzschia* cells from the water at a rate faster than that before the silt was added. Within 30 minutes after the silt was added, the clam was again filtering *Nitzschia* cells from the water at a normal rate. It was observed that not one clam closed during our experiments in which silt was added to the water. Loosanoff and Tommers (1948) in their experiments also found that a majority of the oysters kept their shells open most of the time when silt was added.

From our experiments it appears that the *Chlorella* cells had an unfavorable effect upon the filtering rate of the clam. It was observed that clams, which in previous experiments with other species of algal cells had remained open consistently during the entire period of sampling, usually opened and closed at irregular intervals in the presence of *Chlorella*. Also these clams were the only ones that remained closed for some time when returned to running sea water. Since filtering rates used in this investigation were based on continuous sampling for periods of up to 3 hours, the irregular opening and closing of the clam in the presence of *Chlorella* made it difficult to obtain data for that species. Even though *Chlorella* cells are somewhat larger than *Nannochloris* cells, the filtering rate was usually lower for clams in suspensions of *Chlorella*. Almost always large quantities of pseudofeces were formed when the clam was in suspensions of *Chlorella*. This occurred in suspensions of other

species of algae only when large numbers of cells were present. The presence of *Chlorella* cells in mixed suspensions with another species resulted in a lowered filtering rate for the other species. From our experiments it is also apparent that the older *Chlorella* cultures had a more pronounced effect than the newer cultures.

SUMMARY

The filtering rate of the hard clam, *Venus mercenaria* L., was determined in a series of experiments in which the clams were placed in unialgal and mixed suspensions of radioactive-labeled phytoplankton. The term "filtering rate" was interpreted to mean the volume of water from which the phytoplankton or other particles were removed per unit of time. Four species of unicellular algae were used in these experiments.

1. A comparison of filtering rates of the same clam in various concentrations of *Nannochloris* during a period of 2½ months showed no correlation between initial concentration of this algal species and its rate of removal.

2. More water was filtered per gram of meat by small clams than by large ones.

3. Clams had higher filtering rates in suspensions of diatoms than in suspensions of the smaller green algae. In suspensions of diatoms, the average filtering rates ranged from 3 to 6 liters per hour, while in suspensions of green algae the highest average filtering rates rarely exceeded 2 liters per hour.

4. Filtering rates were less in suspensions of diatoms containing either small numbers (400,000 per liter) or large numbers (170 million per liter) than in suspensions containing intermediate numbers (5 million to 75 million per liter).

5. When diatoms were in mixed suspensions with *Nannochloris* the average filtering rates, based on the rate of removal of *Nannochloris*, were higher than those obtained when the clam was in unialgal suspensions of *Nannochloris*. Lower average filtering rates were obtained for the clam in mixed suspensions of *Nitzschia closterium* and *Chlorella* cells than in unialgal suspensions of *Nitzschia*.

6. The filtering rate of the clam was higher in natural phytoplankton populations than in unialgal suspensions of green algae, but lower than in unialgal suspensions of diatoms.

7. Addition of silt to algal suspensions resulted in an instantaneous decrease in the filtering rate of the clam.

8. The clam formed large quantities of pseudofeces in the presence of high concentrations of algae, in all suspensions of *Chlorella*, and after silt was added.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

FACTORS CAUSING DECLINE IN SOCKEYE SALMON OF KARLUK RIVER, ALASKA

By GEORGE A. ROUNSEFELL

FISHERY BULLETIN 130

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ABSTRACT

Cyclic fluctuations in the sockeye salmon runs of Karluk River (Alaska) coincide with those of adjacent streams, indicating that these fluctuations have a common cause. After removal from the records of the broods the variation in the returns caused by various climatic and biological factors, it is clear that the sockeye salmon have a dome-shaped reproduction curve. The general decline in abundance can be ascribed to a lower survival rate from spawner to returning adults in recent years. There is evidence that this lowered survival rate results partially from seasonal distribution of escapement and partially from heightened mortality of the young during fresh-water residence. Smolt populations in a 15-year period, ranging in numbers from 4,700,000 to 13,200,000, show a linear relation with total weight of the whole smolt biomass indicating that within this range competition for food between young of the same brood in the lake is of no importance. At least a portion of the general decline is tentatively ascribed to heightened predation in recent years since destruction of the former cyclic character of the runs has lessened natural control of predators through a reduced amplitude of the oscillations in number of spawners.

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FACTORS CAUSING DECLINE IN SOCKEYE SALMON OF KARLUK RIVER, ALASKA

By George A. Rounsefell, *Fishery Research Biologist, Bureau of Commercial Fisheries*

Karluk River with its connecting lakes is the largest of several highly productive sockeye-salmon (*Oncorhynchus nerka*) streams in the northwest and southwest portions of Kodiak Island (fig. 1). Because this important fishery has continued to decline over many years, it has been the subject of much study by the Fish and Wildlife Service and its predecessors.

Purpose of the Study

The sockeye salmon run of Karluk River was selected for this detailed study for three reasons: (1) this valuable run has continued to decline despite efforts to maintain it by providing an adequate number of spawners, (2) at no other locality do we possess such a long series of observations on the numbers of fish in the run, numbers of spawners, ages of seaward migrants and returning adults, concomitant data of the fishery, and the limnology of the nursery lake, and (3) because of the great variation in both fresh water and ocean residence of the Karluk River sockeye salmon the study promised to yield information of great value in deducing principles of general applicability to management of salmon resources.

Although several types of data are available, these are insufficient in some respects to fully answer some of the pertinent questions. Nevertheless, in this analysis we have sought to postulate reasonable hypotheses to explain the observed facts. This has been done in order to afford a basis for action in accordance with the knowledge now available. There are several points requiring additional research, the results of which may modify some of the explanations given herein. Meanwhile the conclusions and hypotheses advanced furnish a basis both for the planning and execution of further research and for immediate action toward arresting and perhaps reversing the long downward trend of an important salmon resource.

NOTE.—Approved for publication June 3, 1957. Fishery Bulletin 130.

History of the Karluk Investigations

The scientific investigations were not placed on a continuous and systematic basis until 1921. However, such was the importance of the Karluk fisheries that studies were commenced as early as the summer of 1889, when the United States Fish Commission sent Dr. Tarleton H. Bean to Alaska. He spent from August 2 to September 27 at Karluk, and August 17 to 21 at Karluk Lake. In this first published report (Bean 1891) on the Karluk salmon runs he describes the spawning in various streams and includes a reconnaissance survey of Karluk Lake and a portion of Karluk River. He took samples of young fish to determine the hatching dates, sampled the other fishes, and made a series of temperature observations.

Early data on Karluk may be placed in two categories, (1) the description of the fishing and records of the catches and (2) information on the spawning in Karluk Lake, its tributaries, and Karluk River by the few persons who undertook the arduous hike over muskeg and up the shallow winding river to the lake. After the 1889 reconnaissance survey of Tarleton Bean 14 years elapsed before the lake was again visited in 1903 by Cloudsley Rutter. Although he spent some time at the lake, the description given from his notes by Chamberlain (1907) is very brief. Notes on short visits to the lake by Ward T. Bower in 1911, Edward M. Ball in 1917, and by Henry O'Malley and Charles H. Gilbert in 1919 are given by Gilbert and Rich (1927). The first rather complete survey of the spawning grounds was made by O'Malley and Gilbert in 1921. Thereafter (with the exception of 1923 and 1925) the lake has been visited each year.

In 1926 Willis H. Rich with a small field party made an accurate survey of the lake, including soundings, and commenced the collection of limnological data published in 1932 (Juday, Rich, Kemmerer, and Mann) for the 1926–30 period.

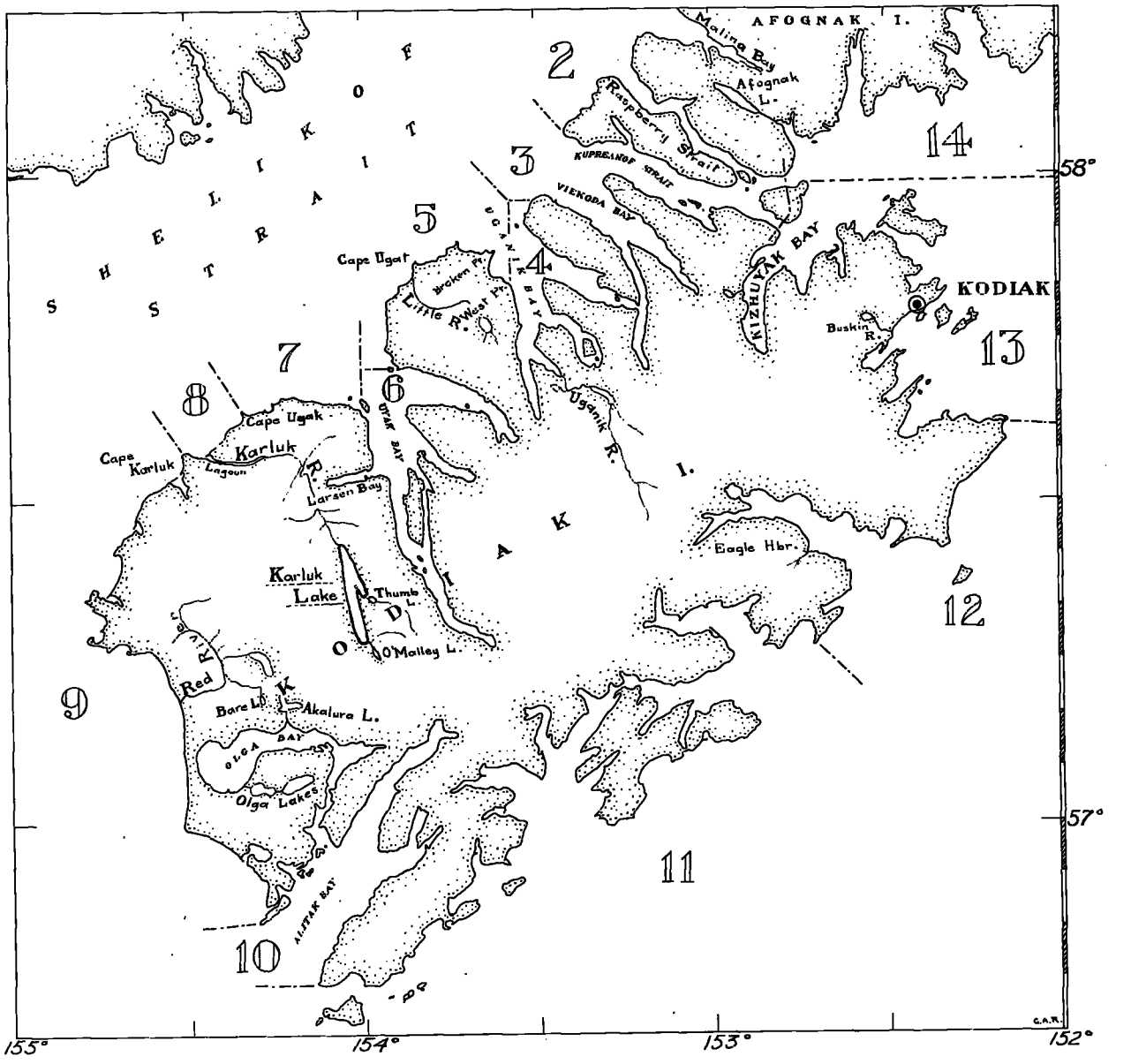

FIGURE 1.—Map of Karluk Lake and vicinity.

The early statistics of Karluk and notes on the fishery were collected by A. B. Alexander, fishery expert on the Fish Commission steamer *Albatross* in 1898 and 1899 (Moser 1899, 1902). The statistics of the fishery up to 1927 are given in Rich and Ball (1931).

In 1921 a weir for counting adult salmon on their upstream migration was placed in the river at the head of the lagoon and maintained there until 1941. From 1942 to 1944 it was installed about 20 miles up the river near the head of Larsen Bay. Since 1945 it has been operated at a site about 300 yards below the outlet of Karluk Lake. The principal reasons for finally locating the weir at the lake outlet instead of farther down the river were the difficulty in maintaining it when high

water brought down excessive quantities of aquatic weeds, and (in the even-numbered years) the clogging of the weir by the carcasses of thousands of pink salmon (*Oncorhynchus gorbuscha*) that spawn chiefly in the river below the lake.

General life history of Karluk sockeye

The general life history of the Karluk River sockeye salmon has been well established by Gilbert and Rich (1927) and Barnaby (1944) from extensive data collected continuously since 1921. The chief features are portrayed in figure 2. In year 0 the parents (of several age groups) ascend the river, spawn in the streams tributary to Karluk Lake and in the lake itself, and die. The spawning may commence late in June and continue until late in the fall. The great majority of the fish in the early run spawn in the tributary streams, large and small; a few spawn on gravelly beaches in the lake itself. Those ascending the Karluk after the end of July spawn both on the lake beaches and in the stream gravels, but the larger tributaries are preferred. It is estimated (Nelson and Edmondson, 1955) that about 75 percent of all the spawners use the streams, the remaining 25 percent the lake beaches. In some years, a few thousand late-arriving sockeye spawn in the main Karluk River below the outlet of the lake.

The eggs hatch during late winter or early spring, but the fry remain buried in the gravel until they have absorbed the yolk sac. During the following spring and summer, after absorbing the yolk, the fry struggle up out of the gravel; those in the tributary streams descend into the lake. We are not certain what happens to the fry from nests in the main river below the lake. The races of sockeye spawning below Chilko Lake in the Fraser River system for instance, habitually spawn below a lake, and the young must swim upstream into the lake. At Karluk, although the spawning below the lake has not been generally regarded as a regular occurrence, large numbers may spawn here in some years. (See appendix L.)

Although some of the young probably drift down the river to produce the few sea-type fish found in the returns, Philip Nelson writes that he has witnessed this group of young working upstream through the weir pickets. The observations of Johnson (1956) on the upstream movements of sockeye fry hatched below Babine Lake are strong confirmation of this habit.

The majority of the fry (fig. 2) reach the lake and live a pelagic existence for a varying length of time. Most of them leave the lake in the late spring and early summer (late May through July) of their third or fourth year of life. Extensive marking experiments have shown that the survival during their sojourn at sea, which may vary from less than 1 to 4 years, approaches 20 percent. Survival is higher for the older and slightly larger 4-year smolts than for the 3-year smolts.

The adults from the spawning of one year will return to the river from 3 to 8 years later after spending 0 to 4 summers in the lake and less than 1 to 4 summers at sea. The majority normally return as mature adults in their fifth year.

The runs at Karluk occur over an usually long period of time. The first sockeye may start running in mid-May and the last of the run may be entering the river in October.

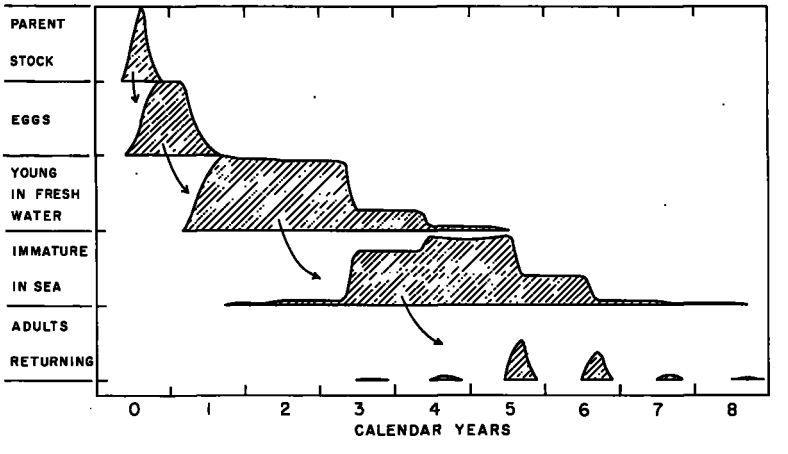

FIGURE 2.—Time diagram of life history stages.

Scope of the report

Because of the large amount of data available, and the necessity of showing how it was treated to prepare it for analysis, the bulk of the detailed data have been placed in the appendix to this report so as not to interfere unduly with the presentation of the analyses.

The first step was to define the field by determining what catches of sockeye salmon could be logically attributed to the Karluk population. Following this it was necessary to determine whether the short-term fluctuations in the Karluk runs occurred only in that stream or simultaneously in adjacent areas.

After it was established that the sockeye runs in Karluk and the neighboring streams exhibit concomitant fluctuations in abundance, analyses were made to determine the effect on freshwater survival of various climatic factors; and to remove these effects from the data to discover the true character of the sockeye reproduction curve. In addition to the variations in reproductive success induced by climatic fluctuation, the removal of the climatic effects from the data made it possible to observe another effect, viz., a significant difference in survival between broods spawned in even- and odd-numbered years, which has been attributed to the great disparity in abundance between the even- and odd-year pink salmon populations that apparently compete for spawning space with the sockeye.

Having also adjusted the data to discount the effects on sockeye survival of the 2-year cyclic variation in pink-salmon abundance, the adjusted data for survival according to number of spawners were now analyzed to determine the nature of the reproduction curve. The result was a constantly decreasing survival rate with an increasing number of spawners; with a greater number of spawners, the returning runs were smaller than the parent runs. It was also discovered that the decline in recent runs was caused by a lower rate of survival per spawner in recent years, so that the decline continued despite the large proportion of fish permitted to spawn.

Another phenomenon apparent in the data was the persistent cyclic character of the runs during the earlier years of the fishery. Because it was a 5-year cycle it has usually been ascribed to the normal dominance of the 5-year age group in the mature adults. However, analysis shows that because of the changes in survival rate with the number of spawners, coupled with the variations in age composition of the runs, this explanation is untenable. The persistence of the cycle, despite fluctuations in climatic and other factors, indicated that it was density-dependent. Analysis shows a significant negative relation between the density of young in the lake (young in their third and fourth years) and the survival of broods that were in the lake as fry during the same year. Since the 3- and 4-year olds average 2½ years older than the fry the result is a negative 2½ year correlation between runs, thus accounting for the positive 5-year cycle.

The reasons for the long-term decline in abundance are discussed from the standpoint of physical and biological factors. The small extent of the spawning beds in relation to the lake area for growth of the young is considered a factor in determining the decreased survival per spawner as the number of spawners increases.

An analysis of the numbers and weights of the seaward-migrating smolts shows that the decreased survival cannot be ascribed directly to intraspecific competition for food. The fact that the largest broods have the largest individual smolts indicates that the relative survival of each year class may be at least partially dependent on the annual food density so that survival is highest when growth is fastest.

The individual size, number, and total biomass of the smolts are compared for Karluk and Cultus Lakes. It would appear that the much greater growth rate of Karluk smolts may be partially caused by the fact that the high summer temperatures restrict the Cultus Lake smolts to the hypolimnion during most of the growing season.

Although direct intraspecific competition for food is dismissed as a factor in the long-term decline, it is postulated that there is nevertheless a strong influence of lake density of older young on fry survival which may take the form of cannibalism. This competition preserved the 5-year cycle as the numerous young from the dominant broods lowered the survival from the smaller broods, and vice versa.

Two types of predators are discussed, density-dependent and nondensity-dependent, according to whether their abundance is or is not controlled to a significant degree by the abundance of the salmon. The nondensity-dependent type tend to

take a fixed amount of salmon. This may have tended to accentuate the cyclic character of the runs during the early years since they reduced survival from small runs, while for the very large runs a small reduction, especially of the spawning adults, would tend to increase total survival. For the small runs of recent years the nondensity-dependent predators would render it difficult to obtain good survival until the number of spawners passed a threshold for which the amount taken by the predators would have little influence.

The density of the young coho salmon residing in Cultus Lake in British Columbia has been shown to be dependent on the density of young sockeye salmon. At Karluk the average number of adult coho spawners entering the lake averaged 8,800 over a 9-year period indicating high potential predation by young cohoes.

Both the lake-residing arctic charr, *Salvelinus alpinus* and the anadromous Dolly Varden charr, *Salvelinus malma*, are abundant at Karluk. More than 80,000 of the latter have been trapped and destroyed at the weir during their annual downstream migration in a single season.

If we postulate that these fish predators are density-dependent on young sockeye, it is apparent that the cyclic nature of the sockeye runs during the earlier years could have effectively controlled their abundance. During the earlier period of 42 years (1887–1928) the amplitude of the oscillations between high and low numbers of sockeye spawners was more than twice as great as in the following 25-year period (1929–53).

A fourth important factor influencing the survival rate per spawner is the effect on mortality of the age at which the parr transform into smolts and migrate seaward. Multiple regression analysis of average smolt lengths, temperatures, numbers of smolts migrating, and total biomass of the smolt migrations, shows that the threshold-size for the parr to transform into smolts is chiefly dependent on the number of fish in the total biomass. Thus, the higher the lake density of young, the younger (and smaller) are the migrating smolts. This implies a longer lake residence, and therefore lower survival, of the young from smaller broods.

In seeking for confirmation or denial of the foregoing hypotheses a study was next made of certain phases of the life history of the sockeye.

Analysis of seasonal occurrence of the runs over the 30 years from 1921–50 showed the sockeye entering the river from mid-May to mid-October. Three peaks of abundance occurred, the first and most evident peak is in mid-June, the second from late July to early August, and the third in early September.

The seasonal age composition of the runs was then studied. This showed that the seasonal occurrence of each age group is rather distinctive. The relative period during the season when each age group enters the river is governed by two factors: fresh-water age and ocean age. Except for the very few adults that entered the sea as fry, the age at the time of downstream migration has a negative effect on the season of return; the 2-year migrants return first, followed by the 3-, 4-, and lastly, the 5-year migrants.

The ocean age, however, has a contrary effect. The fish spending 4 seasons in the sea run first, followed by the 3-, 2-, 1-, and 0-ocean age groups.

Of the 18 commonly occurring combinations of fresh-water and ocean-age fish, only 8 groups are sufficiently numerous to contribute substantially to the run. These eight include all age groups in which the fish migrated seaward in their second to fourth year and spent 1 to 3 seasons in the ocean.

Analysis of the size of smolts leaving the lake shows that within any one season's migration the larger smolts of each age group migrate first. Marking experiments by Barnaby (1944) show that within each age group of smolts those leaving the lake earlier in the season tend to remain a shorter time at sea. The 4-year smolts also tend to stay at sea for a shorter period than the 3-year smolts. Thus it becomes apparent that the fastest-growing smolts are first to reach maturity.

The possibility of two or more distinct races of sockeye at Karluk is explored and rejected on present evidence, since it can be demonstrated that the peaks of seasonal occurrence in the run can be fully explained by the distinctive patterns of seasonal occurrence of fish belonging to the various age groups. Furthermore, it can be shown by correlation analysis that there is a significant relation in the abundance of fish of the same brood year maturing at different ages and running in different parts of the season in the same or the following calendar year.

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A study of the average age at maturity for the brood years of 1919–42 confirms the conclusion of Barnaby (1944) for a shorter period of time (1920–29) that the age at maturity has been increasing in recent years.

An explanation of this phenomenon of increasing age is found in the relation of brood size (mature adults) to age at maturity. The number of 5-year old fish is positively correlated with brood size ($r=0.78$, while the numbers of 6- and 7-year-old fish are negatively correlated ($r=-0.78$ and -0.60, respectively). Thus, this negative relation between average-age and brood-size is the result of the young of the smaller broods (accentuated in recent years by declining abundance) tending to remain an additional year in the lake.

Since man is the chief predator of the salmon run, an analysis was made to discover whether his manner of fishing could affect the survival rates per spawner. The chief portion of his catch has been consistently taken from the center portion of the run, leaving the very early and very late migrating fish almost untouched. No indication exists that this has had any effect on the seasonal occurrence of the runs, but it is postulated that this may have decreased the return per spawner, since the eggs and fry from very early or very late spawning were shown to be more likely to be affected by unfavorable climatic conditions.

The remainder of the report discusses in some detail the pros and cons of various hypotheses that have been advanced in the past to explain the dwindling runs, and advances hypotheses which appear to be supported by the data.

RELATION BETWEEN RUNS OF KARLUK AND OTHER LOCALITIES

Before proceeding with an analysis of the Karluk runs there are two questions which need to be answered. First, are the records of catches of Karluk River sockeye sufficiently accurate for our purpose? Second, if we are satisfied on the first point, do we find the fluctuations at Karluk to be unique, or is there a significant relation between fluctuations in abundance in Karluk and in adjacent streams that indicates a common cause of variation?

Catch allocations between Karluk and adjacent rivers

Accurate records of the catches of sockeye that are bound for the Karluk River are very important to any study of the causes for shifts in abundance of the runs. The catches of Karluk sockeye as given in the available records, apart from any minor discrepancies, are subject to two principal sources of possible error.

1. Inclusion in the early Karluk records of salmon taken in adjacent rivers. In this regard Rich and Ball (1931, p. 665) state,

> In 1896 * * * For the first time salmon were reported from Uganik, "Ayagulik" (probably intended for Ayakulik or Red River,) Kaguayak, and Little River, but the estimated catches at these places were excluded from the Karluk catch. It is believed, however, that in several years before and after 1896, Karluk catch statistics were slightly in error due to the inclusion of fish taken at other localities, but no attempt has been made to correct this, except as indicated in the footnotes following table 14.

2. Possible errors in determining the destina- of salmon caught in salt water at some distance from the rivers.

As to the first point, we have estimated the catches for Little River, Uganik River, and Red River prior to 1903, for the years in which they were included in the published totals for Karluk and have subtracted them. These estimated catches are likely minimal since they are based (table 3) on the best 5-year average catch, which of course, was made at a later period when these fisheries had been fully exploited for a number of years. The dates of 1888 for the commencement of fishing at Little River and Uganik River and of 1889 for the Red River are from the reports of Moser (1899, 1902). It will be noted as a result that the figures for Karluk production prior to 1903 are slightly less in some years than those given by earlier authors.

As to the second point Barnaby (1944) includes as Karluk sockeye all fish caught between Cape Karluk, about 3 miles west of the mouth of the Karluk River, and West Point, about 6 miles inside the western shore of Uganik Bay and about 75 miles northeasterly from the mouth of the Karluk River.

Catches could be allocated with confidence to particular rivers during the earlier years of the salmon fisheries when the catches were made chiefly with beach seines close to the mouths of the streams, or as at Karluk, in brackish lagoons at their mouths. After the advent of purse seines, gill nets, and traps the chances for taking salmon in one area bound for more than one stream were increased. In 1926 and 1927 traps were

placed near Broken Point just inside of Uganik Bay on the western shore and it was immediately suspected that they were largely taking Karluk salmon. Accordingly, Rich and Morton (1929) tagged and released 700 sockeye salmon at Broken Point on August 19 and 20, 1927, to determine the destination of these fish (see table 1).

On the basis of this tagging experiment it was concluded that all sockeye captured between Cape Karluk on the west and West Point to the northeast should henceforth be considered as bound for the Karluk River and be included in the catch of that river. There could be several objections to this allocation on the basis of this lone experiment, which can be summarized:

1. The experiment was performed so late in the season as to yield no information on the earlier runs (76 percent of the Karluk run is normally over by the week ending August 23).

2. Because the Red River run was temporarily at a very low ebb, the Red River fishery was closed to fishing for several years, including 1927, so that no tags could be recovered there, and had the area been open, the number of tags recovered during 1927 would have been less than in years of normal-size runs.

3. Three tags were recovered at Alitak, beyond the Red River area, indicating that there might have been more bound for the Red River area.

4. Seven tags were recovered in Cook Inlet, Raspberry Strait, and Viekoda Bay, all east of the point of tagging, suggesting that some of the fish may have passed the mouth of the Karluk River traveling eastward.

5. Thirteen tags were taken in the southern arm of Uganik Bay from fish that were probably bound for Uganik River, a sockeye stream in the east arm of Uganik Bay. This run, like that of the Red River, was at a low ebb during the period embracing 1927. In the 23-year period from 1889 to 1911 the catch from Uganik Bay, which at that period was not taken by traps and presumably was made near the head of the bay, ranged from a low of 22,000 in 1897 to a high of 366,000 in 1896. The average catch was 123,000 sockeye with only 6 years falling below 100,000. By 1925, the last year before the traps were driven on the west shore near Broken Point, the catch was only 4,646. A weir was maintained in the Uganik River from 1928 to 1932, inclusive. During this 5-year period the average escapement up the river was only 24,609 sockeye salmon.

TABLE 1.—*Tagging experiments on sockeye salmon, 1922 to 1929, showing recoveries either on Kodiak-Afognak Islands, or from localities beyond* [1]

Locality of release	Date of release			Number released	Locality of recapture								Total recaptures	Percent moving to or beyond Kodiak Island
	Month	Day	Year		Cook Inlet	Afognak Island [2]	Uganik Bay	Uganik to Uyak Bay [3]	Uyak Bay	Karluk	Alitak	?		
ALASKA PENINSULA														
Unga Island	June	30	1922	601	4								54	7.4
Do	do	2-5	1923	120									13	0
Do	do	7	1923	575		1							105	1.0
Do	do	23	1923	499									213	0
Do	do	26	1923	499									110	0
Do	do	27	1923	137	1								53	1.9
Do	do	27	1923	859	1					1			277	.7
Do	July	4	1923	110									43	0
Do	do	6	1923	633	1						1		172	1.2
Nicholaski Spit	do	11-17	1928	461	1		1	1					30	10.0
COOK INLET														
Flat Island	June	14	1929	127				3					29	10.3
Do	do	27	1929	45									10	0
Do	July	23	1929	18									7	0
Nubble Point	June	26	1929	138		1		2					46	6.5
Do	July	18	1929	13									5	0
UGANIK BAY														
Broken Point	August	19-20	1927	700	2	5	67	132	107		3	1	[4] 317	
TOTAL RECOVERIES														
Alaska Peninsula				4494	8	1	1	1		1	1		1070	1.2
Cook Inlet				341		1		5					97	6.0

[1] Gilbert (1923), Gilbert and Rich (1925), Rich and Morton (1929), Seton Thompson (1930).
[2] Includes Afognak Island, Raspberry and Malina Straits, and Viekoda Bay.
[3] Includes Cape Ugat and Little River.
[4] 86 additional tags seen on salmon passing Karluk weir.

6. Tagging experiments in Cook Inlet and along the south side of the Alaska Peninsula (table 1) showed that 6 percent of the former and 1.2 percent of the latter moved to localities either on or beyond Kodiak-Afognak Islands.

7. It has been shown in several tagging experiments (Gilbert and Rich, 1925, and O'Malley and Rich, 1919) that the speed of migration increases considerably as the season advances. For this reason, the early-running fish spending a longer time en route are more subject to capture in areas far from their destination. Thus for the Fraser River runs (Rounsefell and Kelez, 1938) the traps took a larger share of the sockeye in years when the runs were early. When the runs were late the fish apparently hurried through the main channels, as only traps along the main route caught a fair share of the run. It is fair to assume that a larger share of the Karluk fish of the early run might be taken elsewhere, and it can only be conjectured as to whether the early arriving fish from other areas taken at Karluk are closely equal in numbers to the early Karluk fish taken elsewhere.

8. After stating that the Alitak fishery seems to be independent of other areas, Rich and Ball (1931) append a footnote saying,

> It has been noted in the past year or two, however, that many of the fish passing through the weirs in this district bear the marks of gillnets. Just where the Olga Bay fish pass through a gill-net fishery is not definitely known but it seems probable that it is along the northwest coast of Kodiak Island.

Despite all objections to the method used for allocating sockeye catches to the Karluk River there is considerable justification for the assumption that the resulting allocations were fairly accurate, at least for the 1904–25 period. The numbers of fish bound for mainland areas taken on Kodiak-Afognak Islands would seem from the tagging experiments to be fairly small. Since, on the other hand, a few of the island-bound salmon are probably taken on the mainland, the total error introduced by these catches must be relatively minor (table 2).

The only sizeable errors would have to come from misallocation of catches of sockeye made in the waters of the islands. Some idea of the relative importance of the sockeye streams can be gained from table 3 showing the areas of the lakes

TABLE 2.—*Catches of sockeye salmon at Karluk and nearby areas*

[In thousands]

Year	Karluk adjusted [1]	Area 5 Little River	Area 4 Uganik River	Area 9 Red River	Area 3 Kupreanof Strait	Area 2 Raspberry Island and Malina Bay	Karluk [2] total run
1882	59						
1883	189						
1884	282						
1885	469						
1886	646						994
1887	1,005						1,546
1888	2,631	*50	*100				4,048
1889	3,056	*106	220	*250			4,702
1890	2,580	*106	191	*463			3,969
1891	2,932	*106	131	*463			4,511
1892	2,140	*106	*143	*463		[3]	3,292
1893	2,198	*106	*143	*463			3,382
1894	2,638	*106	*143	*463			4,059
1895	1,344	*106	*143	*463			2,068
1896	2,070	*106	366	*463			3,185
1897	1,635	*106	22	*463			2,515
1898	965	*106	30	*463			1,485
1899	830	*106	155	*463			1,277
1900	2,074	*106	143	700			3,191
1901	3,629	*106	*100	*450			5,583
1902	2,715	*106	*100	*360			4,177
1903	1,064	*106	*50	*250			1,637
1904	1,639	246	82	167			2,522
1905	1,788	81	2	59			2,751
1906	3,414	35	34	163			5,252
1907	2,930	82	103	312		30	4,508
1908	1,608	86	126	286		7	2,474
1909	924	29	226	201		63	1,422
1910	1,493	47	129	99		43	2,297
1911	1,723	27	133	177			2,651
1912	1,245	6	74	413		29	1,915
1913	868	1	48	293		42	1,335
1914	540	10	56	143		60	831
1915	828	11	24	212	20	42	1,274
1916	2,232	1	15	215	**4	4	3,434
1917	2,350	4	8	222	**0	12	3,615
1918	1,120		2	147	**0	14	1,723
1919	1,105	2	5	80	**1	23	1,700
1920	1,371	1	5	15	2	11	2,109
1921	1,642	1		29	3	77	3,142
1922	658			12	2	17	1,058
1923	728		7	[5]	2	69	1,423
1924	891		4			35	1,954
1925	1,319	6	5		1	28	2,940
1926	2,384	[4] 3	74		2	102	4,918
1927	775	0	**12		**4	**15	1,647
1928	1,198		**9		**11	**3	2,292
1929	381		**57		**9	**21	1,282
1930	238		**21		**2	**18	1,325
1931	867		**20		**5	**5	1,740
1932	771		**39		**17	**7	1,509
1933	1,143		**30		**24	**11	2,111
1934	1,399		**57		**26	**15	2,849
1935	944		**26	337	**37	**21	1,820
1936	1,078		[6]	743	[6]	[6]	2,453
1937	1,071			255			2,336
1938	984			232			2,214
1939	509			174			1,215
1940	452			145			1,268
1941	697			222			1,629
1942	507			220			1,136
1943	806			450			1,727
1944	641			762			1,410
1945	676			659			1,335
1946	228			215			670
1947	110			156			595
1948	657			189			1,410
1949	450			55			1,141
1950	504			145			1,263
1951	149			60			822
1952	219			12			774
1953	77			47			811

[1] Adjusted for estimated catches of other rivers included in Karluk figures.
[2] 1888–1920 equals catch times 1.5385, 1921 and subsequently equals catch plus escapement.
[3] Most of area 2 in Afognak Reservation, no legal fishing 1892–1911.
[4] Area 5 assigned to Karluk catch 1926 and subsequently, except for Rich and Ball figures for 1926 and 1927.
[5] Area 9 closed 1923–1934.
[6] Subsequent to 1935 not available.
*=Estimated catch.
**=Catch minus trap catch.

and their relative productivity. The only other sockeye lake of any size on the islands is Afognak Lake (approximate area of 2.8 square miles, watershed of 32.5 square miles). Thus Karluk Lake has an area about equal to all of the other sockeye lakes on Kodiak and Afognak Island (there are very small lakes with small sockeye runs at several other points in addition to those listed in table 3, e. g., Buskin River, Eagle River, and Kizhuyak Bay).

TABLE 3.—*Lake areas of principal Kodiak Island sockeye streams adjacent to Karluk and their relative productivity since 1903* [1]

Source of water		Area in square miles [2]	Best 5 years	Average catch	Maximum catch any year since 1903	Year of maximum catch
Karluk River	Karluk Lake	15.26				
	Thumb Lake	.31				
	O'Malley Lake	.47				
Total (Karluk River)		16.04	1904–08	2,269,562	3,382,913	1906
Little River	Little Lake	.78	1904–08	105,850	246,131	1904
Uganik River	Uganik Lake	1.25	1907–11	143,436	226,477	1909
Red River	Red Lake	3.27				
	Other lakes	.32				
Total (Red River)		3.59	1941–45	462,772	762,084	1944
Cannery Stream	Akalura Lake	2.18	1917–21	[3] 91,899	[3] 103,777	1917
Olga Creek	Olga lakes	5.29	1917–21	[3] 571,612	[3] 871,723	1917

[1] Before 1904 the records of catches by streams are incomplete.
[2] Planimeter measurement from Geological Survey Topographic Maps, Scale 1: 250,000.
[3] Weir counts, 1923–32, 1937–42 and 1944–51 showed Olga Creek with 6.22 times Cannery Stream so catch was allocated on that basis.

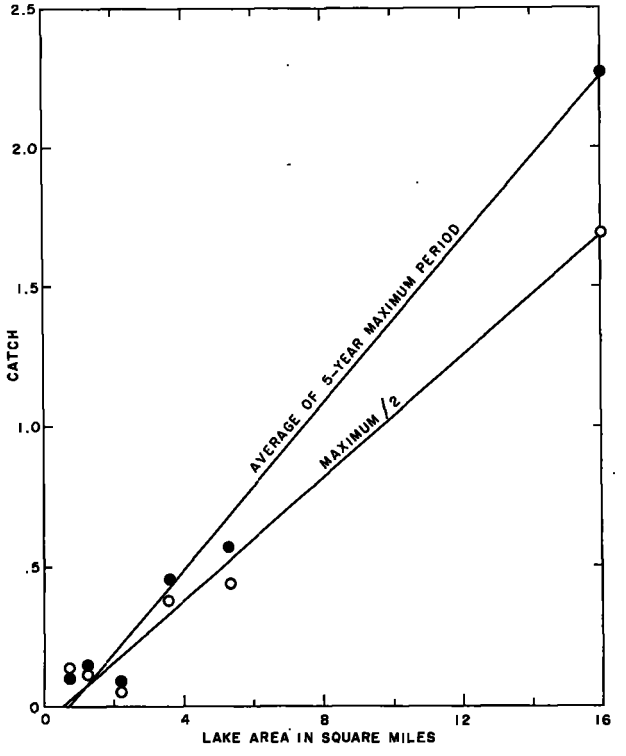

FIGURE 3.—Relation between lake area and potential size of population.

Figure 3 shows that there is a close correspondence between lake area and potential production of sockeye in this general region. A 5-year average was used in order to discount short-term fluctuations in abundance, and since 5 is the dominant age at maturity in this region the use of a 5-year period is indicated. Prior to 1904 the allocation of catches to districts were available in part only, so earlier years were omitted in selecting the 5-year period of maximum catch. Of course the 5-year period selected is not the same for every stream since some streams were depleted during periods when others were not.

For this report, we have tentatively accepted the catch figures for Karluk presented in table 2. It will be noted that previous to 1903 the figures for Karluk production are slightly less than any previously used as we have subtracted the estimated catches for Little River, Uganik River, and Red River, which were included in published totals for Karluk in some of the years.

Comparison of abundance fluctuations in different lake

In determining the cause of the changes in abundance of the Karluk sockeye population it is

important to know whether these fluctuations are confined to Karluk only, or whether they have occurred simultaneously in other populations in the region. In table 4 are shown the total runs for Karluk and Red Rivers, and the weir counts in the Uganik River, Cannery Stream (Akalura Lake), and Olga Creek. For each locality the measure of the run that has been employed has been weighted to make its sum for the period of years available equal to the sum of the total Karluk run for the corresponding period of years. The plotted curves of figure 4 show that the five runs tend to fluctuate together, but the Uganik River series is too short to permit an adequate test of its significance.

For the other four streams the weighted total runs (or weir counts), columns 2 to 5, table 4, have been compared with one another with the following results:

Correlations between runs of sockeye, r

Streams	Cannery Stream	Red River	Karluk River
Olga Creek	.615**	.331	.781**
Cannery Stream		.689**	.506**
Red River			.672**

r^2

Olga Creek	.38	.11	.61
Cannery Stream		.48	.26
Red River			.45

Nearest airline mileage between lakes

Olga Creek	8	11	15
Cannery Stream		1	9
Red River			10

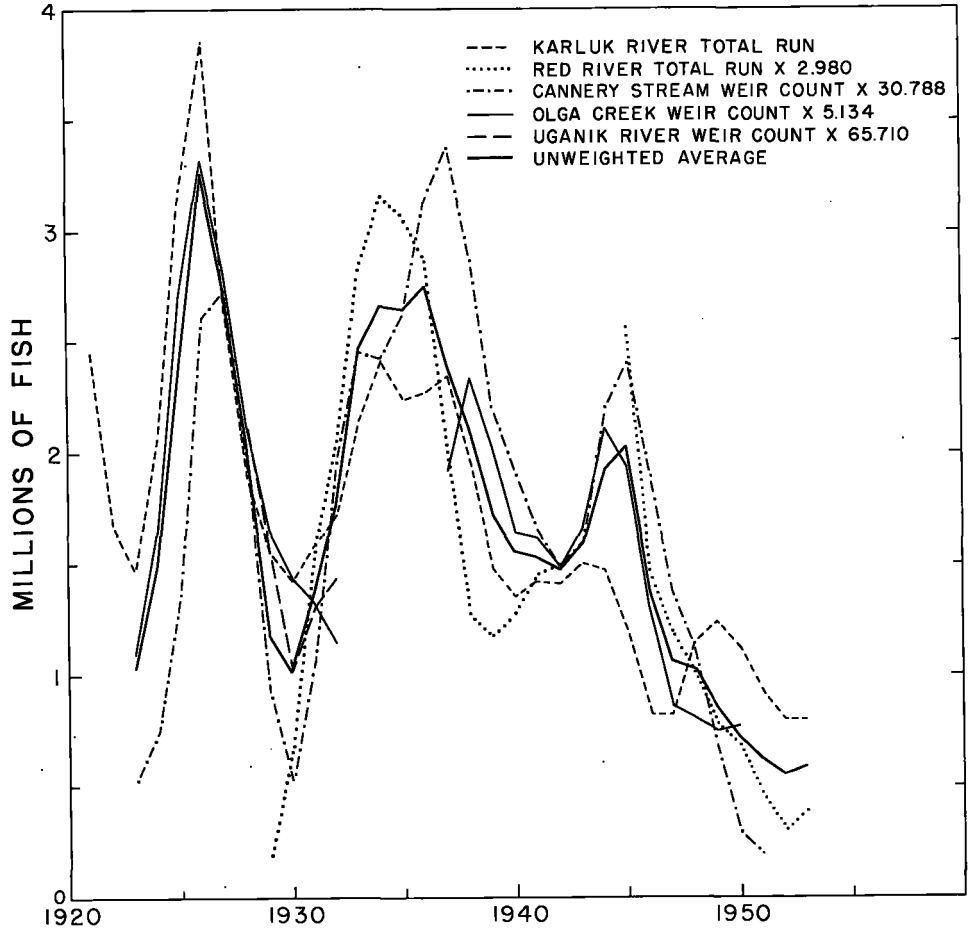

FIGURE 4.—Long-term fluctuations in the runs for Karluk River and other streams in the vicinity, all weighted to equal Karluk for same period of years with available data.

TABLE 4.—*Comparison of Kodiak Island sockeye salmon runs* [1]

[In thousands]

Year	Uganik: weir count	Karluk: total run	Red River: total run	Olga Bay		Trends [2]					Total		
				Cannery Stream: weir count	Olga Creek: weir count								
	A	B	C	D	E	A	B	C	D	E	Sum	Items	Average
1921		3,142					2,447				2,447	1	2,447
1922		1,058					1,670				1,670	1	1,670
1923		1,423		493	863		1,465		534	1,092	3,091	3	1,030
1924		1,954		616	1,550		2,068		747	1,645	4,460	3	1,487
1925		2,940		1,262	2,618		3,188		1,343	2,710	7,241	3	2,414
1926		4,918		3,233	4,056		3,856		2,609	3,322	9,787	3	3,262
1927		1,647		2,709	2,557		2,626		2,725	2,833	8,184	3	2,728
1928	2,366	2,292		2,248	2,161	2,125	1,878		1,940	2,109	8,052	4	2,013
1929	1,643	1,282	86	554	1,556	1,577	1,548	190	916	1,651	5,882	5	1,176
1930	657	1,325	399	308	1,330	1,018	1,418	682	516	1,436	5,070	5	1,014
1931	1,117	1,740	1,842	893	1,530	1,314	1,578	1,506	1,047	1,332	6,837	5	1,367
1932	2,366	1,509	2,181	2,094	940	1,940	1,717	2,068	1,963	1,137	8,825	5	1,765
1933		2,111		2,771			2,145	2,818	2,448		7,411	3	2,470
1934		2,849	3,454	2,155			2,407	3,152	2,424		7,983	3	2,661
1935		1,820	2,548	2,617			2,236	3,058	2,617		7,911	3	2,637
1936		2,453	3,680	3,079			2,266	2,856	3,125		8,247	3	2,749
1937		2,336	1,517	3,725	1,299		2,335	1,990	3,379	1,920	9,624	4	2,406
1938		2,214	1,246	2,986	3,163		1,945	1,269	2,878	2,338	8,430	4	2,108
1939		1,215	1,067	1,816	1,725		1,478	1,165	2,201	2,030	6,874	4	1,718
1940		1,268	1,281	2,186	1,509		1,345	1,282	1,909	1,643	6,179	4	1,545
1941		1,629	1,499	1,447	1,828		1,418	1,446	1,647	1,622	6,133	4	1,533
1942		1,136	1,505	1,509	1,325		1,407	1,503	1,488	1,493	5,891	4	1,473
1943		1,727					1,500		1,601	1,656	4,757	3	1,586
1944		1,410		1,693	1,987		1,470		2,206	2,117	5,793	3	1,931
1945		1,335	3,239	3,233	2,377		1,188	2,573	2,409	1,936	8,106	4	2,026
1946		670	1,240	1,478	1,001		818	1,470	1,894	1,295	5,477	4	1,369
1947		595	1,162	1,385	801		818	1,194	1,370	859	4,241	4	1,060
1948		1,410	1,213	1,232	832		1,139	1,013	1,116	813	4,081	4	1,020
1949		1,141	465	616	786		1,239	775	662	751	3,427	4	857
1950		1,263	957	185	601		1,122	684	293	766	2,865	4	716
1951		822	355	185	1,078		920	458	185	919	2,482	4	620
1952		774	167				795	297			1,092	2	546
1953		811	498				799	388			1,187	2	594
Weight factor	65.710	0	2.980	30.788	5.134								

[1] All runs weighted so that sums of years correspond to same years at Karluk.
[2] Smoothed once by 3's, with double weight on center item.

Out of 6 comparisons, all but 1 were highly significant. The coefficient of determination, r^2, varies in the other 5 comparisons from .26 to .61 showing that the fluctuations in the runs are to a considerable extent controlled by elements common to all.

Although the sea-distance between the mouths of the streams issuing from these lakes varies from about 7 to 75 miles, the lakes lie in a comparatively small area, the greatest distance between any two of them being 15 miles in a direct line. Because they lie in such a small area it is obvious that any major climatic changes must affect them all in the same direction. Clearly, then, we must begin by examining the climatic factors.

EFFECTS OF CLIMATE ON SUCCESS OF REPRODUCTION

The measurement of the effect of climate on the success of reproduction is important from two standpoints. If any one of the climatic factors which have a significant influence show a long-term trend it could conceivably be an important cause of long-term abundance trends. Furthermore, short-term changes in abundance caused by climatic factors serve to obscure the effect of other factors by causing excessive variation in the data. Aside then from the intrinsic value of knowledge of the effect of climatic factors, it is highly desirable to measure their effect so that they may be discounted in further analysis of the abundance data.

In examining the relations between success of survival and the physical environment, we were unable to avail ourselves of the advantages of multiple regression because the different series of data on the ecological factors are not equal, either in number or in specific years represented. The ecological factors have, therefore, been considered one by one. By so doing one loses the effect of interaction between factors. Also, one cannot always be certain of the amount of variation caused by any one factor. For instance, a factor

may not show any significant correlation with survival. However, if this same factor be again related to survival, after the effects of some other factor have been removed, the relation may be statistically significant. By this method of successive elimination it is possible to underestimate the total effect of the factors considered.

We have considered only those elements of the climate for which sufficient records exist and which can logically affect survival or growth at some stage of the salmon's existence. The factors considered were examined only in the order in which they are presented in the text. The factors examined are presented in table 5. The validity of the use of Kodiak air temperatures as representative of the Karluk Lake water temperatures was carefully examined (see appendix I) and verified.

In order to relate these climatic factors to survival it was necessary to have a measure of the success of each season's spawning in terms of survival. The total run (table 2) could not be used directly because the size of the population changed with time. It was, therefore, necessary to use not the run but the size of the returning population in relation to the number of spawners that produced it (table 6). The details concerning the derivation of the escapement and return figures of table 6 are developed in appendix D.

Examination of the data in table 6 reveals that the return per spawner cannot be used directly as a measure of spawning success since the return per spawner is correlated with the number of spawners. The regression of returns on number of spawners is shown in figure 5. The data divide rather sharply into two periods, the break occurring between 1923 and 1924. The relation is not strictly linear, as is illustrated in figure 5 by plots of group averages and empirical curves.

Enactment in 1924 of the White Act empowered the Secretary of Commerce (now Interior) to require a minimum escapement of 50 percent of the run. Thus 1924 became the first season in which the size of the escapement was regulated. Thus there is a natural break between 1923 and 1924, the latter period representing regulated escapements opposed to the chance escapements of earlier years.

In order to obtain a linear relationship the number of spawners was transformed into logarithms. The regressions of return per spawner on the logarithm of the number of spawners are shown in figures 6 and 7 for the early and recent periods. The reason for the considerable fall in the return per spawner after 1923 is not apparent in these data, but as we shall show later, may perhaps be linked with some change in the

TABLE 5.—*Certain climatic factors for Kodiak, Alaska*

Year	Average monthly temperatures °F		Accumulated monthly temperature 45° to 55°F including previous year	Average precipitation April to July in inches
	April–May	October–December		
1869	42.55	38.17		22.78
1870	39.05			12.63
1881				
1882				22.08
1883				28.01
1884				13.50
1885				19.77
1886				11.40
1887				27.22
1888				14.59
1889				20.16
1890				16.77
1895		[2] 42.22		
1896	35.30			
1897				
1898		[2] 39.78		
1899	40.10	[2] 38.98		10.80
1900	41.30	[2] 31.75		19.21
1901	39.70	37.63		
1902	42.25			12.23
1903	40.70	36.33		21.71
1904	41.20	36.57	62.7	10.65
1905	44.25	[2] 37.92		9.60
1906	41.50	37.03		
1907	41.65	34.70		15.61
1908	37.30		45.4	19.19
1909	38.05	[2] 31.23	36.0	20.55
1910	35.70	33.33		20.85
1911	35.45	35.30		16.80
1912				
1913		35.20		18.01
1914	41.00	38.30		23.93
1915	[1] 43.30	35.00		
1916	38.60	31.17	55.1	22.87
1917	39.40	30.27	38.8	15.02
1918			49.2	6.29
1919	39.10	36.00	57.6	20.81
1920	37.15	35.13	48.3	13.57
1921	39.10	37.67	42.4	15.27
1922	38.40	36.77	52.0	15.41
1923	40.55	37.47	57.1	12.79
1924	38.40	37.10	59.7	8.67
1925	38.05	38.07	61.8	13.92
1926	42.50	39.83	71.6	18.01
1927	38.55	33.37	57.6	23.24
1928	39.00	37.60	40.3	21.20
1929	40.80	39.17	57.0	18.28
1930	39.60	36.83	59.9	15.30
1931	41.90	36.97	54.0	16.83
1932	40.70	36.53	51.4	23.76
1933	40.20	34.93	47.4	17.23
1934	40.90	37.80	53.7	21.65
1935	41.80	37.70	59.7	22.69
1936	40.65	38.60	67.9	11.57
1937	40.50	35.60	57.8	26.99
1938	40.60	38.57	44.4	35.24
1939	39.60	34.97	50.2	14.14
1940	43.60	39.27	55.1	25.19
1941		36.07		21.65
1942	44.00	32.03		
1943	40.00	37.33	62.6	
1944	38.90	37.27	56.3	
1945	[1] 39.10	31.83	56.0	
1946	[1] 39.30	34.80	53.1	
1947	39.30	37.07	54.6	
1948	41.60	32.50	49.5	
1949	37.95	36.43	48.3	
1950	38.30	34.07	49.2	
1951	39.30	36.17	50.1	
1952	37.45	37.33	51.6	
1953	40.05	35.97	57.5	

[1] Based on 1 month's record.
[2] Based on 2 months' records.

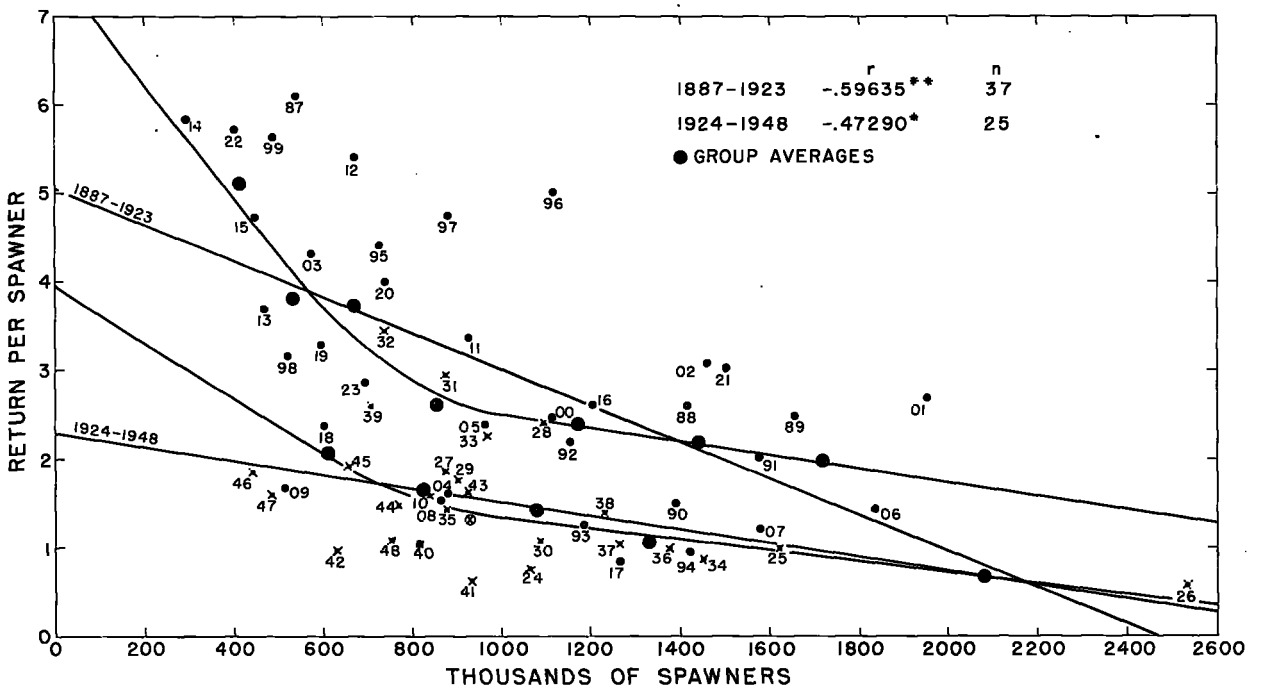

FIGURE 5.—Relation between return per spawner and number of spawners (escapement). This shows both least square curves and empirical curves from grouped averages to illustrate the curvilinearity of the plots.

TABLE 6.—*Showing the number of spawners and the resulting runs from 1887 to 1948*

[In thousands]

Year of spawning	Escapement[1] (spawners)	Returns[2] (progeny)	Returns per spawner	Year of spawning	Escapement[1] (spawners)	Returns[2] (progeny)	Returns per spawner
1887	541	3,292	6.09	1921	1,500	4,494	3.00
1888	1,417	3,382	2.39	1922	400	2,282	5.71
1889	1,646	4,059	2.47	1923	695	1,990	2.86
1890	1,389	2,068	1.49	1924	1,063	809	.76
1891	1,579	3,185	2.02	1925	1,621	1,607	.99
1892	1,152	2,515	2.18	1926	2,534	1,461	.58
1893	1,184	1,485	1.25	1927	872	1,618	1.86
1894	1,421	1,277	.90	1928	1,094	2,630	2.40
1895	724	3,191	4.41	1929	901	1,587	1.76
1896	1,115	5,583	5.01	1930	1,087	1,172	1.08
1897	880	4,177	4.75	1931	873	2,578	2.95
1898	520	1,637	3.15	1932	738	2,538	3.44
1899	447	2,522	5.64	1933	968	2,186	2.26
1900	1,117	2,751	2.46	1934	1,450	1,261	.87
1901	1,954	5,252	2.69	1935	876	1,250	1.43
1902	1,462	4,508	3.08	1936	1,375	1,353	.98
1903	573	2,474	4.32	1937	1,265	1,334	1.05
1904	883	1,422	1.61	1938	1,230	1,587	1.29
1905	963	2,297	2.39	1939	706	1,831	2.59
1906	1,838	2,651	1.44	1940	816	858	1.05
1907	1,578	1,915	1.21	1941	932	575	.62
1908	866	1,335	1.54	1942	629	607	.97
1909	498	831	1.67	1943	921	1,495	1.62
1910	804	1,274	1.58	1944	769	1,141	1.48
1911	928	3,434	3.70	1945	659	1,263	1.92
1912	670	3,615	5.40	1946	442	822	1.86
1913	467	1,723	3.69	1947	485	774	1.60
1914	291	1,700	5.84	1948	754	811	1.08
1915	446	2,109	4.73	1949	691	----------	----------
1916	1,202	3,142	2.61	1950	759	----------	----------
1917	1,265	1,058	.84	1951	673	----------	----------
1918	603	1,423	2.36	1952	556	----------	----------
1919	595	1,954	3.28	1953	734	----------	----------
1920	738	2,940	3.98				

[1] Prior to 1921 equals catch times 0.5385 (35/65).
[2] 1921–48 based on actual returns, other years equals catch and escapement 5 years later.

seasonal distribution and variation in size of the escapements.

The residuals (table 7) of the return per spawner on $\log_{10}$ number of spawners (plus or minus deviations of the return per spawner from the regression line) were derived from the regression curves of figures 6 and 7. These residuals, plotted in figure 8, show long-term fluctuations that could scarcely be considered random.

If we let y equal returns and x equal number of spawners, the formula used in fitting these regressions is $\log y = x\epsilon^{a-b \log x}$ which can also be written as $y=(a-b \log x)x$ (see plot of x and y values in fig. 19). For purposes of fitting it was more convenient to use the straight line form of the equation $y/x=a-b \log x$. A comparison of this and an alternative method of deriving residuals of return on escapement is given in appendix H.

The use of the residuals of the return per spawner on the logarithm of the number of spawners for comparison with climatic effects removes the necessity for an extremely complex analysis in which allowances would have to be made both for actual abundance of the parent broods and for long-term trends in the abundance

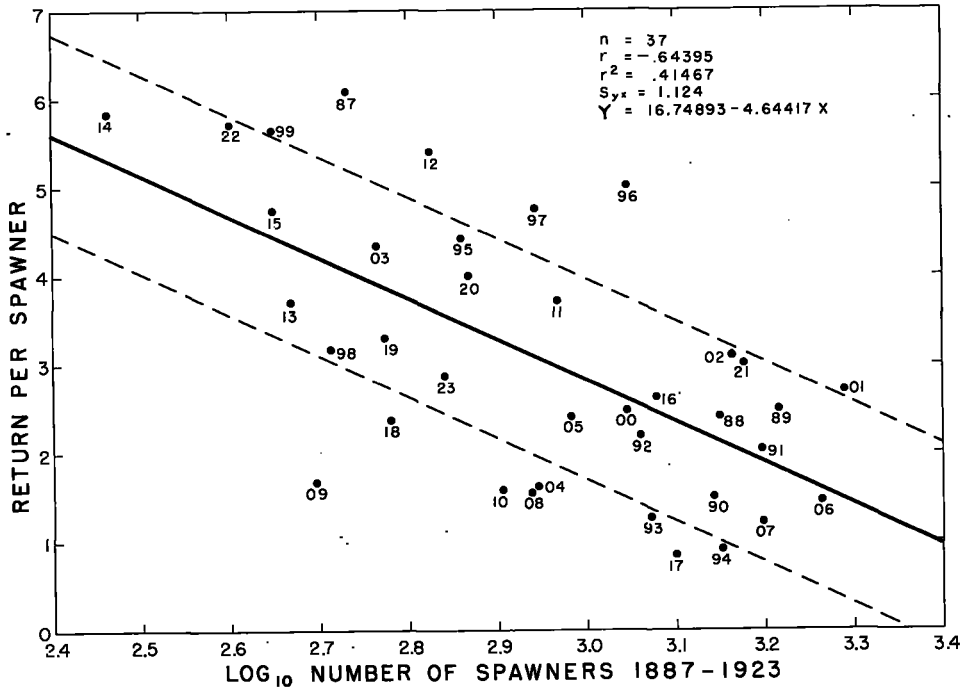

FIGURE 6.—Regression of return per spawner on log number of spawners, 1887 to 1923.

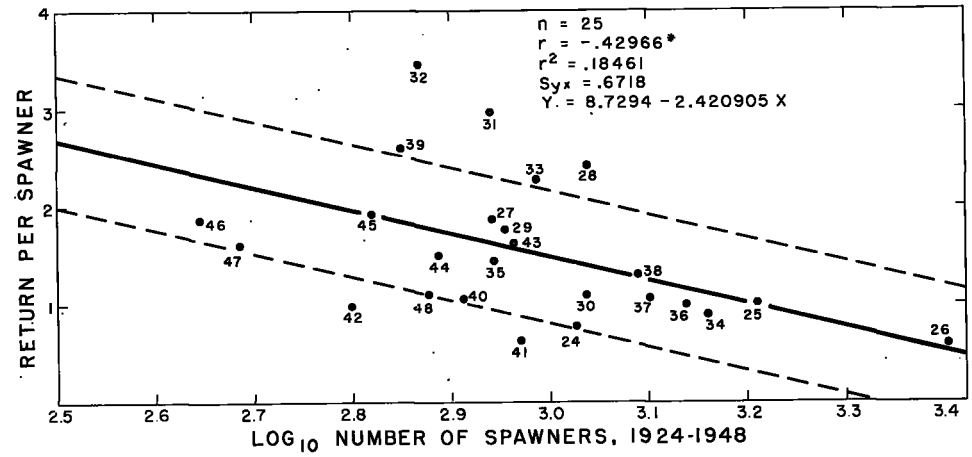

FIGURE 7.—Regression of return per spawner on log number of spawners, 1924 to 1948.

of the runs. In table 7 (column 2) the residuals are shown as "residuals plus three" as a matter of convenience to give all the residuals a positive value, obviating the inconvenience of working with plus and minus values.

In the following sections the comparison of these residuals with climatic factors is explained, and the corrections shown in columns 3, 4, 5, and 7 of table 7 are derived.

Effect of autumn temperatures on survival of eggs

There is evidence for other species of *Oncorhynchus* that there may be a relation between autumn temperatures and survival. Thus in southeastern Alaska experiments on the pink salmon (*O.*

TABLE 7.—*Residuals of return per spawner on $\log_{10}$ number of spawners corrected for ecological factors*

Year of spawning	Residuals (plus three)	Corrections to residuals for temperature factors			Residuals corrected for temperature factors	Correction for April–July rainfall (inches)	Residuals corrected for all physical factors
		October–December °F	Accumulated °F	April–May °F			
1887	5.02				5.02	−.28	4.74
1888	3.28				3.28	−.11	3.17
1889	3.67				3.67	−.49	3.18
1890	2.35				2.35		2.35
1891	3.13				3.13		3.13
1892	2.65				2.65		2.65
1893	1.79				1.79		1.79
1894	1.82				1.82		1.82
1895	3.93	0		1.23	5.16		5.16
1896	5.40				5.40		5.40
1897	4.66				4.66		4.66
1898	2.02	0		−.34	1.68	.41	2.09
1899	4.19	0		−.30	3.89	−.16	3.73
1900	2.87	.78		−.22	3.43		3.43
1901	4.23	0		−.05	4.18	.12	4.30
1902	4.03		.02	−.40	3.65	−.02	3.63
1903	3.41	0		−.33	3.08	.39	3.47
1904	1.55	0		.46	2.01	.56	2.57
1905	2.50	0		−.25	2.25		2.25
1906	2.85	0	.04	−.21	2.68	−.36	2.32
1907	2.33	.11	.51	.57	3.52	−.16	3.36
1908	1.45			.39	1.84	−.08	1.76
1909	.45	.89		1.09	2.43	−.07	2.36
1910	1.33	.42		1.17	2.92	−.31	2.61
1911	3.74	0			3.74		3.74
1912	4.77				4.77	−.23	4.54
1913	2.35	0		−.36	1.99	.12	2.11
1914	3.53	0	−.15	.22	3.60		3.60
1915	3.28	0	.58	.14	4.00	.05	4.05
1916	3.17	1.00	−.03	−.12	4.02	−.34	3.68
1917	1.51	1.13	−.15		2.49	1.14	3.63
1918	1.53		0	−.03	1.50	−.07	1.43
1919	2.41	0	.21	.61	3.23	−.10	3.13
1920	3.55	0	−.10	−.03	3.42	−.35	3.07
1921	4.01	0	−.15	.20	4.06	−.36	3.70
1922	4.04	0	−.10	−.40	3.54	.02	3.56
1923	2.31	0	−.02	.20	2.49	.73	3.22
1924	2.36	0	.73	.32	3.41	−.16	3.25
1925	3.03	0	−.15	.01	2.89	−.23	2.66
1926	3.08	0	.31	.15	3.54	.08	3.62
1927	3.24	.57	−.15	.01	3.67	−.05	3.62
1928	4.02	0	−.09	−.39	3.54	−.21	3.33
1929	3.17	0	−.13	−.18	2.86	−.36	2.50
1930	2.70	0	−.08	−.15	2.47	−.31	2.16
1931	4.33	0	.03	−.40	3.96	.10	4.06
1932	4.65	0	−.13	−.36	4.16	−.28	3.88
1933	3.95	0	−.10	−.38	3.47	−.02	3.45
1934	2.79	0	.42	−.17	3.04	.04	3.08
1935	2.83	0	−.15	−.40	2.28	.23	2.51
1936	2.85	0	.14	−.40	2.59	.29	2.88
1937	2.83	0	−.05	−.40	2.38	.79	3.17
1938	3.04	0	−.15	−.18	2.71	−.21	2.50
1939	3.75	0		.30	4.05	.19	4.24
1940	2.37	0			2.37	−.02	2.35
1941	2.07	0	0	.40	2.47		2.47
1942	2.01	.72	−.16	−.32	2.25		2.25
1943	3.06	0	−.15	.05	2.96		2.96
1944	2.74	0	−.12	.05	2.67		2.67
1945	3.01	.76	−.15	−.08	3.54		3.54
1946	2.53	.09	−.04	−.08	2.50		2.50
1947	2.38	0	0	−.22	2.16		2.16
1948	2.32	.76	−.03	.36	3.41		3.41

gorbuscha) are highly suggestive. Hanavan and Skud (1954) state concerning survival of young from known numbers of spawners:

> 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.

There is also evidence for the Columbia River chinook salmon (*O. tshawytscha*) that winter temperatures subsequent to spawning have an effect on survival as measured by ultimate returns of adult salmon (Silliman 1950). For an 11-year period he obtained a correlation coefficient of 0.337 between survival and the overall range of temperatures which compares closely with 0.363 (significant) for Karluk. Although this series of years was too short to permit detailed analysis, he suggests that the relationship should logically be curvilinear since once winters are warm enough to avoid freezing of eggs, little or no improvement can be expected from further increases in temperature.

In table 5 are presented average monthly air temperatures (see appendix I for the relation between Kodiak air temperatures and Karluk Lake water temperatures) at Kodiak for two periods of months, (1) October to December, (2) April and May. The same table also includes the accumulated monthly average degrees of temperature by 2-year periods falling between 45° and 55° F., and the average monthly precipitation in inches from April to July, inclusive, for Kodiak.

The October–December temperatures are shown in figure 9. Long-term changes in the trend are clearly evident and there appear to be short-term fluctuations also. The feature of chief interest to this study is the pronounced difference in the level of the trend during different periods of years, e. g., from 34° F. in the years close to 1913 to over 37° F. from 1924 to 1938. A difference of 3° F. during the period soon after spawning, while the eggs are still in a very sensitive stage, could have a marked effect on survival.

The regression of the residuals (of return per spawner on $\log_{10}$ number of spawners) on the October to December average temperature is given in figure 10. Over the total range of tem-

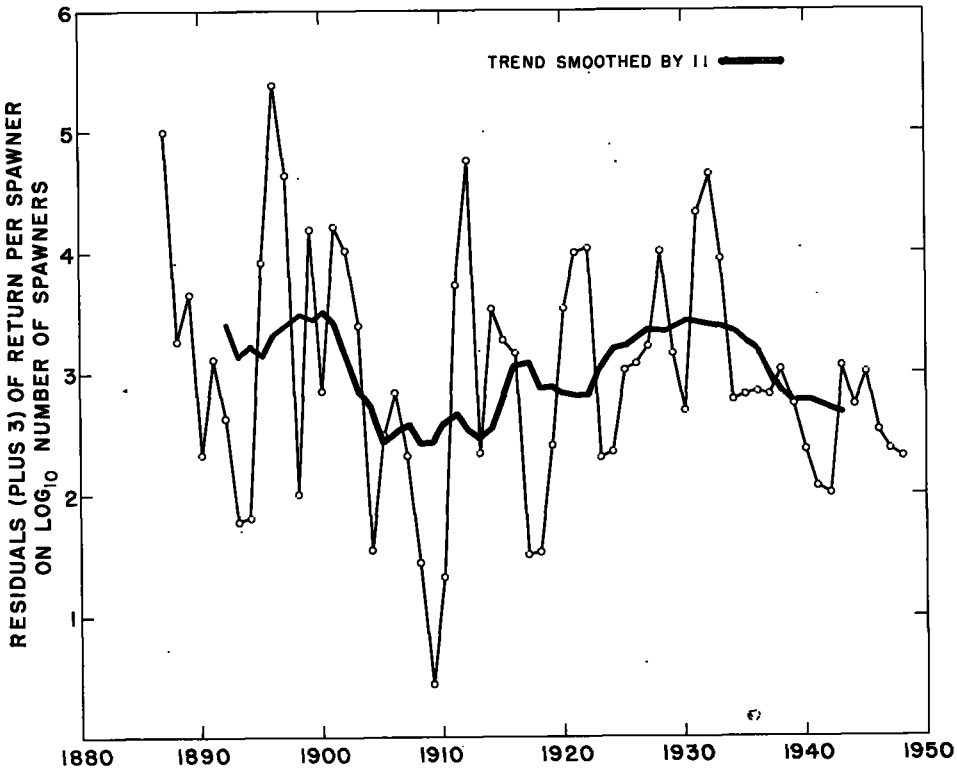

FIGURE 8.—Residuals of return per spawner on log number of spawners showing long-term trends.

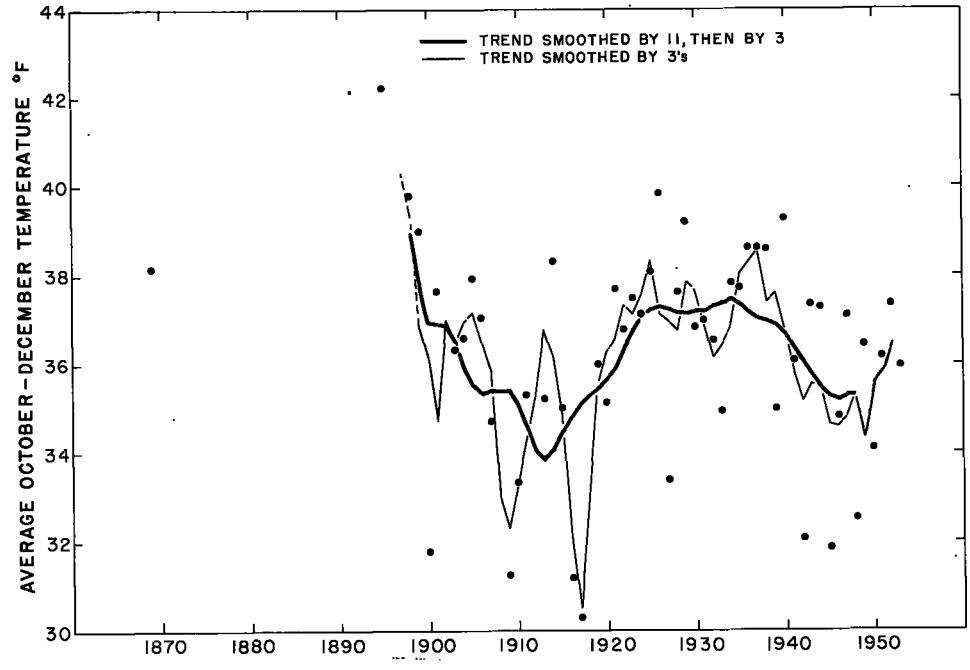

FIGURE 9.—Annual and smoothed trends of air temperature for October to December, inclusive, at Kodiak.

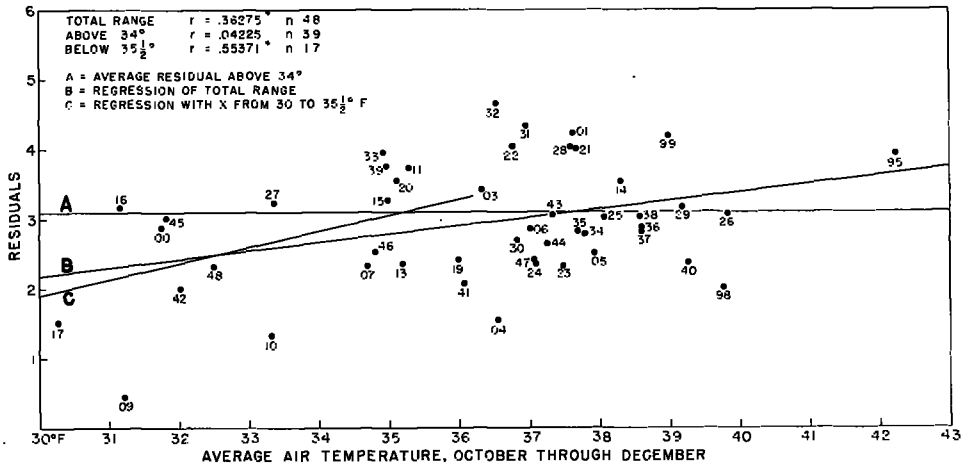

FIGURE 10.—Regression of residuals (Y) of return per spawner on log number of spawners on October–December average air temperature at Kodiak (X).

peratures the correlation is only 0.363, which, although statistically significant is rather low. Inspection of figure 10 shows, however, that this is caused by a lack of any correlation at the higher temperatures. That is, October–December temperatures are a limiting factor on survival only when they fall below a certain threshold. Thus above 34° F. the correlation is nonexistent (0.042), while from 30° to 35.5° the correlation is 0.554 and significant.

To allow for the effect of October–December temperatures the regression of the residuals (Y) on temperatures from 30 to 35.5 degrees has been plotted in figure 10 (curve C) and extended to cut curve A, which is the average of the residuals having a temperature (X) above 34° F. All residuals with an X below 35 degrees (34.9° or lower) were then corrected for autumn temperature by adding the difference between curves A and C. The net effect is that in 11 out of the 48 years with data the autumn temperatures were sufficiently low to affect survival of the eggs.

Effect of length of growing season on survival of young

The second factor considered was the effect of temperature on survival through its effect on growth of the smolts. Since the desideratum was a measure of the length of the growing season, we have employed the accumulated average monthly temperatures above 45° F., omitting for any month any excess over 55° F. As the great majority of the smolts migrate to sea in their third year (after spending two full summers in the lake) the accumulated temperatures for the two calendar years succeeding the year of spawning have been used (see table 5).

These accumulated temperatures are shown in figure 11 plotted against the residuals (corrected for the October–December temperature subsequent to spawning) for return per spawner against $\log_{10}$ number of spawners. Linear correlation throughout the range of accumulated temperatures is practically nonexistent (0.0144), but for the range of accumulated temperatures below 60° F. it is 0.385, and significant.

Obviously, y as a function of x is curvilinear. Note that the last 5 points out of 6 on the left and the last 4 points on the right fall below the average. The shape of the empirical curve shown was determined from the grouped averages.

The curvilinear correlation was determined from the deviations, z, of the individual y's from the empirical curve according to the formula:

$$\overline{P}^2_{yx}=1-\left(\frac{\sigma_z^2}{\sigma_y^2}\right)\left(\frac{n-1}{n-m}\right) \text{ Ezekiel (1930),}$$

where m was made to equal 3 on the assumption that the regression curve used could have been mathematically represented by an equation with three constants, such as a parabola.

Similarly the standard error of estimate was determined by the formula:

$$\overline{S}^2_{y\cdot f(x)}=\frac{n\sigma_z^2}{n-m}$$

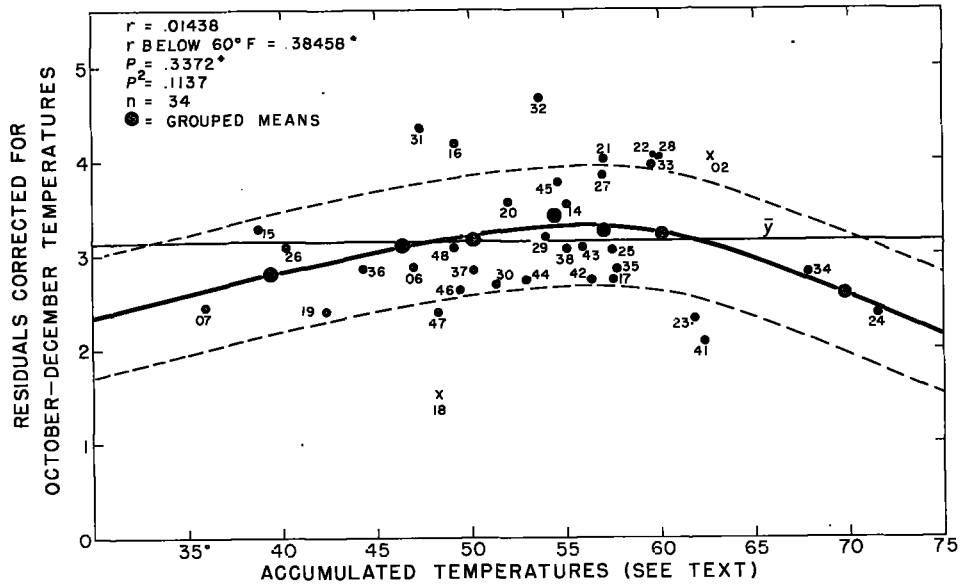

FIGURE 11.—Regression of residuals (see text) corrected for October–December temperature on the accumulated monthly temperatures between 45° and 55° F. for the two calendar years subsequent to year of spawning.

The index of correlation, P of 0.3372 has a probability of less than .05. The standard error of estimate of P is .6277.

The index of determination, P^2 is .1137, indicating that about 11 percent of the residual variation in y (variation remaining after correcting for the October–December temperatures) is associated with these accumulated temperatures.

The residuals of return per spawner on log number of spawners (corrected for the October–December temperatures) were now further corrected by adding the difference between the average Y and the fitted curve for each point. This correction eliminates the influence of the factor considered, at the same time keeping the years corrected on the same basis as those for which lack of data prevents correction for this particular factor.

Effect of spring temperatures on emergence of fry

The third factor to be considered was the spring temperature (April and May) for the year subsequent to spawning. These average temperatures are shown in figure 12 plotted against the residuals corrected as mentioned above. As with the first two factors the relationship is not linear and r is only 0.183 without significance

In the same manner as described above, P was determined to be 0.5203 with a P of less than .01. As for the other factors, the residuals were now corrected by adding the difference between the average Y and the fitted curve for each point. It is clear that the spring temperatures exert an influence on ultimate survival which we tentatively ascribe to an effect on the survival of the fry that are either emerging or about to emerge from the redds. The residuals corrected for all temperature factors are given in table 7.

Effect of rainfall on survival

In considering the possible role of precipitation it was expected that the summer rainfall might have a noticeable effect on ultimate survival through its effect on success of spawning. Figure 13 shows the residuals (corrected for the temperature factors) plotted against total rainfall from June to August. The linear coefficient of correlation is only 0.287 over the total range of rainfall, but there seems to be a tendency for the residuals to decrease with low rainfall. Below 13.5 inches of rain the coefficient of correlation increases to 0.388, but the available years are too few to establish statistical significance, as P is slightly larger than 0.05. Since definite statistical proof of a relationship could not be established no corrections for this factor were attempted.

Considering the widely held opinion that water levels during the spawning period are important to success of reproduction, the lack of correlation in these data is a little surprising. However, the lack of correlation may not be due to the lack

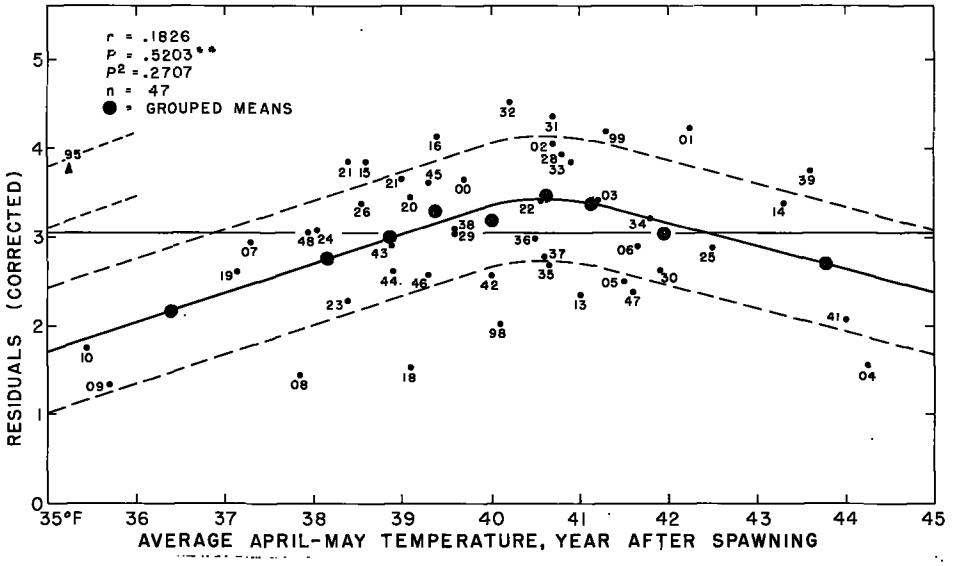

FIGURE 12.—Regression of corrected residuals on the average April–May air temperature at Kodiak.

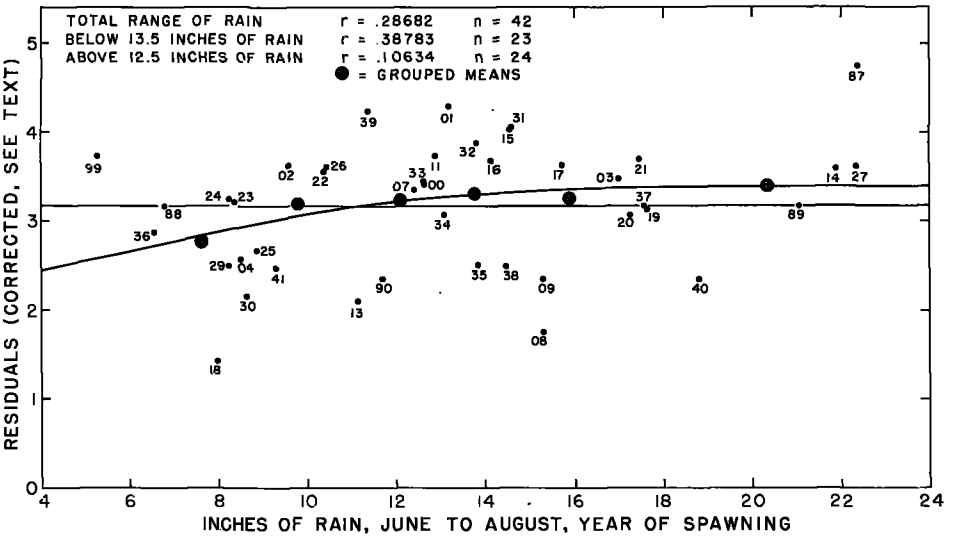

FIGURE 13.—Regression of corrected residuals on the total rainfall from June to August, inclusive, at Kodiak.

of effect of water levels on survival; rather, the lack of any significant correlation may be ascribed to the lack of a sufficiently accurate measure of rainfall at Karluk. In country as mountainous as Kodiak Island, with a high mountain barrier between the observation point at Kodiak and the point of reference, Karluk Lake, the Kodiak rainfall may not be sufficiently representative of Karluk rainfall.

That waterlevels during the spawning period can have a very marked effect on sockeye survival is indicated by the relationship between rainfall and spawning on the Skeena River (Brett 1951). An explanation of these Skeena River data is given in appendix E.

A relation was discovered between the residuals and the rainfall in spring and early summer of the year following spawning. Such a relationship has a logical explanation for this is the period during which the fry from the spawning of the previous autumn would normally be emerging from the redds, and dry streambeds, or floods, would certainly decrease their survival. As before, the correlation was not high, but this may also be related to the fact that the rainfall data may not be truly representative of actual precipitation.

The relation is shown graphically in figure 14. As is quite usual with this type of data linear correlation over the total range of rainfall in nonexistent, r is 0.039. However, below 16 inches of rainfall the correlation is 0.535 and significant. Above 15 inches of rain the correlation of −0.309 is not quite statistically significant. A slight minus correlation with higher rainfall would be a logical consequence as the emerging fry would be damaged by floods. Unfortunately, the data in hand for monthly rainfall at Kodiak do not reveal flood conditions at Karluk. The index of correlation for the empirical curves formed by joining the linear curves for the two segments of the range is 0.316 and significant.

The corrections for the residuals and the corrected residuals are given in table 7, and table 8 shows the return per spawner corrected for all the available physical factors.

TABLE 8.—*Return per spawner corrected for physcial factors*

Year	Corrected return per spawner	Number of factors corrected	Year	Corrected return per spawner	Number of factors corrected
1887	5.81	1	1918	2.26	3
1888	2.28	1	1919	4.00	4
1889	1.98	1	1920	3.50	4
1890	1.49		1921	2.69	4
1891	2.02		1922	5.23	4
1892	2.18		1923	3.77	4
1893	1.25		1924	1.65	4
1894	.90		1925	.62	4
1895	5.64	2	1926	1.12	4
1896	5.01		1927	2.24	4
1897	4.75		1928	1.71	4
1898	3.22	3	1929	1.09	4
1899	5.18	3	1930	.54	4
1900	3.02	2	1931	2.68	4
1901	2.76	3	1932	2.67	4
1902	2.72	3	1933	1.76	4
1903	4.38	3	1934	1.16	4
1904	2.63	3	1935	1.11	4
1905	2.14	2	1936	1.01	4
1906	.91	4	1937	1.39	4
1907	2.24	4	1938	.75	4
1908	1.85	2	1939	3.08	3
1909	3.58	3	1940	1.03	2
1910	2.86	3	1941	1.02	3
1911	3.70	1	1942	1.21	3
1912	5.17	1	1943	1.52	3
1913	3.45	3	1944	1.41	3
1914	5.91	3	1945	2.45	3
1915	5.50	4	1946	1.83	3
1916	3.12	4	1947	1.38	3
1917	2.96	3	1948	2.17	3

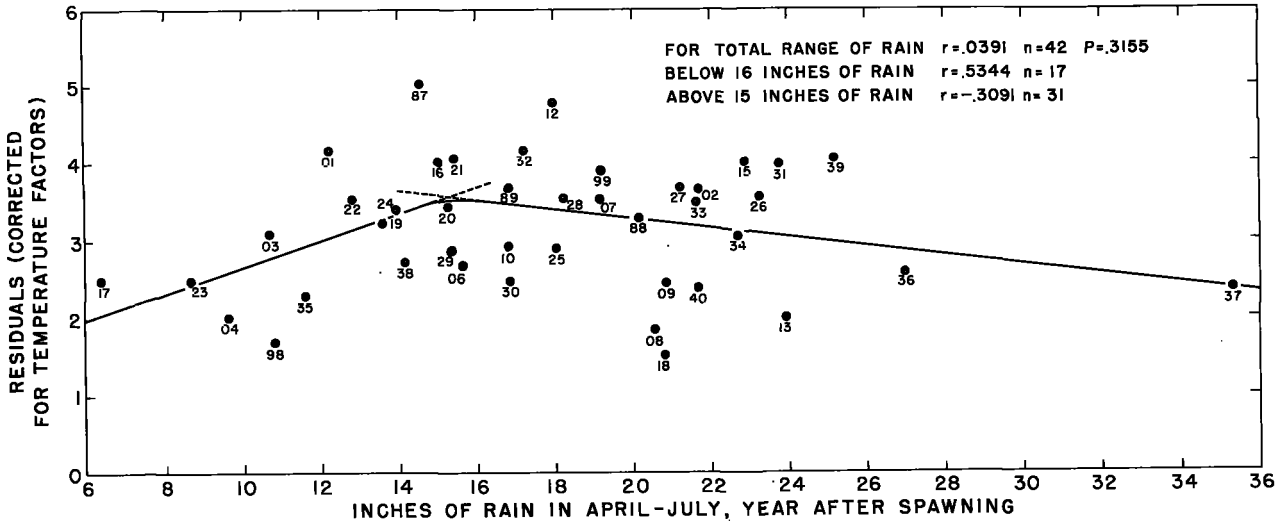

FIGURE 14.—Regression of corrected residuals on the total rainfall from April to July, inclusive, at Kodiak in the year subsequent to spawning.

SOCKEYE ABUNDANCE IN THE ODD- AND EVEN-NUMBERED YEARS

It has long been conceded that the runs of pink salmon to the Karluk River can be detrimental to successful reproduction of the sockeye. It has been generally held that this detrimental effect is confined to the occasional year when the predominant even-year population of pink salmon reaches a peak so that large numbers overflow from their normal spawning beds in the main river below the lake. Entering the lake they then ascend the tributary streams and compete with the sockeye for the limited spawning gravels.

Such a straightforward explanation while having the merit of simplicity does not explain all the facts. If we first examine the records for the pink salmon, we find that for some unaccountable reason the even-year population has maintained its dominance since the earliest available records. Tremendous numbers of pink salmon are recorded at Karluk in 1880 by Bean (1891) and in 1890 by Moser (1899); both of which are even years. The

catches since 1908 in area 8 at the mouth of the Karluk (available through 1935) and the weir counts are shown in table 9.

TABLE 9.—*Catches of pink salmon at mouth of Karluk River (Area 8) and weir counts of pinks*

[In thousands]

Even years	Catches	Weir counts	Odd years	Catches	Weir counts
1908	233		1909		
1910	105		1911	9	
1912	293		1913	12	
1914	1,287		1915	13	
1916	2,319		1917	1	
1918	336		1919	6	
1920	635		1921		
1922	894		1923	10	
1924	2,483	[1] 4,000	1925	6	
1926	86	15	1927	3	
1928	18	5	1929		12
1930	1	116	1931	140	43
1932	1,388	1,440	1933	32	108
1934	1,048	1,002	1935	7	6
1936	?	526	1937	?	6
1938		1,715	1939		32
1940		957	1941		133
1942		[2] 107	1943		[2] 0.2
1944		193	1945		[3] 16
1946		[3] 83	1947		0.05
1948		41	1949		0.05
1950		87	1951		0.04
1952		37	1953		0.1

[1] Estimated.
[2] Weir moved from river mouth upstream to Portage near head of Larsen Bay.
[3] Weir moved to outlet of Karluk Lake.

The most striking feature shown by these data is the ability of the even-year pink runs to recover after overpopulation (as in 1924) has decimated them. The odd-year runs, on the other hand, have never been able to achieve dominance. From table 9 we have constructed figure 15, which shows for the odd years from 1929 to 1943 (before the counting weir was moved to the lake outlet) the number of pink salmon returning per spawner plotted against the number of pinks spawning in the preceding (even) year. There is some suggestion that the return per spawner in an odd year is inversely related to the number of pinks spawning in the preceding even year. The explanation is not contained in the data; we can only surmise concerning the relationship.

If the relationship is due to predator activity it is necessary to postulate a predator having both a high reproductive potential and a short life history. One might also speculate on the possibility of contamination of the spawning beds by some etiological agent that would destroy most of the eggs or fry of the year following a big year spawning.

Neave (1952) in attempting to explain this odd- and even-year disparity says:

> Attention was especially directed to the probable effect of predators during the migration of salmon fry to the sea, in inflicting relatively heavier losses on smaller populations. When a population exceeds or falls below certain limits of size it is likely to be subject to influences which tend to maintain the direction of change or at least to oppose a return to the former level.

His explanation is too simple in that it cannot explain the quick rise of the even-year cycle to abundance after falling below the odd year in numbers.

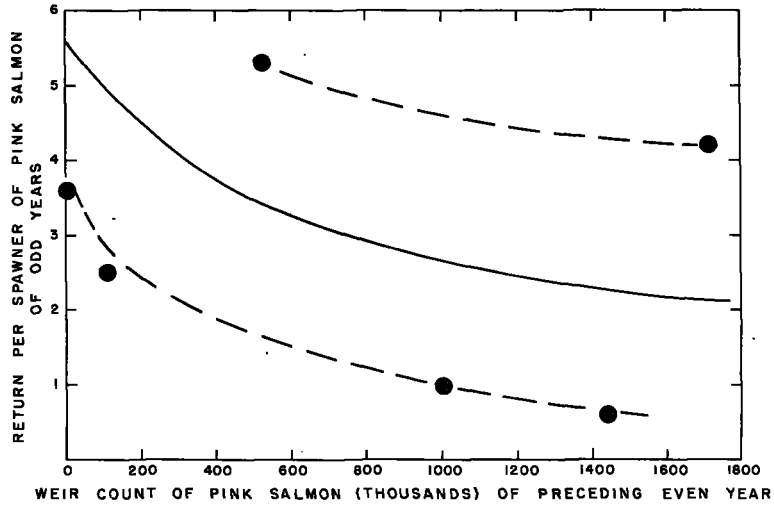

FIGURE 15.—Apparent relation between the return per spawner for pink salmon of odd-numbered years and the weir count of pink salmon of each preceding even-numbered year.

However, it is beyond the scope of this paper to inquire into the many factors that may operate to maintain the dominance of one pink salmon population (in this case the population spawning on the even-numbered years) over another. The chief purpose of this digression has been to show that this phenomenon has existed at Karluk as far back as our records go. Thus we may, with considerable confidence, assume that the even-year pink runs exceeded those of the odd years during those periods in which we lack data on pink-salmon abundance.

Regardless of the cause of the even-year dominance in the pink salmon it is possible to decide whether it has a significant effect on the survival of sockeye. In table 10 are shown the numbers of sockeye (corrected for the four physical factors already discussed) that returned from the spawning escapements of the 60 years from 1889 to 1948, inclusive.

An analysis of variance is as follows:

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	59	764,331.184		
Odd and even	1	16,968.017	16,968.017	5.724*
Cycle years	4	128,433.6	32,108.4	10.831**
10-year periods	5	473,664.884	94,732.977	
Within cycle years (error)	49	145,264.683	2,964.585	

TABLE 10.—*Returns corrected for physical factors*
[In ten thousands]

First year of spawning in 5-year cycle	Year of cycle										5-year cycle	10-year period	
	1		2		3		4		5			Odd	Even
	Odd	Even	Odd	Even	Odd	Even	Odd	Even	Odd	Even			
1889	326			207	318			252	148		1,251		
1894		128	408			559	418			167	1,680		
Sums	454		615		877		670		315		2,931	1,618	1,313
1899	232			337	539			398	251		1,757		
1904		232	206			167	354			160	1,119		
Sums	464		543		706		752		411		2,876	1,582	1,294
1909	178			230	343			346	161		1,258		
1914		172	245			375	374			136	1,302		
Sums	350		475		718		720		297		2,560	1,301	1,259
1919	238			258	404			209	262		1,371		
1924		175	100			284	195			187	941		
Sums	413		358		688		404		449		2,312	1,199	1,113
1929	98			59	234			197	170		758		
1934		168	97			139	176			92	672		
Sums	266		156		373		373		262		1,430	775	665
1939	217			84	95			76	140		612		
1944		108	162			81	67			164	582		
Sums	325		246		176		143		304		1,194	681	513
Odd and even sums	1,289	983	1,218	1,175	1,933	1,605	1,584	1,478	1,132	906			
Sum of cycles	2,272		2,393		3,538		3,062		2,038		13,303		
Sums of 10-year periods											13,303	7,156	6,147
10-year averages											221.717	238.53	204.9

$\frac{221.717}{238.53} = .929514$

$\frac{221.717}{204.9} = 1.082074$

This shows that the returns in the odd years are significantly higher than in the even years. Furthermore, this difference does not occur in haphazard fashion. The odd-year returns are higher than the even-year returns in each of the six 10-year periods and also within each of the 5 cycle years. In figure 16 the logarithms of the subtotals for odd- and even-year returns are shown both for 10-year periods and for cycle years (from table 10). This shows no particular trend but rather that the difference is quite consistent.

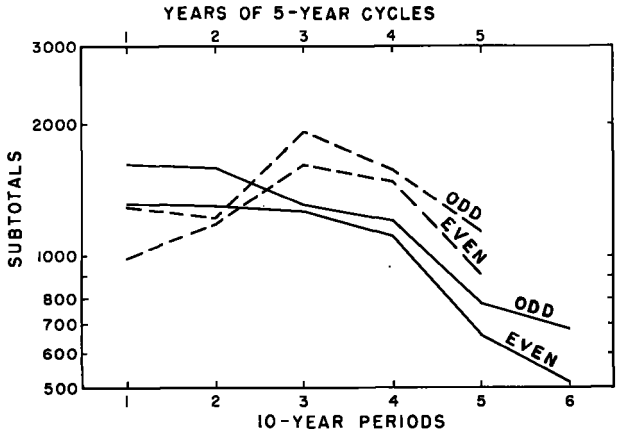

FIGURE 16.—Logarithms of the subtotals for odd- and even-year pink salmon returns for both 5-year cycles (broken line) and for 10-year periods.

Because the logarithmic differences between odd and even years are both consistent and fairly constant, the returns shown in table 10 have been corrected to equalize the difference by multiplying the even years by the factor 1.082074, or 221.717/204.9 and the odd years by the factor 0.929514 or 221.717/238.53. The corrected returns are given in table 11.

The chief manner in which the even-year pink salmon runs may affect the even-year sockeye runs is through direct competition for spawning space. Since the pinks spawn later than most of the sockeye they can destroy many of the sockeye redds in years in which large numbers of pinks reach the lake. How often does this occur? From the records of field parties visiting the lake in various years this would appear to happen only on even years when pinks are especially numerous. Thus in 1924 when the escapement of pink salmon to the river was estimated at 4 million, it is estimated by Gilbert and Rich (1927) that one-fourth to one-third of this number entered the lake. However, in 1932 when the weir count showed 1,440,000 pinks, J. T. Barnaby (field

TABLE 11.—*Returns corrected for physical factors and for odd- and even-numbered years*

[In thousands]

Year of spawning	Returns	Returns per spawner	Log return per spawner (+ 1.0)	Residuals of log return vs. spawners (× 10)	Year of spawning	Returns	Returns per spawner	Log return per spawner (+ 1.0)	Residuals of log return vs. spawners (× 10)
1887	2,921	5.40	1.732	.72	1918	1,475	2.45	1.389	−1.89
1888	3,496	2.47	1.393	.85	1919	2,212	3.72	1.571	.11
1889	3,029	1.84	1.265	.37	1920	2,795	3.79	1.579	.45
1890	2,238	1.61	1.207	−1.08	1921	3,751	2.50	1.398	1.19
1891	2,961	1.88	1.274	.24	1922	2,264	5.66	1.753	1.05
1892	2,721	2.36	1.373	−.21	1923	2,435	3.50	1.544	−.04
1893	1,380	1.17	1.068	−3.14	1924	1,898	1.79	1.253	−1.72
1894	1,382	.97	.987	−3.16	1925	934	.58	.763	−4.74
1895	3,795	5.24	1.719	1.80	1926	3,071	1.21	1.083	1.53
1896	6,044	5.42	1.734	3.06	1927	1,815	2.08	1.318	−1.70
1897	3,883	4.41	1.644	1.58	1928	2,025	1.85	1.267	−1.47
1898	1,811	3.48	1.542	−.68	1929	913	1.01	1.004	−1.51
1899	2,152	4.81	1.682	.50	1930	635	.58	.763	−3.26
1900	3,650	3.27	1.515	1.10	1931	2,175	2.49	1.396	2.36
1901	5,013	2.57	1.410	2.85	1932	2,132	2.89	1.461	2.57
1902	4,303	2.94	1.468	1.78	1933	1,584	1.64	1.215	.85
1903	2,333	4.07	1.610	.22	1934	1,820	1.26	1.100	.42
1904	2,513	2.85	1.455	−.30	1935	903	1.03	1.013	−1.47
1905	1,916	1.99	1.299	−1.60	1936	1,503	1.09	1.037	.42
1906	1,810	.98	.991	−1.73	1937	1,634	1.29	1.111	.98
1907	3,286	2.08	1.318	.66	1938	999	.81	.908	1.34
1908	1,733	2.00	1.301	−1.74	1939	2,021	2.86	1.456	2.40
1909	1,657	3.33	1.522	−.96	1940	909	1.11	1.045	−1.35
1910	2,488	3.09	1.490	−.24	1941	884	.95	.978	−1.64
1911	3,192	3.44	1.537	.66	1942	823	1.31	1.117	−1.26
1912	3,748	5.59	1.747	1.91	1943	1,301	1.41	1.149	.14
1913	1,497	3.21	1.507	−1.22	1944	1,173	1.53	1.185	.06
1914	1,861	6.40	1.806	1.20	1945	1,501	2.28	1.358	1.26
1915	2,280	5.11	1.708	.77	1946	875	1.98	1.297	−.08
1916	4,058	3.38	1.529	1.51	1947	622	1.28	1.107	−1.83
1917	3,480	2.75	1.439	.83	1948	1,770	2.35	1.371	1.70

notes) observed "not over 100 pinks" on the spawning streams entering Karluk Lake.

This evidence from examination of the spawning streams is difficult to evaluate for two reasons. First, because the field parties attempted to visit the lake during the height of the sockeye spawning, and thus may sometimes have missed the pink salmon that arrived later. Secondly, after the weir was moved from downriver to the lake outlet in 1945 some pinks have passed through in every season, varying from less than a hundred to 16,000 in odd years and from 37,000 to 87,000 in even years.

It is our guess that a larger and more constant fraction of the pink salmon population enters the lake each year than was formerly supposed. This helps to explain the consistency with which the odd year sockeye returns exceed those of the even years.

It is probable that this reflection of the pink salmon cycle in the returns from sockeyes spawning the same season also may indicate that a larger proportion of the sockeyes spawn in the main river below Karluk Lake than available records would indicate (see appendix L).

TYPE OF REPRODUCTION CURVE

In order to study the changes in the sockeye population it is desirable to understand the manner in which the size of the population changes. Many of the theoretical considerations are rather fully discussed by Ricker (1954). Under conditions in which there are definite spatial limitations he suggests a domed reproduction curve. If we let x equal number of spawners, and y equal the number of adult salmon returning, his formula is:

$$y=xe^{1-x} \text{ or } \log y=\log x+(1-x).$$

His method of fitting by trial and error is too cumbersome, however. We have used a linear least square fit. The formula is:

$$\log y/x=a-bx \text{ or } \log y=(a-bx)+\log x$$

which is equivalent to his formula as it can be expressed as

$$y=xe^{a-bx}.$$

The regression of the $\log_{10}$ return per spawner (from table 11) on number of spawners,

$$\log y/x=a-bx$$

is shown in figures 17 and 18. The data were broken into two periods 1887–1928 and 1929–1948

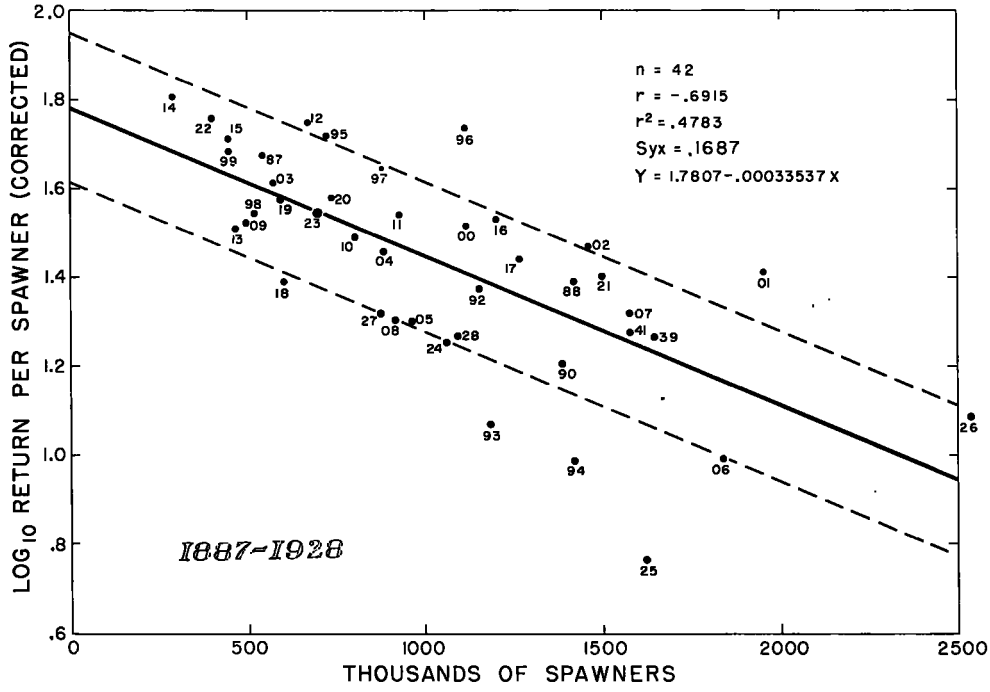

FIGURE 17.—Regression of log return per spawner (corrected for physical environment and for odd and even years) on number of spawners for 1887 to 1928 period.

as there is a definite break after 1928. It will be noted that the two slope coefficients, b, are very similar, 0.0003354 and 0.0003347, also, the standard errors of estimate 0.1687 and 0.1696.

This means that the two reproduction curves are practically identical, except for the level of reproduction. This is shown in figures 19 and 20. In figure 19 is also shown the curve resulting from the linear fit of the return per spawner on log number of spawners:

$$y/x=a-b \log x \text{ or } y=(a-b \log x)x$$

which is equivalent to $\log y=xe^{a-b \log x}$. This curve gives a slightly better fit to the data, r is $-.752$ whereas for the other curve r is $-.692$. However, the second curve eventually cuts the

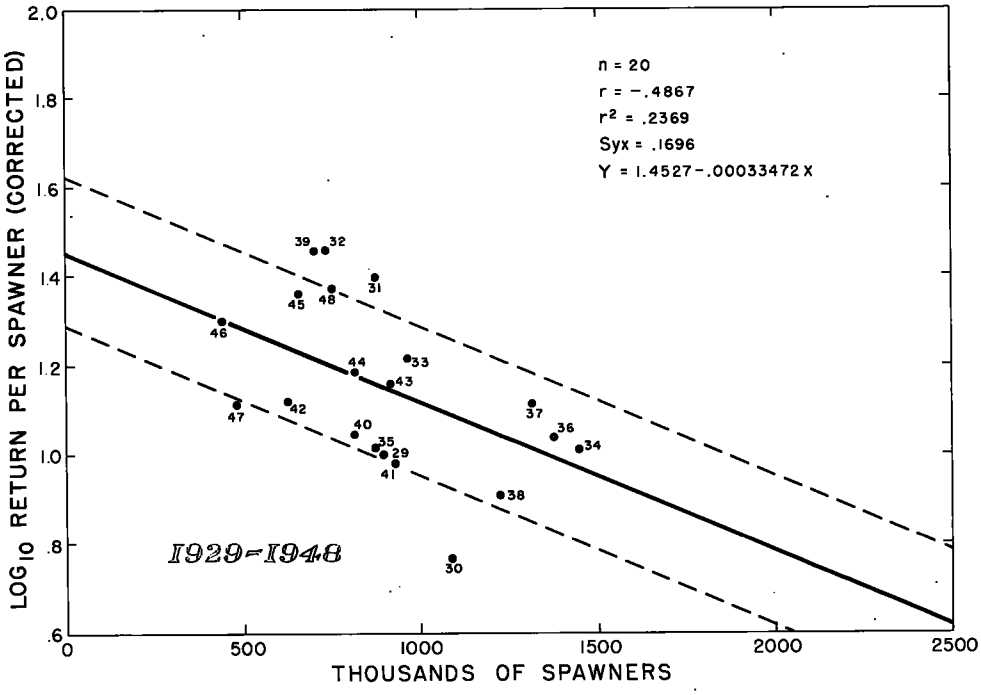

FIGURE 18.—Regression of log return per spawner (corrected for physical environment and for odd and even years) on number of spawners for 1929–48 period.

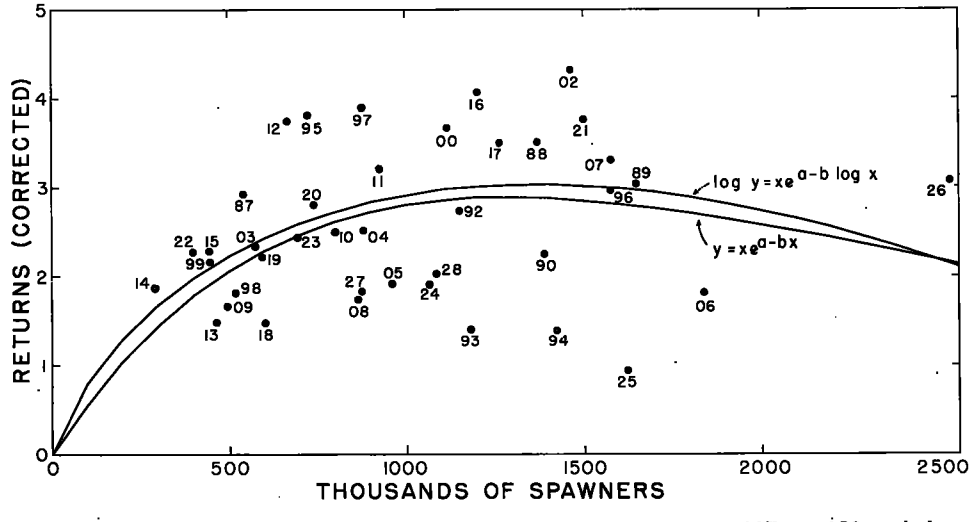

FIGURE 19.—Returns (corrected) on number of spawners for the 1887 to 1928 period.

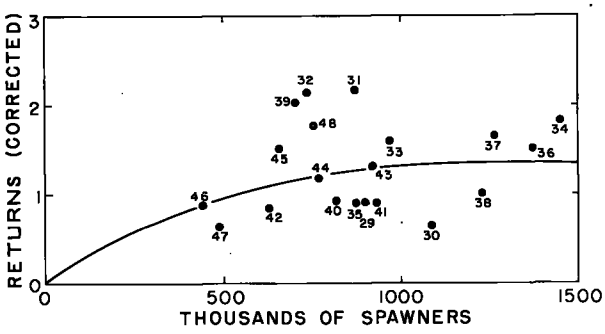

FIGURE 20.—Returns (corrected) on number of spawners for the 1929 to 1948 period.

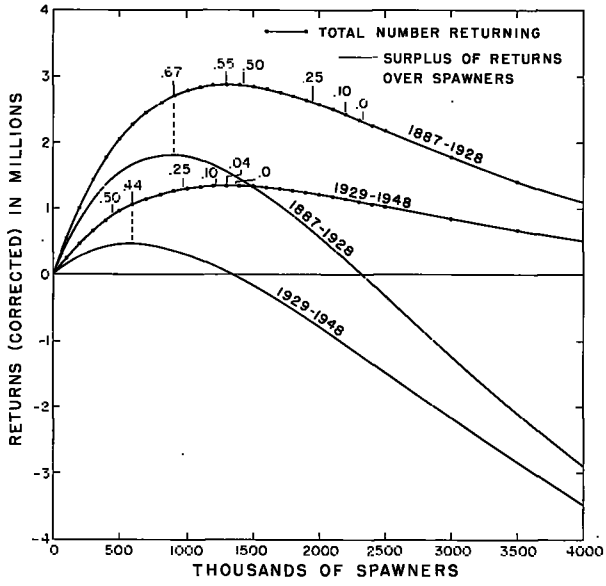

FIGURE 21.—Reproduction curves (corrected for physical factors and for odd and even years) showing the returns for various numbers of spawners, and also the surplus of returns over number of spawners.

base line, which the first curve approaches asymptotically. From this standpoint the first curve is probably more realistic.

MEANING OF REPRODUCTION CURVES

The reproduction curves for the period 1887–1928 and for the more recent 20-year period from 1929–48 are shown in figure 21 together with the resulting surpluses of returns over number of spawners. It will be noted that for the earlier period the returns were approximately double those of the later period for an equivalent number of spawners. However, this caused a tremendous difference in the available surplus.

During the early period the highest surplus, 1,811,000 occurred with 900,000 spawners, whereas during the later period the highest surplus, 472,000 occurred with 600,000 spawners. The average number of spawners was 1,037,000 in the earlier years and 894,000 in the later.

On the curves in figure 21 are indicated the equilibrium points for various rates of removal by the fishery of the returning adults. For the earlier years the largest returns occurred at a removal rate of .55 and the largest available surplus (on a continuing basis) occurred at a rate of .67. By way of contrast the same points for the later years occurred at rates of .04 and .44.

Owing to the varying effect of the various environmental factors the abundance would, of course, fluctuate about these points. However, in general, the average abundance in the earlier period, in the absence of any fishery, would have been about 2,320,000. As the fishery developed the number of spawners would be decreased and the population would ascend the right limb of the reproduction curve, resulting in larger runs. That this bears some relation to reality is shown by the stability of the runs during the first three cycles of the fully developed fishery as follows:

Years	*Returns (table 6)*
1887–91	15, 986, 000
1892–96	14, 051, 000
1897–01	16, 339, 000

The paramount question is what caused the long-term decline in the runs. Certainly the decline was not due to lack of a sufficient number of spawners. However, as will be shown later, the spawners have not been drawn equally from all parts of the run. This has meant that although 50 percent of the number in each migration have been permitted to spawn, the reproductive potential of the 50 percent allowed to spawn was less than 50 percent of the reproductive potential in the original migration. Thus, although there has not been overfishing in the usually accepted sense of taking too many fish, it appears likely that there may have been overfishing by taking too high a proportion of the fish with the highest reproductive potential.

The long-term decline cannot be ascribed to the effects of those changes in temperature and rainfall or in pink salmon abundance, which we have discounted through the removal of most of their effects.

There is one peculiarity of the sockeye population at Karluk that has not been adequately explained, namely, the 5-year "cycles" in the size of the run. For many years these cycles were both persistent and consistent but in the late 1920's the "dominant" years of the past (the 1891 and 1892 cycles) lost their dominance; in fact, the 5-year cycles became rather obscure. This can be seen in figure 22 which shows the ratio of each year's return to the moving 5-year average.

In 10 successive cycle years the 1891 and 1892 cycles each fell below the 5-year trend once during the early years of the fishery. The lowest cycle for abundance was that of 1894 which fell well below the trend for 8 successive cycle years.

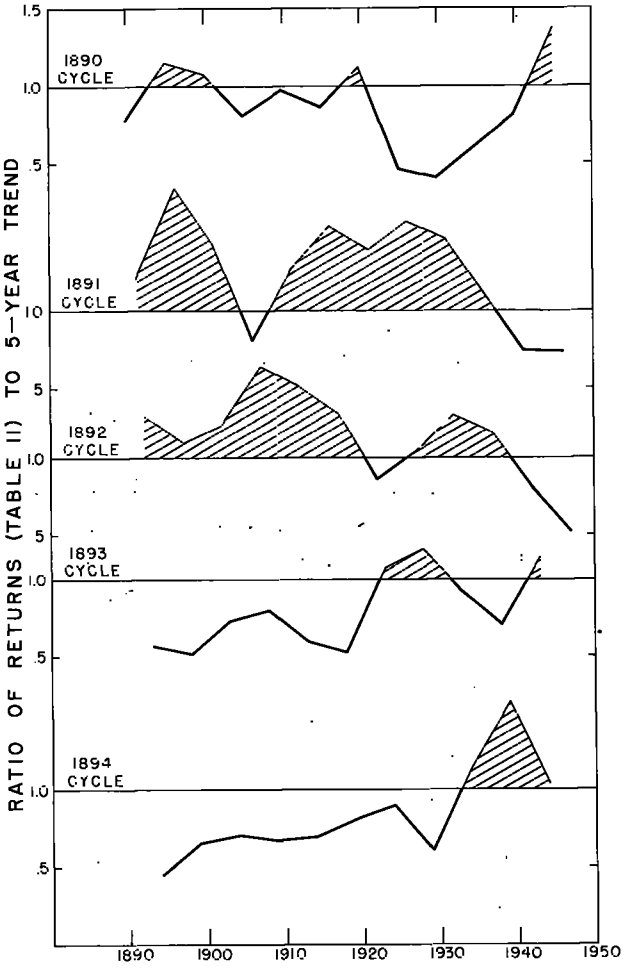

FIGURE 22.—Ratio of each year's returns to that of a 5-year moving average of returns by 5-year cycles commencing in 1890, 1891, 1892, 1893, and 1894.

These cycles have not gone unnoticed in the past. Gilbert and Rich (1927) state:

> Since the Karluk salmon are predominately five-year fish, we anticipate a correlation between the run of any year and that of the fifth year preceding, the fifth year following, etc. With the exception of one of the six cycles, it is apparent from the graph that the Karluk runs consist of two good years followed by three poor years—the good years are those ending in the figures 1, 2, 6, and 7, and the poor years end in the figures 3, 4, 5, 8, 9, and 0.
>
> No one can examine such a series of data without being impressed by the conspicuous correlation between the size of the catch in the corresponding years of the several cycles. There is a remarkably uniform tendency in each cycle, as shown on the graph, for the catch of the second year to be smaller than that of the first, for that of the third to be smaller than that of the second, for the catch of the fourth year to be about the same as that of the third, and for that of the fifth year to be greater than that of the fourth. If it can safely be assumed that spawning escapements are in the main roughly proportional to the catch, it becomes apparent that they are the predominating factor in determining the size of the runs.

Barnaby (1944) states:

> It can be concluded from the fact that a statistically significant correlation of over 0.6 exists between the catches at 5-year intervals and that no statistically significant correlation exists between the catches at 4-year or 6-year intervals that the runs of Karluk red salmon from 1895 to 1921, inclusive, were composed largely of 5-year fish.

As a result of the force of logic, that 5-year cycles should be expected from fish that mature chiefly at 5 years of age (and die after spawning), this view that the cycles are the result of age composition has been rather generally accepted, and until recently has gone largely unchallenged. It will be especially noted that this cyclic effect, if dependent on number of spawners, must postulate equal returns per spawner for all sizes of spawning escapements. That this is not true is clear from figure 21. The return per spawner continually declines as the number of spawners increases. The same phenomenon is apparent in the sockeye runs to the Fraser River (Rounsefell 1949, fig. 4).

The view that age alone could not account for cycle dominance is discussed at length by Ricker (1950). He states concerning the Fraser:

> The old big cycle had persisted through many decades of the historical period and for an undetermined period previously. Right up to the time it was accidentally destroyed it showed no signs of diminishing its domination of the river. This fact at once suggests that the big cycle somehow was acting unfavorably upon the off cycles, and actually prevented them from becoming numerous.

The equilibrium points for several rates of exploitation are shown in figure 21. Under any constant rate of fishing, regardless of the number of spawners one commences with, the number returning in successive generations will move toward these equilibrium points. It becomes obvious then, that the continued existence of dominant cycle years must depend upon some density-dependent reaction between the various years, whereby the big years tend to keep down the small years, and vice versa.

Gilbert and Rich (1927) state:

> With the present requirement of a minimum escapement of 1,000,000 fish, which has been in force since 1925, it is hoped that the level of productivity may once again be raised, but it will not be until the season of 1930 that the catch will be affected by the regulation.

The attempt to raise the size of the returns, especially in the off years, by requiring a minimum escapement (this was in addition to the requirement of a 50-percent escapement) did not bring forth the hoped-for results. It did soon destroy the dominance of the former "big" years, but without a concomitant increase in the runs.

We have attempted to explore this relation between years as it affects the returns from each year by examining the data for density-dependent relations between brood years.

The residuals of $\log_{10}$ returns per spawner (from table 11) against number of spawners are shown in table 11, column 5. These residuals are plotted in figure 23 against $\log_{10}$ ratio of the corrected returns for each year (from table 11) divided by the average observed return for the second and third preceding year. The observed returns (by freshwater age) of sockeye that would have been in the lake in their third and fourth year of life (from table A5 of Appendix C) are used as a measure of the density of 3- and 4-year-old young sockeye in the lake during the season that the fry of the year in question are emerging from

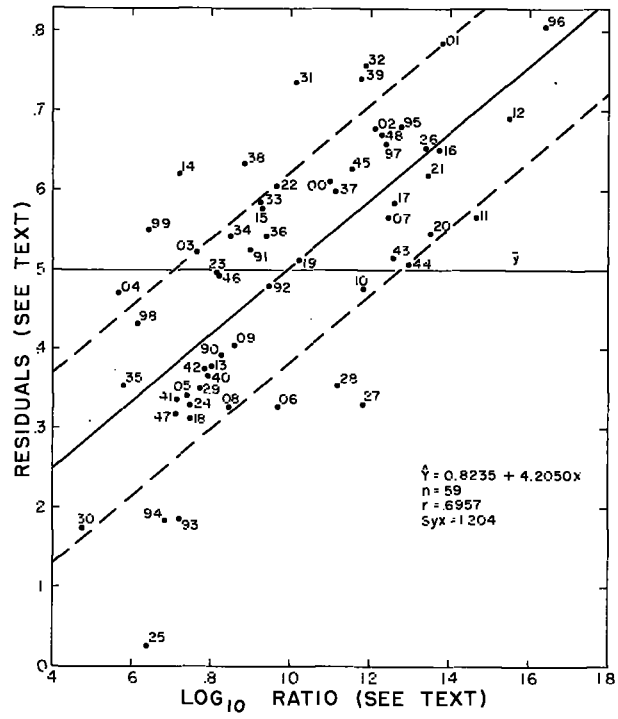

FIGURE 23.—Residuals (corrected, see text) of log return per spawner on number of spawners plotted against the logarithm of the ratio of each brood's returns to that of the average returns for the second and third preceding years.

the gravels of the tributary streams and of the lake itself. The relationship is close; r is .70.

This indicates that for any particular number of spawners the expected return per spawner is increased or decreased, according to the relative density of 3- and 4-year-old sockeye in the lake.

Although lacking the data to prove the actual existence of this phenomenon, Ricker (1950) hints that such a relation is indicated by the persistent dominance of particular cycles in the Fraser River sockeye. He states:

> Although the great bulk of sockeye food is plankton, there is a good possibility that these older sockeye, particularly after they have lived for two growing seasons, can consume young sockeye fry of later cycles. This has not yet been observed, but residual sockeye of 2 years of age have been found to eat young fish of other species, so there is little reason to doubt that they can consume sockeye fry.

Residual sockeye are known to occur in Karluk Lake. Ricker (1940) states,

> . . . J. T. Barnaby has informed the writer that, in the course of his investigations of Karluk Lake, Kodiak Island, Alaska, he has obtained three specimens of residual sock-

eye. It should be noticed, however, that before gill-nets were used in 1932, their existence in Cultus Lake was not suspected; and since very few sockeye lakes have been explored in this manner, it may even be that they occur naturally wherever there is an anadromous stock.

The young sockeye migrating from Karluk Lake average very much larger, and older, than those of Cultus Lake (fig. A4), so there is an even greater probability that the older groups of young consume large quantities of the fry. The existence of such a relationship may help to explain how the dominant cycle year can occasionally fall very low (the returns from the year class of 1906, table 6), yet rapidly regain its ascendancy, since the young from such a poor dominant cycle year as 1906 are not exposed to the same high density of older sockeye as are the low cycle years. Similarly, even when environmental conditions allow a fair return from one of the low cycle years it is pushed down again in the succeeding cycle when the young are again exposed to high density of older young.

It will be noted that this relationship can explain the apparent 5-year periodicity in the runs. The cause of the periodicity is not the 5-year age of maturity (based on a positive regression), but the lake density of young sockeye (based on a negative regression). This negative regression being for conditions 2½ years previous (effect of 3 and 4 year olds on 1 year olds) would, of course, cause an apparent positive 5-year cycle.

The residuals of the $\log_{10}$ return per spawner against log ratio of returns to the average observed return for 2 and 3 years before were corrected for this negative regression. The corrected log return per spawner is in table 12, column 2. The regressions of the corrected log return per spawner on number of spawners appear in figures 24 and 25, and the regression of total corrected returns on number of spawners appears in figure 26.

The effect of removal of the variability caused by lake density of the older young sockeye can be seen by comparing figures 21 and 26. The steeper slope of the right limb of the earlier return curve of figure 26 indicates that during the earlier years the large returns from large numbers of spawners were aided by the presence of cycles whereby the fry of the "dominant" cycle years encountered a lower density of older young in the lake.

With this effect of lake density removed the earlier years would have produced the highest returns with less than 1,100,000 spawners instead

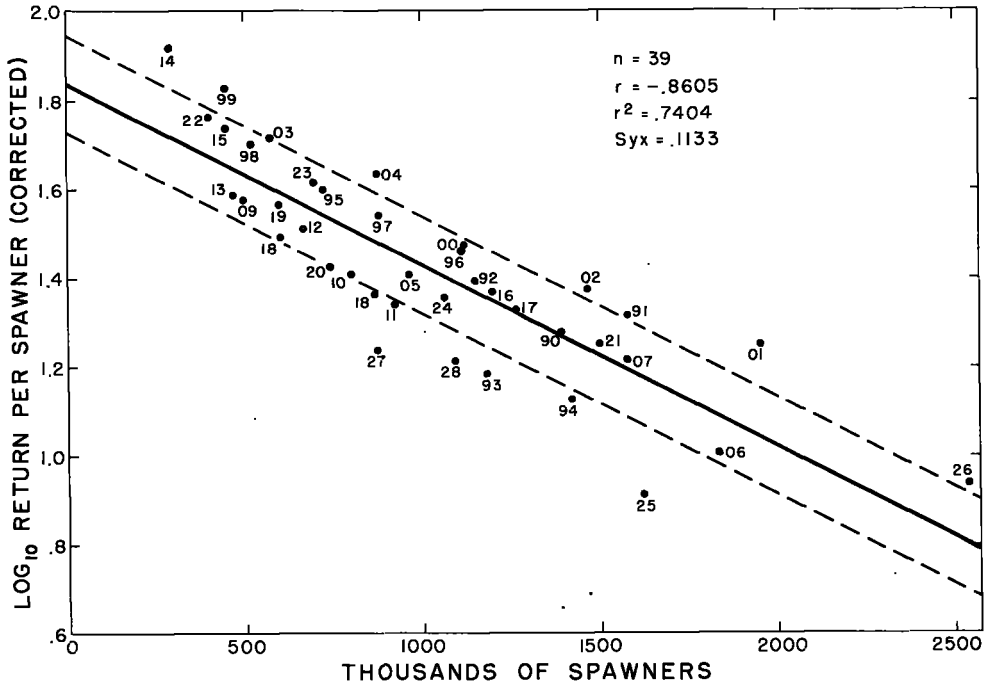

FIGURE 24.—Regression of log return per spawner (corrected for six factors, see text) on number of spawners for the 1887 to 1928 period.

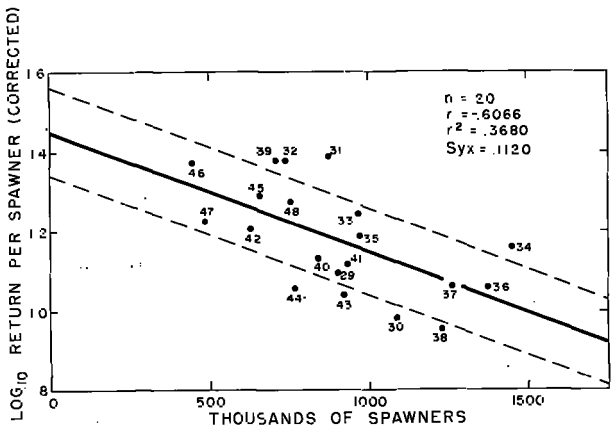

FIGURE 25.—Regression of log return per spawner (corrected for six factors, see text) on number of spawners for the 1929–48 period.

of with 1,300,000 and the greatest surplus with 750,000 spawners instead of with 900,000. Thus figure 26 shows that when the lake density factor is removed the earlier and later years approach much closer in the optimum number of spawners required to produce the maximum surplus. In figure 21 the points were at 900,000 and 600,000 spawners, whereas with the lake density factor removed the points are at 750,000 and 650,000 spawners.

TABLE 12.—*Returns corrected for climate, for odd- and even-numbered years, and for density of young in the lake, 1890–1948*

Year of spawning	Corrected log return per spawner (+1.0)	Corrected return per spawner	Total corrected return	Year of spawning	Corrected log return per spawner (+1.0)	Corrected return per spawner	Total corrected return
1890	1.276	1.852	2,572	1920	1.426	2.667	1,968
1891	1.312	2.051	3,239	1921	1.248	1.770	2,655
1892	1.391	2.460	2,834	1922	1.762	5.781	2,312
1893	1.183	1.524	1,804	1923	1.617	4.140	2,877
1894	1.125	1.334	1,896	1924	1.356	2.270	2,413
1895	1.599	3.972	2,876	1925	.911	.815	1,321
1896	1.461	2.891	3,223	1926	.936	.863	2,187
1897	1.539	3.460	3,045	1927	1.237	1.726	1,505
1898	1.701	5.024	2,612	1928	1.212	1.629	1,782
1899	1.828	6.730	3,008	1929	1.096	1.236	1,114
1900	1.470	2.951	3,296	1930	.982	.959	1,042
1901	1.246	1.762	3,443	1931	1.387	2.436	2,127
1902	1.375	2.371	3,466	1932	1.377	2.382	1,758
1903	1.706	5.082	2,912	1933	1.242	1.746	1,690
1904	1.633	4.295	3,792	1934	1.158	1.438	2,085
1905	1.406	2.547	2,453	1935	1.186	1.535	1,345
1906	1.001	1.002	1,842	1936	1.057	1.140	1,568
1907	1.211	1.626	2,566	1937	1.060	1.148	1,452
1908	1.362	2.301	1,993	1938	.952	.895	1,101
1909	1.576	3.767	1,876	1939	1.378	2.388	1,686
1910	1.408	2.559	2,057	1940	1.128	1.342	1,095
1911	1.337	2.173	2,017	1941	1.094	1.242	1,158
1912	1.511	3.243	2,173	1942	1.203	1.596	1,004
1913	1.587	3.864	1,804	1943	1.036	1.086	1,000
1914	1.917	8.260	2,404	1944	1.056	1.138	875
1915	1.733	5.408	2,412	1945	1.289	1.945	1,282
1916	1.367	2.328	2,798	1946	1.368	2.333	1,031
1917	1.325	2.114	2,674	1947	1.224	1.675	812
1918	1.491	3.097	1,867	1948	1.271	1.866	1,407
1919	1.561	3.639	2,165				

REASONS FOR LONG-TERM DECLINE IN ABUNDANCE

The foregoing analyses indicate that when most of the environmental sources of variability are removed there remains a high residual relationship between the number of spawners and the expected returns. The return per spawner decreases logarithmically as the number of spawners increases, resulting in a domed reproduction curve.

The 5-year periodicity in the runs appears to have been caused by the effect of the lake density of older young on the survival of the young of subsequent years. The decreased periodicity in recent years through the decline of the former "dominant" years may have been brought about largely by the increased proportion of the run, which through regulation has been permitted to spawn in the low years of abundance. The more even rate of competition between older young and the fry of each brood resulting from this loss of periodicity in the runs may have contributed to the general decline (fig. 32).

The possible role of predators in bringing about the decline in the Karluk returns has always been largely dismissed because it was thought that overfishing alone was the cause. In more recent years, as large escapements failed to bring large returns, there has been a school of thought that suggests a declining productivity of the waters.

It is apparent that the decrease in the size of returns in recent years cannot be assigned to overfishing of the spawning stock in the usually accepted meaning of the term. The spawning stock has been kept high through strict control of the catch, so that the decline is not caused by an insufficient number of spawners. The decline becomes apparent in a lowered return per spawner.

Aside from fishing, there are two chief sources of mortality, and it is to changes in these sources of mortality that we must look for an explanation of the changes in rate of survival as shown by the lowered return per spawner in recent years. These sources can be listed under two headings: physical and biological.

Changes in mortality caused directly or indirectly by changes in the physical environment we have discounted as far as the data warrant. Although the physical factors exhibit variations that often trend in one direction for several years,

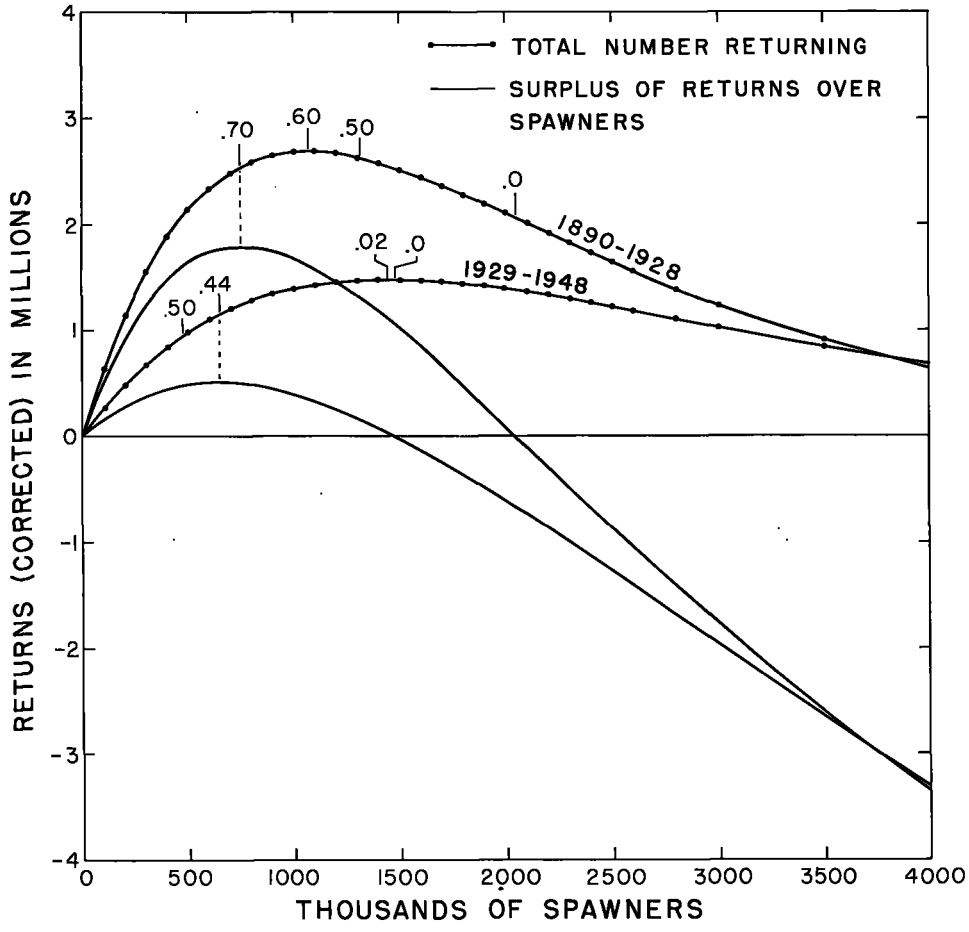

FIGURE 26.—Reproduction curves (corrected for physical factors, odd and even years, and lake density of older young) showing for early and later periods the returns for various numbers of spawners, and also the surplus of returns over number of spawners. The figures along the curves are the equilibrium points for several fishing rates.

there are no long-term trends in the available observations to indicate that the physical environment can be charged with the long-term decline.

The second source of mortality is to be found in the biological environment, which can affect mortality in several ways.

Effect of spatial competition on mortality

This may be primarily the cause of the domed shape of the reproduction curve, caused by lowered survival to the fry stage as increased numbers of spawners spread out over the less suitable gravels or destroy each other's redds on overcrowded beds. Spatial competition may also be the important factor in the difference in the rate of survival between fry of the odd- and even-numbered years. However, the odd- and even-year difference has been present throughout the period of years considered, so that the recent decline in abundance cannot be ascribed to it.

It is of interest to note that with the larger spawning escapements there is not only a lowered survival per spawner, but the total survival is less. There are two possible explanations for this seeming anomaly. One is that when a spawning bed is badly overcrowded the fish have difficulty in spawning effectively. A pair cannot always hold an area undisturbed but are pushed about by the dense mass of fish and it is probable that many eggs are not properly buried. Likewise, in order to find unoccupied territory the salmon utilize unsuitable beds. This is indicated for instance by field notes of Henry O'Malley and Dr. Charles H. Gilbert in their 1919 trip to Karluk Lake (Gilbert and Rich 1927, p. 13), which state,

About half way on west side is a creek (Grassy Point creek) about 6 feet wide and now 6 inches deep, thickly beset with dead and living fish. Temperature 46°. In the lowest 1,000 feet (paced) we counted 1,400 dead salmon, and estimated that side branches contained as many more (4,800 in all), and that there are fully as many live salmon as dead ones. It is safe to say, counting those now preparing to enter the mouth, that there are 10,000 fish spawning in the lower 1,000 feet of the stream. Apparently about 1 mile of stream with spawning in progress, and probably 50,000 fish in all.

Gulls were thick at mouth of creek and some were encountered higher up. They were feeding on drifting eggs, which could be seen in every eddy. Creek bottom of coarse cobbles and gravel, very hard, apparently not dug up. Seems impossible eggs could be buried, and loss must be enormous.

A second cause of lower total survival from the larger escapements may be the destruction of spawn by the spawning activities of the late-comers. Thus Gilbert and Rich (1927, p. 20–21) quote from the field notes taken by Fred R. Lucas in 1924 as follows:

O'Malley River.—Red salmon were spawning in this stream in larger numbers than ever noticed before by the writer. Believe it would average a pair to each square yard, except in the so-called "pothole," where they had spawned earlier. Two visits in August in previous years disclosed comparatively few fish in this stream. Apparently the red spawning here is at its height in September. Thousands of humpbacks had spawned here and some red eggs had been dug out. The reds were now digging out the humpback eggs. Behind every rock and in every eddy piles of humpback eggs lay. Within 22 steps the writer counted 12 piles that would average 5 gallons to a pile; and behind a small island about 6 feet in diameter there were more than a 50-gallon barrel full of humpback eggs. These eggs were all dead; had been dug out and drifted around before passing the tender stage. A small percentage of red eggs was among them . . .

Canyon Creek.—This is the best red stream on the lake this year. Some dead humpbacks were at the lower end, but live and dead reds were thick all the way to the falls. Some of the early red eggs are being dug out by present spawners.

Thumb River.—More reds spawning here than in previous years. . . . Great numbers of humpbacks have spawned here and the reds are now busily working over the same ground. Humpback eggs, with some red eggs, were piled in heaps in eddies and shallows on the right-hand side. Apparently the humpbacks had dug up the early red nests, and what eggs were past the tender stage were still alive but drifting around.

It was thought by Gilbert and Rich (1927) that despite these unavoidable losses the total egg deposition was larger in years of large runs and they so state:

Undoubtedly the late comers dig up many of the nests of those that came earlier, and destroy a regrettably large number of eggs; but they replace those they destroy with fresh lots of their own eggs, and many of the earlier eggs must escape destruction. Even in years of very heavy runs, when waste of eggs is excessive, the net result is probably a more complete seeding of all available gravels than occurs during runs of more moderate dimensions.

Gilbert and Rich are probably correct in assuming that larger numbers of spawners usually leave more eggs in the spawning gravels than smaller numbers. There are no present data, however, to indicate the relative numbers of fry emerging. It is entirely possible that the disturbance of the earlier spawned eggs that are not dug out (some still in the tender age) combined with the additional growth and spread of fungus helped by the large numbers of widely distributed crushed eggs may greatly lower the fry production from an over-spawned bed. Another possible explanation may be the lack of sufficient oxygen in the gravel to satisfy the requirements of too large an egg deposit. Wickett (1954) has demonstrated for chum salmon eggs in Nile Creek that some portions of a spawning bed may lack sufficient oxygen and that this may be aggravated by siltation.

Effect of competition for food on mortality

This can be treated under two headings, i. e., interspecific and intraspecific competition. It would be extremely difficult to believe that the decline could be ascribed to intraspecific competition for food. For such to be the case one would have to postulate a tremendous decrease in the production of food organisms, because the recent runs of less than one-half the earlier runs would scarcely be so drastically affected unless the food supply was also very drastically reduced. As a matter of fact the difference between the food requirements for the early and late periods should be measured by the size of the runs of adjacent years since the young of two broods are both abundant in the lake at the same time. The highest and the lowest totals for runs of any 2 adjacent years in each of the six 10-year periods for the observed returns (table 6) are:

10-year period	Total returns in thousands for 2 adjacent years		Lowest/highest
	Highest	Lowest	
			Percent
1889–98	9,760	2,762	0.28
1899–1908	9,760	3,250	.33
1909–18	7,049	2,105	.30
1919–28	7,434	2,416	.32
1929–38	5,116	2,511	.49
1939–48	2,689	1,182	.44

The 2 highest adjacent years out of the last 10 are only 28 percent of the highest of the 1889–98 period. This would be in the order of a fourfold reduction in food production before it could even start to have an effect on the present populations.

The relative importance of the parts played by number of migrants as against size of migrants in determining the number of returning adults has not been clearly settled. This is often because available data are not adequate, either in kind or quantity to properly test the hypothesis.

Foerster (1954) says of Cultus Lake sockeye data for an 18-year period that:

> Analysis of these data indicates a negative correlation between size of migration (in number of smolts) and percentage return of adults which is found (by multiple correlation treatment) to be related principally to the size (weight in grams) of the smolts.

From the data published by Foerster (1954, p. 342) the following statistics have been calculated in which x_1 equals log of average smolt weight, x_2 equals log of number of smolts and y equals log of adults returning:

$r_{12}=-.7268^{**}$ $r_{y_1}=-.2601$

$r_{y_2}=.6758^{**}$ $R=.7549^{**}$

Since r_{12} shows a very high negative correlation between average weight and number of smolts, it is important to consider the partial correlations which are:

$$r_{13.2}=.4564\ P>.05 \text{ and } r_{23.1}=.7340\ P<.01$$

$$r^2_{13.2}=.2083 \text{ and } r^2_{23.1}=.5387$$

$$R^2_A=.5126$$

These partial correlations indicate that the influence on the number of returning adults of individual smolt weight is only about 21 percent ($r^2_{13.2}=.2083$), whereas the influence of number of smolts is about 54 percent ($r^2_{23.1}=.5387$). Furthermore, the influence of smolt weight may not be significant as P is greater than .05.

A further analysis was made in which x equals log of the weight of the biomass of smolts of each brood and y equals log of the adults returning: r equals .753**, and $r^2=.57$ which is a little larger than r^2_{y2} of .46 when y is estimated from number of smolts alone. (See figure 27.)

It is evident that at Cultus Lake the variability in returns is related chiefly to changes in numbers of smolts, and only in small degree to changes in average weight.

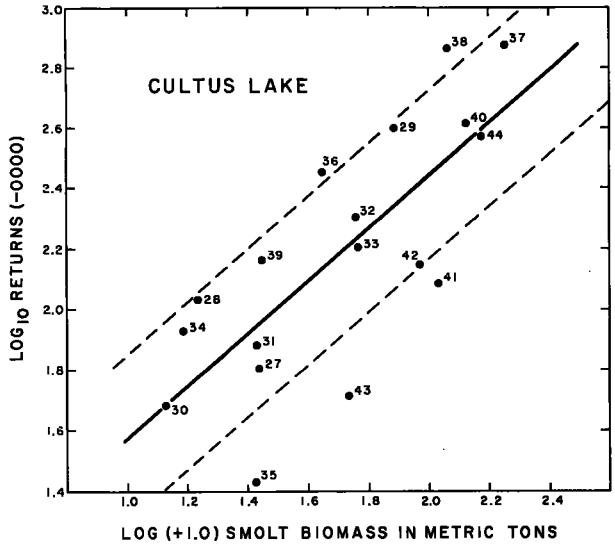

FIGURE 27.—Regression of log return on log biomass of smolts for Cultus Lake, British Columbia (data from Foerster 1954).

At Karluk over a 14-year period from 1923–37 (except 1933, see appendix J) the length of 3-year smolts showed a positive correlation coefficient of .60 with the number migrating, which is the reverse of conditions at Cultus Lake where size and number showed a high negative correlation. This can probably be explained by the fact that at Cultus Lake the young sockeye population (fig. 29) is larger in relation to its food supply than at Karluk.

Further evidence that competition for food is not the important factor at Karluk is shown by analysis of the smolt production (see tables A–9 through A–12 in Appendix F). Table A–9 and figure A–4 show that the Cultus Lake smolts, although very small as they leave the lake in their second year, are heavier for their length than those from Karluk. The Babine Lake smolts of the Skeena River appear to be intermediate. These characteristics are a function of form and are of no significance in themselves.

In tables A–10 and A–11 the total biomass of the smolt migrations is shown for Karluk and Cultus Lakes for periods of 15 and 18 years, respectively. For Karluk Lake the linear correlation between biomass and number of smolts is 0.968 (fig. 28). It is obvious that the runs during the 15-year period considered were not sufficiently large for the smolts to compete for the available food supply. Considering the reduced size of the

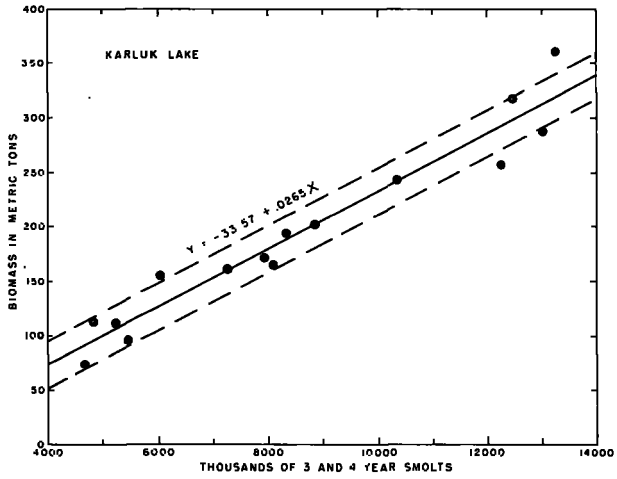

FIGURE 28.—Regression of biomass of migrating smolts on number of smolts for Karluk Lake, 1926–40.

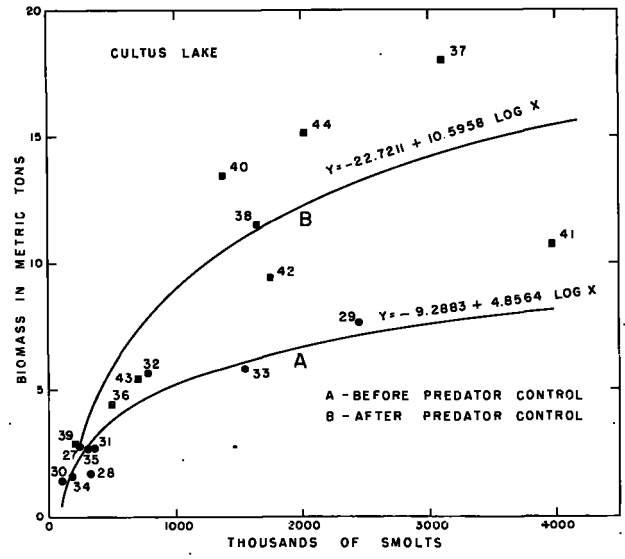

FIGURE 29.—Regressions of biomass of migrating smolts on log number of smolts for Cultus Lake, 1927–44.

populations of recent years compared with past years, this is a logical sequence if the food supply is unimpaired.

Furthermore, the slope of the regression line shows that the smolts from larger populations were actually larger individually. This suggests that although there may be no food competition between the young of a year class at Karluk, the relative survival of each year class may be dependent on the annual food density so that the survival is highest when growth is fastest.

The reverse is apparently true for Cultus Lake. In figure 29 are shown the curves for biomass versus the logarithm of the number of smolts. The correlation coefficients for biomass versus log number of smolts are 0.95 for the 9 years before control of predators (and food competitors, e. g., squawfish (*Ptychocheilus oregonensis*)), and 0.83 for the 9 years following the institution of controls. Both correlation coefficients have a probability of less than 0.01.

It would appear that the food supply of Cultus Lake is insufficient to enable the biomass of smolts to increase in proportion to their numbers. The closeness of the semilogarithmic fit suggests immediately that the increasing competition between smolts as their numbers increase sets an asymptotic level on the biomass. This level was apparently doubled by control of the numbers of other fishes.

As is shown by Ricker and Foerster (1948) the higher the survival rate of the young the smaller will be the loss of production through mortality of young which have already consumed a portion of the available food. Therefore, the raising of the asymptotic level approached by the weight of the biomass of migrating smolts can occur within limits without any increase in available food, merely through raising survival by curbing loss due to predation.

The weight of the smolt biomass migrating from Karluk Lake is truly amazing. The average comes to 41.4 pounds per acre (table A–12). The total standing crop of all fishes from 51 North American lakes (Rounsefell 1946) is less than 40 pounds per acre in lakes over 100 acres. The annual sport and commercial take of fish from the highly productive Wilson reservoir in Tennessee with 15,500 acres is only 32.0 pounds per acre. It must be remembered that the biomass of migrating smolts does not include the great mass of younger parr remaining in the lake. The lake is also inhabited by large populations of both alpine and Dolly Varden charrs, young of coho and king salmon, young steelheads, and quantities of sticklebacks.

Most of the available limnological data for Karluk and Cultus Lakes are not strictly comparable. Perhaps the best comparison of their potential productivity is shown by the differences in water transparency. From Juday et al. (1932)

and Ricker (1937b) the following Secchi disc readings in meters are extracted:

Lake	July	September	October
Thumb	3.6	2.5	
O'Malley	4.8	3.9	
Karluk	7.2	6.8	
Cultus		16.2	16.0

Although the Cultus Lake readings were very scant Ricker says in confirmation,

> In the course of taking plankton samples from 1932 onward the instruments could be seen as they descended, down to 13–15 metres, throughout most of the year.

It would be difficult to believe that the difference in smolt biomass production between Karluk and Cultus Lakes could be entirely dependent upon the difference in plankton production. The effect of another related factor, namely, temperature, also merits consideration.

The best data available on the effect of water temperature on growth of young sockeye are contained in an excellent report by Donaldson and Foster (1941). They held groups of sockeye fingerlings for 6 months in six tanks with individually controlled water temperatures and recorded by fortnightly intervals the grams of food consumed and grams of change in the total weight for each lot of fish. Using these data we have plotted figure 30 showing the efficiency of growth (increase or decrease in weight of fish/weight of food fed) against water temperature. The points on the empirical curve are grouped averages.

Figure 30 shows that like all cold-blooded vertebrates the sockeye is restricted in the range of temperatures suitable for growth. As expected growth is very slow below 40° F., increasing rapidly with increase in temperature until a plateau of favorable growth conditions is reached extending from about 45° to 68° F. The optimum range of temperatures is about 48° to 56° F., after which growth declines gradually with increasing temperature up to about 67.5°. At this point the growth curve falls steeply, and above 70° F. the sockeye lose weight.

Available data concerning the surface water temperatures of Karluk and Cultus Lakes (Ricker 1937b; Juday et al., 1932; and Barnaby 1944) are shown in figure 31. Except for 1935 and 1936 the Karluk observations are scant. However, for the 7 years with observations only 1926 and 1936 (both warm years) show any surface temperatures

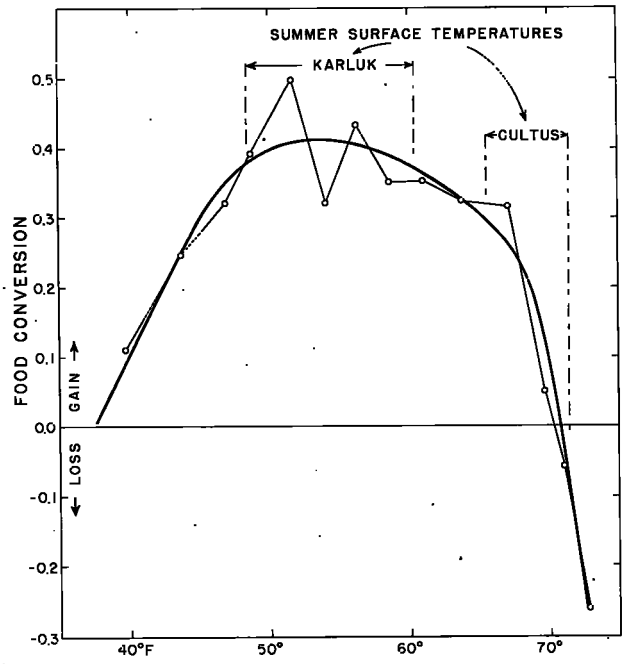

FIGURE 30.—Growth of young sockeye in 2-week periods, as shown by food conversion, at different water temperatures (data from Donaldson and Foster, 1941). For superimposed summer surface lake temperatures see figure 31.

above 14° C. At Cultus Lake for the 3 years of observations none fell below 19° C. after June 20 until September 14, a period of 85 days or 12 weeks.

It is clear that whereas the surface waters of Karluk Lake are seldom if ever too warm for efficient growth of young sockeye, the surface waters of Cultus Lake become too warm for an extended period in midsummer. Foerster (1937) shows that the annual migration of smolts from Cultus Lake terminates as the surface temperature rises. Over an 8-year period 80 percent of the smolt migration on the average had passed out of the lake by the time the surface water reached 10.6° C.; the maximum was reached in 1935 when 80 percent were out at a temperature of 12.5° C. When the temperature reached 13° C., the daily migrations decreased greatly. On the average, the migrations ceased entirely at 17.5° C. (range from 14.4° in 1930 to 20.1° in 1933).

Foerster comments,

> It is suggested, therefore, that the cessation of migration is definitely related to the creation in the epilimnial waters of the lake of a temperature blanket through which yearling sockeye, presumably late in responding to the

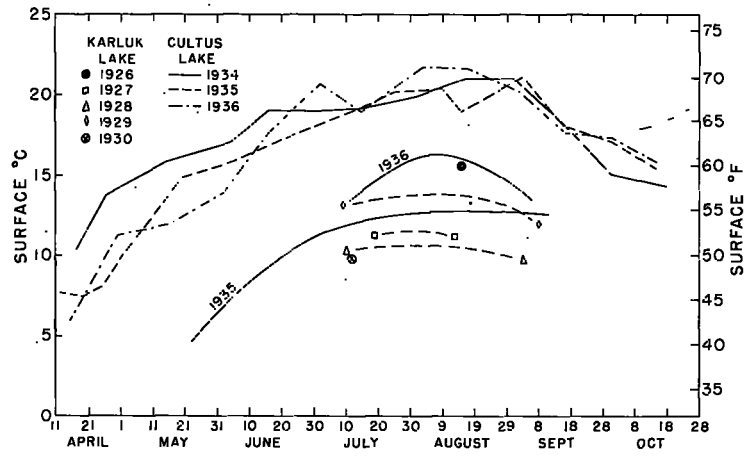

FIGURE 31.—Surface water temperatures during the warm season at Cultus Lake, 1934 to 1936 (upper curves), and at Karluk Lake in various years from 1927 to 1936 (lower shorter curves). Individual readings for 1935 and 1936 at Karluk omitted.

migration stimulus, are unable to pass. As a result they return to the deeper waters of the lake, there to remain until the migratory influence is again felt the following spring.

At Karluk Lake the smolt migration is much later than at Cultus Lake; the height of the migration at Karluk occurs during the first two weeks in June, whereas the Cultus Lake migration reaches its height in April. Furthermore, at Karluk the migration continues into July. There is other evidence that the young utilize the surface waters during the warmer parts of the year.

Gilbert and Rich (1927) quote from the field notes of E. M. Ball for September 13, 1917, while at Karluk Lake,

> From sundown, until darkness prevented further observation, the lake was alive with feeding fingerlings.

Even though the young sockeye are pelagic in the lake they are occasionally caught with beach seines, i. e., J. T. Barnaby collected them with a seine on August 8 and September 18, 1927.

Bare Lake, a small lake in the Red River drainage only 12 air miles from Karluk, is too shallow to have a thermocline, yet it has a regular run of sockeye.

It would appear that Cultus Lake is in reality marginal for sockeye because of the high summer temperatures which force the salmon to live in the narrow stratum of water adjacent to and beneath the thermocline. In Karluk Lake, on the contrary, the young can feed at the surface throughout the summer. This is the most logical explanation of the vast superiority of Karluk Lake for growth and for total production per area of sockeye smolts.

Effect on mortality of intraspecific competition which could take the form of cannibalism

As shown by the analysis of the effect of lake density of young sockeye on the survival of future broods, this is probably an important cause of fluctuations in survival. The importance of this factor can best be grasped by comparing the curves for the later with those from the earlier years, before the "dominant" cycle years had been destroyed (fig. 32). Obviously the effect of intraspecific competition was to raise the survival from the larger spawning stocks of the dominant years and to lower the survival from the low year broods, the young of which would feel the full pressure of competition in the lake from the numerous young of the dominant years.

During this early period the above described effect gave the dominant cycle years an advantage in survival that kept them dominant despite the variations in survival from other causes. An equal number of spawners in an off year yielded a lower return than in a dominant year, because the young had to face a larger number of young from the previous dominant broods. The net result was a tendency for the years with dominant broods to remain large and the years of low broods to remain small.

When the take of the fishery was regulated to permit a larger proportion of spawners in the low years this delicately-balanced natural cycle was

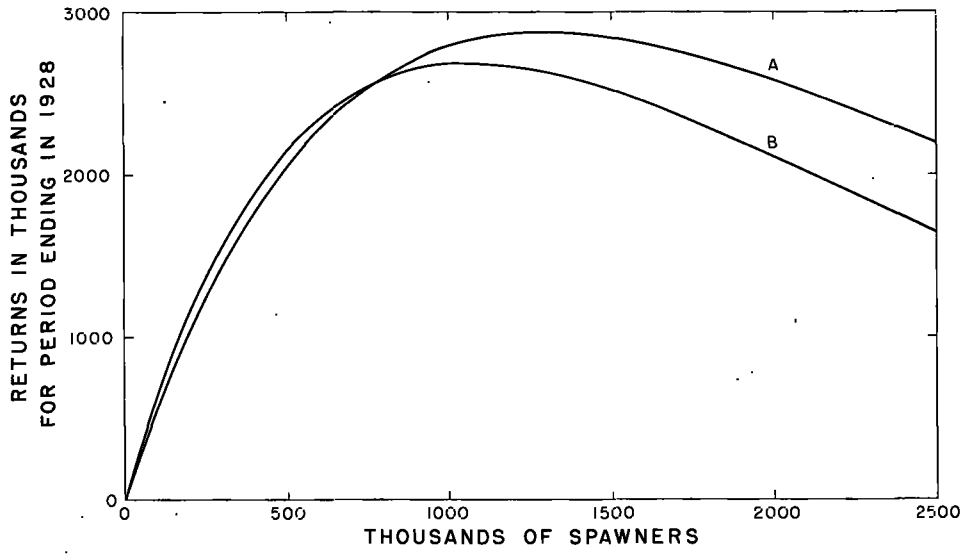

FIGURE 32.—Reproduction curves derived from return per spawner on number of spawners for the period of years ending in 1928 showing curves corrected (*B*) and uncorrected (*A*) for lake density of the older young at time of fry emergence.

destroyed. This tended to equalize the intraspecific competition between years.

Effect of predation on mortality

The sockeye in fresh water has numerous predators: bears, mergansers, gulls, young of the coho and king salmon (*Oncorhynchus kisutch* and *O. tshawytscha*), the steelhead rainbow trout (*Salmo gairdneri*), the fresh-water sculpin (*Cottus aleuticus*), the Dolly Varden trout or charr (*Salvelinus malma*) and its close cousin, the alpine charr or red lake charr (*Salvelinus alpinus*).

Although the data are admittedly meager we can form some notion of the probable abundance of predators and the amount of depredation. In doing so it would be best to try to make some differentiation between types of predators. The first type, (1) are those that may fluctuate in abundance independently of the abundance of sockeye. They may be referred to as nondensity-dependent. The second type, (2) are those that depend sufficiently on sockeye for food so that their abundance is controlled, at least to a significant extent, by the abundance of sockeye. They are referred to as density-dependent predators.

Predators of the first type would be more apt to take a rather fixed number of sockeye, irrespective of sockeye abundance. Their net effect would be to render it difficult for sockeye in years of low abundance to recuperate until they pass a threshold of abundance sufficient to offset the amount taken by the predator. As a matter of fact, when the escapement is sufficiently large for the expected return to fall along the right limb of the reproduction curve (fig. 32), the loss of some adult spawners could actually increase the expected return.

Predators of this first type include land mammals. Shuman (1950) dismisses predation by the smaller mammals as insignificant, but stresses the high predation by the Kodiak bear, which he believes increased in numbers at Karluk in the 1940's owing to the absence of hunters, natural increment, and migration from areas occupied by military installations.

From actual weir counts of bear-killed salmon in Moraine Creek, a tributary of Karluk Lake, as well as observations on bear-killed salmon and on incidence of bears on other streams he estimated a minimum bear kill of unspawned salmon of 94,000 in 1947, which would be 19.4 percent of the escapement of 485,000. A large bear population could account for an appreciable portion of the difference in the returns per salmon between early and late years, since predation by bears could be important when runs are small.

Predators of the first type also include birds. Assessment of damage is difficult for many species of birds because of the variety of foods taken.

The bald eagle will attack adult salmon in the streams, but there is no reason to believe that eagles are of any but minor importance as predators.

The American merganser, according to White (1937), rears its broods on the streams where it consumes large quantities of salmon and trout, although it will eat any fish available. Its appetite is enormous; he found that a young bird ate an average of more than a third of its own weight each day.

In contrast to White's findings on Cape Breton Island, Munro and Clemens (1937) found in British Columbia, that salmon were not so important an item, and that they ate more fresh-water sculpins. However, mergansers were collected throughout the year. Salmon were an important item in certain localities, especially during the downstream fry migration in the spring. Although mergansers eat salmon eggs, they believed that the eggs eaten were largely loose eggs not buried in the gravel, which would constitute a loss in any event.

Young sockeye salmon could be subject to merganser predation at two periods. The first would be after emergence from the gravel and before completing the descent to the lake; the second would be during the smolt migration from the lake to the sea. As mergansers also take fresh-water sculpins, young trout, and stream-dwelling young coho and king salmon, it would be a difficult task to judge the balance between beneficial and harmful effects without extensive data.

Birds were stressed as destructive by Bean (1891):

> Chief among the destroyers of the young fish are terns, gulls, ducks, and loons, which are very common in that region. I shot some terns and gulls near the south end of Karluk Lake and upon holding them up by the legs small salmon dropped out of their mouths. Towards the end of August the shallow parts of Karluk River were visited by hundreds of gulls, chiefly young of *Larus glaucescens* and *L. brachyrhynchus*, which were feeding upon young salmon.

This is at variance with the findings of Munro (1928) in British Columbia. Here the glaucous-winged gull was feeding on salmon carcasses and loose salmon eggs. In August the main Karluk River would be unlikely to contain many sockeye fry, but there might be fry of the coho and king salmon. When Bean visited Karluk in the summer of 1889 there should have been numerous pink salmon fry from the even-year spawning of 1888, but towards the end of August seems late for pink salmon fry to remain in fresh water, and there would seem to be some question concerning the chief food of the concentration of gulls observed.

For the fish predators it would be advantageous to know whether or not their density is dependent on the density of sockeye. There is some information bearing on this subject for the coho salmon, *Oncorhynchus kisutch*, at Cultus Lake. Foerster and Ricker (1953) give the mean length of lake-residing coho salmon in their third year together with the number of sockeye migrants leaving the lake the same spring and the mean December-to-March air temperature before the migration. Their data cover 6 years and they found no statistically significant correlations. However, if one employs the logarithm of the number of sockeye migrants the correlation with coho length is .71 (r is .75 for P of .05). The multiple correlation coefficient of coho size on temperature and on the logarithm of number of sockeye migrants is .80 (R is .81 for P of .05), indicating that the growth of young coho is increased by an increase in abundance of young sockeye.

The existence of a marked relationship between coho growth and number of young sockeye in the lake is a strong indication that the survival of coho from young to adult is influenced strongly by young sockeye abundance. This follows because it has been shown by many investigators that the larger coho smolts have a higher rate of survival from time of seaward migration until their return. At Karluk this relationship holds between smolt size and survival for the sockeye so that it is reasonable to assume that at Karluk it also holds for the coho.

This view that the coho depend largely on young sockeye at Cultus Lake is stated by Ricker (1941):

> Coho are perhaps the only species which would suffer severely from a scarcity of sockeye, for their only considerable alternative food is insects, which during much of the year are not available.

A count of coho salmon was not made during every year at Karluk, and in many years the weir was removed before the last of the coho had ascended. By averaging the weekly count by the number of years with available data it was possible to arrive at an estimate of the average coho escapement (table 13). During 10 years of the 1926–37 period the average escapement through

the weir near the river mouth was nearly 21,000. In 1945 the weir was placed at the outlet of Karluk Lake. In the 9 years from 1945–53 the average escapement into the lake was about 8,800 cohoes, sufficient to maintain a large number of young coho predators.

TABLE 13.—*Escapement of coho salmon by weeks when weir was at river mouth and at lake outlet*

Week ending	1926–28 and 1931–37		1945–53		Average counts	
	Count	Number of years	Count	Number of years	Early period at lower weir	Later period at lake outlet
Aug. 23			9	4		2
Aug. 30	3,345	4	237	6	836	40
Sept. 6	3,531	7	722	7	504	103
Sept. 13	15,406	9	1,973	8	1,712	247
Sept. 20	42,776	10	8,219	8	4,278	1,027
Sept. 27	79,371	10	9,815	8	7,937	1,227
Oct. 4	26,309	10	18,260	9	2,631	2,029
Oct. 11	22,422	10	15,561	5	2,242	3,112
Oct. 18	1,575	2	1,929	2	788	964
Oct. 25			69	1		69
Sum					20,928	8,820

The most numerous of the fish predators are the two charrs. DeLacy and Morton (1943) made a study of these charrs at Karluk. They state:

Perhaps the most conspicuous feature in the life history of the dolly varden is its habit of migrating regularly to and from salt water. At Karluk the seaward movement occurs in the latter part of May and in early June. Although the majority of the population participates in the migration, it is known that some dolly vardens remain behind, because adult representatives of the species are present in the Karluk system during late June and early July, at a period when no charrs are moving either up or down the river. The return migration from salt water to fresh water takes place from mid-July until September after an average residence in the ocean of approximately 60 days, as determined from tagging experiments.

Concerning the red lake or alpine charr they state:

Until late June, insects are the most common food eaten by these charrs. As soon as the red salmon begin to spawn in the tributaries of the lake in late June or early July, schools of lake charr may be found congregated about the mouth of each stream. At this time of the year they eat not only the salmon eggs that drift downstream into the lake, but also other food material dislodged in the streams by the spawning salmon. Later in the season as the disintegrating carcasses of the dead, spawned-out salmon accumulate in the lake, fragments of this flesh become the most common item in the diet of the lake charr. Fish caught in shallow portions of the lake feed heavily on sticklebacks during certain seasons. Cottids, salmon fingerlings, and young charr are found occasionally in their stomachs. During September, insect material again resumes its earlier position as an important source of food.

The great abundance of these charrs is attested by the numbers that have been caught and destroyed during the down-stream migration of the Dolly Varden. This ran as high as 82,000 in 1937 and over 50,000 in 1938 and again in 1939. Considering that these represent only a portion of the Dolly Varden population, it is plain that the two charr populations require a great quantity of food.

That these charrs can be destructive to young fry migrating down-stream is shown by Pritchard (1936) whose data we have summarized in table 14. It should be noted that the coho described above as being density dependent on sockeye abundance took fewer fry than the Dolly Varden.

Barnaby (1938, p. 33) says,

At Karluk Lake it was noted that charrs take a very heavy toll of red salmon fry in the spring at the time the young fish are entering the lake from the spawning streams.

The destructiveness of the Dolly Varden charr is attested also by Ricker (1933) who states concerning their predation at Cultus Lake,

Individually these are more destructive to sockeye than are any other fish in the lake. The specimens taken in the nets ranged from eleven to twenty-seven inches in length, and all fed largely upon young salmon. The greatest numbers were found in May and in mid-July, when stomachs contained an average of 17 sockeye each, and individual fish had as many as 90.

The predation was not confined to the large Dolly Varden, he adds that,

A number of Dolly Varden, 5–6 inches long, were taken at the counting fence in the outlet of the lake during the spring migration of yearling sockeye. Even these small fish were able to eat the migrant sockeye, as well as many small coho fingerlings.

If we make the wholly reasonable assumption that these charr populations increase in the wake of a large spawning of sockeye and decrease after a small spawning we can readily perceive how they might be an important factor in causing long-term changes in the rate of survival.

While discussing predation mention should be made of another species abundant in Karluk Lake, the 3-spined stickleback, *Gasterosteus aculeatus*. Evermann and Goldsborough (1907, p. 273, listed as *G. cataphractus*) mention specimens collected from a large school in Karluk River near the Lake in 1903 by Cloudsley Rutter that ranged from 2 to 4 inches. There seems to be little

TABLE 14.—*Food of predator fish in McClinton Creek, British Columbia, during springs of 1931 and 1933* (from Pritchard 1936)

Species of predator	Number of specimens	Number of salmon fry in stomachs	Number of stomachs empty	Number of stomachs containing insects	Salmon fry per specimen	Common name of predator
Cottus sp.	165	187	98	1	1.1	Freshwater sculpin.
Salvelinus malma	76	616	6	1	8.1	Dolly Varden charr.
Salmo clarki	11	12	6	0	1.1	Cut-throat trout.
Oncorhynchus kisutch[1] and *S. clarki*	1,523	3,917	188	17	2.6	Mixed.[1]
Oncorhynchus kisutch	385	1,072	76	0	2.8	Coho salmon.
All species	2,160	5,804	374	19	2.7	

[1] Estimated by Pritchard to be over ninety percent *O. kisutch*.

evidence that they are actual predators. Kincaid (1919) says,

> The damage done by the Stickleback is out of proportion to his size as he is able to kill the fry of larger fish, notably the salmon, for which reason the Stickleback is known locally as the salmon killer.

Bigelow and Schroeder (1953, p. 309) say of the same species,

> It is a proverbially pugnacious fish, using its spines with good effect as weapons of offense and defense, even on fishes much larger than itself. It feeds indiscriminately on the smaller invertebrates, on small fish fry, and on fish eggs, to which it is exceedingly destructive in fresh water.

Concrete evidence of destruction of salmon fry by sticklebacks appears to be lacking. White (1930) carried out experiments in 1927 and 1928 in which he placed 1,000 trout fry each (*Salvelinus fontinalis*) in screened sections of a stream. In one section he added 200 adult 3-spined sticklebacks, in another he placed 25 larger trout, and in both years he tried one section with both 200 sticklebacks and 25 larger trout. Losses in the last experiment were 85 percent in both years. Losses with trout alone were 78.6 percent and with sticklebacks alone 54.4 percent. Unfortunately, no controls were run to determine survival in the absence of either trout or sticklebacks. However, the difference between the 85 percent and the 78.6 percent with and without sticklebacks is too small to even consider its significance.

Salmon fry are much larger than the fry of the brook trout, so that there would seem to be even less chance of any destruction.

During the earlier years when the fluctuations in the runs were of greater magnitude the predator populations would have had a large range in size, whereas in later years, when the range of fluctuations was much less, the predator populations likewise would fluctuate less. Under such conditions it would be difficult for salmon of the dominant years to become re-established. The effort to obtain a large number of spawners in every year would assure the predators a constant food supply, and the fry of all brood years would be subject to heavy predation.

There is the possibility that during the period when the runs were cyclic in character the frequent occurrence of years with low numbers of spawners aided in keeping the predator populations under control. Table 15 gives the frequency of the numbers of spawners in the early and late periods. During the early period, 10 years, or nearly 1 year out of 4 had less than 600,000 spawners, whereas in the later period only 3 years, or 1 year in 8, had so few spawners. The large number of spawners in many of the early years may have aided also in controlling predators, since their large increase in numbers following the big years would render them more susceptible of damage in the low years.

TABLE 15.—*Frequency of number of sockeye salmon spawners (in thousands)*

Number of spawners	1887–1928	1929–53
200–300	1	
301–400	1	
401–500	4	2
501–600	4	1
601–700	3	4
701–800	2	6
801–900	5	3
901–1,000	2	4
1,001–1,100	2	1
1,101–1,200	4	
1,201–1,300	2	2
1,301–1,400	1	1
1,401–1,500	4	1
1,501–1,600	2	
1,601–1,700	2	
1,701–1,800		
1,801–1,900	9	
1,901–2,000	1	
above 2,000	1	
Total	42	25

The difference between the early and recent periods in number of spawners is perhaps better illustrated by the differences between the minimal and maximal numbers. Since a 5-year cycle is being discussed and as the two series of years are unequal in number, perhaps the best measure is afforded by comparing the 20th and 80th percentiles of the frequencies in table 15 as follows:

Percentiles	Frequency class	
	Early years	Recent years
20	501–600	601–700
50	901–1,000	701–800
80	1,801–1,900	1,001–1,100
80–20	1,300	400
(80–20)/50	1.37	0.53

This comparison shows that the amplitude of the oscillations between high and low numbers of spawners was over twice as great in the earlier as in the more recent period.

Effect on mortality of age of smolts at migration

The Karluk smolts average about 3 to 4 times heavier than those from Cultus Lake. While all but a small minority of Cultus Lake smolts migrate in the spring of their second year, the second year migration at Karluk is very small. The majority migrate in their third year, a fair number leave in their fourth year, and small numbers leave in their second and fifth years (table 17).

As shown later in the section on life history, the average age of the sockeye increased rather steadily in the returns from the broods spawned from 1919–43. This increase can be attributed chiefly to an increase in the proportion of smolts remaining an additional year or years in the lake prior to seaward migration. Speaking of this phenomenon Barnaby (1944, p. 293) says,

> The change in the period of time spent in fresh water is considered to be due to unfavorable environmental conditions, which may also adversely affect the survival value of the population.

According to his view, the fact that the smolts tend to remain longer in the lake is an indication of poor growing conditions, but the evidence may indicate the contrary.

Evidence that better growing conditions tend to cause migration of smolts at a later age is suggested by the older average age of the smaller year classes (figs. 48, 49, and 50) at Karluk. The excellent growing conditions that apparently exist especially for the smaller broods may be keeping the smolts in the lake for a longer period. The earlier age at migration of the Cultus Lake smolts, which encounter much less favorable growing conditions, might seem to support this view.

Against this explanation the fact is mentioned by Foerster (1944) that older smolts in the same brood are nearly always smaller (in this instance, third year fish) than younger smolts (second year fish) at the time the younger smolts leave the lake. It has been suggested, therefore, that there is a threshold size which must be attained before migration. We cannot fully subscribe to this hypothesis, but incline to the view (see appendix J for details) that migration is induced both by size and density of young. The threshold size for migration then will vary (within limits) inversely with the weight of the biomass of young.

Further confirmation of the inhibition of migration by too rapid growth is given by Foerster (1938, p. 186) who states,

> . . . there is evidence to indicate that the larger size of the latest groups of liberated fish, rather than weighting the data favorably by an abnormally high survival, affected them in opposite fashion by contributing to the nonmigration of individuals. It has recently been observed by Ricker (1938) and referred to in a previous paper (Foerster 1937a) that in some years at least, if not in every year, there occur in Cultus Lake certain populations of sockeye the individuals of which remain in the lake and mature. Specimens have been taken in small-mesh gill nets and have been found maturing in their second, third, or fourth years. These sockeye show distinct differences in color, size, habits, and sex ratio to the common landlocked sockeye (*O. nerka kennerlyi*) and Ricker has given to them the name "residual" sockeye.
>
> These "residual" fish, according to Ricker, are believed to result, in part, from normal young sockeye of anadromous stock which have experienced unusually rapid growth during their first or second years and do not respond to the migratory stimuli in the spring.

If the size-threshold to be attained before migration were not partially density-dependent, then there would be almost no smolt migration at Cultus Lake in years when young were abundant because the fish would be too small. Likewise in years of very low abundance practically all would migrate for the contrary reason.

If this hypothesis is correct, it offers a reasonable explanation at Karluk both for the older fresh-water age of the smaller year classes, and the trend toward an older fresh-water age in recent years as the size of the runs decreased. Furthermore, it would aid in keeping the smaller runs small and the larger runs large. The remedy

lies in increasing the number of young in the lake, either by larger escapements or by increasing survival of the young.

LIFE HISTORY OF THE KARLUK RIVER SOCKEYE

Before discussing further the meaning of the foregoing analyses there are certain aspects of the life history that should be examined to determine their bearing on population abundance. Since 1921 there have been extensive collections of some types of data and these have been studied from this viewpoint.

Seasonal occurrence of the runs

The details of determining the seasonal occurrence of the runs are given in appendix A. Figure 33 shows the normal curves of the occurrence of the run for three 10-year periods and for the 30-year period from 1921 to 1950, inclusive.

The curves show three modes. The first mode has always been clearly recognized, but the last two modes have usually been considered as only one. Thus Barnaby (1944) says:

> There is a definite mode in June, a minimum during the week ending July 12, followed by a second mode. The second mode itself is slightly bimodal; however, the data for any single year clearly show that the minimum occurs during the period of the week ending July 5 to the week ending July 19 and only one mode is present during the fall run. It appears that there are two distinct red salmon runs to the Karluk River each year, the spring run which reaches a maximum during June and the fall run which reaches a maximum between the last week of July and the first week of September.

Data for 10 years were available to Barnaby contrasted with that for 30 years at present. With this additional data, the point concerning the modes has become clear. Note that in figure 33 the fall run is bimodal in each of the three 10-year periods. The question concerning the presence of a lower minimum between the first two modes is largely a matter of the spacing of the modes. The first two modes are 7½ weeks apart and the last two 5 weeks apart. It is clear that these modes are not due to chance, so that if seasonal occurrence alone is to be used as a criterion for postulating separate populations one must postulate not two, but three populations. We will show later that these modes are caused by seasonal differences in age composition.

Age composition of the runs

Sockeye salmon of Karluk River vary considerably in age at maturity, returning at 3 to 8 years of age. Within each of these age groups there is a further differentiation according to the proportion of the time spent in fresh-water and marine environments. Although the bulk of the young leave the lake in the late spring of their third or fourth year of life (reckoning from the time of egg deposition) a few remain in the lake until their fifth year, some leave in their second year, and an undetermined number drop down the river to the sea during their first summer without any period in the lake. Likewise, the growing period at sea varies from part of one summer to four summers.

In the years for which ages of the run are analyzed, 1922 and 1924–49, 21 different combinations of fresh-water and ocean ages were read. Three combinations, 3_3, 5_1, and 5_5, occurred only

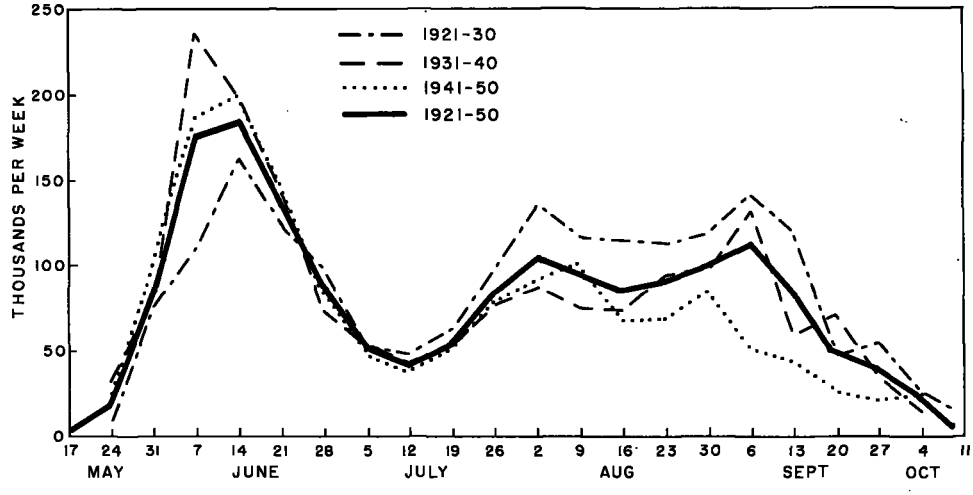

FIGURE 33.—Showing by weeks the normal seasonal run of sockeye entering the Karluk River by 10-year periods from 1921 to 1950.

once; 18 groups occurred more regularly. Ages are denoted by two figures, thus 5_3 means a fish returning to spawn in its fifth year, which migrated to sea in the spring of its third year.

The details of determining the age composition of the runs and the detailed tables are given in appendix B.

Relation of age of seaward migration and age at maturity with the season of return migration to the river

The seasonal occurrence of each age group is rather distinctive. Comparison of the different age groups (tables A–3 and A–4, appendix) gives convincing evidence that the time of the returning migration of each age group is governed by two factors: fresh-water age and ocean age. Except for the few adults that entered the sea as fry (3_1 and 4_1 groups) the age of downstream migration has a negative effect on the season of return; the 2-year migrants run first, followed by the 3-, 4-, and finally the 5-year migrants.

The ocean age, on the contrary, has a positive effect. The 4-ocean fish run earliest, followed in succession by the 3-, 2-, 1-, and 0-ocean groups. This is best seen in table A–4 which is on a cumulative basis.

The cumulative curves of percentage seasonal occurrence by weeks are shown in figures 34 to 38.

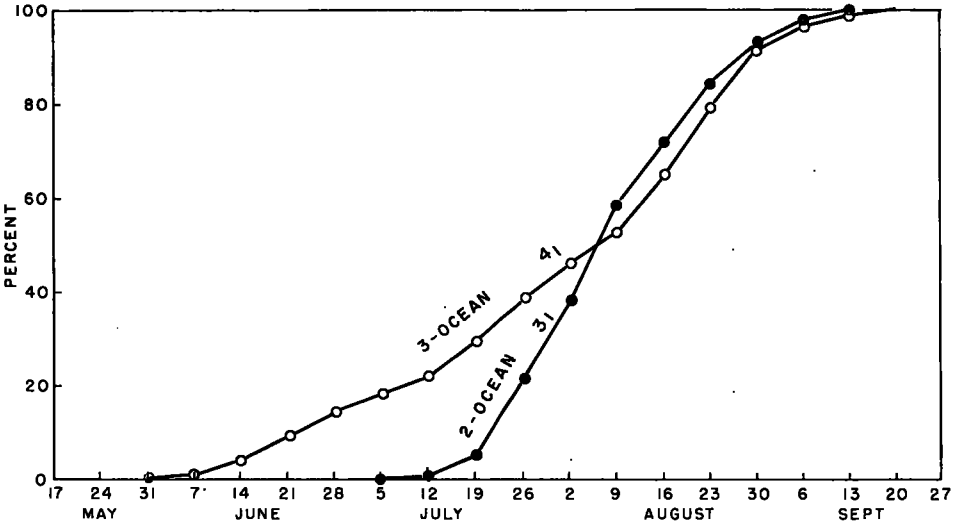

FIGURE 34.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 1-year-old seaward migrants.

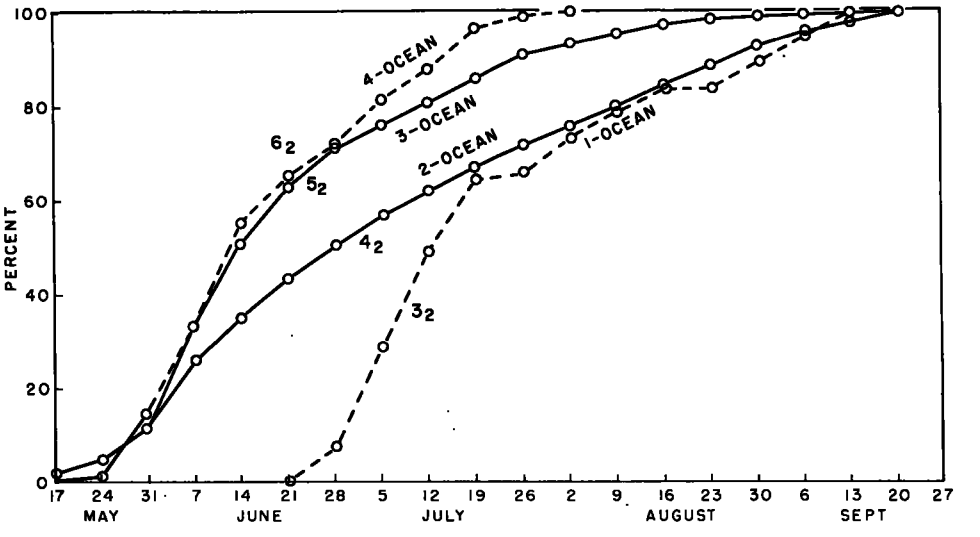

FIGURE 35 —Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 2-year-old seaward migrants.

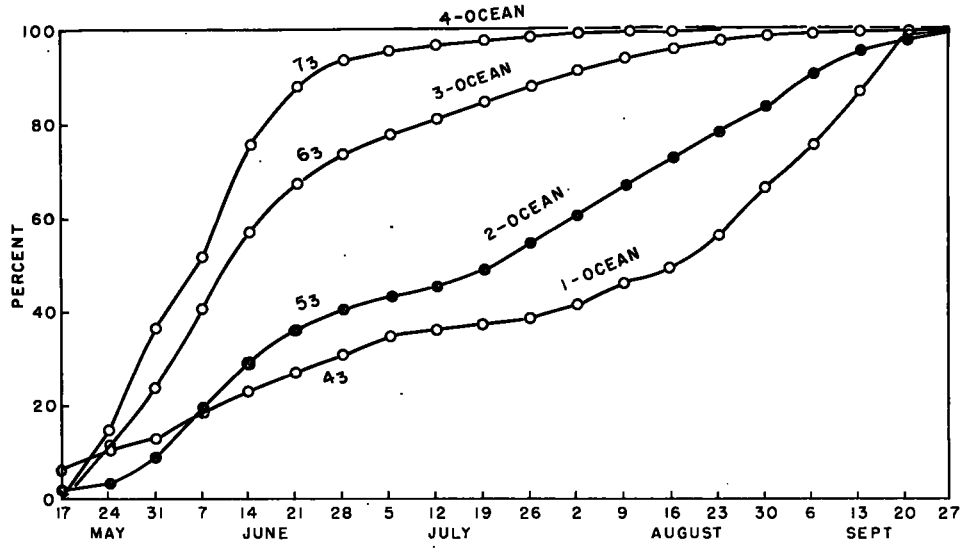

FIGURE 36.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 3-year-old migrants.

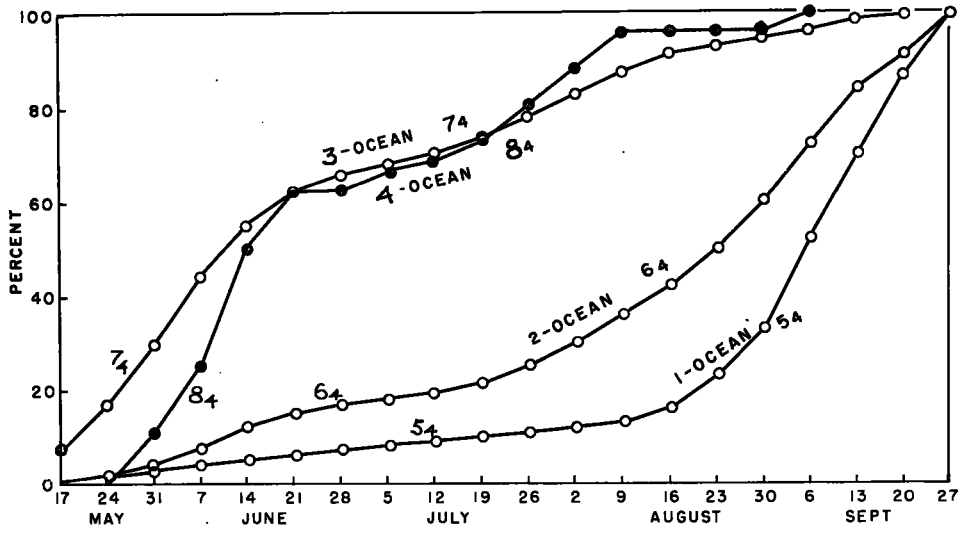

FIGURE 37.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 4-year-old migrants.

The effect of the time spent in the ocean on the season of return migration is very apparent. For each group of migrants, those that remained longest at sea migrated earliest in the season, and those spending the least time at sea migrated latest.

The relation of age at time of seaward migration on the seasonal period of returning migration of adults, irrespective of ocean age, is shown in figure 39 and table 16. In this table the number at each age is weighted according to the normal annual numbers of each age combination. Thus, the curve for migrant age 1 is composed of the curve (table 16) for the 3_1 group weighted by 937 and of the 4_1 group weighted by 1,675; the weights employed for each age group are given in table 17.

Only 8 of the 18 commonly occurring age combinations make any substantial contribution to the runs. These include all the groups in which the migrant age is 2 to 4 with the ocean age 1 to 3. All groups are unimportant in which either the migrant age or the ocean age falls higher or lower than these middle ranges.

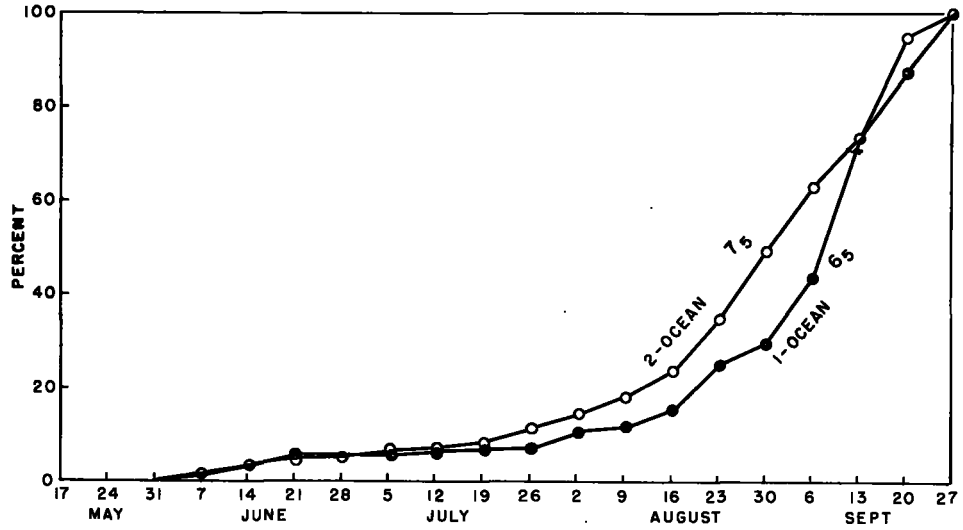

FIGURE 38.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 5-year-old seaward migrants.

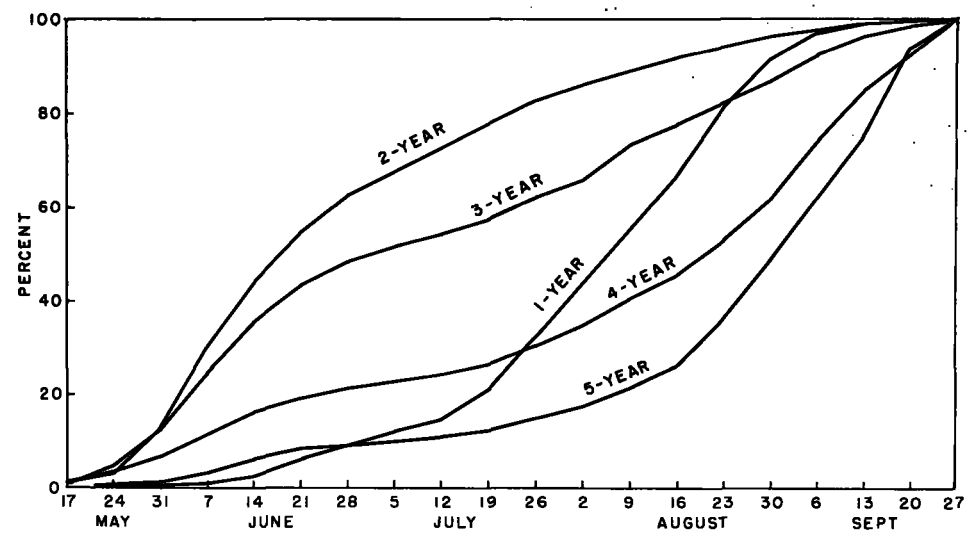

FIGURE 39.—Cumulative percentage seasonal occurrence by age at time of seaward migration of adult sockeye derived from 1- to 5-year-old seaward migrants.

The relation of the time spent at sea on the seasonal period of the returning migration of adults, without regard to age at time of seaward migration, is given in table 18 and shown in figure 40.

When figure 39 is compared with figure 40, the opposing effects of migrant age and ocean age on the seasonal occurrence are very obvious.

In order to show more clearly the effects of age on seasonal occurrence a multiple regression was calculated in which:

X_1 = Total age.

X_2 = Age at time of seaward migration.

Y = Percent of an age group accumulated by the end of the week ending on July 26.

The week ending July 26 was chosen as it represents the approximate midpoint of the runs (54 percent accumulated). Twelve age groups were used (table 17) omitting all with less than 1,000 fish and also the 4_1 group, as the 1-year migrants do not conform to the remainder of the runs. The totals for each group for July 26 are shown in table A4.

TABLE 16.—*Cumulative percentage occurrence of adults according to their age at time of seaward migration*

Week ending	Age at time of seaward migration				
	1	2	3	4	5
May 17	0.0	1.0	0.9	1.2	0.0
May 24	.0	2.9	4.8	3.1	.5
May 31	.2	12.1	12.3	6.2	1.2
June 7	1.0	30.1	24.6	11.6	3.6
June 14	2.9	43.9	35.9	16.3	6.6
June 21	6.4	54.3	43.7	19.6	8.6
June 28	9.7	62.2	48.4	21.7	9.4
July 5	12.2	67.6	51.5	23.1	10.1
July 12	14.7	72.5	54.0	24.5	11.1
July 19	21.3	77.9	57.2	26.8	12.4
July 26	33.0	82.6	62.1	30.4	14.7
Aug. 3	43.9	86.0	67.9	35.0	17.7
Aug. 9	55.3	88.8	73.4	40.4	21.2
Aug. 16	67.5	91.6	77.9	45.7	26.1
Aug. 23	81.2	94.0	82.3	52.9	36.1
Aug. 30	91.8	96.2	86.8	62.0	48.9
Sept. 6	97.0	97.6	92.3	74.0	61.7
Sept. 13	99.3	99.0	96.4	84.7	75.4
Sept. 20	100.0	99.9	98.5	92.3	94.0
Sept. 27	100.0	100.0	100.0	100.0	100.0

TABLE 17.—*Normal age distribution of annual run of sockeye, May 17 to September 27, for 1922 and 1924–49*

Age group	Number of fish	Total age	Number of fish	Migrant age	Number of fish	Ocean age	Number of fish
3_1	937	3	1,009	1	2,612	0	131
3_2	72						
4_1	1,675	4	38,457	2	38,125	1	51,592
4_2*	15,928*						
4_3*	20,723*	5	947,548	3	1,211,010	2	1,262,383
4_4	131						
5_2*	21,990*	6	640,636	4	423,571	3	363,906
5_3*	895,479*						
5_4*	30,079*	7	51,618	5	4,661	4	1,967
6_2	135						
6_3*	293,387*	8	711				
6_4*	346,396*						
6_5	718						
7_3	1,421						
7_4*	46,554*						
7_5	3,643						
8_4	411						
8_5	300						
Total	1,679,979		1,679,979		1,679,979		1,679,979

*Age groups contributing materially to the runs.

TABLE 18.—*Cumulative percentage occurrence of adults according to their ocean age*

Week ending	Ocean age at time of return				
	0	1	2	3	4
May 17	0.0	2.5	0.5	2.4	0.0
May 24	.0	4.4	2.3	11.0	10.2
May 31	.0	6.8	7.6	22.1	29.2
June 7	.0	9.7	16.4	40.2	44.8
June 14	.0	12.5	24.6	55.7	69.2
June 21	.0	14.8	30.4	66.1	80.7
June 28	.0	16.9	34.0	72.2	85.2
July 5	.0	19.3	36.3	76.0	88.2
July 12	.0	20.3	38.5	79.0	90.1
July 19	.0	21.1	41.5	82.6	92.3
July 26	.0	22.5	46.4	86.2	94.8
Aug. 2	.0	24.1	52.6	89.9	97.0
Aug. 9	.0	26.7	58.8	92.9	98.8
Aug. 16	13.1	29.6	64.3	95.2	98.8
Aug. 23	26.2	36.8	70.2	96.8	99.2
Aug. 30	50.8	46.8	77.0	98.0	99.2
Sept. 6	66.9	61.5	85.6	98.8	100.0
Sept. 13	86.9	76.8	92.4	99.5	
Sept. 20	96.2	92.0	96.3	99.9	
Sept. 27	100.0	100.0	100.0	100.0	

The resulting correlations were $r_{12}=0.59$, $r_{y_1}=0.18$ and $r_{y_2}=-0.68$. The β coefficients, however, give the measure of the relation of each X to Y divorced from the effect of the other factor:

$$\beta_{Y_{1.2}}= 0.88$$

$$\beta_{Y_{2.1}}=-0.88$$

$$\hat{Y}=17.67+24.37\ X_1-30.01\ X_2$$

The β-values show that migrant age and total age have exactly equal and opposite effects in determining the season of migration.

The effect of early migration on time of run may be linked with the fact that those leaving the lake at the younger ages appear to be the

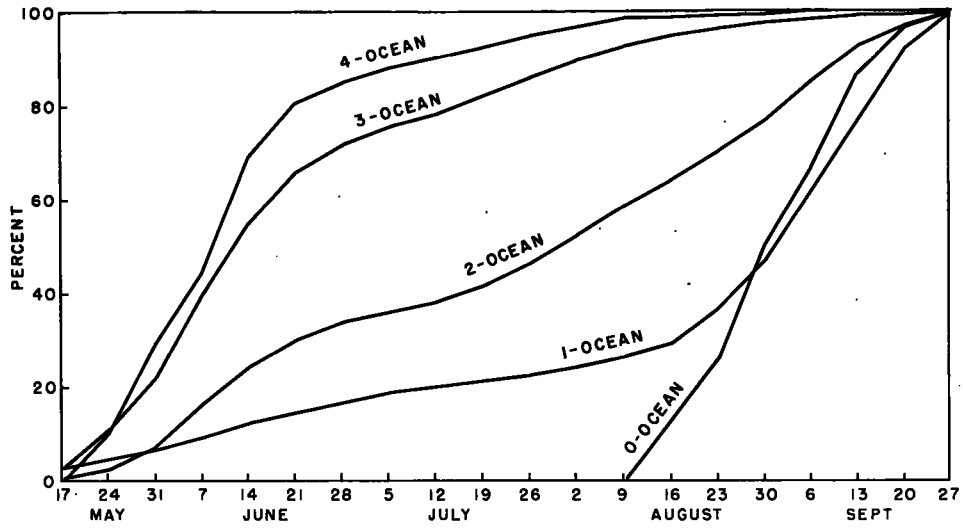

FIGURE 40.—Cumulative percentage seasonal occurrence by ocean age of adult sockeye derived from fish spending 0 to 4 seasons in the ocean.

fastest-growing individuals of each brood. In most organisms the age at maturity is closely related to the rate of growth. Table 19 shows the relation between size and time of seaward migration. The season of seaward migration coincides with the commencement of the period of most rapid growth. Since the 3-year-olds are growing relatively faster than the 4-year olds, their decrease in size is more masked by growth. The 4-year-olds clearly show that the largest individuals of the group were first to leave the lake.

Relation between season of smolt migration and ocean age

There is a definite relation between the time at which the smolts migrate and the length of their stay in the sea. Barnaby (1944) gives data for marking experiments conducted on different dates in 1932. In the second and fourth experiments the fish were marked by excision of the adipose and one pectoral fin. Since the results from these and a previous experiment in 1930 showed that the pectoral-marked fish suffered heightened mortality, we have omitted the second and fourth markings. The first and third markings (15,000 fish each) employed the adipose and right ventral (pelvic) and adipose and left ventral, respectively.

The first lot (first experiment) was taken on May 27 and 28; the second lot (third experiment), on June 6, 7, 8, and 9. Thus, the two lots average 12 days apart. The results are as follows:

Ratio of 2-ocean to 3-ocean fish in returns

Age at release	Marking dates		
	May 27–28	June 6–9	Both dates
3	2.46	1.37	1.76
4	2.94	1.95	2.41

It will be noted that the 4-year-olds tend to stay a shorter time at sea than the 3-year-olds (ratio of 2.41 against 1.76). There is a sharp decrease in the proportion of 2-ocean returns from the second lot. Since we have shown (table 19) that the larger smolts of each age are first to leave the lake, it becomes apparent that the fastest-growing smolts are first to reach maturity.

The 4-year-old smolts tend to compensate for their greater age at seaward migration by a shorter sea life than the 3-year-olds. Within the group itself the faster-growing also tend to mature earlier (fig. 41), as the ratio of 2- to 3-ocean fish in the lot that migrated seaward earlier.

Do the Karluk sockeye belong to one population?

This question deserves careful study and elucidation, because the system of regulation depends on the answer. The prevalent opinion that there are races depends chiefly on the knowledge that different races of sockeye are found in some large river systems, such as the Fraser, and these races traverse the main channel leading to the different tributaries at different seasons. There has also

TABLE 19.—*Lengths of seaward migrants by weeks as percent of length during week ending June 7*

Year	3-year-old migrants				4-year-old migrants			
	May 31	June 14	June 21	June 28	May 31	June 14	June 21	June 28
1925		99.65				96.08		
1926	100.48	99.33			100.84	95.94		
1927		102.12	101.15			100.64	98.84	
1928		98.85	96.93			99.15	96.10	
1929	102.41	98.17			100.50	94.24		
1930	98.46	103.66	101.18	98.40	100.37	101.56	97.24	90.40
1931	99.16	100.45	98.54		102.60	96.79	94.74	
1932	99.72	99.94	100.15	103.16	101.52	96.43	91.86	96.54
1933	99.43	98.74		95.26	101.38	96.60		93.97
1934	102.09		101.01		105.12		96.20	
1935	99.72	99.23			99.80	96.87		
1936	102.63	97.66			104.76	96.14		
1937	98.83	99.33	97.82		100.40	99.76		
1938	98.34	101.08	101.41		97.77	98.69	97.85	
1939		100.16	99.15			96.36	92.51	
1940	99.09	98.18			102.60	97.33		
1941	101.11	96.29			102.60	100.22		
1947	98.24				100.16			
1948	98.66		96.08		96.45		101.37	
1949		97.05				98.47		
1950	100.68	99.58	101.69	103.64	99.63	98.09	98.75	98.31
Sums	1,599.05	1,789.47	1,095.11	400.46	1,616.50	1,759.36	965.46	379.22
Items	16	18	11	4	16	18	10	4
Average	99.94	99.42	99.56	100.12	101.03	97.74	96.55	94.81

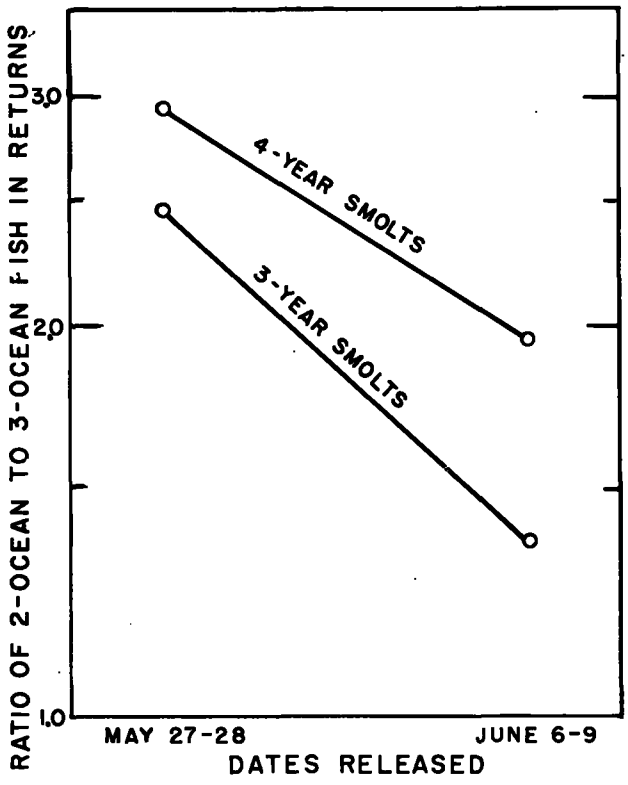

FIGURE 41.—Relation of season of smolt migration on the ocean age of the returning adults.

been a strong indication that at least two races may exist in the Chignik River, which enters Shelikof Strait from the mainland on the opposite shore from Karluk. However, neither the Fraser nor the Chignik present the same picture as Karluk.

The main Fraser constitutes merely a passageway for the salmon bound to particular lake systems. The question of two or more populations in a single lake as at Karluk is not involved. The Fraser salmon are predominately of one age so that the problem of varying age at maturity affecting the season of migration does not arise.

The Chignik system contains two large lakes, one deep oligotrophic lake on the southern side of the Alaska Peninsula, and one shallow eutrophic lake on the northern side of the peninsula so that two races, each growing in a different ecological situation are possible.

Let us examine for the Karluk system the available evidence for and against the existence of different races. The basis for the hypothesis of two races is the shape of the curve for the seasonal occurrence of the run and the fact that surveys of the spawning grounds seem to indicate a pronounced midsummer lull in spawning activity. There also is some evidence that whereas the earlier spawners use all of the streams entering the lake, the later spawners use chiefly the larger streams and the lake itself. None of these facts, however, necessarily have any bearing on whether there is more than one self-perpetuating race of sockeye in the lake.

Before examining contrary evidence we might briefly examine the above facts to see whether they can be consistent with a single population. First, let us look at the curve of seasonal occurrence (fig. 33). This indicates two or possibly three distinct modes, and as the data cover a 30-year period there is no reason to doubt their authenticity. The curves of occurrence by age groups (table A3) show that there are not two but three distinct modes in both the 5_3 and 6_4 age groups, other age groups show at least one or two of the same three modes. If races are to be postulated on the shape of the curve of seasonal occurrence alone, we must admit of three rather than two populations.

A lull in the seasonal run to the river for one or more age groups of the population is not sufficient evidence of more than one population. There are many other explanations. One of these is the fact that those fish of an age group that are fully mature at the beginning of the season hasten to the river, causing a heavy initial run. This explanation is supported by the fact that those age groups with a long sojourn at sea run early in the season, their run corresponding with the early maturing 5_3 and 6_4 fish, while age groups with a short sojourn at sea run late in the season since they require additional summer growth to attain maturity.

The evidence for only one population of sockeye at Karluk is rather conclusive. In figures 42 to 45 are shown as percentages by weeks the seasonal occurrence of the runs of several age groups.

It will be noted in each instance that the 1-ocean-age fish, 3_2, 4_3, 5_4, and 6_5 ran latest in the season. Of this group the ones with the shorter fresh-water sojourn ran earlier, being the faster growing smolts. The 2-ocean-age fish, 4_2, 5_3, 6_4, and 7_5, ran earlier than the 1-ocean fish, and as in the 1-ocean group, the order of their abundance in relation to the season was governed by their fresh-water history. Thus the 4_2 fish ran pre-

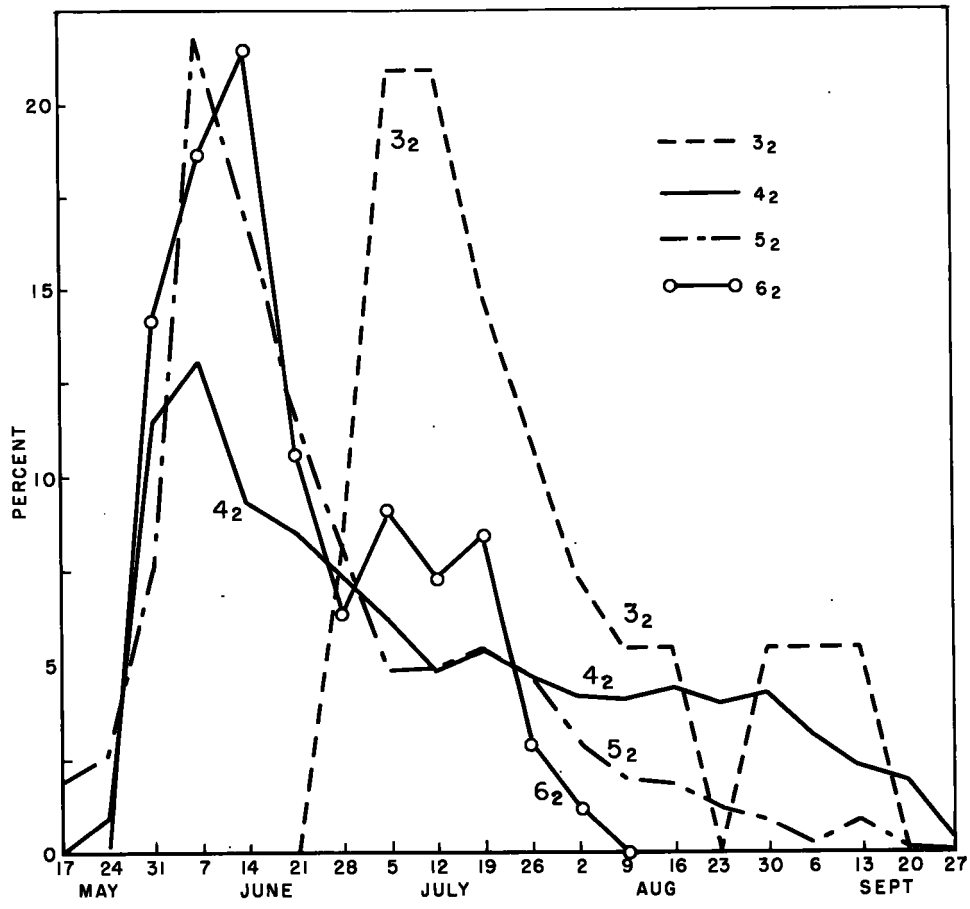

FIGURE 42.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 2-year-old seaward migrants.

dominantly in the early summer attaining 50 percent by the week ending on June 28. The 5_3 group averaged 3 weeks later (48.9 percent by July 19), followed 5 weeks later by the 6_4 fish (50.5 percent by Aug. 23) and ending with the 7_5 group (49.3 percent by Aug. 30).

The same sequence of events holds true for the 3- and 4-ocean-age groups. These seasonal age relations show that the season of migration is linked with age, not with race.

If the runs were to consist of two populations, the spring (and early summer) and the fall (and late summer) portions of the runs would, of course, vary independently. However, the reverse is the case. The number of 4_3 fish (reference to figure 43 will show run predominantly in the fall) is highly correlated with the number of 5_3 fish running the following year, $r=.956$, which is highly significant (table 20).

TABLE 20.—*Correlations between adults of the same brood year from smolts descending to the sea in their third year, but returning at different ages*

X	Y			
	5_3	6_3	7_3	5_3+6_3
4_3	.956**	−.100	−.172	.909**
5_3		.006	−.182	
6_3			.716**	

The 5_3 age group always comprises the largest share of the runs. It is also the only age group that runs strongly during both spring and fall. To test the relationship of the spring and fall components of this run the group has been divided into two portions: those running before July 19 and those running later (table 21).

Since the variance was correlated with the mean in these series, the data were transformed to

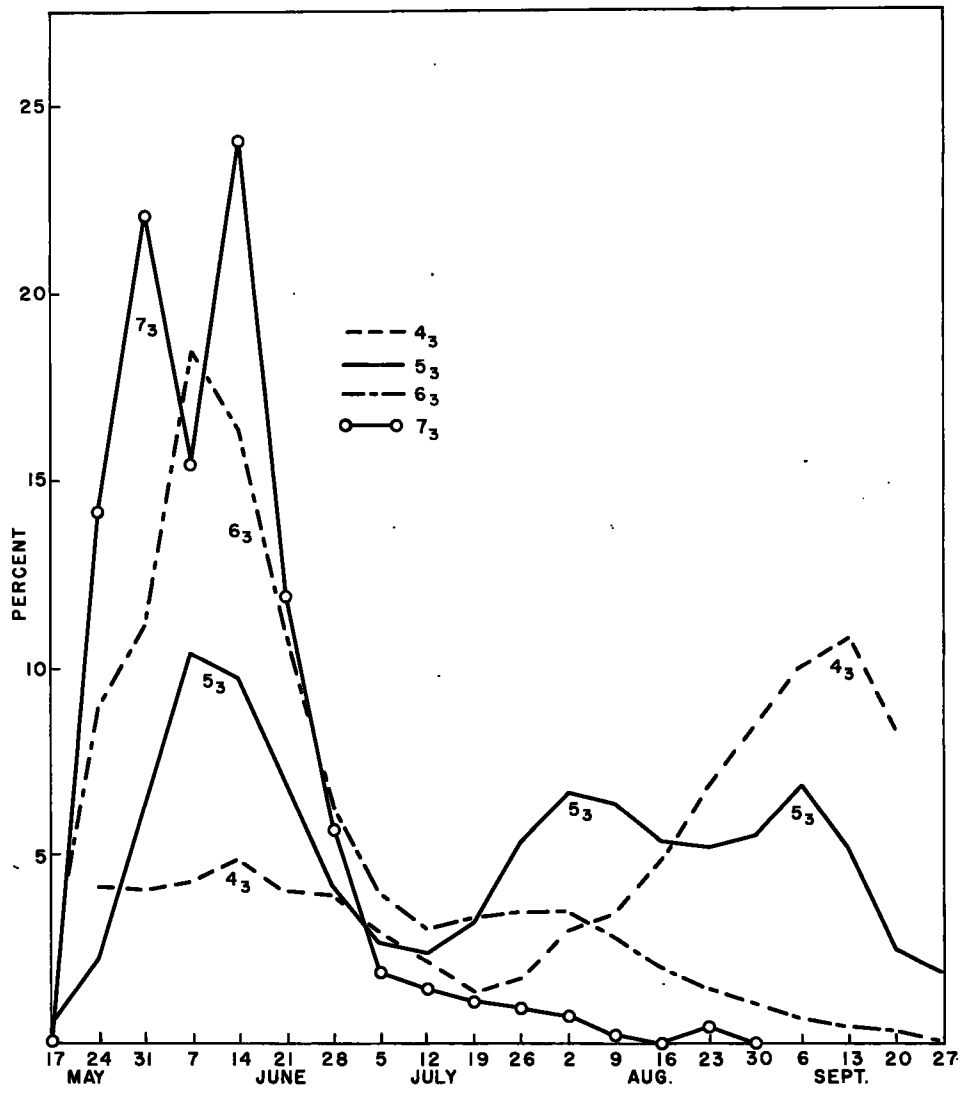

FIGURE 43.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 3-year-old seaward migrants.

logarithms. Plots of temperature data showed that there is a positive relation between temperature and the proportion of 5_3 fish returning in the fall. Therefore, a multiple correlation was calculated to show the relation between the late-running 5_3 fish, Y, the early-running 5_3 fish, X_1, and the sum of the degrees of temperature (air) for Kodiak above 40° F, during July and August, X_2, the results are as follows for 1924–49 (except 1941 for which July temperatures were not available):

Logarithm of number of late-running 5_3 fish	Logarithm of number of early-running 5_3 fish	Accumulated monthly air temperature over 40° F at Kodiak during July and August
Y	X_1	X_2
Correlation of Y with X's	0.81854**	0.28461
Standard regression of Y on X's	.8071**	.2472

This indicates that about 64 percent of the variation in numbers of late-running 5_3 fish is associated with variations in the numbers of early-running 5_3 fish of the same brood.

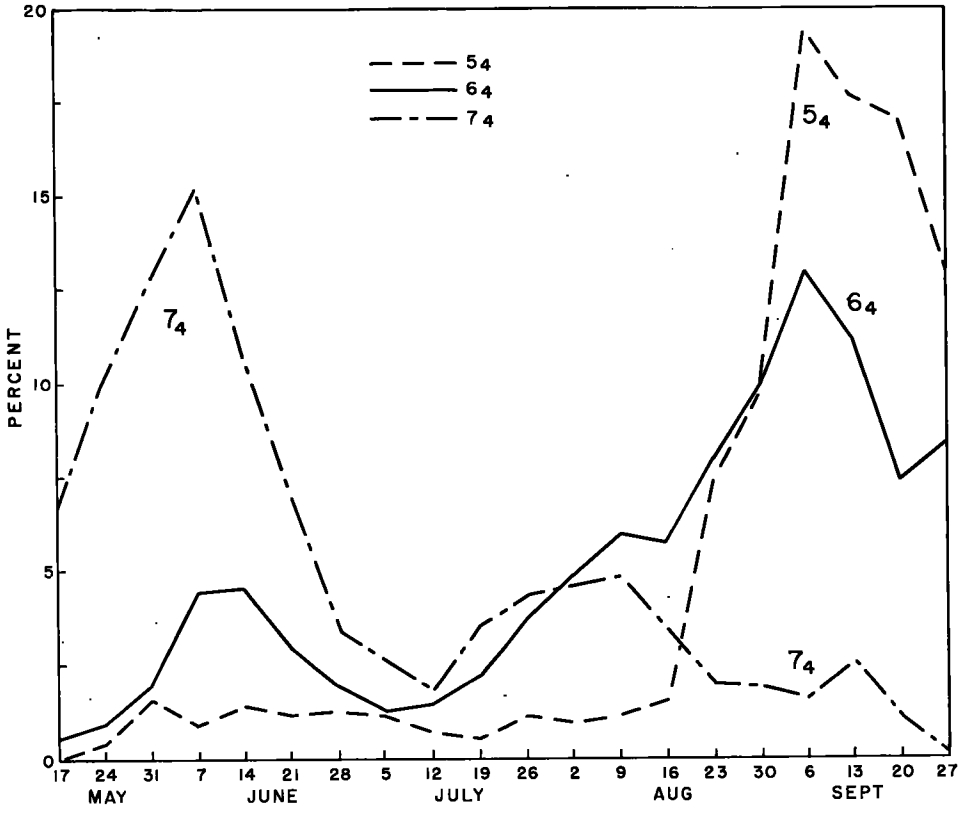

FIGURE 44.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 4-year-old seaward migrants.

TABLE 21.—*Numbers of sockeye of age 5_3 occurring early and late in the season*

Year	Numbers in the run			Dates of occurrence of percentiles of run				
				Total run			Early run	Late run
	Early run (to July 19, in thousands)	Late run (after July 19, in thousands)	Total run [1] (thousands)	25th	50th	75th	50th	50th
1922	132	560	692	July 27	Aug. 22	Sept. 7	June 25	Aug. 30.
1924	676	716	1,393	June 15	July 26	Aug. 25 ca.	June 14	Aug. 21.
1925	629	1,357	1,985	June 26	Aug. 2	Aug. 24	June ?	Aug. 15.
1926	1,469	2,491	3,960	June 17	Aug. 4	Aug. 26	June 6	Aug. 21.
1927	627	513	1,140	June 12	July 6	Aug. 4	June 13	Aug. 10.
1928	533	674	1,206	June 16	July 27	Aug. 13	June 10	Aug. 12.
1929	170	216	386	...do...	July 23	Aug. 16	June 14	Aug. 14.
1930	251	417	668	June 13	July 29	...do...	June 10	Aug. 11.
1931	239	552	741	July 6	Aug. 5	Aug. 25	June 16	Aug. 21.
1932	499	251	751	June 8	June 22	July 29	June 12	Aug. 9.
1933	611	369	979	June 7	June 18	Aug. 9 ca.	June 11	Aug. 9 ca.
1934	409	303	712	...do...	June 28	Aug. 20 ca.	June 9	?
1935	256	248	504	June 10	July 14	Aug. 8	June 10	Aug. 10 ca.
1936	659	1,050	1,708	June 17	July 30	Aug. 25	June 12	Aug. 20 ca.
1937	1,178	412	1,589	June 7	June 17	July 22	June 11	Aug. 23.
1938	784	543	1,326	June 10	June 26	Aug. 14	...do...	Aug. 25.
1939	177	181	358	June 16	July 20	Aug. 16 ca.	June 16	Aug. 26 ca.
1940	238	181	419	June 4	July 6	Aug. 10	June 9	Aug. 14.
1941	265	570	835	June 17	Aug. 7	Aug. 26	June 2 ca.	Aug. 22.
1942	356	245	601	June 10	July 3	Aug. 6	June 13	Aug. 18.
1943	590	359	950	June 11	June 28	Aug. 22 ca.	June 16	?
1944	364	432	796	June 13	July 22	...do...	June 11	Aug. 18 ca.
1945	181	82	264	June 9	June 22	July 27	June 13	Aug. 6 ca.
1946	64	58	123	June 12	July 11	Aug. 8	June 16	Aug. 10.
1947	64	94	158	June 21	July 26	Aug. 7	...do...	Aug. 5.
1948	614	388	1,003	June 8	July 3	July 29	June 12	Aug. 2.
1949	250	346	596	June 15	July 24	Aug. 7	...do...	Aug. 6.

[1] Slight discrepancies due to rounding off figures.

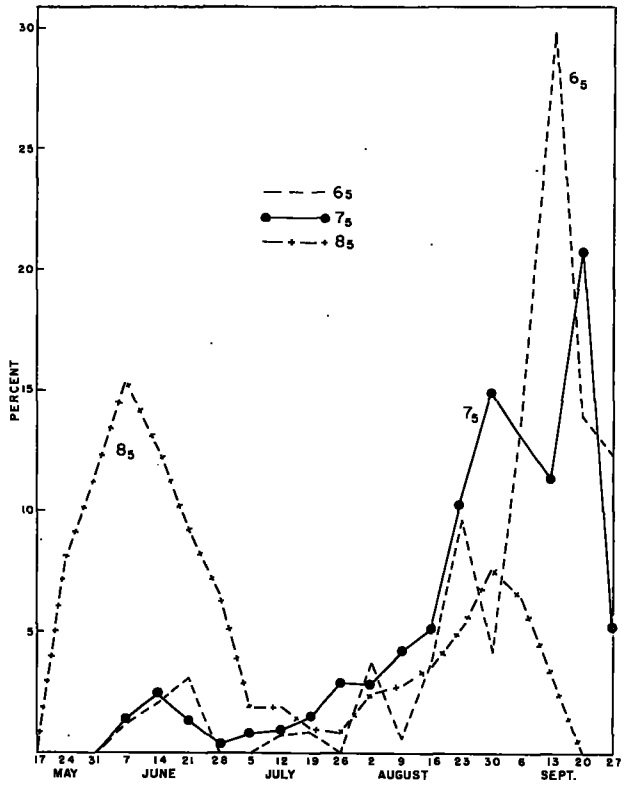

FIGURE 45.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 5-year-old seaward migrants.

So far we have shown that grilse of 4_3 age (running chiefly in the fall) are undoubtedly of the same population as the fish of the 5_3 age group returning in the following year and running strongly during both spring and fall. Also a strong correlation has been found between the spring and fall-running fish of the 5_3 group.

Some of the smolts leaving the lake in their third year also return as the 6_3 and 7_3 age groups. The 7_3 group is so minor (table A-5) that it can safely be ignored, but the 6_3 group is the third largest, exceeded only by the 5_3 and 6_4 groups.

Because of the numerical importance of this 6_3 age group, and the fact that its members run chiefly in the spring (84 percent normally enter the river before July 19), it could conceivably be argued that it constitutes a separate and self-perpetuating population. Of course, in order for this to be true its members would have to either spawn apart from sockeye of the 5_3 age group or (which would seem highly improbable) seek out individuals of the same age group with which to spawn. Although either alternative seems too improbable to warrant serious consideration we shall examine the evidence pro and con.

The total numbers of the 6_3 group are not significantly correlated with the total numbers of the 5_3 group of the previous year, r equals .006 or with the 4_3 group of the same year class, r equals —.100. However, there are sound biological reasons why these correlations of total numbers are not expected to be significant. The number of 6_3 fish is dependent both on the total number of survivors of the brood year and on the number that mature at an earlier age, so that when a high proportion of 3 fresh-water fish of a brood mature in their fifth year, there are fewer remaining to mature in their sixth year.

To show the relation between brood size and the proportion maturing in their sixth year, the percentage of each brood year (1920–42 brood years) returning as 6_3 fish has been correlated with the total numbers of the same brood year returning at all ages. The correlation coefficient of —.5567 while not denoting a high degree of relationship is highly significant. The explanation of this relationship may be twofold. First, the number of survivors may be greater from brood years with faster-growing (and therefore larger) smolts. When fish are larger they tend to return at younger ages, resulting in a lesser percentage of 6_3 fish from brood years producing large runs. Secondly, there is undoubtedly a significant natural mortality during the additional year in the sea so that when a smaller percentage of a brood remain at sea until their sixth year, the total number ultimately returning to the river is greater.

There is, however, a significant relation between the 6_3 and the *late-running* 5_3 fish that is somewhat obscured by other factors. To remove the effect of these factors in order to determine the degree of relationship it was first necessary to obtain two sets of residuals. The first set, for the 6_3 fish, are the residuals (which we will call set A) from the regression of the percent that the 6_3 fish were of the total of each brood year of smolts migrating to sea in their third year, on the total numbers of returning adults in each brood year. The second set (which we shall call set B) for the late-run 5_3 fish, are the residuals from the regression of the logarithms of the late-run 5_3 fish on the logarithms of the early-run 5_3 fish with the temperature factor held constant.

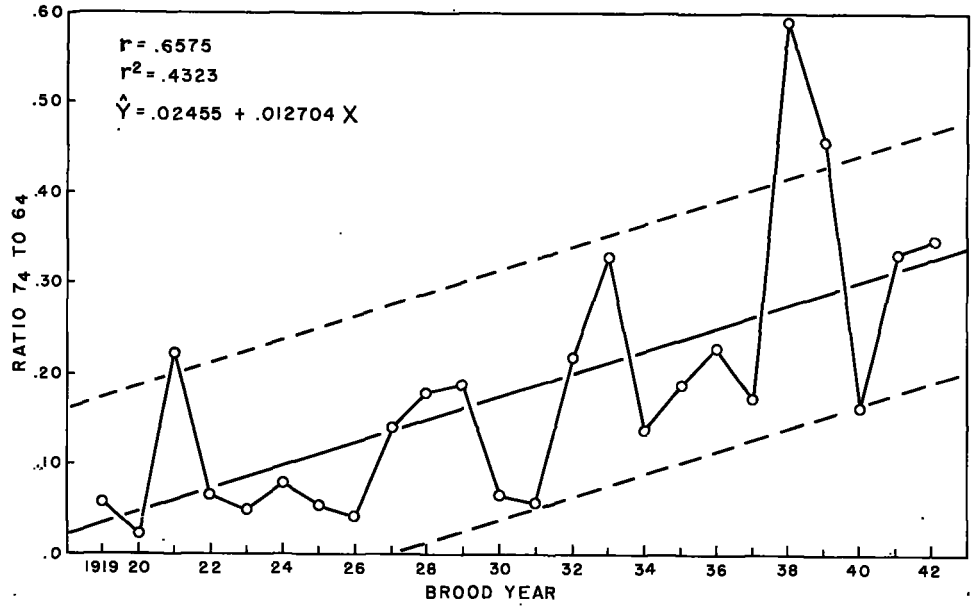

FIGURE 46.—Regression of the ratio of 7_4 to 6_4 of the same brood on time.

The coefficient of correlation between the residuals of set A and set B, −0.5045 is statistically significant at the 5 percent level. This indicates two things: first, that the 5_3 and 6_3 fish belong to the same population, and second, that the fluctuations in the numbers of 6_3 fish are determined chiefly by the fluctuations in rate of growth of the 3-freshwater age group.

In summary, the evidence strongly indicates that the Karluk sockeye salmon comprise one population, since the number of fish of the same brood running at different seasons, and even in different years, are significantly correlated.

Increase in average age at maturity

Barnaby (1944) pointed out that there seemed to be an increase in age of the sockeye from the brood years of 1920–29. He concludes that since the evidence from his marking experiments does not indicate any marked change in the ocean mortality of either the 3-year or the 4-year seaward migrants, the change may be due to an increase in the length of fresh-water residence. He further suggests that this may be linked with a decreased rate of growth in fresh water.

To test this theory over a longer period of time the proportion of 7_4 age fish to the 6_4 age fish of the same brood was correlated with time for the brood years of 1919–42 (24 years). The correlation coefficient of +0.658 is highly significant. The average ratio of $7_4/6_4$ rose from 0.03 for the 1919 brood to 0.33 for the 1942 brood (fig. 46).

The same correlation was tried using only the late-running 6_4 fish (running after July 19) and the correlation coefficient was +0.761. This indicates clearly that the number of spring-running 7_4 fish is closely correlated with the numbers of fall-running 6_4 fish. As the ratio appeared to fluctuate more widely as its value increased the logarithm of the 7_4/late-running 6_4 ratio was correlated with time resulting in a correlation coefficient of +0.812 (fig. 47). The antilogs of the regression line show an increase from .05 to .54 in the 7_4/late-running 6_4 ratio between the 1919 and 1943 brood years (fig. 47).

That increasing age of seaward migrants is a general phenomenon and not connected with one age group of seaward-migrating smolts is shown by the correlation coefficient of +0.579 between the ratio of 6_3 fish to late-running 5_3 fish against time.

Having established that the average duration of lake residence, as shown by the seaward-migrant ages of the returning adults, has increased steadily and markedly over a period of 24 years, we shall next inquire into the underlying cause.

Relation of size of brood to age at maturity

Since the increase in average age of the adult sockeye has been occurring during a period when

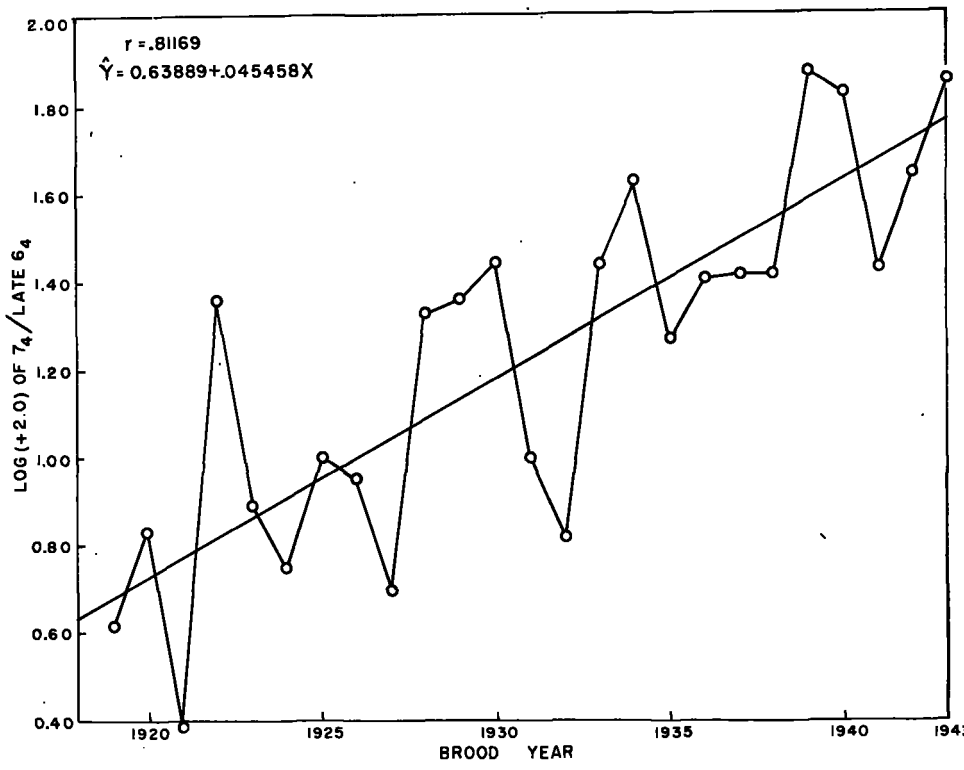

FIGURE 47.—Regression of log of ratio of 7_4 age fish to late-running 6_4 sockeye of the same brood on time.

the runs are declining in size, one should therefor inquire whether there is any relation between age at maturity and size of the brood. In table 22 we have shown the percentage of 4,[1]5, 6, and 7-year-olds in each of the 23 broods from the spawning of the years 1920–42, inclusive. The coefficients of correlation of age percentage on brood-size are:

Age at maturity	Coefficient of correlation
4 (plus a few 3)	0.26
5	.78**
6	—.78**
7 (plus a few 8)	—.60**

The regressions of age percentage on brood size are shown in figures 48 and 49, and all four curves are combined in figure 50. The linear regressions obviously do not give the best fit if the curves are extrapolated for larger broods. In fact, table 23 shows clearly that for larger broods linear extrapolation would yield more than 100 percent. Therefore in figure 50 and the bottom portion of table 23, it was necessary to make empirical curvilinear fits from grouped averages, for all but the 4-year-olds.

TABLE 22.—*Percent at certain ages in returns from brood years*

Brood year	Total returns (—000)	Percent at each age			
		[1] 4	5	6	[2] 7
1920	2,849	2.03	72.35	25.16	0.46
1921	4,494	4.31	89.45	5.54	.69
1922	2,282	6.62	55.99	36.48	.91
1923	1,990	2.76	61.08	35.24	.91
1924	809	2.01	48.72	47.27	2.01
1925	1,607	.73	50.52	45.73	3.02
1926	1,461	2.82	57.89	37.15	2.14
1927	1,618	1.69	48.76	45.34	4.21
1928	2,630	1.22	39.22	54.11	5.45
1929	1,587	1.12	51.00	42.27	5.61
1930	1,172	5.87	50.72	39.80	3.61
1931	2,578	4.75	71.22	22.18	1.86
1932	2,538	2.45	65.25	28.87	3.43
1933	2,186	2.99	62.35	32.01	2.66
1934	1,261	5.68	33.11	56.19	5.02
1935	1,250	.78	38.90	53.23	7.09
1936	1,353	1.15	65.11	28.85	4.90
1937	1,334	1.50	46.57	48.23	3.70
1938	1,587	2.25	61.98	30.58	5.20
1939	1,831	1.89	46.95	46.10	5.06
1940	858	1.86	45.69	48.67	3.78
1941	575	2.71	26.66	58.94	11.70
1942	607	1.18	32.95	53.81	12.07

[1] Plus a few 3-year-olds.
[2] Plus a few 8-year-olds.

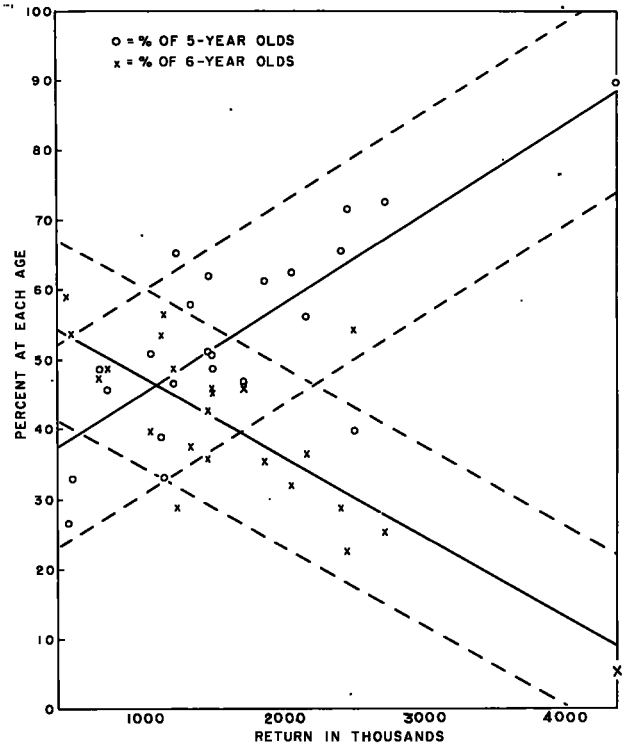

FIGURE 48.—Regressions of percent of 5-year-olds and of percent of 6-year-olds on the size of the returning brood of which they are a portion.

The relation of brood size to age percentage may be easily converted to average age for each brood size from table 23. Thus during the period 1922 and 1924–49 (table 16) the average run of 1,680,000 sockeye averaged 5.42 years in total age, which compares closely with 5.41, the average age calculated from table 23 for a run of 2,000,000. The average calculated ages for runs of 500,000 to 4,000,000 are:

Size of run	Average age
500,000	5.69
1,000,000	5.58
1,500,000	5.49
2,000,000	5.41
3,000,000	5.26
4,000,000	5.15

This negative relation between average-age and brood-size is caused primarily by the young of the smaller broods tending to remain an additional year in the lake (p. 136).

Seasonal distribution of the escapement

The seasonal distribution of escapement has not paralleled the seasonal occurrence of the runs.

TABLE 23.—*Curves for estimating ages of Karluk sockeye in returns of varying size*

Number in returns (—000)	Percent at each age by linear least square fit				
	4	5	6	7	Total
0	1.73	30.48	60.04	7.75	100.00
1,000	2.24	43.37	48.69	5.71	100.01
2,000	2.75	56.26	37.34	3.66	100.01
3,000	3.26	69.14	25.99	1.61	100.00
4,000	3.76	82.03	14.64	—.43	100.00
5,000	4.00	95.00	3.00		
6,000	4.30	100.00			
	Percent at each age by empirical fit from grouped averages				
0	1.7	25.5	62.8	10.0	
250	1.8	30.5	58.7	9.0	
500	2.0	35.0	55.0	8.0	
750	2.1	39.3	51.6	7.0	
1,000	2.2	43.5	48.2	6.1	
1,250	2.4	47.0	45.3	5.3	
1,500	2.5	50.4	42.3	4.8	
1,750	2.6	54.1	39.2	4.1	
2,000	2.8	57.0	36.7	3.5	
2,250	2.9	60.0	34.1	3.0	
2,500	3.0	63.0	31.4	2.6	
2,750	3.2	65.9	28.8	2.1	
3,000	3.3	68.7	26.3	1.7	
3,250	3.4	71.2	24.0	1.4	
3,500	3.5	73.6	21.6	1.3	
3,750	3.6	76.1	19.2	1.1	
4,000	3.8	78.2	17.0	1.0	
4,250	3.9	80.3	15.0	.8	
4,500	4.1	82.2	13.1	.6	
4,750	4.2	84.1	11.3	.4	
5,000	4.4	85.8	9.5	.3	
5,250	4.5	87.4	7.9	.2	
5,500	4.6	88.8	6.4	.2	
5,750	4.7	90.1	5.1	.1	
6,000	4.9	91.2	3.9	.0	
6,250	5.0	92.0	3.0		
6,500	5.2	92.7	2.1		
6,750	5.3	93.3	1.4		
7,000	5.4	93.8	.8		
7,500	5.8	93.9	.3		
8,000	6.0	94.0	.0		

This is similar to conditions on the Fraser River (Rounsefell and Kelez, 1938, pp. 764–765) where the fishing during the early years was concentrated on the peak of the run with the result that this portion was depleted early in the history of the fishery. The total runs, catches, and escapements for the 30-year period from 1921 to 1950 are given in tables 24, 25, and 26. The tendency for low escapements during the middle of the season and high escapements both early and late is very marked.

The percent of the run escaping by time periods is given in table 27 and figure 51. This arouses the question of whether the central portion of the run has declined more than the early and late portions. If each portion were to represent a more or less separate and self-sustaining population such a tendency should show. However, if the entire run is one population with the time of seasonal run determined largely by varying ecological conditions to which each brood is subjected, then all portions should show the same general trends.

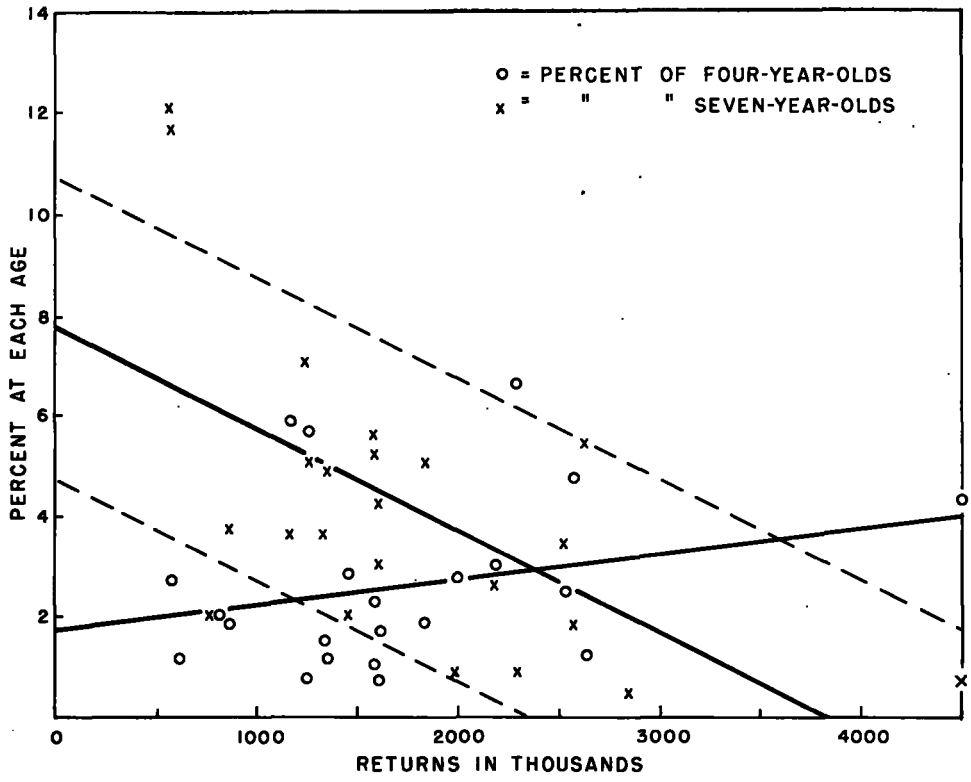

FIGURE 49.—Regressions of percent of 4-year-olds and of percent of 7-year-olds on the size of the returning brood of which they are a portion.

TABLE 24.—*The total run of sockeye to the Karluk River, 1921 to 1950*

Year	Total run by periods in thousands							
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season	Total run
1921	22	523	589	932	847	230	1,077	3,143
1922	10	135	200	216	395	102	497	1,058
1923	73	275	206	407	370	94	464	1,425
1924	91	457	314	349	?	?	742	1,953
1925	63	536	276	954	876	239	1,115	2,944
1926	561	845	466	1,138	1,773	137	1,910	4,920
1927	62	517	256	402	268	82	350	1,587
1928	166	587	335	598	320	89	409	2,095
1929	76	310	117	229	309	87	396	1,128
1930	44	287	149	337	253	184	437	1,254
1931	63	289	190	338	561	184	745	1,625
1932	49	432	207	273	274	177	451	1,412
1933	27	757	296	305	357	71	428	1,813
1934	204	893	288	316	?	?	669	2,370
1935	162	548	168	294	227	132	359	1,531
1936	183	603	283	613	675	96	771	2,453
1937	5	1,087	345	298	507	94	601	2,336
1938	0	938	285	396	?	?	595	2,214
1939	84	455	227	189	209	51	260	1,215
1940	269	303	104	229	?	?	363	1,268
1941	226	289	102	367	?	?	645	1,629
1942	153	289	151	195	284	64	348	1,136
1943	155	675	290	163	?	?	444	1,727
1944	99	503	173	294	?	?	341	1,410
1945	60	702	254	217	89	13	102	1,335
1946	65	248	136	104	39	78	117	670
1947	5	219	69	176	119	7	126	595
1948	179	449	265	424	86	8	94	1,411
1949	34	380	162	397	162	6	168	1,141
1950	48	460	170	267	270	48	318	1,263
Sum	3,238	14,991	7,073	11,417	------	------	15,342	52,061
Minus 1924 and 1934	2,943	13,641	6,471	10,752	------	------	13,931	47,738

TABLE 25.—*The total catch of Karluk River sockeye, 1921 to 1950*

Year	Total catch by periods in thousands						
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Total
1921	0	35	394	591	567	56	1,643
1922	0	40	102	175	318	23	658
1923	0	141	126	254	199	10	730
1924	0	116	180	139	?	?	891
1925	0	42	151	663	467	0	1,323
1926	0	235	317	773	1,050	12	2,387
1927	0	34	180	310	191	0	715
1928	0	110	201	469	195	26	1,001
1929	0	57	83	87	0	0	227
1930	0	1	103	50	2	1	157
1931	0	106	147	189	243	67	752
1932	0	159	157	215	143	0	674
1933	0	403	158	193	65	7	826
1934	0	371	249	?	?	?	919
1935	0	280	157	175	43	0	655
1936	0	348	199	531	0	0	1,078
1937	0	300	259	227	285	0	1,071
1938	0	206	190	354	234	0	984
1939	0	209	179	114	2	5	509
1940	0	13	62	201	155	20	451
1941	0	152	52	231	259	5	698
1942	0	134	106	127	139	1	507
1943	0	280	215	106	204	0	806
1944	0	266	154	221	0	0	641
1945	0	349	203	109	15	0	676
1946	0	36	96	96	0	0	228
1947	0	31	22	55	2	0	110
1948	0	104	222	330	1	0	657
1949	0	73	114	263	0	0	450
1950	0	172	118	199	0	15	504
Sum	0	4,803	4,896	------	------	------	22,928
Minus 1934	0	4,432	4,647	7,447	------	------	22,009
Minus 1924 and 1934	0	4,316	4,467	7,308	4,779	248	21,118
Percent	------	20.44	21.15	34.61	22.63	1.17	100.00

TABLE 26.—*The total escapement of Karluk River sockeye, 1921 to 1950*

Year	The escapement by periods in thousands*							
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season	Total
1921	22	488	195	341	280	174	454	1,500
1922	10	95	98	41	77	79	156	400
1923	73	134	80	153	171	84	255	695
1924	91	341	134	210	?	?	287	1,063
1925	63	494	125	291	409	239	648	1,621
1926	561	610	149	365	723	125	848	2,534
1927	62	483	76	92	77	83	160	872
1928	166	477	134	129	125	63	188	1,094
1929	76	253	34	142	309	87	396	901
1930	44	286	46	287	251	183	434	1,087
1931	63	183	43	149	318	117	435	873
1932	49	273	50	58	131	177	308	738
1933	27	354	138	112	292	64	356	987
1934	204	522	39	?	?	?	?	1,450
1935	162	268	11	119	184	132	316	876
1936	183	255	84	82	676	96	772	1,375
1937	5	787	86	71	222	94	316	1,265
1938	0	732	95	42	?	?	361	1,230
1939	84	246	48	75	207	46	253	706
1940	269	290	42	28	?	?	187	816
1941	226	137	53	136	?	?	380	932
1942	153	155	45	68	144	64	208	629
1943	155	394	75	56	?	?	241	921
1944	99	236	19	73	?	?	342	769
1945	60	353	51	107	75	13	88	659
1946	65	211	40	9	39	78	117	442
1947	5	189	46	121	117	7	124	485
1948	179	345	43	94	85	8	93	754
1949	34	307	48	134	162	6	168	691
1950	48	288	52	68	270	33	303	759
Sum	3,238	10,186	2,179	-------	-------	-------	-------	29,135
Minus 1934	3,034	9,664	2,140	3,653	-------	-------	9,194	27,685
Minus 1924 and 1934	2,943	9,323	2,006	3,443	-------	-------	8,907	26,622

*Adjusted to date of catches at mouth of Karluk River to discount time spent in upstream migration to the counting weir.

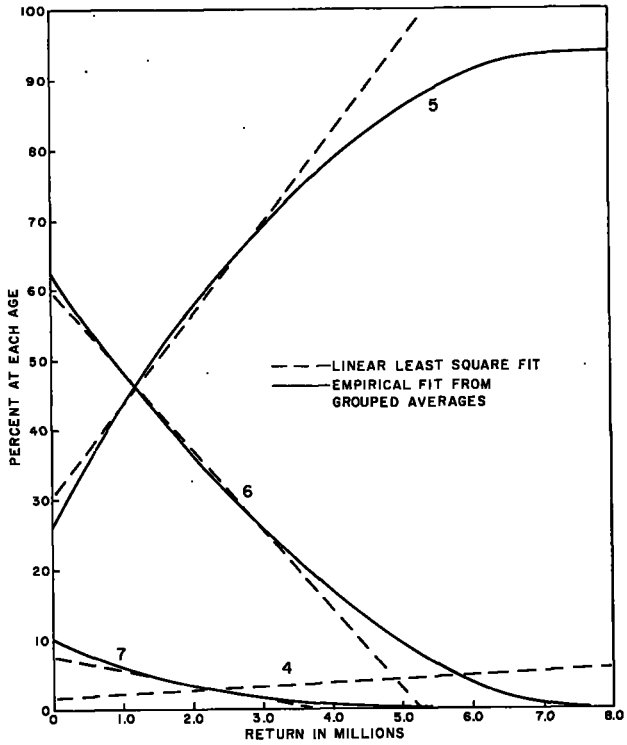

FIGURE 50.—Showing the linear least square and the empirical fit from grouped averages to the percent of fish returning at each age on the size of the brood of which they are a part.

Table 28 and figures 52 and 53 show the runs and escapements by spring, summer, and fall periods. It will be noted in figure 52 that the three seasons show the same general pattern of decline. The 1931–35 period is low as 1934 data on seasons are incomplete, necessitating omission of that year. The escapements (fig. 53) for the spring and fall seasons are obviously a function of the size of the runs. As the 1921–25 escapements are largely the source of the 1926–30 runs, and so forth, it is also clear that the relative size of the spring and fall escapements bears no relation to the relative size of the ensuing seasonal runs.

The summer escapement fell off rapidly and remained very low, yet the summer runs followed the same pattern as the other runs. It is almost necessary to conclude that the three seasons followed the same general pattern and did not respond to changes in the escapement for the respective seasons.

Thompson (1950) attempted to show that the decline in the Karluk runs was caused by a decline in the summer runs, accompanied by a relative increase in the spring and fall runs. This is similar to the drop in the summer sockeye run to the Fraser (Rounsefell and Kelez, 1938, p. 764). However, the drop in the Fraser run could be attributed to a decline in the races of sockeye that migrated through the fishery at a particular season. This is not the same at Karluk.

The data presented by Thompson on Karluk seasonal case-pack (taken from his mimeographed figures) for the 25 years from 1895 to 1919 for one cannery are compared in figure 54 with the seasonal catch at Karluk for 28 of the 30 years for which data are on hand from 1921–50. These curves refute the proposition that the seasonal catch bears any close relation to the seasonal run (compare figs. 33 and 54), or that the data he presents can be interpreted as showing any relative decrease in the summer run.

The slightly lesser importance of the fall catch in the later years can well be due to the early closing of the fishing season in many of the late years. All evidence appears to point to one pop-

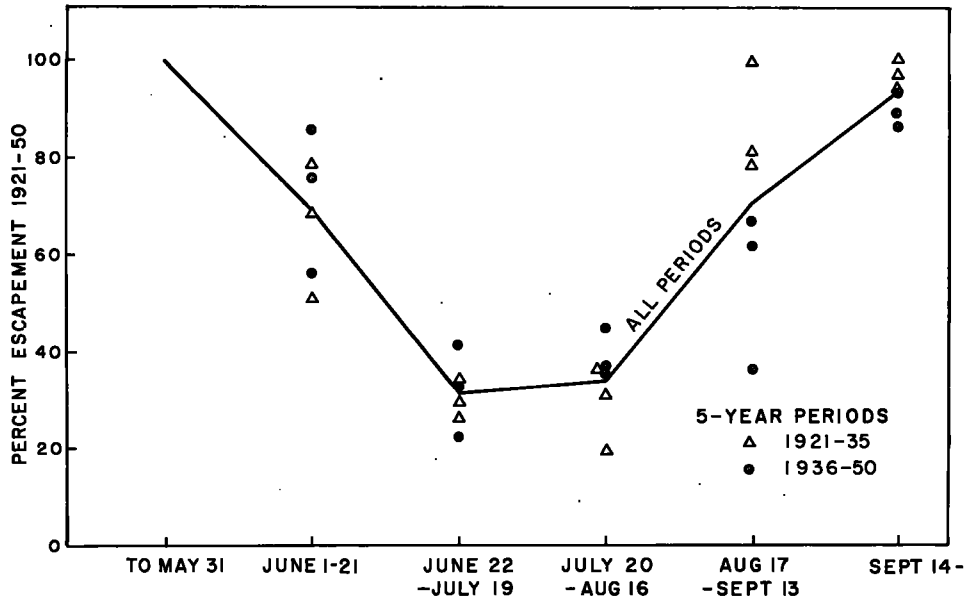

FIGURE 51.—Percentage of the run escaping through the fishery, by 4-week periods, from 1921–50.

TABLE 27.—*Percentage of total run escaping by periods, 1921 to 1950*

Year	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season
1921	100.0	93.3	33.1	36.6	33.1	75.7	42.2
1922	100.0	70.4	49.0	19.0	19.5	77.5	31.4
1923	100.0	48.7	38.8	37.6	46.2	89.4	55.0
1924	100.0	74.6	42.7	60.2	------	------	38.7
1925	100.0	92.2	45.3	30.5	46.7	100.0	67.1
1926	100.0	72.2	32.0	32.1	40.2	91.2	44.4
1927	100.0	93.4	29.7	22.9	28.7	100.0	45.7
1928	100.0	81.3	40.0	21.6	39.1	70.8	46.0
1929	100.0	81.6	29.1	62.0	100.0	100.0	100.0
1930	100.0	99.7	30.9	85.2	99.2	99.5	99.3
1931	100.0	63.3	22.6	44.1	56.7	63.6	58.4
1932	100.0	63.2	24.2	21.2	47.8	100.0	68.3
1933	100.0	46.8	46.6	36.7	81.8	90.1	83.2
1934	100.0	58.5	13.5	------	------	------	------
1935	100.0	48.9	6.5	40.5	81.1	100.0	88.0
1936	100.0	42.3	29.7	13.4	100.0	100.0	100.0
1937	100.0	72.4	24.9	23.8	43.8	100.0	52.6
1938	------	78.0	33.3	10.6	------	100.0	60.7
1939	100.0	54.1	21.1	40.2	99.0	90.2	97.3
1940	100.0	95.7	40.4	12.2	------	------	51.5
1941	100.0	47.4	52.0	37.1	------	------	58.9
1942	100.0	53.6	29.8	34.9	50.7	100.0	59.8
1943	100.0	58.4	25.9	34.4	------	100.0	54.3
1944	100.0	46.9	11.0	24.8	100.0	100.0	100.0
1945	100.0	50.3	20.1	49.3	84.3	100.0	86.3
1946	100.0	85.1	29.4	8.7	100.0	100.0	100.0
1947	100.0	86.3	66.7	68.8	98.3	100.0	98.4
1948	100.0	76.8	16.2	22.2	98.8	100.0	98.9
1949	100.0	80.8	29.6	33.8	100.0	100.0	100.0
1950	100.0	62.6	30.6	25.5	100.0	68.8	95.3
1921–25	100.0	75.8	41.7	36.8	36.4	85.8	46.9
1926–30	100.0	85.6	32.3	44.8	61.4	92.3	67.1
1931–35	100.0	56.1	22.7	35.6	66.8	88.4	74.5
1936–40	100.0	68.5	29.9	20.0	80.9	97.6	72.4
1941–45	100.0	51.3	27.8	36.1	78.3	100.0	71.9
1946–50	100.0	78.3	34.5	31.8	99.4	93.8	98.5
1921–50[1]	100.0	69.3	31.5	34.2	70.5	93.0	71.6

[1]Average of 5-year periods.

ulation of sockeye at Karluk, the adults returning at various ages and seasons, the age and season depending to a large extent on varying ecological conditions.

DISCUSSION

Before formulating an hypothesis to explain the facts brought out by the foregoing analyses it may be worthwhile to discuss briefly the explanations for the general decline made by various persons at various times. These will be discussed one at a time, the list includes the following:

a. Long-term changes in the physical environment.
b. Increased predation on young sockeye.
c. Overfishing on one (or more) of several discrete populations in the Karluk runs.
d. Overfishing in general.
e. Reduction in lake fertility.

Long-term changes in the physical environment

The data on temperature and rainfall shown, exhibit fluctuations covering periods of several years. Nevertheless, over the whole period of years of available data (table 5 and fig. 9) there is no general change either in temperature or rainfall. Therefore, although they are the cause of some of the short-term fluctuations the available evidence indicates that those two physical factors cannot be the cause of the general decline.

Increased predation on young sockeye

This theory for the decline was never fully advocated by biologists but rather by some of those entrusted with the management and enforcement of the fishing regulations, and many persons in the fishing industry. Unfortunately, the whole theory fell into disrepute on two grounds. (1) No

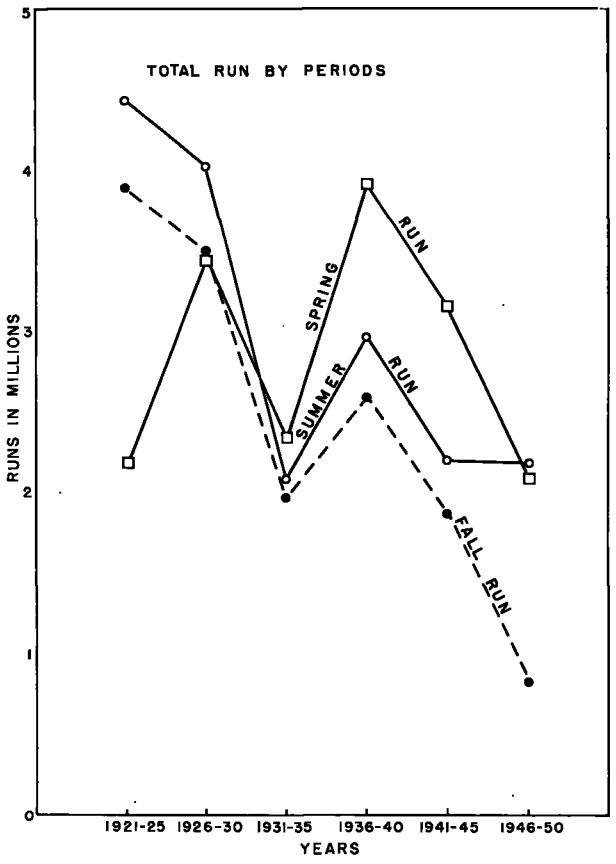

FIGURE 52.—Comparison by 5-year periods of the spring, summer, and fall runs.

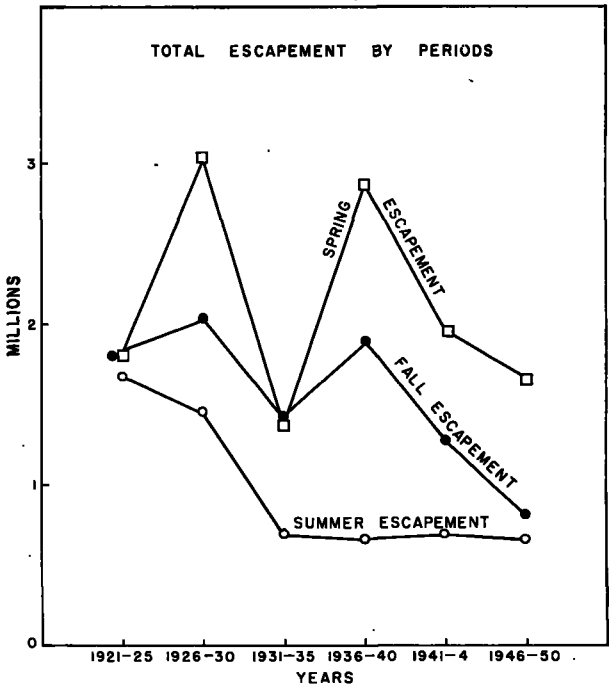

FIGURE 53.—Comparison by 5-year periods of the spring, summer, and fall escapements.

adequate tests, such as were made at Cultus Lake, were carried out in Alaska so that no accurate measure of the effect of destroying predators was obtained. (2) The destruction of predators was carried out over a wide area in Alaska, chiefly on the basis of bounties to native fishermen (Hubbs 1940), and financed by the Territory and by the canners. Naturally, bounty seekers fished for predators only where they were most abundant and most easily captured.

Capture of only a portion of a predator population at the time when it is at a peak may result in increased future predation. Let us postulate a population of a million predators, which in the course of events will soon be reduced to 300,000

TABLE 28.—*Runs and escapements by 5-year periods, 1921–50 (in thousands)*

Period of years	Total run by periods			Total escapement by periods			Total run	Total escapement	Average total run per period	Average total escapement per period
	to June 21	June 21 to Aug. 16	Aug. 17 to end of season	to June 21	June 21 to Aug. 16	Aug. 17 to end of season				
1921–25	2,185	4,443	3,895	1,811	1,668	1,800	10,523	5,279	3,508	1,760
1926–30	3,455	4,027	3,502	3,018	1,454	2,026	10,984	6,498	3,661	2,166
1931–35*	2,327	2,071	1,983	1,379	680	1,415	**6,381	**3,474	2,127	1,158
1936–40	3,927	2,969	2,590	2,851	654	1,889	9,486	5,394	3,162	1,798
1941–45	3,151	2,206	1,880	1,968	683	1,259	7,237	3,910	2,412	1,303
1946–50	2,087	2,170	823	1,671	655	805	5,080	3,131	1,693	1,044
Grand total	17,132	17,886	14,673	12,698	5,794	9,194	49,691	27,686		
Minus 1921–25	14,947	13,443	10,778				39,168			
Minus 1946–50				11,027	5,139	8,389		24,555		
Escapement as percent of runs during the ensuing 5-year periods				73.77	38.23	77.83		62.69		

*Minus 1934.
**Includes 1934.

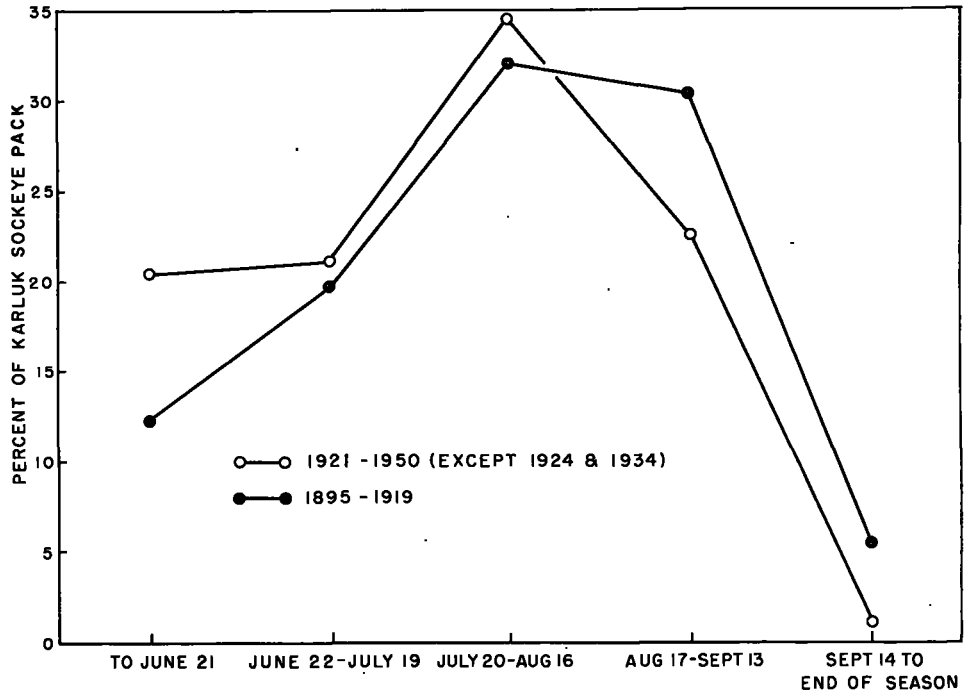

FIGURE 54.—Percent of the sockeye pack canned during different portions of the season for the 1895–1919 period compared to the 1921–50 period.

through natural control (in this instance, lack of sufficient young sockeye for food). If we now capture 400,000 of this predator population the remaining 600,000 will have more food per predator and survival will likely exceed the 300,000 which would have survived without any attempted control. Thus, a smaller predator population will thrive better than a larger in seasons when the number of young salmon prey are too small to support the greater number of predators.

At Karluk the destruction of predators was confined to attempting to destroy large numbers of Dolly Varden charrs by seining or trapping at the salmon-counting weir during their annual downstream migration in May and June. In the 21 years from 1922 to 1942 the annual reports of the Alaska Division mention the destruction of Dolly Vardens during 15 years. During the 9 years in which the numbers destroyed are recorded they vary from 3,000 to 81,500. The work was hampered by high water and by the desire to avoid harming the downstream sockeye migrants. These migrants commence their seaward migration soon after that of the Dolly Vardens and there is considerable overlap.

DeLacy and Morton (1943) have shown that many Dolly Vardens are found in the tributaries of Karluk Lake during the season when those that have migrated downstream are at sea, so it is obvious that not all the Dolly Vardens were subject to capture at the weir.

Since DeLacy and Morton (1943) also found large numbers of nonmigratory alpine charr (*S. alpinus*) in Karluk Lake, the utility of the destruction of Dolly Vardens alone is questionable. Certainly it does not constitute any test of the results that might accrue from a full-scale program of predator control.

Overfishing of one (or more) of several discrete populations in the Karluk runs

This theory depends of course on the existence of discrete populations. One advocate of this theory is Thompson (1950) whose hypothesis of summer overfishing of a discrete population is based on a comparison between the salmon pack of earlier years and the weir counts of salmon bound for the spawning grounds in later years. As figure 54 shows, one can not compare pack during one period with escapement in another period as escapement was not uniform in different parts of the season.

The existence of a midsummer lull in the runs led many to postulate the existence of "spring" and "fall" runs of salmon belonging to self-perpetuating populations. This theory has long been generally accepted without any proof. For many years the attempt to assure a spawning stock for the spring and fall runs has doubtless contributed to the condition whereby the smallest relative escapement has been coming from the salmon running in the center portion of the season. This is unfortunate since the eggs and young of these fish are more apt to encounter favorable temperature conditions.

As abundant proof has been offered to show that only one population exists this topic need not be be pursued further.

Overfishing in general

This theory for the decline at Karluk once seemed thoroughly reasonable. It was based on the idea that the existence of the 5-year cycles in the run (during the earlier years) is adequate proof that the returns are in direct proportion to the escapement since the majority of the run are usually 5 years of age. As we have shown, the returns are not directly proportional to the escapement. The reproduction curve shows a decreasing survival rate with an increasing number of spawners. It has also been shown that the cycles persisted despite this type of reproduction curve because of the relation between the survival of young fry and the lake density of older young, whereby the large numbers of young from the larger broods exerted an unfavorable influence on the young of the smaller broods and vice versa.

Good escapements of spawning fish were obtained in every year following the enactment of the White Act of 1924. However, instead of following the principle of allowing 50 percent of the run to escape, an attempt was made through closure of fishing to obtain a larger proportionate escapement in the low years by requiring a minimum of a million spawners. As we have shown, this did not halt the decline in the runs (it may have accelerated it) because it soon destroyed the balanced cycles, that had endured for many years, which favored the survival of the large broods and militated against the small broods. This increase of the escapements in the low years quickly damped the former regular oscillations in the numbers of young sockeye in the lake. This trend toward stabilization of the annual numbers of young produced removed the natural control of density-dependent predators which were no longer held in check by alternate feasts and famines.

The belief that the decline in the runs was caused by overfishing was abandoned as untenable after increased runs did not result when ample spawning fish were reserved over a period of years. It is not the rate of exploitation that has changed, but the ability of the populations to withstand even a greatly diminished rate.

Reduction in lake fertility

After all other explanations for the general decline in abundance failed the most popular explanation has been a supposed progressive decline in fertility of the waters of Karluk Lake. The only evidence to which advocate of this proposition can point is the long-term decline in abundance of the runs combined with the failure to discover any alternative explanation. The fact that there has been a tendency for the average age at maturity to increase has also been cited in support of this theory. The increase in average age is confirmed but it is also found that the age composition of each brood varies with the size of the brood, the largest broods having a younger average age. The increase in average age can therefore be explained wholly on the basis of the smaller returns, since (see appendix J) small broods of young tend to remain longer in the lake because their small biomass raises the individual threshhold size necessary for seaward migration.

If the increase in age at return were due to increased intra-specific competition from lowered lake fertility, then smaller broods should tax the food supply less, grow faster, and show a lower average age. The reverse is true.

The hypothesis that the decline in the runs has come about through a gradual decline in lake fertility is based on theoretical grounds. It is known that the carcasses of the dead spawners contribute a large quantity of chemicals, of which nitrogen and phosphorus are important, to the lake waters; also that these chemicals are used to produce food organisms consumed either directly or secondhand by young sockeye.

The truth of the theorem depends on the truth of three major premises, to wit: (1) That the decomposing carcasses furnish a very large share of the nutrients available to the primary food organisms, (2) That there has been a large but gradual

decline in the number of spawners and, (3) That the fertility of the lake has actually fallen to a significant degree.

Those who accept the three major premises appear to be divided into two schools of thought concerning the manner in which the runs are presumed to be affected. One school holds that the fertility of the lake in any period depends to a large extent on the gradual release, over a long period of years, of chemicals stored from the carcasses of adults that spawned in the lake many years before. They reason that since there has been a decline in the number of spawners, this storehouse is gradually becoming exhausted.

The other group contends that because of a continuous decline in the number of spawners the nutrients available each year from decomposing carcasses are becoming increasingly insufficient.

The storage and gradual release theory requires proof since practically all work on fertilization of waters has been carried out in farm ponds and small shallow lakes in which the volume of water is extremely small in relation to the area of bottom deposits. Karluk Lake (Juday et al., 1932) has a maximum depth of 126 meters (413 feet) and a mean depth of 48.6 meters (159 feet).

The constant loss of chemicals through lake outflow also makes it appear unlikely that any long-term decline in fertility could be caused by any using up of chemicals stored in the lake itself over long periods. Between 1926 and 1940 (tables 26 and A–11) the 3- and 4-year smolts leaving the lake weighed 194 metric tons per year, or about 200 metric tons if we allow for the few 2- and 5-year smolts. The average escapement of sockeye into the lake was 1,120,000 fish. Allowing 2 kilos per fish this yields 3,360 metric tons of adults so that the ratio of income to outgo stands at about 17 to 1. If we assume ocean mortality to have been relatively constant over the years this ratio should have been about the same during the earlier years.

Concerning the relative quantities of terrigenous phosphorus and that contributed by the salmon carcasses, Nelson and Edmondson (1955) state,

> . . . 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.

Although published data on the chemistry of the streams tributary to Karluk Lake are too scanty to make any formal prognosis, those available seem to show that the importance of the salmon carcasses as the source of nutrient materials may have been overemphasized in the past. In table A–15, appendix K, is shown the soluble phosphorus for tributary streams of Karluk Lake from published data.

We believe these data indicate that there is a natural increase in soluble phosphorus between the upper and lower reaches of these streams and that the above-mentioned figures of 0.008 and 0.029 mgm./l. do not take this into account. The water in the upper portion of a stream will contain less soluble phosphorus but Nelson and Edmondson apparently averaged these upstream values in with the values taken at the mouth before the salmon arrived, to obtain the figure of 0.008. Using only observations from the same areas of the streams (table A–15) the data suggest that the annual terrigenous contribution of soluble phosphorus exceeds the extra supply during the 2- to 3-month period when the salmon carcasses are decomposing.

Using the more reliable estimates of total phosphorus it is also suggested (appendix K) that the terrigenous contribution of total phosphorus is larger than the total phosphorus from most annual escapements.

As to the second theory, reduction of escapement, the present analysis of the runs show from the reproduction curve that the largest total runs come from moderate numbers of spawners, so that in prefishing years (see 0 fishing rate on upper curve in fig. 21) the runs very likely averaged only slightly more than 2 million fish. If adequate data should confirm the suggestion that the terrigenous phosphorus annually entering the lake is equivalent to nearly twice the amount contained in the carcasses of 1 million adult sockeye, then the reduction in the total phosphorus content of the lake caused by reduced escapements is in the order of 10 to 15 percent over a period of about 75 years.

Intraspecific competition for food (within the range of 4 to 13 million smolts) would seem to be ruled out as a limiting factor not only by the highly significant linear relationship between

number of smolts and their total weight, but by the actual increase in individual weight in the larger broods. Thus, if we correlate the number of smolts migrating (column 5, table A–11) with the weight of the individual 3-year-old smolt in the migration of the same year (column 4, table A–10) the coefficient of correlation is 0.5936 and significant. This strongly indicates that survival to the smolt stage is partially a positive function of rate of growth. This does not mean that the density of food organisms is not important. The interpretation suggested is that when the density of food organisms is high two results occur: the survival is enhanced by the increased growth rate, resulting in a large brood, and the size of the individual fish tends to be large.

Were the annual survival of young dependent on available food at some short critical period there would be no logical reason to expect any effect on the relative size of the survivors of different broods. Therefore, the chief cause of this relationship can be assumed to be heavier losses through predation on the slower-growing broods. This does not answer the question as to whether there has been any long-term decline in fertility of the lake, since a lower level of predation (in the absence of intraspecific food competition) undoubtedly would raise the rate of survival.

To sum up the foregoing the general decline in rate of survival can stem principally from three causes:

1. Increased predation on the young through lack of control of the density-dependent predators. This may have come about through a decrease in the amplitude of the oscillations, formerly so pronounced, in the number of spawners.

2. Higher mortality of young caused by increased loss to predators during a longer sojourn in the lake before making the seaward migration. This longer sojourn appears to be due principally to an insufficiently large total weight of young in most years to induce early migration.

3. Heavier losses from predation in the lake caused by a slower rate of growth. Since there is good evidence against the existence of any significant intraspecific competition for food in recent years, the smaller average individual smolt size of the less numerous broods may indicate a slower growth rate in recent years, possibly caused by a drop in lake fertility. With a slower rate of growth more of the slow-growing broods would be taken by the same number of predators. However, the same differential mortality between broods may have been occurring in former years but have become more pronounced with more predators so that the data cannot confirm but certainly cannot deny a drop in lake fertility.

The foregoing analysis of lake fertility (see appendix K) is based of course on the assumption that there has been no significant change over the period of the fishery in the annual contribution of terrigenous phosphorus (or other nutrients). It does not, however, take into account the possibility that there may have been a gradual long-term decline in the chemicals leaching into the lake from the watershed. The soils in the general area of southwestern Alaska have been enriched from time to time by deposits of volcanic ash. The marked effect on fertility in certain lakes following the Katmai eruption of 1912, and the subsequent enrichment of the soils, is described by Eicher and Rounsefell (1957). The Karluk watershed was just south of the area of ash deposit from Katmai (10 inches fell at Kodiak) but probably it has received ash deposits in the more distant past.

The destruction of the former cycles of big and small years that prevailed over several decades may have had a much greater effect than we can ascertain. The portion of the effect that we have removed statistically is only that portion that is caused by intraspecific competition between broods (probably including some degree of cannibalism). The general decline that could have been caused by multiplication of species density-dependent upon sockeye (predation and competition could both be involved) because of the cessation of control over these other species when the cycles were destroyed, cannot be estimated from these data.

In regard to the second point it has been shown that there appears to be a threshhold size which a young fish must attain in order to become a smolt and migrate seaward, and that, further, this threshhold size is a variable that changes inversely as the weight of the biomass of smolts in the migration.

Concerning the effect of biomass of young in inducing migration from Cultus Lake, Foerster and Ricker (1948, p. 204) state,

> The yearling stock is thus 28 percent of the lake's total g in of sockeye biomass in years before (predator) control,

and 44 percent of it after control, on the average. The apparent improvement in utilization of production is therefore about 55 percent. However, yearling stock is not exactly the same thing as yield, and in some of the years before control a large part of it did not migrate.

It is not possible from the data to know which of these three points is paramount but all may have been instrumental in causing the general decline. Because we have no good measure of the mortality in the lake of young that remain an additional year before migrating, it is not possible to assign one portion of the decline to heightened mortality of young up to their third year and another portion to the additional mortality on the proportion of the young that remain an additional year on account of lack of a sufficiently high biomass of smolts to induce migration.

We have no positive evidence to support the theory of declining fertility, but let us suppose that it might be feasible to increase fertility through artificial fertilization of the waters. Would this result in a greater survival of young sockeye? It might at first, however, if the fertilization were continued the predators would merely need to increase to lower the survival rate to the point where most of the advantage of the increased growth from the larger quantity of available food was being lost by heightened mortality, so that the end result might be no increase in the weight of the smolt biomass migrating from the lake unless predator control were conducted simultaneously. The experiments of Nelson and Edmondson (1955) show that sockeye growth was increased by fertilization of Bare Lake, a 120-acre unstratified lake lying near Karluk in the Red River watershed. Experiments on larger stratified lakes are now needed to determine the feasibility of fertilization of lakes similar to Karluk.

Control of predators density-dependent upon sockeye may be accomplished by varying the food supply of these predators through great variations in the abundance level of young sockeye from year to year. In order to take full advantage of such control it may even be necessary to re-establish the former cycles. This natural control having been destroyed it may be very difficult to restore the runs unless these other fishes are controlled by man.

A somewhat similar situation is recorded by Smith (1955) for brook trout in Crecy and Gibson Lakes, New Brunswick. He concludes,

Stocking alone was found to be ineffective in Crecy and other lakes of the area (Smith 1952a). Stocking of Gibson Lake, when a barrier was present in the outlet to prevent escapement of planted trout, was also ineffective. Fertilization and stocking when applied together led to improvement of the yield of trout from Crecy Lake, but, as we have seen, only temporarily until predator control was undertaken.

It has been shown for Cultus Lake (Rounsefell 1946, see fig. 3) that control of other fishes greatly increased the total poundage of seaward migrants. This increased biomass of migrants was obtained without an increase in actual productivity of the lake. This follows because under conditions of heavy predation a large portion of the food consumed by young sockeye does not contribute to the final biomass. Predator control at Cultus Lake accomplished two things: (1) it raised the survival rate so that fewer spawners could supply all the young required (2) it raised the conversion rate of natural food into sockeye migrant flesh so that more or larger smolts could result from the same lake area.

It appears from the preceding that the difference in survival rate between early and recent years stems from two causes: higher mortality in recent years from the time of egg deposition to the third year, and in recent years a higher mortality of fish after their third year because more of them remain an additional year in fresh water.

The remedy for both lies in increasing the biomass of smolts. To increase the number of spawners without regard to sources of mortality might help by increasing egg deposition to a point where the number of smolts produced was large despite heavy mortality in the lake, perhaps large enough to gain the additional benefits of earlier smolt migration.

This method appears to be highly wasteful. If the same results can be achieved without an increased number of spawners the economic benefits will be large indeed. We, therefore, recommend trying certain logical steps, including control of predation on adults and young, improvement of spawning grounds, some shift in the seasonal proportion of the run reserved for spawning, and experiments to determine the feasibility of increasing growth rate by fertilization of large stratified lakes.

The collection of sufficient field data to determine the role of each predator or competitor will be so involved and time consuming that a direct

approach is indicated. This would involve excluding from the lake all potential anadromous predators, coho and king salmon, charrs, and trouts, and in the lake itself in netting or trapping to remove all possible charrs.

The effect of controlling the fresh-water sculpin could be measured by experiments on paired streams. Shapovalov and Taft (1954, p. 251–256) show that two species of sculpin, *Cottus asper* and smaller *Cottus aleuticus* can be controlled in California streams by low barrier dams. The sculpins make a definite annual downstream migration. On returning, the sculpins are unable to pass the low dam used for an experimental fish trap, and so they were soon heavily depleted above the dam. From 3,357 sculpins moving downstream the first year, the run fell to 337 in 3 years and to 30 sculpins in 8 years. In neighboring Scott Creek no sculpins now live above a low dam built in 1908, although they are still abundant below it.

Since *Cottus aleuticus* Gilbert is also the fresh-water sculpin present in the Karluk River system (Evermann and Goldsborough, 1907) a trial of this method of control is clearly indicated.

That the Karluk River sculpins probably also perform definite migrations is perhaps indicated by the experience of Cloudsley Rutter (Chamberlain 1907). During the night of June 25, 1903, a fyke net with a 25-foot wing spread set at the outlet of Karluk Lake in the river took 738 sculpins.

Since the desired objective is to produce the largest surplus of returns over number of spawners, we suggest strict control of predation on the spawning salmon, by bears.

A study needs to be made jointly by biologists and engineers to determine the costs of making physical improvements in the limited spawning area available in the streams. These might include the placing of large boulders to stabilize shifting gravel bars, establishing very low dams in spawning areas to keep the beds from becoming exposed in dry weather, or freezing deeply in winter, making additional space for spawning by removal of excess boulders, and construction of flood control headwater dams with controlled outlets to provide stabilized stream flows.

Concerning the relation between the time of run and the time of actual spawning, Gilbert and Rich (1927, p. 27) state,

> The first fish to appear are, in general, well advanced toward spawning and certainly do not linger long in the lake before seeking the spawning gravels. The earliest spawning has not been observed, but it is believed to take place not later than the middle of June. From that time until late in the fall uninterrupted spawning is in progress in suitable gravels about the shores of the lake and in all favorable tributaries.

On the average, neither the very early nor the very late spawners are as successful as those spawning in midseason. The analyses showed that because of the deleterious effects on survival of low autumn (11 out of 48 years) and late spring (about 14 out of 47 years) temperatures, survival depends to some extent on the season of spawning. It would be best then to abandon the idea of obtaining a spring and fall group of spawners, but rather to encourage the canning of the early and late fish, and insist on a higher percentage of the summer fish being in the escapement. This should, on the average, raise the survival per spawner, which would increase the runs during all parts of the season.

The Bare Lake experiments (Nelson and Edmondson, 1955) have shown that the growth rate of young sockeye can be increased by fertilization in a small unstratified lake. The feasibility, both biologically and economically of fertilization of Karluk Lake should be determined by experiments on a lake larger and much deeper than Bare Lake.

SUMMARY

After the inception of canning in 1882 the Karluk River sockeye catches rose quickly to a maximum and then declined gradually over several decades. Catch records are available since 1882 plus actual weir counts of the upstream-migrating salmon since 1921. Ages of salmon in the runs by weeks are available for 1922 and continuously since 1924.

Runs in the neighboring streams show the same secular changes in abundance (after removal of the short-term 5-year cycle) as the Karluk runs, indicating a common cause. The changes in survival at Karluk are significantly correlated with variations in temperature. Autumn temperatures averaging below 34° F. lower survival from the eggs then in the spawning gravels. April and May temperatures affect the survival of the brood resulting from eggs deposited the previous season, the effect probably being greatest

on eggs deposited the previous late spring. Either too low or too high a temperature lowers survival; the optimum survival range lies between 39° and 42° F. The accumulated monthly temperature between 45° and 55° F. for the two years succeeding egg deposition affect survival of young, presumably by affecting growth. The optimum survival occurs between an accumulation of 45° to 60° F. Greater or lesser accumulation lowers survival.

Rainfall for the period April to July in the year following deposition of the eggs affects survival of a brood, presumably through the effect of drought or floods on the fry emerging from the gravel. For this period survival declines sharply as the total rainfall falls below 14 inches. Above about 20 inches of rain the survival only decreases gradually, probably owing to freshets.

Survival of sockeye from broods of odd-numbered years is very significantly and consistently higher than from broods of even-numbered years. The even-numbered years are those of the cycle of pink salmon that has remained dominant at Karluk at least as far back as 1880.

The survival from any brood is negatively correlated with the numbers of young sockeye two and three years older in the lake during the season the brood emerge as fry. This 2½-year negative correlation between fry survival and lake density of older young results in a positive 5-year cycle in the runs, which has previously been erroneously ascribed to the effect of age.

After statistical removal of the variation caused by these physical and biological factors it is clear that the sockeye has a dome-shaped reproduction curve. This indicates that, on the average, the largest available surplus of returning adults over the number of spawners occurs with intermediate numbers of spawners.

The general decline in the sockeye population can not be ascribed to the above factors since they exhibit short-term, not long-term fluctuations. Neither is the decline caused by the number of spawners, which has been fairly high in recent years. The decline is caused by a lowered survival rate in recent years.

Analysis of the age composition of both the seaward-migrating smolts and the returning adults shows that the particular portions of the season at which adult sockeye return to the river (extending from May to October) is governed by two equally strong and opposing factors: smolt age and ocean age. Smolts leave the lake in the late spring and early summer of various years of life. These years in the usual order of importance are 3, 4, 2, and 5. Some young enter the sea in their first year but so few sea-type adults return and the mortality is doubtless so high that the relative number is unknown. With the exception of these few sea-type fish, those leaving at the younger ages tend to return earlier in the season during their spawning run. However, those remaining the shortest time in the sea (they remain from less than 1 summer to 4 summers at sea) tend to return later in the season.

It is shown conclusively that the modes of abundance in the curve of total annual runs to the river are caused by the different times at which these different age combinations of smolt- and ocean-age fish return and not, as previously supposed, to any racial differences. This lack of races is further borne out by significant correlations between fish of the same brood that return at different ages in different portions of the season.

A tendency for an increase in the average age of the returning sockeye in more recent years has been ascribed previously to loss of lake fertility. This increase in average age is confirmed, but it is also shown that the average age of return of each brood is correlated with the size of the brood. Larger returns contain more younger fish. This increase in average age thus may be merely the result, without necessarily any causal relation, of the dwindling runs in recent years.

It is shown that the relation between numbers and biomass of the annual Karluk smolt migration is strictly linear, indicating no intraspecific competition for food within the range of smolt populations available in the data (4,675,000 to 13,226,000). At Cultus Lake the smolt biomass shows a linear relation to the logarithm of the number of smolts, indicating that the food supply is being heavily taxed by the larger populations. Karluk Lake produces more than four times the weight of smolts per acre as Cultus Lake. This is probably caused by the difference in surface water temperatures which in Karluk Lake are optimum for young sockeye growth but in Cultus Lake are so warm that the young are confined for 3 months to the stratum adjacent to the thermocline. This shows that the continual decline in the Karluk

runs is not caused by intraspecific competition for the available food.

The attempt to stabilize the runs by obtaining a high number of spawners in every year has largely destroyed and obscured the former cyclic character of the runs. During the period when these cycles were present the number of spawners fluctuated in a more or less regular manner from very high to very low (lower than most recent years). This wide variation in number of spawners resulted in wide oscillations in the numbers of young sockeye present in the lake and therefore available as food for predator fishes. These regular oscillations in the supply of available prey may have acted as a control on the abundance of predators.

Apart from knowledge of the tremendous abundance of fish predators at Karluk, young of coho and king salmon, Dolly Varden charrs, alpine charrs, steelhead rainbow, and freshwater sculpins, there is scant quantitative data on them, but their great importance is clearly indicated.

RECOMMENDATIONS FOR ACTION

This report is an attempt to postulate reasonable hypotheses to explain the observed facts. In some instances the data are sufficient to afford definite proof, but in others they can only furnish strong indications. Therefore, in evaluating the final recommendations it must be borne in mind that only further careful research can fully prove, or for that matter disprove, the validity of some of the hypotheses upon which they must rest.

Furthermore, where more than one factor is indicated as operating to bring about some condition, the data are not always sufficient to yield any good estimate of which factor is the more important. Bearing these limitations in mind, but also realizing the necessity for action to arrest the declining abundance, conclusions have been reached that, although they later may be modified, give a basis for action consonant with the present state of our knowledge.

It is concluded that the survival rate can be increased in six ways listed more or less in the order of their importance: (1) by eliminating so far as practicable all predator species of fish from Karluk Lake and its tributaries, (2) by regulating the fishing in such a manner that greater numbers of spawners are from the middle portion of the runs and smaller numbers from the early and late portions of the runs, since the spawning success of the latter is often adversely affected by autumn and spring temperature conditions, (3) by restoring insofar as practicable the former cyclic character of the runs in order to lessen competition between the older young and fry, and perhaps give some measure of natural control of predators. Because of the present low state of the runs this should be accomplished by providing a higher proportion of spawners on big runs rather than by decreasing the proportion on smaller runs, (4) by increasing growth rates through fertilization of the lake waters (if it is proved to be economically feasible), (5) by physical improvement of the spawning beds, (6) by increasing the egg deposition of the potential spawners through control of predators on the adult run.

Recommendations 2, 5, and 6 are all designed to obtain the largest possible number of fry per potential spawner. This is doubly important with the present small runs.

Recommendation 1 is of great importance at present. If, after restoration of larger runs, it is found that either through natural predator control (see recommendation 3), or through accelerated early growth (see recommendation 4), the artificial control of predators is no longer necessary, it may be possible to discontinue it. Both 1 and 4 are designed to increase the biomass of young by lowering predation. One will also increase the biomass, even without increasing available food supplies, by conserving food otherwise lost by predation after consumption. Four may be necessary to supplement 1, at least at first, since the biomass of the present small broods, even with predator control, may not sufficiently lower the threshold size at seaward migration to induce seaward migration at an early age without faster growth.

Recommendation 3 might not have to be carried out if predators are strictly controlled, but this is uncertain because the data available do not give sufficiently clear indications of the relative importance of predators and intraspecific competition (possibly cannibalism). This is a point on which research is sorely needed.

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The material on which this report is based was collected by numerous individuals over a long period of years. Very little data after 1936 have been published. Dr. Willis H. Rich and the late

Dr. Charles H. Gilbert were responsible for initiating the continuous investigation in 1921 and for guiding it for many years. Joseph T. Barnaby was in charge for several years, followed by Allan C. DeLacy, the late Richard F. Shuman, and Philip R. Nelson. Other biologists who spent one or more seasons at Karluk include Alan C. Taft, Seymour P. Smith, the late Merrill Brown, George J. Eicher, and W. Markham Morton. Grateful acknowledgment is due these and others who collected portions of the data.

This report has drawn freely upon the data of other biologists. Special mention is due the work of Drs. R. Earle Foerster and William E. Ricker at Cultus Lake, British Columbia, which clarified many of the underlying principles of salmon biology. Clyde C. Taylor has been most helpful in criticism of the statistical procedures.

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APPENDIX A

NORMAL SEASONAL OCCURRENCE OF THE RUNS

Because the weir was not in operation for portions of some years, a weighted average could not be taken. The numbers in the runs are available by weeks. The weir counts are added to the commercial catch allowing a 7-day lag for earlier years and an 11-day lag for the later years when the weir was farther upstream. The 7- and 11-day lags were determined by special tagging experiments (unpublished) designed to measure the speed of migration from Karluk Lagoon to the weir sites.

In order to obtain the normal shape of the curve of occurrence the numbers of fish in all years were added for the period May 31 to August 16, since the data for every year were complete for this period. Each year's data were then weighted by the ratio of the run during this period to the 30-year average. This gave each year equal weight in determining the shape of the curve as well as making it possible to determine the correct shape at the ends of the curve where data for some years were lacking (table A–1).

TABLE A–1.—*Seasonal norm of occurrence of the runs in thousands of fish, 1921–50*

Week ending	Total run	Percent	Cumulative percent	Years with data
May 10	4.9	0.28	0.28	1
May 17	4.2	.25	0.53	9
May 24	20.2	1.16	1.69	30
May 31	88.6	5.09	6.78	30
June 7	178.5	10.26	17.04	30
June 14	187.0	10.75	27.79	30
June 21	137.4	7.90	35.69	30
June 28	86.5	4.97	40.66	30
July 5	51.2	2.94	43.60	30
July 12	44.0	2.53	46.13	30
July 19	56.6	3.25	49.38	30
July 26	85.8	4.93	54.31	30
Aug. 2	105.6	6.07	60.38	30
Aug. 9	97.7	5.61	65.99	30
Aug. 16	86.0	4.94	70.93	30
Aug. 23	92.2	5.30	76.23	29
Aug. 30	100.3	5.76	81.99	28
Sept. 6	111.5	6.41	88.40	24
Sept. 13	84.4	4.85	93.25	22
Sept. 20	48.2	2.77	96.02	22
Sept. 27	37.7	2.17	98.19	21
Oct. 4	21.6	1.24	99.43	17
Oct. 11	10.2	.59	100.02	9
Oct. 18	0.0			1
Total	1,740.3	100.02		

APPENDIX B

AGE COMPOSITION OF THE RUNS

The list of ages found in the various years (table A–2) may possibly reflect the different interpretations of the scales made by different investigators. The investigations were commenced by Dr. Charles H. Gilbert and Dr. Willis H. Rich (Gilbert and Rich, 1927). They had several assistants in different years and were followed by other investigators. Among those who were at Karluk in various years were Alan Taft, Seymour P. Smith, Merrill Brown, Joseph T. Barnaby (Barnaby 1944), Allan C. DeLacy, W. Markham Morton, Richard F. Shuman, and Philip R. Nelson.

Absence of a minor age group in any particular year does not mean that it may not have been present. None may have been taken in the samples; the few taken may not have been recognized, or the few taken may have been considered as aberrant scales. (Certainly in some years more age groups were found than in others.) This does not necessarily mean that the very minor age groups are invalid. In fact, there is good evidence from the individual pattern of the seasonal run of most groups that they are probably valid.

These minor groups, as shown later, represent such a minor numerical share of the run that their presence or absence can have but slight effect on the interpretation of the data.

For estimating age composition of the runs, samples are available by weeks, but unfortunately there are many weeks, both during the season and at the two ends when samples are not available. Because each age group has its own individual pattern of seasonal occurrence, the practice that has been followed of extrapolating at either the beginning or end of the season by applying the age readings of the nearest available week to the truncated portions of the data can lead to serious discrepancy. It has, therefore, been necessary to determine the normal pattern for each group (fig. A–1).

The method followed was to first determine the average numbers by weeks of an age group for the

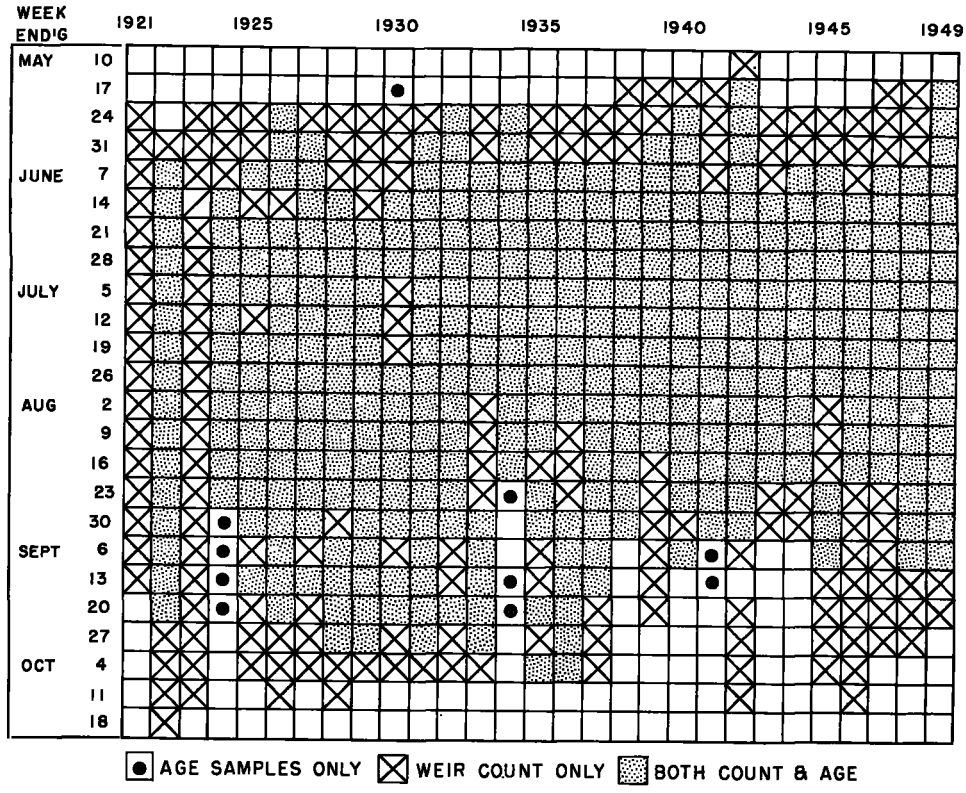

FIGURE A–1.—Availability by weeks for the years 1921–49 of weir counts and age samples of the runs.

TABLE A–2.—*Age groups represented in various years, 1922 and 1924–49*

Year	Age groups																				
	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
1922				x	x	x	x		x	x	x	x		x	x	x		x			
1924			x	x	x	x	x		x	x	x			x	x			x			
1925	x			x	x	x			x	x	x			x	x	x		x			
1926	x			x	x	x	x		x	x	x			x	x	x		x	x	x	
1927	x			x	x	x	x		x	x	x			x	x	x		x	x		x
1928				x	x	x			x	x	x			x	x			x	x		
1929				x	x	x			x	x	x			x	x		x	x			
1930					x	x			x	x	x			x	x		x	x	x		
1931	x			x	x	x			x	x	x			x	x	x	x	x	x		
1932				x	x	x			x	x	x			x	x			x	x		
1933				x	x	x			x	x	x			x	x	x	x	x	x		
1934					x	x			x	x	x			x	x	x		x	x		x
1935		x		x	x	x			x	x	x		x	x	x	x	x	x	x	x	x
1936	x			x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x
1937		x			x	x			x	x	x			x	x	x	x	x	x		x
1938					x	x			x	x	x			x	x	x	x	x	x		x
1939		x			x	x			x	x	x		x	x	x	x	x	x	x	x	x
1940				x	x	x		x	x	x	x		x	x	x	x	x	x	x	x	x
1941					x	x			x	x	x			x	x		x	x	x	x	x
1942				x	x	x			x	x	x			x	x		x	x			x
1943				x	x	x			x	x				x	x			x	x	x	
1944	x	x		x	x	x			x	x	x		x	x	x		x	x	x	x	x
1945		x			x	x			x	x	x		x	x	x		x	x	x	x	x
1946		x		x	x	x			x	x	x		x	x	x		x	x	x	x	x
1947		x			x	x			x	x	x			x	x		x	x		x	
1948					x	x			x	x	x			x	x		x	x	x		
1949					x	x			x	x	x			x	x	x	x	x	x	x	x
	Times age group found																				
1922–31	4	0	1	8	9	9	4	0	9	9	9	1	0	9	9	5	3	9	5	1	1
1932–40	1	3	0	5	9	9	1	1	9	9	9	0	4	9	9	8	7	9	9	4	7
1941–49	1	4	0	4	9	9	0	0	9	9	8	0	3	9	9	1	8	9	7	7	6
All years	6	7	1	17	27	27	5	1	27	27	26	1	7	27	27	14	18	27	21	12	14

period of 10 weeks commencing with the week ending June 14 and finishing with the week ending August 16. Complete data on age and total run were available for all 10 weeks for 18 of the 27 years with age readings, and the average was based on these 18 years.

The next step was to obtain for each year the ratio of the numbers of the age group during as many of the 10 weeks as were available to the number represented in the same weeks by the curve for the 18-year average.

The reciprocal of this ratio for each year was then used to weight each year's data. By this means each year was given approximately equal weight in determining the shape of the normal curve of seasonal occurrence for each age group. By summing the numbers for the various years in each week and dividing by the number of years available, a seasonal norm was obtained.

This method was followed for all the major age groups. For several of the minor age groups the data were too few to employ this method, and the numbers were merely summed by weeks and divided by the number of years (for each week) in which ages were taken. The groups so treated were the 3_1, 3_2, 4_1, 4_4, 6_2, 6_5, 7_3, 8_4, and 8_5 groups. The percentage curves of normal seasonal occurrence for each age group are given in table A–3.

TABLE A–3.—*Normal percentage occurrence of each age group by weeks, 1922 and 1924–49*

Week ending	Age group								
	*3_1	*3_2	*4_1	4_2	4_3	*4_4	5_2	5_3	5_4
May 17	0.00	0.00	0.00	0.00	6.19	0.00	1.81	0.46	0.00
May 24	.00	.00	.00	.89	4.08	.00	2.61	2.24	.45
May 31	.00	.00	.38	11.49	2.25	.00	7.51	6.48	2.61
June 7	.00	.00	1.20	13.10	5.89	.00	21.63	10.39	.91
June 14	.00	.00	2.97	9.27	4.76	.00	17.11	9.78	1.40
June 21	.14	.00	5.45	8.50	4.12	.00	11.78	6.96	1.18
June 28	.14	7.55	5.00	7.31	3.23	.00	8.22	4.19	1.26
July 5	.14	20.86	3.87	6.19	4.31	.00	4.81	2.70	1.17
July 12	.97	20.86	3.34	4.83	1.22	.00	4.87	2.41	.74
July 19	4.35	14.75	7.82	5.39	.98	.00	5.38	3.24	.65
July 26	16.17	1.80	9.09	4.68	1.75	.00	4.66	5.38	1.13
Aug. 2	17.34	7.19	7.37	4.12	2.61	.00	2.88	6.68	.98
Aug. 9	20.33	5.40	6.43	4.07	4.63	.00	1.94	6.42	1.17
Aug. 16	12.32	5.40	12.10	4.34	3.23	13.11	1.78	5.33	2.59
Aug. 23	12.49	.00	14.39	3.99	6.98	13.11	1.16	5.25	7.41
Aug. 30	8.50	5.40	11.84	4.24	10.55	24.41	.85	5.53	9.72
Sept. 6	4.70	5.40	5.30	3.09	8.12	16.38	.13	6.95	19.35
Sept. 13	2.40	5.40	2.37	2.26	11.48	20.23	.82	5.15	17.55
Sept. 20	.00	.00	1.09	1.89	12.99	8.93	.04	2.50	16.88
Sept. 27	.00	.00	.00	.35	.64	3.84	.00	1.96	12.85
	99.99	100.01	100.01	100.00	100.01	100.01	99.99	100.00	100.00

Week ending	Age group								
	*6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	*8_5
May 17	0.00	1.75	0.55	0.00	0.00	6.64	0.00	0.00	0.00
May 24	.00	8.97	.95	.00	14.08	10.01	.00	.00	7.94
May 31	14.36	11.12	1.95	.00	22.01	12.67	.00	10.38	11.40
June 7	18.65	18.37	4.48	1.21	15.44	15.22	1.45	14.81	15.37
June 14	21.45	16.28	4.51	2.01	24.07	10.71	2.42	26.49	12.61
June 21	10.56	10.83	2.95	2.82	11.92	6.84	1.36	10.38	9.15
June 28	6.27	6.35	1.93	.00	5.73	3.48	.34	.00	6.56
July 5	9.08	3.99	1.27	.00	1.83	2.66	.78	4.76	1.90
July 12	7.26	3.03	1.45	.74	1.45	1.82	.96	2.05	1.90
July 19	8.42	3.37	2.22	.87	1.13	3.58	1.49	3.89	1.04
July 26	2.81	3.49	3.73	.00	.94	4.32	2.89	7.89	.86
Aug. 2	1.16	3.51	4.87	3.76	.75	4.58	2.84	7.57	2.42
Aug. 9	.00	2.83	5.94	.60	.19	4.91	4.23	7.78	2.76
Aug. 16	.00	2.05	5.73	3.89	.00	3.49	5.15	.00	3.63
Aug. 23	.00	1.45	7.94	9.66	.47	1.98	10.49	.00	5.18
Aug. 30	.00	1.06	9.77	4.23	.00	1.87	14.93	.00	7.60
Sept. 6	.00	.70	12.94	13.88	.00	1.57	13.05	4.00	6.39
Sept. 13	.00	.45	11.11	30.11	.00	2.53	11.32	.00	3.28
Sept. 20	.00	.31	7.34	13.88	.00	1.05	21.01	.00	.00
Sept. 27	.00	.09	8.37	12.34	.00	.06	5.26	.00	.00
	100.02	100.00	100.00	100.00	100.01	99.99	99.97	100.00	99.99

*Smoothed once by three's.

TABLE A–4.—*Cumulative percentage occurrence of each age group by weeks, 1922 and 1924–49*

Week ending	Age group								
	3_1	3_2	4_1	4_2	4_3	4_4	5_2	5_3	5_4
May 17	0.00	0.00	0.00	0.00	6.19	0.00	1.81	0.46	0.00
May 24	.00	.00	.00	.89	10.27	.00	4.42	2.70	.45
May 31	.00	.00	.38	12.38	12.52	.00	11.93	9.18	3.06
June 7	.00	.00	1.58	25.48	18.41	.00	33.56	19.57	3.97
June 14	.00	.00	4.55	34.75	23.17	.00	50.67	29.35	5.37
June 21	.14	.00	10.00	43.25	27.29	.00	62.45	36.31	6.55
June 28	.28	7.55	15.00	50.56	30.52	.00	70.67	40.50	7.81
July 5	.42	28.41	18.87	56.75	34.83	.00	75.48	43.20	8.98
July 12	1.39	49.27	22.21	61.58	36.05	.00	80.35	45.61	9.72
July 19	5.74	64.02	30.03	66.97	37.03	.00	85.75	48.85	10.37
July 26	21.91	65.82	39.12	71.65	38.78	.00	90.39	54.23	11.50
Aug. 2	39.25	73.01	46.49	75.77	41.39	.00	93.27	60.91	12.48
Aug. 9	59.58	78.41	52.92	79.84	46.02	.00	95.21	67.35	13.65
Aug. 16	71.90	83.81	65.02	84.18	49.25	13.11	96.99	72.66	16.24
Aug. 23	84.39	83.81	79.41	88.17	56.23	26.22	98.15	77.91	23.65
Aug. 30	92.89	89.21	91.25	92.41	66.78	50.63	99.00	83.44	33.37
Sept. 6	97.59	94.61	96.55	95.50	74.90	67.01	99.13	90.39	52.72
Sept. 13	99.99	100.01	98.92	97.76	86.38	87.24	99.95	95.54	70.27
Sept. 20	.....	.....	100.01	99.65	99.37	96.17	99.99	98.04	87.15
Sept. 27	.....	.....	.....	100.00	100.01	100.01	.....	100.00	100.00
	99.99	100.01	100.01	100.00	100.01	100.01	99.99	100.00	100.00

Week ending	Age group								
	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
May 17	0.00	1.75	0.55	0.00	0.00	6.64	0.00	0.00	0.00
May 24	.00	10.72	1.50	.00	14.08	16.65	.00	.00	7.94
May 31	14.36	21.84	3.45	.00	36.09	29.32	.00	10.38	19.34
June 7	33.01	40.21	7.93	1.21	51.53	44.54	1.45	25.19	34.71
June 14	54.46	56.49	12.44	3.22	75.60	55.25	3.87	51.68	47.32
June 21	65.02	67.32	15.39	6.04	87.52	62.09	5.23	62.06	56.47
June 28	71.29	73.67	17.32	6.04	93.25	65.57	5.57	62.06	63.03
July 5	80.37	77.66	18.59	6.04	95.08	68.23	6.35	66.82	64.93
July 12	87.63	80.69	20.04	6.78	96.53	70.05	7.31	68.87	66.83
July 19	96.05	84.06	22.26	7.65	97.66	73.63	8.80	72.76	67.87
July 26	98.86	87.55	25.99	7.65	98.60	77.95	11.69	80.65	68.73
Aug. 2	100.02	91.06	30.86	11.41	99.35	82.53	14.53	88.22	71.15
Aug. 9	.....	93.89	36.80	12.01	99.54	87.44	18.76	96.00	73.91
Aug. 16	.....	95.94	42.53	15.90	99.54	90.93	23.91	96.00	77.54
Aug. 23	.....	97.39	50.47	25.56	100.01	92.91	34.40	96.00	82.72
Aug. 30	.....	98.45	60.24	29.79	.....	94.78	49.33	96.00	90.32
Sept. 6	.....	99.15	73.18	43.67	.....	96.35	62.38	100.00	96.71
Sept. 13	.....	99.60	84.29	73.78	.....	98.88	73.70	.....	99.99
Sept. 20	.....	99.91	91.63	87.66	.....	99.03	94.71	.....	.....
Sept. 27	.....	100.00	100.00	100.00	.....	99.99	99.97	.....	.....
	100.02	100.00	100.00	100.00	100.01	99.99	99.97	100.00	99.99

APPENDIX C

ESTIMATION OF NUMBERS AND OF AGE COMPOSITION OF THE ANNUAL RUNS

Portions of the escapement were not counted during 7 of the years, and scale samples for ages are missing for varying proportions of most seasons. Because each age group has its own pattern of seasonal occurrence a special procedure was evolved to resolve this problem. It was decided that grave errors in estimation would result from extrapolating age readings from the first or last week sampled by applying them directly to the earlier or later portions of the run. Neither have we used any estimates of the run not based on actual catches and on counts at the weir. The percentage of runs without age readings or weir counts, or both, are as follows:

9-year periods	Before July 12	After July 12	Total
1922, 1924–31	27	13	18
1932–40	4	30	16
1941–49	20	34	26
Total	16	23	19.5

In individual years the spring portion lacked as high as 74 percent of the data and the fall portion as high as 71 percent. For this reason the estimates of the age composition that we have derived, as well as the numbers of fish in some of the years when the weir count was incomplete, differ in some degree from previously published material.

Because of the sharp difference in age composition between the beginning and the end of the runs, the portions with missing data were estimated separately for the two halves of the season and divided at the end of the week ending July 19.

The method of estimation, while time consuming, is relatively simple. Utilizing tables A–3 and A–4, the percentage was obtained of each age group that would normally occur during the portion of the year for which age and enumeration data were available. Next the percentage was obtained of each age group that would normally occur during the period up to July 19 for which age data were lacking. The number of fish was then computed (for each age group) that would be required (on the basis of the number and percentage with data) to bring that age group up to normal.

For example, suppose 75 percent of the 6_4 group normally should occur during that portion of the season for which ages and counts of the run were available. Then suppose 15 percent should normally occur during the portion of the season up to July 20 for which data are not available. Further, let us suppose that the 75 percent represents 200,000 fish. Then 200,000 times 15/75 or 40,000 would be the number estimated to occur during the early season.

The estimates of the missing numbers were made for each age group and totaled. This total was then divided by the total enumeration (weir count plus catch) for the period without age data, and the estimated total of each age group was then decreased or increased in proportion to this ratio. By this means the total of all ages was made to agree with the actual enumeration.

The same procedure was followed with the portion of the season following July 19, except that for the 7 years without full enumeration the uncorrected estimates of the numbers of each age group were used for the portion of the season that lacked an actual tally, as we feel that this objective method should give a more accurate estimate than any used previously. The estimates are given in table A–5. The figures were not rounded off because of the incidence of many minor age groups.

TABLE A–5.—*Estimated numbers of each age group of sockeye in the annual runs to the Karluk River, 1922 and 1924 to 1949*

Year of run	Age groups									
	3_1	3_2	4_1	4_2	4_3	4_4	5_2	5_3	5_4	6_2
1922	-----	----	896	6,451	8,750	1,390	3,168	691,889	20,180	-----
1924	-----	----	177	6,131	51,616	-----	5,998	1,392,627	59,482	-----
1925	12,824	----	3,710	37,920	152,187	-----	5,369	1,985,213	70,902	-----
1926	8,115	----	18,760	97,462	21,013	1,064	49,342	3,960,107	10,224	-----
1927	138	----	1,682	3,443	41,329	370	91,568	1,139,945	46,273	-----
1928	-----	----	309	9,749	6,066	-----	3,812	1,205,915	5,687	-----
1929	-----	----	223	5,728	5,722	-----	5,350	386,013	2,988	-----
1930	-----	----	-----	807	40,382	-----	8,493	668,420	135,089	-----
1931	312	----	115	18,334	8,961	-----	5,823	791,366	48,736	-----
1932	-----	----	2,029	17,909	11,780	-----	19,229	750,577	18,982	-----
1933	-----	----	1,245	8,715	7,864	-----	37,339	979,393	14,892	-----
1934	-----	----	-----	63,137	5,641	-----	35,893	711,766	61,576	-----
1935	-----	68	3,012	62,301	57,041	-----	40,573	503,766	50,201	1,591
1936	270	----	691	22,473	38,788	166	82,761	1,708,473	44,539	727
1937	-----	242	-----	14,023	51,029	-----	23,439	1,589,153	43,163	-----
1938	-----	----	-----	57,233	14,099	-----	32,320	1,326,449	4,336	-----
1939	-----	324	-----	1,249	8,503	-----	20,864	357,728	38,842	-----
1940	-----	----	190	7,522	7,531	-----	2,931	418,914	64,477	111
1941	-----	----	-----	6,985	13,067	-----	7,141	834,807	38,897	-----
1942	-----	----	1,036	9,589	25,056	-----	10,097	600,700	10,590	-----
1943	-----	----	7,950	10,684	15,935	-----	33,749	949,714	-----	-----
1944	1,310	56	756	11,613	3,597	-----	49,307	796,302	14,188	624
1945	-----	298	-----	12,185	2,003	-----	127,450	263,751	687	264
1946	-----	484	197	5,284	1,376	-----	22,981	122,794	7,500	501
1947	-----	80	-----	4,995	17,170	-----	12,761	158,208	29,118	-----
1948	-----	----	-----	1,090	6,427	-----	6,848	1,002,605	926	-----
1949	-----	----	-----	809	3,806	-----	1,439	596,380	1,136	-----

It was now possible to compile a table showing the total run divided into catch and escapement and of the adults that returned in later years as a result of the spawning of each year's escapement (table A–6).

TABLE A–5.—*Estimated numbers of each age group of sockeye in the annual runs to the Karluk River, 1922 and 1924 to 1949*—Continued

Year of run	Age groups							
	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
1922	244,057	79,159	619	-------	1,440	-------	-------	-------
1924	83,655	344,990	-------	-------	8,751	-------	-------	-------
1925	122,721	540,873	969	-------	11,312	-------	-------	-------
1926	242,792	471,727	2,273	-------	32,308	4,619	194	-------
1927	119,029	129,311	640	-------	10,369	2,734	-------	169
1928	578,612	253,933	-------	-------	29,087	2,094	-------	-------
1929	340,107	361,192	-------	4,077	16,700	-------	-------	-------
1930	189,581	193,037	-------	25	17,950	215	-------	-------
1931	104,767	628,878	1,446	244	14,764	1,253	-------	-------
1932	71,846	471,048	-------	-------	40,840	7,761	-------	-------
1933	286,175	446,593	563	772	19,737	9,711	-------	-------
1934	783,531	639,920	-------	-------	63,206	3,982	-------	1,016
1935	296,785	370,929	1,386	2,503	115,482	24,504	594	263
1936	195,249	270,434	48	1,243	70,428	15,872	397	443
1937	178,261	388,637	4,786	372	17,937	23,460	-------	1,498
1938	302,051	370,332	316	119	22,562	23,896	-------	597
1939	548,439	149,310	1,998	1,657	80,563	4,680	898	353
1940	301,355	405,807	1,187	3,808	49,276	4,387	142	66
1941	192,065	473,348	-------	2,458	57,231	2,708	310	402
1942	115,449	274,837	-------	1,109	86,652	-------	-------	886
1943	397,851	245,617	-------	-------	62,436	2,387	876	-------
1944	359,434	125,103	-------	2,301	43,218	1,021	1,062	343
1945	665,600	178,251	-------	3,421	76,984	1,334	2,546	226
1946	212,614	204,336	-------	6,763	82,223	2,241	412	292
1947	156,163	182,641	-------	490	31,962	-------	1,413	-------
1948	125,916	200,865	-------	3,436	60,049	1,839	-------	-------
1949	230,855	230,986	374	1,219	68,850	3,226	1,469	450

TABLE A–6.—*Catches, escapements and returns from escapements in thousands of fish, 1919–49*

Year of run	Total run	Catch	Escapement	Return
1919	----------	1,090	----------	[1] 2,160
1920	----------	1,369	----------	2,849
1921	(?)3,143	1,643	(?) 1,500	4,494
1922	1,058	658	400	2,282
1923	1,425	730	695	1,990
1924	1,953	891	1,063	809
1925	2,944	1,323	1,621	1,607
1926	4,920	2,386	2,534	1,461
1927	1,587	715	872	1,618
1928	2,095	1,001	1,094	2,630
1929	1,128	227	901	1,587
1930	1,254	167	1,087	1,172
1931	1,625	752	873	2,578
1932	1,412	674	738	2,538
1933	1,813	845	968	2,186
1934	2,370	919	1,450	1,261
1935	1,531	655	876	1,250
1936	2,453	1,078	1,375	1,353
1937	2,336	1,071	1,265	1,334
1938	2,214	984	1,230	1,587
1939	1,215	509	706	1,831
1940	1,268	451	816	858
1941	1,629	698	932	575
1942	1,136	507	629	[2] 607
1943	1,727	806	921	[3] 1,495
1944	1,410	641	769	----------
1945	1,335	676	659	----------
1946	670	228	442	----------
1947	595	110	485	----------
1948	1,410	657	753	----------
1949	1,141	450	691	----------
Sum for period 1921—43	44,236	19,690	24,546	39,103

[1] Plus 4-year-olds.
[2] Plus 8-year-olds.
[3] Plus 7 and 8-year-olds.

APPENDIX D

ESTIMATION OF ESCAPEMENT

The sockeye salmon fishery at Karluk commenced with the salting of salmon in 1867, but the first cannery was established in 1882 (Moser 1899). For 6 years, from 1882 to 1887 only one cannery operated at Karluk and the pack increased each year.

Three canneries operated in 1888 and five in 1889 (Gilbert and Rich, 1927). Up to this time all fishing had been conducted only in the lagoon and in the river inside the sand spit at the mouth, but commencing in 1889 most of the fishing was carried on outside of the river. For the next few years the catch was limited to a large extent by the capacity of the canneries. This is probably one reason why the catches during the years from 1888–94 were fairly uniform in quantity.

There is some evidence that even during this period the large catches were being made (at least in some years) at the expense of the escapement. Shuman (1950) states,

> While catches are subject to many variables, such as fishing intensity, availability, and economic conditions, it is believed that at Karluk they are a reasonably good index of abundance, and it is further believed that the escapements (spawning populations) have decreased proportionately to the decrease in abundance. By *a posteriori* reasoning, the escapements prior to the advent of commercial fishing must have been at least 3 million fish annually. In the first 10 years of operation of the Karluk weir (1921–30) the mean annual escapement was 1.2 million, while for the past 3 years the mean escapement was only 0.4 million.

Prior to the advent of commercial fishing the escapement and the total run are practically one and the same. After 1888 when the fishery was well established the escapement in order to bear the same relation to the catch in earlier years that it did after the weir was established would have had to be larger than the commercial catch. This would mean a total run (in the 1888–93 period at least) of about 6 million fish, so that prior to the advent of commercial fishing the escapement would have been about 6 million.

There is reason to seriously doubt that the runs attained such proportions, except perhaps in a very abnormal year. Rather we are inclined to the view that during the earlier years of the fishery, when fishing was practically unrestricted, the

total catch represented a much greater share of the total run than in any year since 1924.

The largest run since 1924 was in 1926. Because of fishing restrictions the commercial take was limited to 2,386,000 fish and 2,534,000 salmon passed the weir toward the lake. Rich visited the lake and states (Gilbert and Rich, 1927),

> Particular attention was given to the spawning of the adult fish, which was made especially interesting and important by the remarkably fine run and escapement of 1926. The spawning escapement was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake.

Observers visited the lake in a number of prior years: Tarleton H. Bean in 1889, Cloudsley Rutter and M. H. Spaulding (Chamberlain 1907) in 1903, Ward T. Bower in 1911, E. M. Ball in 1917, Henry O'Malley and Charles H. Gilbert in 1919 and 1921, C. H. Gilbert, W. H. Rich, W. P. Studdert, and Fred Lucas in 1922, and Fred Lucas in 1924.

If we assume that Rich's statement is correct, then it is apparent that escapements in earlier years were proportionately smaller than in more recent years. Some measure of this can be gained by comparing the notes of Cloudsley Rutter (Chamberlain 1907, p. 100) with those of Shuman (1950). In 1947 Shuman counted 15,000 salmon (14,826) in Moraine Creek. In 1903 Rutter counted 22,000 (21,756) in the same creek. Since the total escapement in 1947 was 485,000 the escapement of 1903 can be roughly estimated as 22/15 of 485,000 or 711,000. The catch in 1903 was 1,320,000 which would make the escapement only 35 percent of the total run. This is, of course, assuming, which may not be warranted, that spawning in Moraine Creek is representative of the entire run.

A similar situation existed in the sockeye fishery of the Fraser River (Rounsefell 1949). The escapements in the Fraser River from 1894 to 1921 (seven 4-year cycles) averaged 18 percent of the runs, whereas from 1922–45 (six 4-year cycles) they averaged 27.4 percent of the run. Escapements during the earlier period averaged only 65 percent of escapements after 1921. It will be noted that the Fraser fishery was building up slowly with an escapement of slightly more than 25 percent of the runs, which is one-half of the Karluk escapement of recent years, under which the Karluk fishery has continued to decline.

Another factor, possibly minor, that until now has been ignored in discussing escapements is the role of the Karluk hatchery, which was operated in 1891 and again from 1896 to 1916. It was in operation during the same era that sockeye fry were planted in the Fraser River at New Westminster. Results from the planting of fry at the mouth of the Karluk River undoubtedly were equally nonproductive. However, the Karluk run was much smaller than that of the Fraser so that salmon taken out of the escapement for the hatchery may have made a significant reduction in the escapements of the poorer years.

The chief loss from the hatchery was not so much in the numbers of salmon actually stripped as in the large numbers of fish that were killed in handling or that died in the corrals in which they were held for ripening. From various sources table A–7 has been compiled. The number of eggs stripped is shown a year later than are the other statistics as they were reported by fiscal years commencing July 1, and few eggs were ever taken in June. It is obvious that the numbers of salmon captured and held for spawning greatly exceeded the number surviving to be stripped. Bower (1912, p. 75) says,

> There is a tremendous mortality of fish held in corrals and ponds, due no doubt to crowding so many fish together in a limited space, and the loss is particularly heavy during the latter half of July when the water warms up. The season of 1910, the last for which complete statistics are available, is typical of conditions at Karluk. From June 7 to August 10, 1910, a total of 85,623 adult salmon were impounded. Of these fish a total of 42,174, or nearly 50 percent, died and were of no use whatsoever.

In order to determine certain population parameters it was necessary to postulate the escapements prior to the establishment of the counting weir in 1921. Any empirical estimation is subject to legitimate criticism, but the decline in the fishery is of such magnitude that any reasonable estimate will suffice for our purpose.

In constructing table 6 our calculations from the weir counts and age samples were utilized from 1921–49. For prior years we have estimated escapement as 53.85 percent of the catch (based on 35 percent escapement of the total run). An estimate of fish impounded for the hatchery as shown in table A–7 was not subtracted from the estimated escapement.

Table A–7.—Artificial propagation at Karluk

Year (calendar)	Reported number of eggs per female stripped	Number of females stripped	Number of males stripped	Total number stripped	Total impounded	Number of eggs in millions (fiscal years)	Estimated number of eggs per female impounded (calendar years)	Estimated number of salmon impounded
1891								4,699
1892						2.5		
1896								6,015
1897		2,285		3,348	6,640	3.2	1,280	6,640
1898						8.5		8,459
1899		2,837				4.5		19,737
1900		5,524			79,753	10.5	242	79,753
1901						19.3		61,654
1902						32.8		43,985
1903						23.4		52,820
1904						28.1		85,526
1905						45.5		69,361
1906					18,000	36.9	2,150	18,000
1907						38.7		89,850
1908						47.8		75,752
1909						40.3		84,962
1910				43,449	85,623	45.2	579	85,623
1911	2,826	14,516	14,770	29,286		49.6		77,008
1912						41.0		85,714
1913	3,109					45.6		65,038
1914	2,542					34.6		56,767
1915	2,620					30.2		77,256
1916						41.1		1,880
1917						1.0		
Average number eggs per female impounded							1,063	
Average number of eggs per salmon impounded (1063/2)							532	

APPENDIX E

RAINFALL AND SPAWNING SUCCESS

For the Skeena River sockeye, Brett (1951) attempted to determine the effect of precipitation in August and September on success of reproduction for the 1920–34 period. He used multiple correlation with four variables: seeding (estimates of numbers spawning), precipitation, production (returning adults taken in catch at various ages from each seeding), and catch (in the brood year). His "seeding" is a ranked estimate-of-escapement that is not significantly correlated with catch in the brood year (r is .38 and P.05 is .51). Precipitation and production gave a correlation of .56 (P of .05 is .51). Precipitation and production with seeding held constant gave a partial correlation of .64 (P of .05 is .53, P of .01 is .66).

Brett has assumed linear relations both between the returns (production) and number of spawners ("seeding" or catch), and also between rainfall and returns. Analysis of his data (fig. A–2 and A–3) shows that the ranked seeding is probably a very poor estimate of escapement. The second portion of figure A–2 shows that the catch in the brood year is probably a good relative measure of escapement since the $\log_{10}$ production/catch in brood year shows a high negative correlation with catch in the brood year, $r=-.79$ and P of .01 is .64. The lower portion of figure A–2 shows the reproduction curve resulting from this relationship.

The residuals of $\log_{10}$ production/catch in the brood year versus catch in the brood year are shown in figure A–3 as the ordinate and inches of rainfall in August and September as the abscissa. The correlation is .59 with $P.05=.51$ and $P.01=.64$. However, if we exclude 1920 data the correlation is very high .75 with $P.01=.66$. The curve shown in figure A–3 is calculated without 1920. It would appear that the function is probably curvilinear, and, as the Karluk data seem to indicate, the production reaches a maximum and then declines if rainfall is excessive.

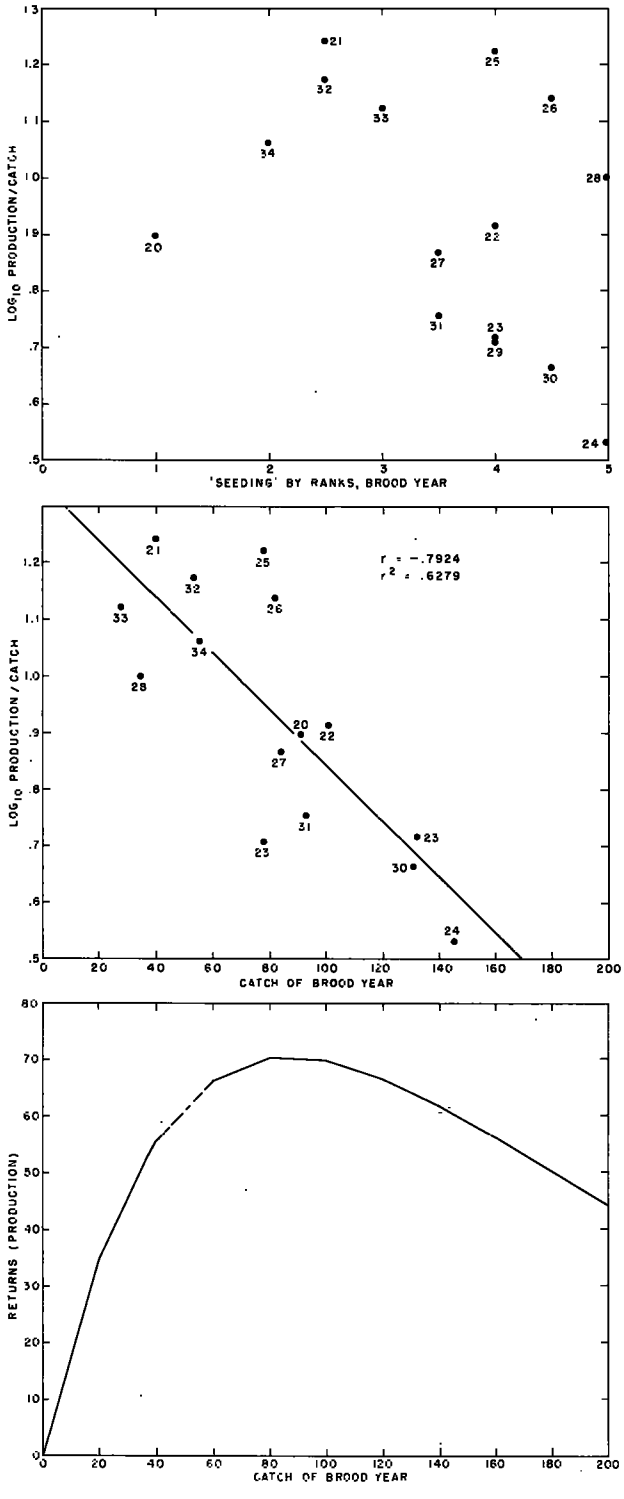

FIGURE A–2.—Relationship between spawners and returns for the Skeena River.

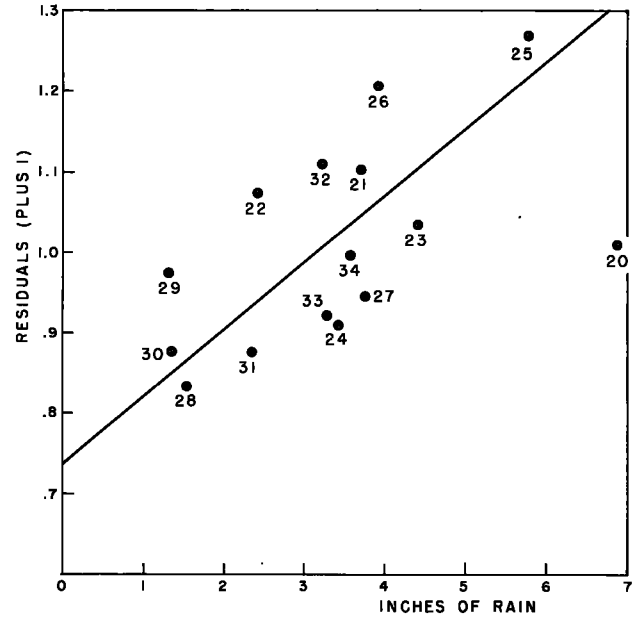

FIGURE A–3.—Relation between late summer rainfall and relative success of spawning as given by the residuals of log production/catch of brood year versus catch of brood year for the Skeena River.

APPENDIX F

DATA ON CULTUS LAKE SMOLT MIGRATIONS AND RETURNS

TABLE A–8.—*Analysis of data on smolt migrations and returns from sockeye of Cultus Lake*

[Data from Foerster 1954]

Year of smolt migration	Number of smolts (–000)	Average length cm.	Average weight gm.	Returning adults in escapement (–00)
1927	250	10.07	11.0	64
1928	336	8.08	5.1	109
1929	2,460	6.86	3.1	398
1930	104	10.70	12.8	48
1931	365	9.08	7.3	76
1932	779	9.02	7.3	202
1933	1,556	7.22	3.7	161
1934	184	8.66	8.4	85
1935	324	9.26	8.2	27
1936	498	9.80	8.9	288
1937	3,112	8.42	5.8	756
1938	1,640	8.8	7.0	736
1939	217	10.5	12.8	145
1940	1,375	9.9	9.7	411
1941	3,979	6.3	2.7	122
1942	1,752	8.1	5.4	141
1943	694	9.2	7.8	52
1944	2,012	8.9	7.5	373

APPENDIX G

CALCULATION OF NUMBER AND BIOMASS OF KARLUK SMOLT MIGRATIONS

The length-weight curves in table A–9 are derived from linear least square fits of the logarithms of length and weight. For Karluk the average lengths and weights for each centimeter length interval for three weekly sampling periods were used. In fitting, these averages were weighted by the numbers involved.

In constructing table A–10 the 2- and 5-year migrants, which usually account for about 2 to 5 percent of the returning adults were omitted because of the lack of adequate data on their survival. The length for the week ending June 7 was used because it was sampled in all years, and is about midway in the smolt migration. The average weights in grams for the lengths given were from figure A–4.

The number of smolts of each age leaving the lake was estimated from the number of adults surviving, by utilizing the smolt to adult survival rates determined from marking experiments. Barnaby (1944) found for 6 years that the rates for all smolts were 20.8 percent (this year with incomplete returns), 22.3, 21.0, 23.6, 20.5, and 20.5 percent. For the 3-year smolts the survival rate was 17.4 percent and for smolts leaving in their fourth year the rate was 25.7 percent.

Table A–11 shows the 3- and 4-year smolts combined by the years in which they left the lake rather than by brood year. This has been done in order to assess the total biomass of smolts leaving the lake in any one year (minus the 2- and 5-year smolts).

TABLE A–9.—*Length and weight of seaward-migrant sockeye (fork length in millimeters, weight in grams)*

Length (mm.)	Weight		
	Karluk Lake [1] (gms.)	Cultus Lake [2] (gms.)	Babine Lake [3] (gms.)
60		2.21	
65		2.76	
70		3.47	
75		4.29	3.94
80		5.22	4.90
85		6.29	6.01
90		7.49	7.28
95		8.85	
100	9.01	10.35	
105	10.46	12.02	
110	12.06	13.87	
115	13.81		
120	15.73		
125	17.82		
130	20.08		
135	22.53		
140	25.18		
145	28.04		
150	31.10		
155	34.32		
160	37.86		
165	41.60		
170	45.56		

[1] Based on 1031 specimens, May 28–June 13, 1936.
[2] Based on average lengths and weights of total migrations 1927–44 (Foerster 1954).
[3] Based on average lengths and weights of smolts in second year 1950–53 (Dombroski 1954).

TABLE A–10.—*Size, number, and weight of 3- and 4-year smolts from each brood year, 1922–37*

Brood year	Size of smolts migrating week ending June 7				Adults from brood year according to migrant age		Estimated number of smolts leaving lake		Total biomass of smolts	
	Length (mm.)		Weight (gms.)		Age 3 (-000)	Age 4 (-000)	Age 3 [1] (-000)	Age 4 [2] (-000)	Age 3 (Metric tons)	Age 4 (Metric tons)
	Age 3	Age 4	Age 3	Age 4						
1922	135.6	145.9	22.8	28.5	1,744	318	10,023	1,237	228.52	35.25
1923	135.8	145.9	22.9	28.5	1,587	385	9,120	1,498	208.85	42.69
1924	132.6	143.4	21.2	27.3	582	210	3,345	817	70.91	22.30
1925	129.8	145.7	19.9	28.4	779	805	4,477	3,132	89.09	88.95
1926	130.1	140.1	20.0	25.2	904	540	5,195	2,101	103.90	52.95
1927	126.7	139.7	18.5	25.0	1,046	529	6,011	2,058	111.20	51.45
1928	129.9	142.9	20.0	26.8	1,777	771	10,212	3,000	204.24	80.40
1929	131.8	147.2	20.9	29.5	1,018	503	5,850	1,957	122.26	57.73
1930	137.7	147.8	23.9	29.6	705	339	4,052	1,319	96.84	39.04
1931	138.9	153.7	24.8	33.3	1,944	457	11,172	1,778	277.07	59.21
1932	142.0	142.6	26.3	26.6	1,992	494	11,448	1,922	301.08	51.13
1933	132.7	125.8	21.3	18.2	1,930	203	11,092	790	236.26	14.38
1934	119.5	130.2	15.5	20.1	676	502	3,885	1,953	60.22	39.26
1935	120.2	142.9	15.7	26.8	621	625	3,569	2,432	56.03	65.18
1936	128.7	142.1	19.4	26.4	958	377	5,506	1,467	106.82	38.73
1937	131.8	138.3	21.0	24.3	1,014	302	5,827	1,175	122.37	28.55

[1] Times reciprocal of 17.4 percent or 5.747.
[2] Times reciprocal of 25.7 percent or 3.891.

TABLE A–11.—*Number and total weight of smolts leaving Karluk and Cultus Lakes in various years, 1926–44 (weight in metric tons)*

[Number in thousands]

Year of seaward migrations	Karluk Lake [1]				Cultus Lake [2]	
	Weight			Number	Weight	Number
	Age 3	Age 4	Ages 3 and 4			
1925	222.52					
1926	208.85	35.25	244.10	10,357		
1927	70.91	42.69	113.60	4,843	2.75	250
1928	89.09	22.30	111.39	5,294	1.72	336
1929	103.90	88.95	192.85	8,327	7.63	2,460
1930	111.20	52.95	164.15	8,112	1.33	104
1931	204.24	51.45	255.69	12,270	2.67	365
1932	122.26	80.40	202.66	8,880	5.69	779
1933	96.84	57.73	154.57	6,009	5.79	1,566
1934	277.07	39.04	316.11	12,491	1.54	184
1935	301.08	59.21	360.29	13,226	2.66	324
1936	236.26	51.13	287.39	13,014	4.43	498
1937	60.22	14.38	74.60	4,675	18.05	3,112
1938	56.03	39.26	95.29	5,522	11.48	1,640
1939	106.82	65.18	172.00	7,938	2.78	217
1940	122.37	38.73	161.10	7,294	13.34	1,375
1941		28.55			10.74	3,979
1942					9.46	1,752
1943					5.41	694
1944					15.09	2,012
Sum			2905.79	128,252	122.56	21,647
Average			193.72	8,550	6.81	1,203
1927–1935:						
Sum					31.78	6,368
Average					3.53	708
1936–1944:						
Sum					90.78	15,279
Average					10.09	1,698

[1] Omitting the smolts leaving in second and fifth years, usually 2 to 5 percent.
[2] Calculated from Foerster (1954, table 1).

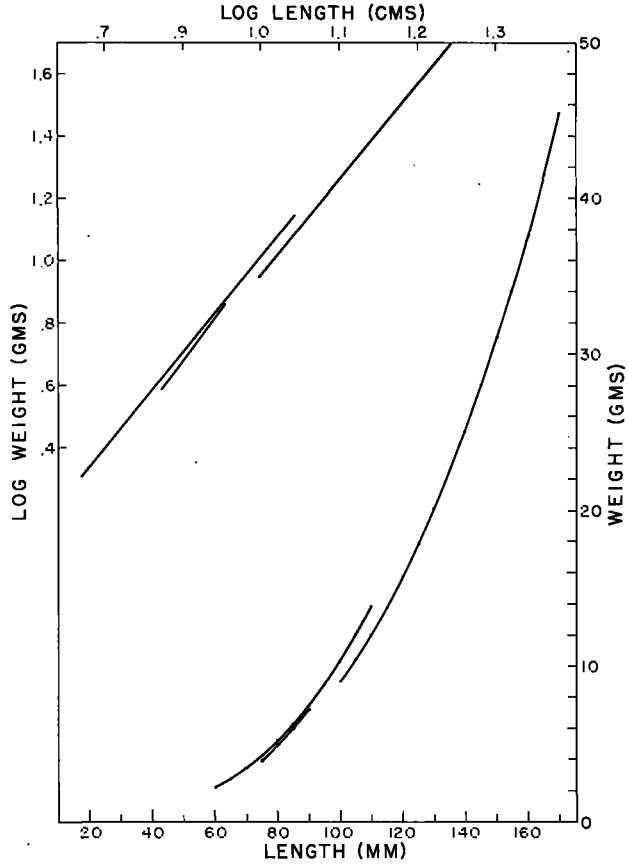

FIGURE A–4.—Length-weight curves for sockeye smolts from Karluk, Cultus, and Babine Lakes.

TABLE A–12.—*Comparison of Karluk and Cultus Lakes* [1]

Item	Karluk	Cultus
Area:		
Square miles	16.04	2.42
Acres	10,266	1,550
Watershed: Square miles	108.67	32.0
Annual rainfall:		
Kodiak 1916–41, inches	57.2	
1933–35, inches		61.8
Volume of lake: Acre feet	1,556,851	175,470
Total precipitation on watershed: Acre feet	331,749	105,472
Minimum outlet flow:		
August 1928 (7 cu. meters), c. f. s.	247	
Late summer (1/2 cu. meter), c. f. s.		18
Annual number of smolts:		
Average per acre	833	776
Maximum per acre	1,288	2,567
Biomass of migrating smolts:		
Metric tons, average	193.7	6.8
Kilos per acre, average	18.8	4.4
Pounds per acre, average	41.4	9.7
Kilos per acre, maximum	35.1	11.6
Pounds per acre, maximum	71.1	23.5
Ratio of lake volume to total precipitation on watershed	4.7	1.7

[1] Physical data for Cultus Lake from Ricker (1937b).

APPENDIX H

COMPARISON OF ALTERNATE METHODS FOR DERIVING RESIDUALS OF RETURN ON ESCAPEMENT

In the section of this report dealing with the effect of climate on success of reproduction the residuals of return on escapement employed are derived from the formula (letting y equal return and x equal escapement):

$$y/x = a - b \log x \qquad (1)$$

This corresponds to:

$$y = (a - b \log x)x \qquad (2)$$

which can be written (See fig. 19) as:

$$\log y = x\epsilon^{a-b \log x} \qquad (3)$$

The question was raised by reviewers of the draft of this report as to whether use of a ratio in fitting (formula 1) may yield biased residuals.

This point has been tested by comparing the residuals derived from other formulae with those derived from formula 1 above. Since it was suggested that it might be advantageous to correct for time in years because of the declining run, a time factor was used in some of the tests.

Letting y equal return, x equal escapement and t equal time, three regressions were calculated:

$$\log y = a + b \log x + b_{y_{1.2}}\, t + b_{y_{1.3}}\, t^2 \qquad (4)$$

$$\log y = a + b \log x + b_{y_{1.2}}\, t \qquad (5)$$

$$\log y = a + b \log x \qquad (6)$$

The residuals of log y on log x were then calculated for each formula (holding t and t^2 at $\bar{t}$ and $\bar{t}^2$ in the appropriate formulae). These residuals were then compared with those derived from formula 1 above. The period 1887–1923 was used to give comparisons with figures 5, 6, and 19.

Comparison of residuals of y (formulae 4, 5, and 6) on residuals of y (formula 1):

Formulae	r	r^2	Syx
4 and 1	0.8884	0.789	0.088
5 and 1	.9290	.863	.070
6 and 1	.9342	.873	.069

It will be noted that the correlations between the sets of residuals are all high, the highest occurring between residuals of formulae 6 and 1. These are plotted in figure A–5. There appears to be a slight tendency toward curvilinearity in their relation as shown by the empirical curve drawn through the grouped means. The standard error of estimate about the empirical curve is

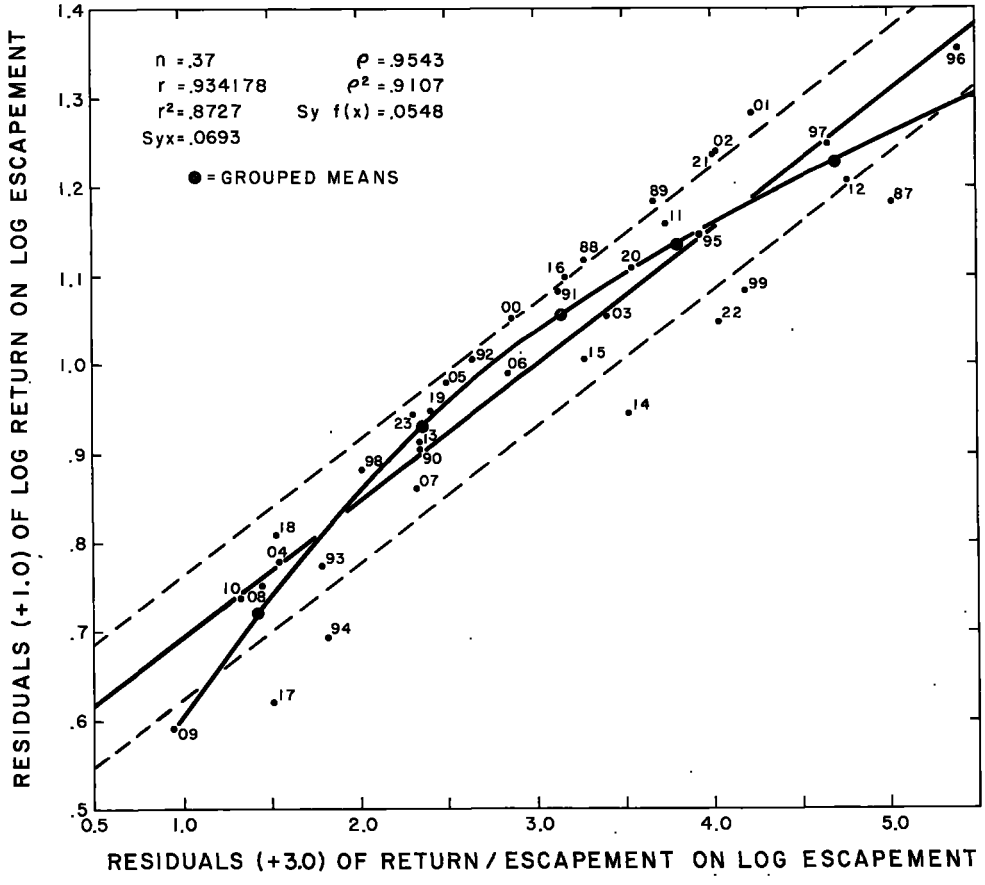

FIGURE A–5.—Comparison of residuals of return on escapement derived by two methods.

.055 compared to 0.69 for the linear regression. The index of correlation, P, for the empirical curve is 0.9543 compared to the linear correlation coefficient of 0.9342. However, the difference between the two (Fisher, 1936, p. 206), 0.188 is less than its standard deviation, 0.242, and hence not statistically significant.

APPENDIX I

RELATION OF KODIAK AND KARLUK TEMPERATURES

Because the only extended series of records of climatic conditions were taken at the town of Kodiak, they were employed in this study so that the degree of association between Kodiak and Karluk conditions is important in evaluation of the data. That the daily temperatures of the air and surface of the sea at various points around Kodiak Island are closely associated was shown by Rounsefell (1930) from a series of temperatures from April through September, 1926.

Water temperatures for Karluk Lake were published for certain dates by Juday et al. (1932) for the 1926–30 period and by Barnaby (1944) for 1935 and 1936. The summer temperatures for these years for surface and 10-meter depths are shown in table A–13. These have been correlated (fig. A–6) with Kodiak air temperatures for a 30-day period ending on the date the water temperature was taken. Both series of water temperatures show a high significant correlation with the air temperature. As expected the surface-water temperature is more variable than the temperature at 10 meters.

TABLE A–13.—*Comparison of Kodiak and Karluk summer temperatures, 1926–36* [1]

Date			Karluk Lake temperature		Kodiak air temperature 30-day period to date shown [2]
Year	Month	Day	Surface	10 meters	
			° F	° F	° F
1926	August	15	60.08	56.30	56.80
1927	July	19	52.34	49.46	51.21
Do	August	13	51.98	50.54	52.77
1928	July	10	50.36	47.30	50.67
Do	September	3	49.46	49.46	53.02
1929	July	9	55.76	49.10	51.18
Do	September	8	53.60	52.70	55.48
1930	July	12	49.64	46.94	50.28
1935	June	28	51.80		49.72
Do	July	11	52.88		51.52
Do	do	30	53.42		54.50
Do	August	13	53.96		54.80
Do	September	6	54.86		54.36
1936	June	28	56.48		55.08
Do	July	11	53.96		57.61
Do	do	18	56.30		58.64
Do	August	7	62.78		59.65
Do	do	13	59.90		59.01
Do	do	27	59.00		57.52
Do	September	9	55.86		55.16

[1] Karluk temperatures 1926–30 from Juday et al. (1932), 1935–36 from Barnaby (1944).
[2] Derived from mean monthly temperatures weighted by number of days falling in each month.

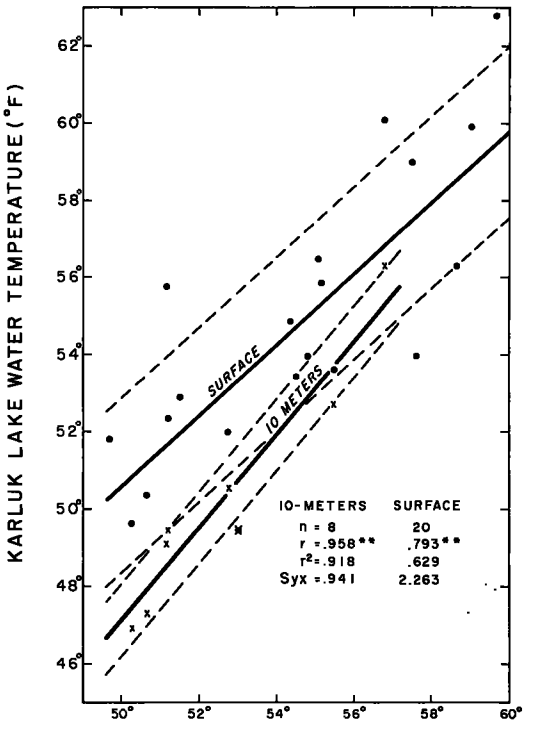

FIGURE A–6.—Comparison of Karluk Lake water temperatures with Kodiak air temperatures for the preceding 30-day period.

This indicates that average monthly air temperatures at Kodiak are a useful and fairly reliable indication of Karluk water temperatures.

APPENDIX J

RELATION OF AGE OF SMOLTS AT MIGRATION TO TEMPERATURE, SIZE, AND NUMBER

The question of an increase in the average age of smolts is a troublesome one. It was shown that the broods with larger returns have a larger proportion of younger fish, but this can perhaps be explained by the additional mortality resulting from a greater age at maturity.

It has been suggested by some authors that an increased age of smolt at Karluk has been caused by lack of sufficient fertility of the lake. However, figure 28 showing the strong linear relation between numbers and biomass of smolt migrations refutes this suggestion.

The question has been raised as to whether the increased smolt age has been accompanied by a decrease in smolt size. Figure A–7 shows that the average length of the 1922–37 broods (migrating in their third year from 1925–40 and in their fourth year from 1926–41) at time of migration from the lake varied widely with no apparent trend (r for time and length equals −0.29 and is not significant).

In an attempt to answer the question as to what causes a smolt to migrate we have calculated a multiple regression in which

y=the ratio of smolts migrating in their third year to smolts of the same brood migrating in their fourth year (columns 8 and 9, table A–10).

x_1=length of smolts migrating in their third year (column 2, table A–10).

x_2=mean June–July air temperature at Kodiak year of migration.

x_3=total numbers of 3 year smolts and 4 year smolts leaving lake (from 2 different broods, column 5, table A–11) year of the migration.

The resulting correlations are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	June–July temperature (X^2)	Number 3 and 4 smolts migrating (X^3)
Correlations of Y with X's	0.4534	0.9152**	0.6705**
Standard regressions of Y on X's	.0583	.7966**	.2600

R=0.9365**.

However, examination of table A–14 shows that the apparent high correlation with temperature is largely due to the extremely high 3/4 smolt ratio for the 1933 year class and the correspondingly extreme temperature of 58.20° F. It would appear that this extreme temperature had some physiological effect which caused a very much heavier migration than normal for the length, greatly reducing the length-ratio correlation.

The distinct possibility of such a physiological effect is substantiated by the work on temperature tolerance in Pacific salmon by Brett (1952). He showed (p. 300, fig. 22) that young sockeye acclimated at 5° C. had a preference (modal preference) of 10 to 11° C., and even for young sockeye acclimated at 10° C. the modal preference was 12 to 13° C. with the upper limit of one standard deviation at about 14.5° C. This upper limit of 14.5° C. is almost exactly equivalent to the 58.20° F. the 3-year-olds of the 1933 brood encountered in June and July of 1936.

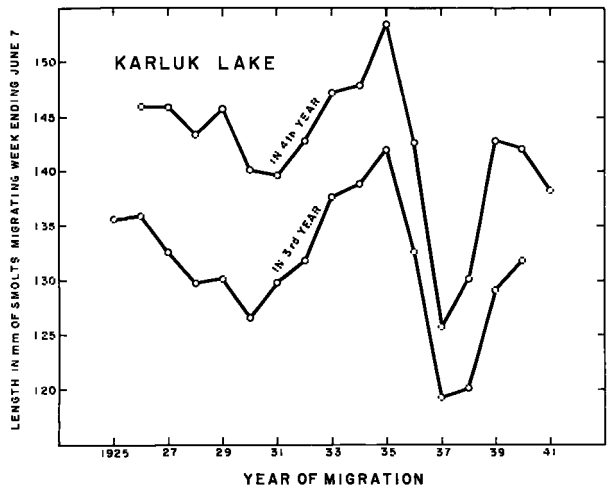

FIGURE A–7.—Lengths of Karluk smolts migrating in their third and fourth year.

Since this temperature was far above any of the other years we recalculated the multiple regression

TABLE A–14.—*Factors influencing age of smolts at time of seaward migration*

Year of spawning	Ratio of smolts migrating in year 3 to those migrating in year 4 (Y)	Length of 3-year smolts (X_1)	Mean June-July Kodiak temperature year when 3-year smolts migrate (X_2)	Number of 3-year and 4-year smolts migrating in year 3-year smolts migrate (X_3)
		Mm.	°F.	(–0000)
1923	6.1	136	55.90	1,035
1924	4.1	133	50.70	484
1925	1.4	130	50.95	529
1926	2.5	130	52.50	833
1927	2.9	127	50.80	811
1928	3.4	130	51.25	1,227
1929	3.0	132	50.80	888
1930	3.1	138	52.30	601
1931	6.3	139	51.30	1,249
1932	6.0	142	52.15	1,323
1933	14.0	133	58.20	1,301
1934	2.0	120	49.90	468
1935	1.5	120	49.00	552
1936	3.8	129	51.20	794
1937	5.0	132	51.75	729
Mean	4.34	131.4	51.91	854.9
Mean without 1933	3.65	131.3	51.46	823.1

excluding the data for the 1933 brood. The resulting correlations are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	June—July temperature (X_2)	Number 3 and 4 smolts migrating (X_3)
Correlations of Y with X's	0.7659**	0.6007*	0.6926**
Standard regression of Y on X's	.4456	.1836	.3461

$R=0.8314^{**}$.

The result is not altogether surprising. It shows that, except perhaps in years of extremely warm early summer temperatures, the temperature plays but a minor role.

Since temperature normally does not appear too important as a factor to induce migration, this variable was eliminated with the following result:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	Number of 3 and 4 year smolts migrating (X_2)
Correlations of Y with X's	0.7659**	0.6926**
Standard regressions of Y on X's	.5472	.3625

$R=0.8186^{**}$.

It will be noted that R is practically the same, .8186, as before, .8314, showing that temperature contributed little to the correlation.

Since number times individual weight equals the biomass of the smolts migrating it was of interest to examine the effect of biomass on the ratio migrating in the third year. The results are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	Biomass migrating (X_2)
Correlations of Y with X's	0.7659**	0.7679**
Standard regressions of Y on X's	.4324	.4406

$R=0.8182^{**}$.

Length and biomass have a correlation coefficient of .7566. This close dependence of biomass on individual size suggests that the survival of the young may be linked with size.

However, at Bare Lake (Fish and Wildlife Service, 1955) the highest ratio 2.0 of 2 to 3 year smolts migrating from one brood (1948 to 1951 broods) was for the 1948 brood, when the total of all smolts migrating in the second year following spawning was 10,199, and the lowest ratio 0.2 was for 1949 when only 4,503 smolts left the lake in the second year after spawning. This occurred despite a progressive increase in smolt size.

APPENDIX K

PHOSPHORUS RELATIONSHIPS IN KARLUK LAKE

The 1927 determinations of soluble phosphorus in streams tributary to Karluk Lake (table A–15) as well as the determinations of total phosphorus both in Karluk Lake and in tributary streams are from Juday, Rich, Kemmerer, and Mann (1932). The 1935 and 1936 determinations of soluble phosphorus in streams (table A–15) are from Barnaby (1944).

If we make the wholly reasonable assumption that the 0.0105 milligrams/liter of soluble phosphorus during the week ending July 5 does not include any phosphorus from salmon carcasses, then it appears that the streams pick up a not inconsiderable quantity of soluble phosphorus between their upper reaches (last column, table A–15) and the lake. If we now subtract this average amount of 0.0105 from the averages of the subsequent weeks we can obtain a summation of the surplus during the summer of soluble phosphorus contributed by salmon carcasses decomposing in the streams.

This summation is 0.1721. The summation of the remaining 0.0105 by 52 weeks yields 0.5460, assuming that the soils are being leached at comparable rates during the remainder of the year. Since Nelson and Edmondson (1955) state that 25 percent of the salmon spawn in the lake and that one-third of the stream carcasses are either washed into the lake or removed by animals or birds, the figure for salmon-derived phosphorus must be doubled to represent the contribution of the carcasses. This gives 0.3442 as the relative contribution of carcasses against 0.5460 as the relative terrigenous contribution of soluble phosphorus. Since the spawning escapements of 1927, 1935, and 1936 averaged 1,041,000 salmon we can accept the 6,100 kilograms of phosphorus given by Nelson and Edmondson (1955) for one million spawners, which would leave an estimated 9,670 kg. (6,100 times 0.5460/0.3442) of soluble phosphorus contributed by the soils and rocks of the watershed.

Perhaps a more reliable method would be to consider only total phosphorus. The average

TABLE A–15.—*Soluble phosphorus in spawning streams tributary to Karluk Lake, 1927 and 1935–36*
[In milligrams per liter of water]

Streams	Taken near mouth during weeks ending on dates shown												Taken above spawning areas
	June	July				August					September		
	28	5	12	19	26	2	9	16	23	30	6	13	
Cold Creek													0.012 .015
Spring Creek		0.002 .006		0.005			0.005	0.022		0.006		0.014	
Moraine Creek		.018 .032		.060 .130	0.060		.135	.022		.014		.030	.004
Cottonwood Creek		.016 .015		.080 .045		0.030	.180	.020				.008 .014	
Grassy Point Creek			0.036 .056			.045		.016 .100				.014 .019	
Alder Creek			.002 .016	.020		.025	.050	.016				.010 .012	
Little Lagoon Creek	0.004		.009 .010 .008	.016				.010					.005 .004 .006 .004
Halfway Creek			.004 .010		.023	.025		.014 .040				.010	.002 .004 .004
Salmon Creek		.004	.016 .018	.060	.015		.005	.025 .050		.018	0.010		
Upper Thumb River		.007	.022 .020	.045	.025 .025		.019	.035 .070		.024	.026		.004
Meadow Creek		.012		.025		.030		.018 .060				.008	
Cascade Creek		.006 .003		.005 .024 .006		.016		.020 .025				.003	Trace.
Canyon Creek		.032 .004		.008 .016				.030				.014	.002
Falls Creek		.000 .000		.005 .006								.006	.003
Sum	.004	.157	.227	.556	.148	.171	.394	.593		.062	.036	.162	.069
Items	1	15	13	17	5	6	6	18		4	2	13	14
Average		.0105	.0175	.0327	.0296	.0285	.0657	.0329	(0.0242)	.0155	.0180	.0125	.0049
Above 0.0105			.0070	.0222	.0191	.0180	.0552	.0224	.0137	.0050	.0075	.0020	

total phosphorus in the lake varied in 8 observations by Juday et al. (1932) from 0.014 to 0.019 mgm./1. with very slight variation from the surface to the deepest part of the lake. Since the lake volume is 1,920 million cubic meters the total P can be estimated at 31,680 kg.

Six observations of total phosphorus in streams (all above salmon spawning areas) yield an average of 0.0175 mgm./1. To estimate the amount contributed by the streams an estimate must be made of the total stream flow. Nelson and Edmondson (1955) estimate the mean outflow of Bare Lake (about 15 airmiles from Karluk Lake) at 6 cubic feet per second. The ratio of the Karluk watershed to that of the Bare Lake watershed is about 93.68 (108.67 sq. miles/1.16 sq. miles by planimeter measurement). From this we can estimate the average outflow of Karluk Lake at 562 c. f. s. The one measured flow we have available is 475 c. f. s. with the lake level at −1 inch. Since from 1927 to 1953 the level has varied from −13 to +18 inches we will accept the 562 c. f. s. as a rough approximation of the true flow.

If the flow is 562 c. f. s., the total yearly outflow would be 656 million cubic yards or 502 million cubic meters. Since inflow must equal outflow the total natural phosphorus from the streams can be estimated at 11,480 kg. As the total phosphorus observations used were taken above the salmon spawning areas, thus eliminating the terrigenous phosphorus that would occur in the lower reaches of the streams, this seems to be a minimum estimate.

From the preceding figures we can make an approximate balance sheet for total kilograms of phosphorus in Karluk Lake (omitting phosphorus in the young salmon and other fishes in the lake) as follows:

	Kilograms
Estimated in Karluk Lake water	31,680
Estimated annual inflow from tributaries	11,480
Estimated annual gain from 1,000,000 carcasses	6,100
Total of chief sources	49,260
Minus loss from outflow (502/1,920 or 26.1 percent)	12,857
Remainder assuming 1,000,000 spawners	36,403
Remainder assuming 500,000 spawners	34,149
Remainder assuming 2,000,000 spawners	40,911

APPENDIX L

SPAWNING OF SOCKEYE IN KARLUK RIVER BELOW KARLUK LAKE

The extent of spawning in the main river below Karluk Lake may not have received as much attention as it may deserve because (1) such spawning often occurred rather late in the season and so was only partially observed by summer field parties visiting the lake, (2) since spawning fish would often be intermingled with fish migrating into the lake it was somewhat difficult to distinguish spawners from upstream migrants, and (3) because of the extremely small percentage of mature fish found that had stream-type scale nuclei indicating they had entered the sea as fry, it has been rather generally considered that the great majority of the offspring of these below-the-lake spawners perish.

Considerable doubt concerning this last point would seem warranted by the observations of Philip R. Nelson (loc. cit.) in which he saw fry ascending into the lake. Furthermore, the consistent negative effect of the number of pink-salmon spawners on the success of returns from sockeye spawners is difficult to wholly explain by competition for spawning beds within the lake and its tributaries, since few pinks entered the lake in years of small or moderate pink runs. If on the other hand, a significant number of sockeye normally spawn below the lake, and if the resulting young contribute a significant proportion of the seaward smolt migration, then the consistent negative effect of pink salmon spawners on the success of sockeye spawning has a more logical explanation as the pinks normally utilize the spawning beds below the lake.

Gilbert and Rich (1927, p. 30) write:

> . . . there are found in the river in spring and early summer a limited number of fry in their first year, which are believed to straggle out to sea during the early part of the season. Apparently they are not moving downward with the regular seaward migration of lake fish, but are observed even after the fingerling migration is past, in the eddies along the banks of the river and among the water weeds along the shore where the current is slack; but they seem to have disappeared before midsummer, and have doubtless gone to sea. . . . as considerable numbers of adult salmon are known to spawn in the river gravels below the lake it is considered probable that the fry in question have had this origin and that they occur numerously . . . . If this is true, their mortality in the sea must be extraordinarily great, for there are relatively few mature fish returning to spawn that have had this early history. In the 1926 run of mature fish, only six-tenths of 1 percent belonged to this group . . . .

Writing on the observations of Cloudsley Rutter, Chamberlain (1907) says of the Karluk:

> The upper course is of moderate current and affords excellent spawning ground, while in addition there are many sloughs to act as nursery ponds for the young.
>
> Throughout May and June [1903] the sloughs of the upper part of the Karluk River contained many sockeye fry or small fingerlings. In a haul May 22 nearly a thousand were taken, many with remnants of yolk. June 21 large schools of small fingerlings were numerous in the upper river, and some were taken with the dip net. June 30 a few fingerlings averaging nearly 2 inches in length were taken in a pool of the river.

Rutter attempted to determine whether any sockeye fry moved out of Karluk Lake down the river. Between June 5 and 28 he made 4 overnight sets with a net with a 25-foot spread in Karluk River at the lake outlet on the shoal side. Although the catch in the 4 sets included large numbers of sculpins and sticklebacks, 185 sockeye parr, and 39 trout, the nets also took on successive nights a few fry (16 fry, 2 fry, and no fry).

After Rutter's 1903 observations the next are those of Edward M. Ball in 1917 (Gilbert and Rich, 1927, p. 12):

> September 12 [1917].—This part of the river (the upper 2 miles) formed the spawning ground of a large number of red salmon, the river bottom being a mass of spawning beds.

O'Malley and Gilbert (Gilbert and Rich, 1927, p. 16) estimated a school of 10,000 sockeye at the foot of the lake in 1919, which they state was not present in 1921 (on Aug. 12).

In 1922, Gilbert and Rich (1927, p. 17) record sockeye spawning in greater abundance than pinks in the quarter-mile of river below the lake.

In 1924, Fred R. Lucas (Gilbert and Rich, 1927, p. 20) in the period September 16 to 24, wrote that sockeye in considerable numbers had spawned and were spawning in the river for one-half to three-quarters of a mile below the lake.

In 1926 (no spawning surveys were made in 1923 or 1925) Gilbert and Rich (1927, p. 26) wrote on August 27:

> . . . it was difficult to estimate the number of fish actually spawning in the upper 2 miles of the river, but I believe there were between 50,000 and 100,000. In addition, there were as many more, approximately, in the river passing up, either to spawn in the upper reaches of the river or to go on into the lake.

All of the information we have available is summarized in table A–16 which starts with 1917 and runs through 1932, the last year for which I had field spawning observation notes. Out of 12 years there are only 3 in which the notes fail to chronicle the spawning in the main river below the lake. In at least 2 years (1926 and 1927) the spawners appear to have approached a quarter of a million.

There is some suspicion that most of these river spawning estimates may be too low in some years because of the sockeye that still remained to ascend after the removal of the weir. In the 14 years from 1922–36, inclusive (except 1924 when the number of pink salmon carcasses broke it early), the weir was removed each year by the following dates: 1922 (October 22); 1926, 1927, 1929 (October 14); 1923 (October 12); 1928 (October 11); 1930, 1933 (October 9); 1931 (October 8); 1925 (October 6); 1932, 1934, 1935, 1936 (October 5).

For 4 of these 14 years the reports state that mature sockeye that had not yet ascended the river were still present in the brackish lagoon inside the river mouth when the weir was removed.

Furthermore, there is little information concerning the spawning areas of a large portion of the late spawners during these years because the spawning ground observations were terminated long before all the spawners had had time to reach the lake as shown in the following tabulation:

Year	Date of last recorded spawning ground observations	Date of weir removal	Intervening days plus 11-day lag (lower weir to lake migration time)
1922	Aug. 22	Oct. 22	72
1923	(2)	Oct. 12	
1924	Sept. 24	Aug. 21[1]	?
1925	(2)	Oct. 6	
1926	Aug. 27	Oct. 14	59
1927	Sept. 22	Oct. 14	34
1928	Sept. 5	Oct. 11	47
1929	Sept. 12	Oct. 14	43
1930	Sept. 10	Oct. 9	40
1931	Sept. 27	Oct. 8	22
1932	Sept. 5	Oct. 5	41
Sum			358
Average number of days at end of season during which spawners counted through the weir could reach lake unobserved			44.8

[1] Weir washed out as a result of large number of pink salmon carcasses.
[2] No survey.

TABLE A–16.—*Sockeye spawning in Karluk River below Karluk Lake in certain years from 1917 to 1932*

Year of spawning	Observer	Source of data	Area of spawning	Estimated number
1917	Edward M. Ball	Gilbert and Rich (1927)	Upper 2 miles	Large.
1918	No survey			
1919	O'Malley and Gilbert	Gilbert and Rich (1927)	At foot of lake	10,000.
1920	No survey			
1921	O'Malley and Gilbert	Gilbert and Rich (1927)	None up to Aug. 12	
1922	Gilbert and Rich	....do....	Upper $\frac{1}{4}$ mile	Greater abundance than pinks.
1923	No survey			
1924	Fred R. Lucas	Gilbert and Rich (1927)	Upper $\frac{1}{2}$ to $\frac{3}{4}$ mile	Considerable numbers.
1925	No survey			
[1] 1926	Gilbert and Rich	Gilbert and Rich (1927)	Upper 2 miles	50–100 thousand and more coming on Aug. 27.
1926	Howard H. Hungerford	Warden report	1. Between lower weir and weir near Larsen Bay.	Many.
			2. Above Larsen Bay weir	150,000.
			3. Lower weir to lake total	250,000.
1927	Seymour P. Smith	Field notebooks	Upper $1\frac{1}{2}$ miles	10–15 per 10 sq. yards, plus many already dead (158–238 thousand).
1928	S. P. Smith and Alan C. Taft	....do....	None mentioned	
1929	Merrill Brown (Boucher and Sundberg).	....do....	....do....	
[2] 1930	J. T. Barnaby	....do....	Lake down to Deep Hole	50–100 thousand on Sept. 10.
[3] 1931	....do....	....do....	Below lake	15,000 on Sept. 19, but one-third dead so is an underestimate.
1932	....do....	....do....	For 2 to 3 miles below lake	Two-thirds of 5,000 spawners on Aug. 31.

[1] Considerable numbers not yet ascended when weir removed on Oct. 14.
[2] Weir removed Oct. 9 with a few sockeye still in lagoon and river very low.
[3] Weir removed Oct. 8 with a few sockeye still in lagoon.

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ANADROMY IN NORTH AMERICAN SALMONIDAE

By GEORGE A. ROUNSEFELL

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ABSTRACT

Although there is a considerable range of variation in anadromy between species of the same genus, each of the four genera of North American Salmonidae occupies a different position in degree of anadromy exhibited. Arranged in descending order of degree of anadromy, the genera are *Oncorhynchus*, *Salmo*, *Salvelinus*, and *Cristivomer*.

There is a close correspondence between lethal stream temperatures for the young of certain species and the anadromous habits of those species.

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ANADROMY IN NORTH AMERICAN SALMONIDAE

By GEORGE A. ROUNSEFELL, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

In discussing the anadromous pattern of the salmonids, inevitably the question of landlocked versus anadromous species or varieties arises. Intelligent discussion of this question demands that the terms be at least tentatively defined. The word "landlocked" as it is and has been used is, of course, a misnomer in the majority of cases; only rarely is a population denied access to the sea. Offhand I can recall only two specific cases. One involves the ponds of Cape Cod, many of which lack an outlet, the excess runoff draining into the sandy soil; the other the rivers in Baja California, which for most of the year disappear into their stony watercourses. These rivers of the Sierra Madre of Baja California are the home of the famed San Pedro Martir trout, *Salmo gairdneri nelsoni*.

Of course, many salmonids live above impassable falls. Such fish are not technically landlocked insofar as access to the sea is concerned. However, they are isolated in that any individuals which migrate downstream can never return. Such a situation is favorable to the development of resident races of a species. The more-usual situation is for so-called landlocked races or species to occupy streams or lakes with access to the sea freely traversable in both directions. Furthermore, in many cases both resident and anadromous salmonids, even of the same species, may occupy the same waters for at least part of the year.

The term "anadromous" is likewise difficult to define with a nice degree of exactitude. It is all very well to say that it means "up-running," but before a fish can run up it must first establish residence in the sea. In anadromy, one is confronted with a surprising divergence. The typical life history of the anadromous salmons of the genus *Oncorhynchus*—the five eastern Pacific salmons—includes from less than 1 year to 4 years at sea, with the average probably a little more than 2. The anadromous members of the genus *Salmo*—*salar*, *gairdneri*, *clarki*, and *trutta*, the Atlantic salmon, the steelhead rainbows and cutthroats, and the European sea trout—likewise usually spend about 2 years at sea before reaching maturity.

There is another group of salmonids, the charrs, in which certain stocks usually regarded as anadromous typically spend only a small portion of each season in the sea. These include *Salvelinus malma*, the Dolly Varden charr, and *S. fontinalis*, the eastern brook trout, or more properly, charr, the sea-run members of which are known locally as sea trout or "salters." *Salvelinus alpinus*, the alpine, red lake, or arctic charr, while a freshwater resident in the southern part of its range, also migrates to the sea in the Hudson Bay and arctic regions. Dolly Varden charr of the Karluk River on Kodiak Island, Alaska, were found to spend less than 60 days a year in the sea.

A few species either cannot reproduce, or cannot do so with sufficient success to maintain a natural population, without residing for some time in a marine environment. These species might well be termed "obligatory anadromous." This group includes at least two of the Pacific salmons: the pink, *Oncorhynchus gorbuscha*, and the chum, *O. keta*. The king salmon, *O. tshawytscha*, perhaps should be included. Chamberlain (1907) tells of king salmon being raised generation after generation for 25 years in fresh water at the Trocadero Aquarium in Paris. I have identified as *O. tshawytscha* a salmon fry collected by Dr. Herbert Warfel in Newfound Lake, New Hampshire, from natural spawning. Although there is little doubt that under exceptionally favorable circumstances king salmon can mature and reproduce wholly in fresh water, there is serious question concerning the chances of successful maintenance of a natural population. Commencing as early as 1904 numerous plants were made in many New Hampshire

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lakes, as well as in other New England lakes. Hoover (1936) says, "they have never established a self-sustaining population in fresh or salt water, either in this state or elsewhere in New England." Therefore, I classify the king salmon as obligatory anadromous.

The silver or coho salmon, *O. kisutch*, has shown little tendency to develop natural resident fresh-water populations in North America. Jordan and McGregor (1925) describe a landlocked salmon from Japan, *O. ishikawee*, which is assumed to be a dwarf form of *O. kisutch*. In Montana (U. S. Fish and Wildlife Service, 1951) success has been claimed in holding and maturing silver salmon in fresh water.

In Crater Lake, Oregon, young silvers, *O. kisutch*, were planted to furnish fresh-water angling. Although there are no stream spawning beds available and only steep talus slopes of coarse rubble in the lake, both the silver salmon and rainbow trout reproduced naturally in the lake, according to Hasler and Farner (1942). However, Wallis and Bond (1950) show rather conclusively that although silvers were planted in the lake it was the kokanee (*O. nerka*), the small landlocked form of the sockeye salmon, that actually reproduced. Kokanees were not officially planted in the lake but were introduced, possibly by accidental mixing with silvers in rearing ponds.

Dwarfed, landlocked silvers are reported from Becharof Lake in the Egegik River system of Bristol Bay (personal communication from George J. Eicher, Jr.).

In view of these occurrences in fresh water we believe that *O. kisutch* should not be classified as obligatory anadromous.

The sockeye salmon, *O. nerka*, is the only one of the five Pacific salmons on this continent about which there is no doubt that it can successfully maintain populations wholly in fresh water.

To bring out the differences in degree of anadromy in the Salmonidae, one can compare the pink salmon with the lake charr, sometimes called the togue or mackinaw. At the one extreme, the pink salmon in some localities spawn in the tidal flats off the mouths of streams so that many pass their entire lives without entering strictly fresh water. At the other end of the scale, the lake charr so rarely leave fresh water that the only instances recorded (Ungava Bay and vicinity, Weed 1934) are not established beyond a reasonable doubt. However, Fred Cleaver (personal communication) states that he has a photograph of a lake charr caught in 1939 at the head of tidewater on the Naknek River in Bristol Bay. These two bits of evidence suggest that perhaps *namaycush* is a rare visitor to the sea in the northern part of its range.

Between these two extremes there are several points at which one can draw a line, always bearing in mind that the Salmonidae is an extremely plastic group, so that what we are saying may not always apply to some small segment of a species.

As already noted, the charrs tend to spend only short periods at sea, and furthermore, all the charrs can develop normally without going to sea. In Alaska there are many streams in which most of the Dolly Varden charr go to sea, but at the same time there are populations of stunted Dolly Vardens in many of these same streams living above impassable falls. DeLacy and Morton (1943) found in the Karluk drainage system during the late spring that while the majority of the Dolly Varden charr were making their annual pilgrimage to the sea many could still be found in fresh water in the streams tributary to Karluk Lake. According to Bigelow and Schroeder (1953) the eastern charr, *Salvelinus fontinalis*, seek salt water in the fall after the breeding season and remain there over winter. Speaking specifically of the streams on Cape Cod, they state that the sea trout go down to salt water in November immediately after spawning, to winter there. The charr begin to run again in April, and all of them are in brackish or fresh water by mid-May. The arctic charr, *S. alpinus*, has a more northern range than either *malma* or *fontinalis*, and its habits vary from theirs accordingly; in the southern part of its range the arctic charr tends to be a resident fish, occurring especially in lakes at high altitudes. Even as far north as the Karluk River it is a resident fish. DeLacy and Morton state that only on rare occasions is the arctic charr encountered in the river below Karluk Lake, and specimens are seen in salt water still less frequently.

In the Hudson Bay region, as in central Alaska, the arctic charr occurs at low elevations. Sprules (1952, pp. 11–12) found landlocked charr in a small lake without an adequate outlet, but in general the charr populations in the area visit the sea regularly.

He states that—

> The local inhabitants were questioned and were of one accord in their accounts of the spawning habits of char. They stated that quantities of char were netted along the coast during the early summer but that the catch decreased during August and only an occasional specimen was obtained at later dates. The fish begin to move into the estuaries of the large rivers in late July and early August and are congregated at the head of tide by late August. Evidently some time is spent in this brackish water before the fish ascend the rapids into the fresh-water system. The ascent is made, in general, during a spring [high] tide or during periods of heavy rainfall which swells the rivers.
>
> The adult char leave the lakes as soon as the shore ice disappears. Even before the ice breaks up on the open lakes the char may be seen crowding along the flood waters near the shore in the rivers. The Eskimos did not know how long the young char remained in fresh water, but it is probable that at least one year is spent there prior to their first migration to the sea.

In the genus *Salmo*, which includes the Atlantic salmon, the steelhead salmons (or trouts), and the sea trout (Loch Leven trout), the seagoing habit is firmly established; at the same time, all of these species have forms that are resident in fresh water. Furthermore, the presumably anadromous forms of *Salmo* are all perfectly capable of maturing and reproducing in fresh water. This is true even of the anadromous form of Atlantic salmon, *S. salar*—millions of sea-run young have been stocked in fresh-water lakes, and they mature and grow as well as the landlocked form.

The Atlantic salmon is probably the most truly anadromous species of *Salmo* in that almost all of the young normally make a definite downstream migration. In the other species, many of the young may elect to remain in fresh water, never becoming anadromous. This is well exemplified by the planting in Maine of *S. trutta*. For years many plants were made in the Orland River of so-called Scotch sea trout, supposedly an anadromous form of *S. trutta* sometimes called *S. trutta trutta* or *S. levenensis* by taxonomists. This resulted in the occasional return of a few sea-run fish but also in the establishment of fresh-water angling for brown trout. In other rivers, such as the Sheepscot, the planting of brown trout, sometimes classified as *S. trutta fario*, has resulted not only in fresh-water angling, but in the return of quite a number of fine sea trout. Similarly, on the Pacific coast there are some resident fish in practically all steelhead streams, regardless of whether the species is *Salmo gairdneri* or *S. clarki*.

The fresh-water forms of the anadromous salmonids normally use a lake as a miniature sea, ascending its tributaries to spawn. These adfluvial (see Rounsefell and Everhart, 1953, p. 33) species usually are smaller than their anadromous counterparts on account of the more restricted diet (Blair 1938), but otherwise their life histories are very similar, even to the acquiring in many lakes of the same overall silvery sheen characteristic of salmons at sea. In refutation of this idea some have pointed out the habit of the landlocked salmon *Salmo salar sebago* of often spawning in lake outlets. However, it should be noted that the anadromous salmons and trouts also spawn below lake outlets. This is the usual practice of the sockeye (*Oncorhynchus nerka*) below Chilko Lake on the Chilcotin tributary of the Fraser, and it occurs below lakes in Alaska. The fry upon emerging from the gravels of the spawning redds must swim upstream to reach their nursery lake. This is contrary to their actions in the lake tributaries, and the factors that determine which direction the fry will swim are not yet understood.

This upstream movement of great numbers of newly emerged sockeye fry has been observed as a massed living band moving upstream from the lower Babine River spawning grounds into Nilkitkwa Lake and from the upper Babine River spawning area into Babine Lake (Johnson 1956).

Since in some places the fry move downstream and in others upstream, it is difficult to comprehend how their movement can be wholly directed by any such physical factors as temperature or current. It might be suggested that these newly emerged fry, which must seek food immediately or perish, will move upstream in the usual situation of lake-outlet spawning streams. These outlet streams usually have a gentle current, and just below the lake they would contain sufficient plankton for the fry to commence feeding. Such active movement in hours of light if directed upstream toward the oncoming plankton might overcome any downstream drift during hours of darkness, especially since the fry emerge at a season when daylight hours substantially exceed those of darkness.

Whether the dwarfed, fresh-water forms of the basic species of salmonids are the result of genetic characteristics or of environment has been at least partially answered in the case of the sockeye. There are in reality not two, but three, forms of

sockeye, all of which may be present in the same lake. One type is the anadromous form; the second is the dwarfed, landlocked sockeye, called variously kokanee, little redfish, or silver trout; the third type, discovered first in Cultus Lake by Ricker (1938), was termed by him "residual." Presumably these residual sockeye are direct descendants of anadromous parents. The residual sockeye differ from the kokanee in several respects. They remain a dull olive gray at maturity, whereas the kokanee show the bright-red body and green head characteristic of the mature anadromous form. In Cultus Lake, the kokanee spawn early in August and September; the residuals spawn from October to December, like their anadromous progenitors. The residuals are predominately male.

Ricker suggests in a further paper (1940) that the kokanee populations have been derived from anadromous fish in geologically recent times, the residual sockeye representing a step in this process.

The question of whether the kokanee is a separated species or merely a variant of the anadromous form was answered by Foerster (1947). He reared young kokanee and in the spring of 1934, when they were 3 to 4 inches in length, he marked nearly 64,000 of them by removing their pelvic fins. The fish were liberated in Sweltzer Creek, the outlet of Cultus Lake, below the counting fence so that they could not swim into the lake, but would either have to remain in the stream or descend toward the sea.

None of the marked kokanees were recaptured in 1936 when they would have been in their fourth year and were expected to return, as most of the anadromous Cultus Lake sockeye mature in their fourth year. In 1937, however, in their fifth year, examination of 37 percent of the Fraser River commercial catch (756,000 out of 2,225,000 fish) revealed 25 of the marked kokanees had returned from the sea, and 17 more had returned to the counting fence at Cultus Lake. These fish were all fully grown and of a size comparable with that of the usual 5-year-old Fraser River sockeye.

Further experiments on the kokanee were performed as part of the Grand Coulee salmon relocation program on the Columbia River from 1939 to 1943.[1] In a personal communication Hanavan states that Lake Wenatchee, during those years, supported a large population of kokanees uniformly about 7 to 8 inches in length at maturity. Their mature color was a dull olive green, though rarely a red individual was observed on the spawning grounds. None that might be classed as residuals were observed.

In this study of Columbia River salmon, Hanavan and Fulton performed three marking experiments. In the first experiment, 22,000 Lake Chelan fingerling kokanee were marked and released in the Entiat River, resulting in one adult recaptured in the commercial fishery in its fifth year. In the second and third experiments, Lake Wenatchee kokanee were used. The 29,000 marked fingerlings in the second experiment were released in Icicle Creek, a lower tributary of the Wenatchee River, resulting in 79 adults recovered: 3 in their third year and 76 in their fourth. In the third experiment, 60,000 young marked kokanee were released in Lake Wenatchee, their "home" lake. Of these, 302 were recovered as sea-run adults: 3 in their third year, 287 in their fourth, and 12 in their fifth.

Contrary to the Cultus Lake kokanee, the sea-run adults from these experiments were smaller than the normal sea-run stock at maturity. Females averaged 2.4 to 2.7 pounds compared with 3.1 pounds, and males averaged 2.6 to 2.8 pounds compared with 3.4 pounds for marked sea-run stock.

These experiments indicate that the kokanee sockeye have retained the ability to live a marine existence and find their way back to their natal stream. Surprisingly enough, their size at maturity was only slightly less than that of the normal sea-run stocks. Although the difference in size may be genetic, the chief genetic difference between the two forms would seem to lie in the propensity toward anadromy.

There appears, thus, to be some tendency toward lacustrine existence in all anadromous populations and some tendency toward anadromy in all lacustrine salmonids. The presence of adfluvial populations in the headwater lakes of river systems may well be of great advantage to a species by furnishing sufficient seaward migrants to reestablish anadromous populations after streams have been obstructed for a considerable period.

Returns from seaward migrants of the abundant kokanee populations would appear to be the only

[1] Mitchell G. Hanavan and Leonard A. Fulton, U. S. Fish and Wildlife Service, manuscript.

logical source for the large number of adult sea-run sockeye that have attempted at various times to ascend the impassable falls below Lake Chelan or the high dam on the Similkameen River in western Washington. Chapman (1941), who observed these migrations in 1937 and 1938, writes that young, downstream sockeye migrants were reported in an irrigation diversion that takes off from the dam in the Similkameen River. The only source of such migrants is the kokanee population in Lake Palmer, above the dam.

In Maine, occasional Atlantic salmon are found attempting to pass dams that have been impassable barriers for many years. Their source has been disputed, many believing them to be merely strays; however, it is the writer's belief that at least the larger share of such strays are progeny of salmon residing in the lakes upstream from the dam. The fact that for many years young Atlantic salmon of anadromous parentage were stocked in most of the Maine lakes already populated by landlocked salmon may have even intensified the tendency for a small percentage of the young to descend to the sea.

DEGREES OF ANADROMY

Before we can measure the degree to which these different salmonid species are anadromous, we must first establish some criteria. The following six criteria have been used in this analysis:

1. Extent of migrations in the sea.
2. Duration of stay in the sea.
3. State of maturity attained at sea.
4. Spawning habits and habitat.
5. Mortality after spawning.
6. Occurrence of fresh-water forms.

Each criterion has been subdivided into as many categories as appears feasible from our present knowledge. The category signifying the most anadromous condition has been given a weight of 10, the least significant a weight of 0, and the categories between the two have been assigned weights which are, of course, subjective. Although this method can be criticized on the grounds of not being truly quantitative, it does yield a rather satisfactory basis of classification. Perhaps its chief fault lies in the inability to determine the relative merits of each of the six criteria.

The criteria, the categories (with assigned weights in parentheses) arranged in the order of decreasing anadromy, and the species assigned to each category are as follows:

Criterion 1.—Extent of migrations in the sea.

Category *a* (10).—Migrate several hundred miles from their home streams and large numbers occur very far offshore. *Oncorhynchus keta, O. nerka, O. gorbuscha.*

The occurrence of these species in abundance far offshore was demonstrated by Barnaby (1952) and Fukuhara (1953, 1955).

Category *b* (8).—Migrate long distances, but are not abundant far offshore. *Oncorhynchus tshawytscha, O. kisutch; Salmo salar.*

It may be noted that these three species are more piscivorous than the preceding species, which may somewhat affect their remaining closer inshore where more of the smaller pelagic fishes would be encountered.

Category *c* (6).—Migrations chiefly coastwise, somewhat less extensive than in the preceding categories. *Salmo gairdneri.*

The rainbow steelhead is occasionally taken at sea (Fukuhara 1955, Snyder 1921), and they are often captured in salmon traps, even along the outer coast.

Category *d* (4).—Migrations coastwise, chiefly estuarine and usually short. *Salmo trutta; Salvelinus alpinus, S. malma.*

See Grainger (1953), Sprules (1952), and many authors not cited concerning *S. trutta* in Europe.

Category *e* (2).—Migrations in sea very short. *Salmo clarki; Salvelinus fontinalis.*

Neave (1949, p. 21) says of *S. clarki* in the Cowichan River on Vancouver Island, that "In the neighbourhood of the river mouth the cutthroats lead a characteristic estuarine existence moving in and out with the tide. Up-river migrations occur in autumn and spring . . . ."

In southeastern Alaska, the salmon traps take many rainbow steelheads, *Salmo gairdneri*, and often take Dolly Varden charr, *Salvelinus malma*, but cutthroat steelhead, *S. clarki*, are rarely captured even though they may be caught by angling in many southeastern Alaska streams.

The eastern charr, *Salvelinus fontinalis*, likewise is chiefly estuarine. Doan (1948) says that they descend Hayes River into Hudson Bay in the autumn, and in the winter can be caught through the ice at a distance of 7 or 8 miles out

from the shore. White (1942) says that some wandered 8 or more miles from their home stream and ascended other streams.

Category *f* (0).—Rarely or never in the sea. *Salvelinus oquassa, S. aureolus; Cristivomer namaycush.*

Criterion 2.—Duration of stay in the sea.

Category *a* (10).—Entire life spent in the sea and intertidal zone. *Oncorhynchus gorbuscha, O. keta* (intertidal populations).

Pink salmon, *O. gorbuscha*, spawn successfully in intertidal gravels in which the salinity in the redds at high tide may reach a maximum of 30 parts per thousand (Hanavan and Skud, 1954). Hanavan stated (personal communication) that chums, *O. keta*, also commonly spawn in intertidal stream areas and live; and that well-developed chum eggs were turned up several times while he was digging in intertidal stream gravels.

Category *b* (9).—All young enter the sea immediately after emerging as fry and remain until mature. *Oncorhynchus gorbuscha, O. keta* (upstream populations).

It is usually considered that pink- and chum-salmon fry commence feeding after they reach the sea, but there must be some doubt on this point. Pink-salmon fry hatching over 250 miles from the sea above the Hells Gate Canyon of the Fraser have a long journey to reach the sea, and presumably would feed en route. The same reasoning applies with more force to some populations of chum salmon. Gilbert and O'Malley (1921) state that chums spawn as far as 2,000 miles up the Yukon. It would seem impossible for the young to make their descent to the sea without feeding. It is well known that chum-salmon fry stocked in a lake will feed voraciously, grow quickly, and furnish excellent fly fishing. In the Egegik River system, chum-salmon fingerlings are reported (personal communication, George J. Eicher, Jr.), which presupposes a long feeding period in fresh water.

That pink-salmon fry do feed in fresh water, even in short streams, is indicated by the observations of Chamberlain (1907), who states that a few have been found to contain remains of insects, larvae, and crustacea.

Category *c* (8).—A high proportion of the young descend to the sea before their first winter. *Oncorhynchus tshawytscha.*

This category applies especially to the fall-spawning king salmon. However, many young kings, especially those hatching from spring-running parents (which usually spawn far upstream) remain in the streams over winter before descending as smolts. These latter populations of kings more properly belong in the next category.

Category *d* (7).—Majority of young migrate seaward following the first winter. *Oncorhynchus tshawytscha, O. kisutch.*

All young enter the sea with the exception of a few precocious males of *O. tshawytscha* that may mature at a very small size in fresh water. This applies both to the silver, *O. kisutch*, and the spring-running king, *O. tshawytscha*. A very small proportion of the adult silvers taken in British Columbia went to sea as fry, only 22 out of 6,312 fish aged (Pritchard 1940); 54 left in their third year, 2 left at some undetermined older age, and all the rest left in their second year. This average age of smolt migrants varies geographically. I am informed (personal communication, George J. Eicher, Jr.) that the average Bristol Bay silver salmon matures in its fifth year and goes to sea in its fourth, i. e., at an age of 5_4 instead of the predominant 3_2 found in Washington and British Columbia fish.

Category *e* (6).—Majority of the young enter the sea after their first winter, but some may elect to remain in fresh water as residuals. *O. nerka.*

These young sockeye of anadromous parentage which elect to remain in fresh-water are predominantly males.

Category *f* (5).—The young normally enter the sea after their first winter and remain there until mature, but some may remain behind in lakes as normal fresh-water residents. *Salmo salar.*

The anadromous form of *S. salar* apparently becomes easily adapted to an adfluvial existence judging from successful rehabilitation of adfluvial populations in New York State using eggs from sea-run parents (Greeley 1955). This, of course, does not mean that *S. s. sebago* may not differ genetically from the present sea-run stocks, but it does indicate that the transposition from sea-run to adfluvial is relatively easy. For the sockeye placed in the preceding category the transposition is obviously more difficult, judging from the differences between the kokanee, *Oncorhynchus n.*

kennerlyi, and the residual sockeye in fresh water which derive directly from sea-run stock. In this category, as in all of the preceding categories, the fish do not ordinarily reenter fresh water until they return as adults on their spawning migration.

Category *g* (4).—The young enter the sea after the first winter and usually remain at sea until mature, which may take from 1 to 2 or 3 years. *Salmo gairdneri, S. clarki.*

Anadromy is optional and resident fresh-water individuals occur in practically all streams with anadromous stock. Whether there is any inheritable difference in those that develop at sea and those remaining in fresh water has long been the subject of much controversy. Neave (1944) believes that there are two strains of *Salmo gairdneri* in the Cowichan River, British Columbia, one anadromous and the other resident. However, the existence of two strains of *S. gairdneri* in the same waters may depend largely on there being a sufficiently large lake in a stream system to encourage the development of an adfluvial strain. Shapovalov and Taft (1954, p. 158) state,

> While the salmon [*O. kisutch*] go to sea almost immediately, some of the [young] steelhead remain for a whole season in the lagoon or the lower portion of the stream, after which some move out to sea, while others make an upstream migration and then a second downstream migration. While most of the steelhead go to sea before maturing, some fish of both sexes spawn before going to sea, while still others complete their life cycles without going to sea at all.

Briggs (1953) agrees with Neave that two types of *S. gairdneri* occur in the same streams, one anadromous and the other permanently resident in fresh water, basing his conclusions largely on the idea of spatial isolation, since the smaller "rainbows" tend to spawn in smaller tributaries and in shoaler water. No data are given on the age or size of the fish he designated as rainbows.

Experiments to test the pure strain of "rainbow" trout that has been propagated for over 30 years at the Manchester, Iowa, station of the U. S. Fish and Wildlife Service (Ratledge and Cornell, 1953; Carbine 1953) showed absolutely no difference in the migratory tendencies of the Manchester strain compared to nonpure strains from other stations.

Category *h* (3).—The majority of the young enter the sea after the first winter, but some remain in fresh water. A portion of the young that enter the sea may reenter fresh water before maturity. *Salmo clarki, S. trutta.*

Category *i* (2).—The majority of the young enter the sea after the first winter, but some remain in fresh water. The young that enter the sea normally return to the stream before maturity, and may visit the sea more than once before they attain maturity. *Salvelinus fontinalis, S. malma, S. alpinus.*

The annual visit of a portion of the population to the sea is in the nature of a feeding migration. The return migration (usually composed of both immature and adult fish) is often made many months before the spawning period and the adults may continue to feed.

Wilder (1952) has definitely established that in the Moser River, Nova Scotia, the sea trout and fresh-water trout constitute one taxonomic unit. He also found that a much larger proportion of the fish migrated to sea from Mill Brook, which contains a few shallow lakes, than from the main river, which contains several deeper, cooler lakes. This agrees with the findings of White (1941), that *S. fontinalis* moves downstream slowly at low temperatures. With a temperature varying between 0° and 5° C. from April 17 to 28, 1940, only 142 trout moved downstream and of these 36 reversed their direction, while from April 29 to May 11 with the water temperature varying from 5° to 11° C. more than 700 trout descended and only 6 ascended the stream. Wilder concludes that if descending trout encounter cold bodies of water their tendency to migrate is inhibited. This seems to indicate that they are seeking cooler water. If they find a cool lake they may remain instead of continuing to the sea. This behavior is in accord with the comparative upper-lethal-temperature tolerance of *S. fontinalis* and other salmonids discussed in a following section.

According to Bigelow and Schroeder (1953) the eastern charr, *S. fontinalis*, on Cape Cod go down to salt water in November immediately after spawning and return in April, with all of them being in brackish or fresh water by mid-May. However, the same species in Nova Scotia apparently behave in very similar fashion to the Dolly Varden charr in central Alaska. White (1940, p. 176) says,

> Smolts, kelts, and nonmature large fish descend in May and early June to the sea, to remain feeding in the estuary

or near the shore. They began (1939) to ascend the river in late June, and 93 percent of the "run" was in July.

These trout agree with the local salmon in having smolts that become silvery before migration and that are 2 or 3 years old. Trout smolts and kelts remain in the sea only about two months before returning to fresh water.

Salvelinus malma, the Dolly Varden charr, usually descend to the sea in May and return in July at Karluk, but in smaller streams, especially those without lakes, I believe that both young and adults may spend the winter in salt water. Thus in Ketchikan Creek in southeastern Alaska I have taken immature *Salmo gairdneri* by angling throughout the winter in the deeper holes and log jams but never saw a Dolly Varden. In the early summer Dolly Varden of all sizes can be seen entering the mouth of the creek in advance of the salmon runs. Fred Cleaver (personal communication) quotes Robert Vincent of the Alaska Department of Fisheries as saying that in 1956 on Afognak Island *Salvelinus malma* entered Big Kitoi Creek in the fall, spawned in mid-October, and retreated to the sea before winter. It thus would appear that the season and duration of marine life for *S. malma* is dependent partially on latitude (probably relative and actual sea and stream temperatures) and partially on the size and physical characteristics of any particular stream, since in small streams toward the north winter survival may be difficult unless the stream contains a deep, accessible lake.

Category *j* (0).—This last group comprises species that seem to have become thoroughly adapted to life in fresh water. Rarely, if ever, does an individual visit the sea. *Salvelinus oquassa*, *S. aureolus*; *Cristivomer namaycush*.

Criterion 3.—State of maturity attained at sea.

Category *a* (10).—Maturity of gonads usually very advanced, often before the fish enter fresh water. *Oncorhynchus gorbuscha*, *O. keta*.

Category *b* (8).—Maturity of gonads advanced, as fish enter fresh water. *Oncorhynchus tshawytscha*, *O. keta*.

This category applies to the fall-spawning king, *O. tshawytscha*, and a few of the chums, *O. keta*, that make long migrations.

Category *c* (6).—Gonads maturing as the upstream migration commences. *Oncorhynchus kisutch*, spring-run *O. tshawytscha*.

Category *d* (4).—Eggs usually not in advanced stage of maturity when fish reach fresh water. *Oncorhynchus nerka; Salmo gairdneri*, *S. salar*, *S. clarki*, *S. trutta*.

Egg maturation in fresh water may require a few weeks to as long as several months. For instance, over three-quarters of the Quinault Lake sockeye, *O. nerka*, reach the lake before July 7, and some start ascending the river as early as January (Rounsefell and Kelez, 1938; p. 756) yet they spawn in the fall, after maturing their eggs in the deep, cool waters of the lake. The necessity for cool water in which to mature the eggs may account for the fact that only sockeye running late in the fall usually spawn in rivers below lakes, since the water temperatures below the lakes in midsummer are rather high. Thus the U. S. Bureau of Fisheries placed a weir across the Ozette River, on the outer Washington coast in 1926, to hold sockeye for the hatcheries, but the fish, which practically all ascended the river before July 1, could not survive holding in the river, which derived its flow from the surface waters of Ozette Lake. This stage includes the sockeye, *O. nerka*, which is a lacustrine anadromous form with smaller eggs than the four fluvial anadromous *Oncorhynchus* (Rounsefell 1957).

All of these fish move into streams on a spawning migration even though the gonads are seldom in an advanced stage of maturity during this migration. Thus in the Penobscot River adult *Salmo salar* commence running in late April or May but these early arrivals spawn, together with those ascending later, in the late autumn.

Category *e* (2).—Gonads may vary from immature to slightly mature. The upstream migration may include returning young as well as adults and may bear no relation to time of spawning. *Salvelinus fontinalis*, *S. malma*, *S. alpinus*.

Concerning *S. malma*, Evermann and Goldsborough (1907, p. 266) observed the upstream migration of Dolly Varden charr of all sizes at Pablof Falls in Pablof Creek, Chichagof Island, on July 25. They state that the ovaries " . . . were quite small and immature, and this was evidently not their spawning season."

Category *f* (0).—No adults returning from the sea. *Salvelinus oquassa*, *S. aureolus*; *Cristivomer namaycush*.

Criterion 4.—Spawning habits and habitat.

Category *a* (10).—Spawn successfully in the intertidal zone. *Oncorhynchus gorbuscha, O. keta.*

Category *b* (7).—Spawn in streams where there is flowing water. All species of *Oncorhynchus* and *Salmo; Salvelinus fontinalis, S. malma, S. oquassa.*

Cooper (1940), says of *S. oquassa*, the blueback charr, that "It was seldom seen except when it entered streams in October to spawn."

Category *c* (3).—Lake spawners that construct a spawning redd and bury their eggs in similar fashion to the stream spawners. *Oncorhynchus nerka; Salvelinus alpinus, S. fontinalis, S. aureolus* (?).

For *S. aureolus* the available information on spawning (Bailey and Oliver, 1939) indicates that they spawn on shallow reefs in Lake Sunapee within the 10-foot contour. There is no information as to whether they construct a redd as do the other salmonids, with the exception of *Cristivomer.*

Category *d* (0).—Lake spawners that do not construct a spawning redd. *Cristivomer namaycush.*

This category differs from category *c* in that the spawning adaptation to fresh water is so complete, and the urge to make an upstream spawning migration so completely lost, that the fish not only spawn in the lakes, but do so without constructing a redd (Royce 1951). Regarding the selection of a spawning site Royce says (p. 66) that as the fish make no attempt to bury the eggs, the bottom must have crevices into which the eggs can roll, and that the location of these suitable areas of bottom in the lake is primarily determined by currents or wave action which keep the bottom swept clean. Quoting from Royce (pp. 68–70),

> The writer has found no evidence that lake trout select a lake bottom supplied with spring water for the deposition of their eggs . . . .
>
> No nest or redd was built. The males spent their time cruising along close to the bottom, occasionally giving the stones a little fillip with their tails . . . . This activity cleaned several hundred square feet of bottom . . . .
>
> No tendency towards oviposition in any definite place on the spawning area was observed. The trout mated at random over the area cleaned off, and there was no attempt by either sex to bury the eggs . . . .

There is apparently at least one race of *Cristivomer namaycush* that is adfluvial. Dymond (1926, p. 68) says,

> It is said that there exists in Lake Nipigon a sort of lake trout known locally as "black trout," which ascends some of the rivers, notably the Sturgeon river, at spawning time. This form . . . seldom attaining more than four or five pounds in weight. . . . It is a fact, however, that very dark trout, all of medium size, do enter the Sturgeon river at spawning time in large numbers. They also spawn earlier than the trout which spawn in the lake, usually beginning about September 20.

No mention is made of the spawning behavior of this group of lake charr, so we can only assume that they spawn without building a redd.

Criterion 5.—Mortality after spawning.

Category *a* (10).—All die soon after spawning, including fresh-water stocks. All species of *Oncorhynchus.*

Category *b* (5).—A few anadromous adults die soon after spawning; subsequent survival of the others is very low. *Salmo salar, S. gairdneri.*

Category *c* (0).—Spawning does not have a drastic effect on survival. *Salmo clarki, S. trutta;* all species of *Salvelinus; Cristivomer namaycush.*

Criterion 6.—Occurrence of fresh-water forms.

Category *a* (10).—No natural fresh-water populations are known to exist. *Oncorhynchus gorbuscha, O. keta.*

Category *b* (9).—No natural fresh-water populations are known to exist, but adults will mature and spawn in fresh water with very limited success. *Oncorhynchus tshawytscha.*

Category *c* (8).—Fresh-water populations are rare. *Oncorhynchus kisutch.*

Category *d* (7).—Fresh-water form is common, but young of anadromous stock remaining in fresh water are chiefly males and differ from fresh-water stock. *Oncorhynchus nerka.*

Category *e* (5).—Fresh-water forms are common; the young of anadromous stock in streams normally enter the sea with the exception of precocious males. Anadromous stock will form normal adfluvial fresh-water populations, but not fluvial populations. *Salmo salar.*

Category *f* (3).—Fresh-water forms are very common, some of the young of anadromous stock usually remain in streams forming fluvial populations. *Salmo gairdneri, S. clarki, S. trutta; Salvelinus malma, S. fontinalis, S. alpinus.*

Category *g* (0).—No anadromous forms. *Salvelinus oquassa, S. aureolus; Cristivomer namaycush.*

It is of interest that when the species of Salmonidae are plotted (fig. 1) according to the six criteria just considered (see also table 1), each of the four genera occupies a distinct area in the degree of anadromy exhibited.

TABLE 1.—*Degrees of anadromy of normal populations of North American Salmonidae*

[According to six criteria, pp. 175 to 179]

Genus and species	Subjective criterion—						Degree of anadromy
	1	2	3	4	5	6	
Oncorhynchus:							
gorbuscha	10	9–10	10	7–10	10	10	56–60
keta	10	9–10	8–10	7–10	10	10	54–60
tshawytscha	8	7–8	6–8	7	10	9	47–50
kisutch	8	7	6	7	10	8	46
nerka	10	6	4	3–7	10	7	40–44
Salmo:							
salar	8	5	4	7	5	5	34
gairdneri	6	4	4	7	5	3	29
trutta	4	3	4	7	0	3	21
clarki	2	3–4	4	7	0	3	19–20
Salvelinus:							
malma	4	2	2	7	0	3	18
fontinalis	2	2	2	3–7	0	3	12–16
alpinus	4	2	2	3	0	3	14
oquassa	0	0	0	7	0	0	7
aureolus	0	0	0	3	0	0	3
Cristivomer:							
namaycush	0	0	0	0	0	0	0

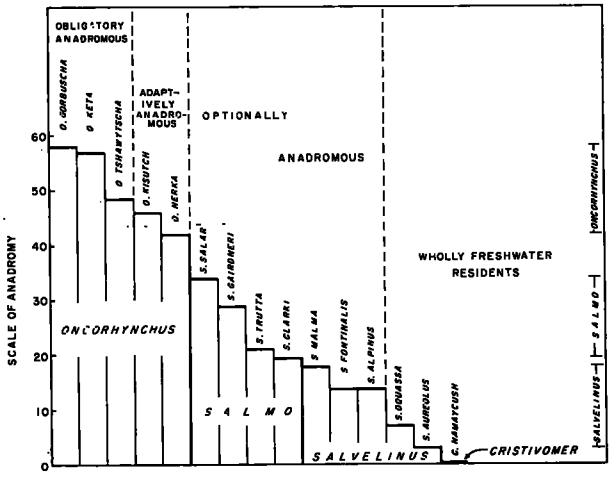

FIGURE 1.—Species of North American Salmonidae classified by degree of anadromy (based on table 1).

The fact that the four genera of North American Salmonidae occupy successive positions in their propensity toward anadromy may be of phylogenetic significance and should not be ignored in any study of their interrelationships.

RELATION OF ANADROMY TO LATITUDE

A rather interesting aspect of anadromy in the North American Salmonidae is the effect of latitude on the degree of anadromy. Different species inhabit different ranges of latitude, but within each species there seems to be a greater degree of anadromy toward the north. Starting with the lake charr, *Cristivomer namaycush*, we find that the only records indicating this species may occasionally visit the sea are for Ungava Bay in the Arctic and Naknek River in Bristol Bay, Alaska.

The arctic or alpine charr, *Salvelinus alpinus*, is known as the sea trout in the Arctic, where most of the populations are anadromous. It has been little studied on the Pacific coast, where it may easily be confused with the Dolly Varden charr; but in the Karluk River, it is lacustrine in habit, only occasional individuals going to sea. On the Atlantic coast also, toward the southern end of its range, the anadromous form of *S. alpinus* is not found, but there are fresh-water groups, such as *S. oquassa, S. aureolus*, and *S. marstoni*, that are either fresh-water counterparts of *S. alpinus* or closely related forms.

For the eastern charr, the northern populations are also more anadromous, since in the southern part of its natural range it is confined to the cooler mountain streams of the southern Appalachians. In New England, anadromous *S. fontinalis* occurs in many rivers on Cape Cod and in Maine. Farther north, on Prince Edward Island and in the southern drainage of Hudson Bay, a large share of the populations visit the sea.

For the genus *Salmo* the evidence is not so clear that latitude affects anadromy. Landlocked *S. salar* occur in lakes in New England, Newfoundland, eastern Canada, and Labrador. That is, the ranges of the landlocked and anadromous forms are similar. The steelhead cutthroat, *S. clarki*, occurs only in the anadromous form in the northern portion of its range in Alaska.

The fact that *Salmo gairdneri* and *S. clarki* have anadromous populations far to the south of any

anadromous populations of *Salvelinus* appears to be related to their being definitely more southern in general distribution and thus able to thrive in waters too warm for *Salvelinus*. *Salmo clarki* does not occur in western Alaska, and *S. gairdneri* avoids the colder situations. Thus, *S. gairdneri* is absent from the Egegik and Ugashik Rivers, the coldest of the main Bristol Bay rivers (personal communication, George J. Eicher, Jr.).

It is interesting to note that the kokanee, *Oncorhynchus nerka kennerlyi*, is not recorded from any of the Alaska sockeye lakes. It does occur in Skilak Lake, in Cook Inlet (personal communication, George J. Eicher, Jr.).

The kokanee does occur in a number of the Fraser and Columbia River lakes and even in many of the coastal lakes, both on Vancouver Island and in the Puget Sound region. This poses an interesting question, namely, What are the factors in the environment which militate for or against anadromy? One factor may be temperature. The salmonids as a group are cold-water species. Those that live in the surface fresh waters in the north must, farther south, spend the summer months in the hypolimnion of the lakes. In southern waters, they cannot exist in shallow lakes that lack a thermocline or in deep lakes in which the oxygen of the hypolimnion is largely exhausted during the summer.

Because in the southern part of their ranges some species are unable to tolerate the surface temperatures of the lakes in summer, any spring migration from the lakes must take place before summer stratification develops. There is much variation among lakes in the date of the establishment of a thermocline and in the rapidity with which it forms. Because of this circumstance there is always the possibility of some young of a normally anadromous fish being trapped in the deeper waters of a lake at the time when they should migrate seaward. Such occurrences not uncommonly happen to anadromous sockeye populations in the southern part of their range.

Whether the trapping of anadromous young by a thermocline has any bearing on the existence of fresh-water forms of a species is not yet fully proved; undoubtedly it favors the existence of the residual form of the sockeye discussed by Ricker (1938), but whether these residual populations are the potential progenitors of landlocked forms is uncertain. Ricker points out that such an origin for the kokanees is not only possible but highly probable. He shows several respects in which the kokanees differ from the residuals, one of the most significant being that of their resistance to certain fresh-water parasites. This resistance must be of genetic origin, but if it can be established by selection, rather than mutation, there is no reason to doubt that the kokanee may have originated independently in many different localities.

RELATION OF ANADROMY TO LETHAL TEMPERATURES

The temperature tolerance of young Salmonidae bears an interesting and significant relation both to the degree of anadromy exhibited by the various species and to special adaptations in their life histories. Table 2 and figure 2 show the upper lethal stream temperatures for the young of several species. The data for *Oncorhynchus* (except *kennerlyi*) are from Brett (1952, p. 305) and the temperatures for the other species have been estimated either by the difference in their regression lines from that of *O. keta* in figure 26 of Brett (taken from Fry, 1947) at 1,000 minutes, or from Black (1953).

TABLE 2.—*Upper lethal temperatures for young Salmonidae in fresh water*

Genus and species	Ultimate upper lethal temperature (° C.) [1]	Estimated upper lethal temperature (° C.)
Cristivomer: namaycush		[2] 23.2
Salvelinus: fontinalis		[2] 24.2
Salmo:		
trutta		[2] 25.5
gairdneri kamloops		[3] 25.7
salar		[2] 26.1
Oncorhynchus:		
tshawytscha	25.1	
kisutch	25.0	
nerka	24.4	
nerka kennerlyi		[4] 23.9
gorbuscha	23.9	
keta	23.8	

[1] From Brett (1952, p. 305).
[2] Derived from figure 26, Brett 1952 (after Fry, 1947) by temperature difference in regression lines at 1,000 minutes from regression line for *O. keta*.
[3] From Black (1953); represents total mortality in 24 hours for fish acclimated at 11° C.
[4] Estimated from Black (1953) as being 0.5° C. lower for 11° C. acclimation temperature and 50% morta lity in 24 hours than for *O. nerka*, as shown in figure 6 of Brett (1952).

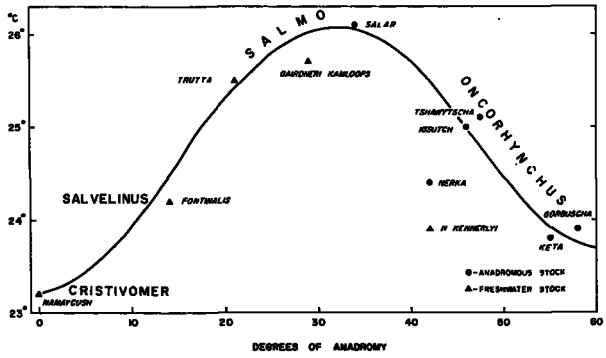

FIGURE 2.—The upper lethal temperatures for the young of certain species of North American Salmonidae in fresh water. (Temperature in degrees Centigrade.)

In those Salmonidae with the lowest upper-temperature limits, *Cristivomer namaycush*, *Oncorhynchus keta*, and *O. gorbuscha*, the young stay in cool water. In *Cristivomer* this is accomplished by keeping in the cool stratum of the lakes, which means retreating to the hypolimnion during summer, especially in more southerly latitudes. In *Oncorhynchus gorbuscha* and *O. keta* the young emerge from the redds quite early in the spring and immediately descend to the sea, thus avoiding high, summer stream temperatures.

It will be noted that although *O. nerka* exhibits a lower degree of anadromy than *kisutch* or *tshawytscha* (fig. 1), the young of *nerka* have distinctly the lower upper-temperature tolerance. This intolerance to higher temperatures fits in with the fact that *nerka* is lacustrine anadromous rather than fluvial anadromous: the young upon emerging from stream redds seek a nursery lake in which to grow. Only lakes that are temperature stratified in summer support runs of *nerka* in its southern range. In the few instances in which young sockeye do not enter a lake, such as the stock spawning in Harrison Rapids in the Fraser River system or the "creek" sockeye found in a few British Columbia streams, the young descend to the sea as fry after the manner of *keta* and *gorbuscha*.

The young of *Oncorhynchus kisutch* and *O. tshawytscha* have a much-higher temperature tolerance than the other members of the genus, as the young of *kisutch* and a fair proportion of those of *tshawytscha* live in the streams during the summer months.

These differences in tolerance of the four fluvial anadromous species of *Oncorhynchus* are reflected in the southern limits of their ranges. For instance, Snyder (1931, p. 16) says,

> Besides the king salmon, three other species enter Klamath River to spawn, namely, the silver salmon (*Oncorhynchus kisutch*), the humpback (*O. gorbuscha*) and the dog salmon (*O. keta*). The humpback and dog salmon are seldom seen and the fishermen are not familiar with them. The silver salmon occur in large nunbers, the migration being later than that of the king salmon.

The king salmon is abundant as far south as the Sacramento River, and the silver salmon occurs in smaller coastal streams south to Monterey. However, the steelhead rainbow, *Salmo gairdneri*, regularly inhabits the coastal streams of southern California—Shapovalov and Taft (1954) say from the United States–Mexico boundary, or possibly even from Baja California northward. This is in keeping with the upper lethal temperatures for the young of *Salmo salar*, *S. trutta*, and *S. gairdneri kamloops*—all of which are higher than for any species of the other genera.

The anadromous cutthroat, *Salmo clarki*, according to Snyder (1940), ranges only as far south as Mad River, north of San Francisco. DeWitt (1954) has extended this range slightly, to the Eel River. This suggests that the upper lethal temperature for the young of *clarki* may be somewhat lower than for the young of *S. gairdneri*. Since the tolerance for the anadromous *O. nerka* is higher than for the adfluvial *O. nerka kennerlyi*, it is probable that the upper lethal temperature for anadromous *S. gairdneri* may similarly be higher than for the adfluvial *S. gairdneri kamloops*.

Brett's regression curve (1952; fig. 26) for *Salvelinus fontinalis* did not parallel regression curves for the other species, in that it had a steeper slope. Therefore, the upper lethal limit could not be obtained with the same degree of assurance. However, the relative position of *S. fontinalis* is undoubtedly correct, since it cannot tolerate midsummer temperatures in the main portions of many streams thickly populated with the parr of *Salmo salar*. In such situations *fontinalis* seeks the cooler, spring-fed tributaries.

The lower limits of lethal temperatures are not so well defined as the upper, but in general there must be some correspondence between them. The only species of *Oncorhynchus* in the Arctic Ocean are *gorbuscha* and *keta*. Thus Dymond (1940) records both *gorbuscha* and *keta* from the mouth of the Mackenzie River. He mentions a notable

run of *keta*, some weighing 20 to 25 pounds, in the Mackenzie in 1914, and in 1930 one was captured 5 miles below Fort Smith in the Slave River, tributary to the Mackenzie. Kennedy (1956) reports a chum salmon taken in Great Slave Lake. Dymond also mentions that Borisov (1928) notes a chum salmon taken in the Lena River of northern Siberia.

That members of the genus *Salmo* cannot tolerate as cold situations as the other genera is indicated by their comparative distribution. On the Pacific coast, *S. clarki* does not extend beyond southeastern Alaska and *S. gairdneri* is absent from the colder rivers of Bristol Bay.

On the eastern side of the continent, *Salvelinus alpinus* extends to Baffin Island, but *Salmo salar* only to the Koksoak River in Ungava Bay (Dunbar and Hildebrand, 1952) and in very small numbers in west Greenland.

A most significant feature of the lethal temperature limits found in the various species is the manner in which these limits affect the life histories. For instance, it has already been noted that *Salvelinus alpinus*, *S. fontinalis*, and *S. malma* are all regular visitors to the sea in the northern part of their ranges, but toward the southern end their low upper-temperature tolerance confines them to the cooler waters found at higher altitudes.

SUMMARY

The Salmonidae are very plastic and exhibit all degrees of anadromy. Six criteria have been used to classify them according to degree of anadromy. (1) Extent of migrations in the sea, (2) duration of stay in the sea, (3) state of maturity attained at sea, (4) spawning habits and habitat, (5) mortality after spawning, and (6) occurrence of fresh-water forms.

Gaging the degree of anadromy by these criteria, each of the four genera occupies a different position. *Oncorhynchus* is the most anadromous, following in decreasing degree by *Salmo*, *Salvelinus*, and *Cristivomer*.

In general, within a species the degree of anadromy is greater toward the northern end of the species' range.

The length of time the young of several species are exposed to high stream temperatures is closely related to their upper-lethal-temperature tolerance. This is reflected both in the short stream life of species of lower tolerance to temperature and in the more southerly distribution (except at high altitudes) of *Salmo* and the two species of *Oncorhynchus—tshawytscha* and *kisutch*—species which show greater temperature tolerance.

Species with the lowest upper-lethal-temperature tolerance probably have also the lowest lower-lethal-temperature tolerance, since they range farther north—*Oncorhynchus gorbuscha* and *O. keta* into the Arctic Ocean, *Salvelinus alpinus* in Baffin Island, and *Cristivomer* in deep Arctic lakes.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

HIGH-SPEED PLANKTON SAMPLER

BY ELBERT H. AHLSTROM, JOHN D. ISAACS, JAMES R. THRAILKILL, AND LEWIS W. KIDD

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ABSTRACT

A high-speed plankton sampler is described, and performance tests are discussed in this paper. The sampler was designed to supplement, and, in certain cases, to supersede standard plankton nets. The sampler is so constructed that it can be fastened to the towing cable at any point, hence samplers can be used in series to sample different depth levels simultaneously. The samplers are towed at normal ship's speed between hydrographic stations; each sampler obtains a horizontal strip sample of the plankton at the level at which it is hauled. The usual length of haul has been 10 miles. The depth sampled and the amount of water filtered by a sampler during a haul are recorded on a strip of 35-millimeter acetate film. Tests were made to determine the comparative effectiveness of high-speed samplers and standard 1-meter plankton nets in delimiting the distribution and abundance of fish eggs and larvae. Both types of gear seem to be equally effective in delimiting the horizontal distribution of eggs and larvae. Standard nets are more versatile in depth sampling, as they can be operated to any desired depth; high-speed samplers have been operated only between about 60 meters deep and the surface, when hauled at normal ship's speed. The most marked advantage of high-speed samplers over conventional gear is that samples obtained with the former are far more representative of the mean density of plankton organisms.

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HIGH-SPEED PLANKTON SAMPLER

By E. H. AHLSTROM, *U. S. Fish and Wildlife Service*, JOHN D. ISAACS,[1] *Scripps Institution of Oceanography*, JAMES R. THRAILKILL, *U. S. Fish and Wildlife Service*, and LEWIS W. KIDD,[1] *Scripps Institution of Oceanography*

Because of the diversity in size, motility, and distribution of plankton, there is no one type of plankton sampler yet devised that can obtain a fully representative sample of all organisms in the water. Every type of plankton collector is selective in one way or another. Samples obtained with plankton-collecting gear may be classified, on the basis of distance covered in obtaining the samples, into two principal categories: spot samples and strip samples. Each has its limitations and its advantages. The conventional 1-meter plankton net used in a standard oblique tow is hauled only a short distance, seldom more than ¼ mile; hence it is regarded as a spot sampler.

The Isaacs high-speed sampler, to be described in this paper, was designed to supplement the information obtained with conventional 1-meter nets. At the time of its development, the California Cooperative Oceanic Fisheries Investigations (then the California Cooperative Sardine Research Program) was just getting under way. The plan of operation under the program was to cover a widespread grid of hydrographic stations approximately 40 miles apart. It was desired to construct a collecting device that could obtain information on plankton distribution by taking a strip sample while the ship was running full speed ahead between stations.

HISTORICAL REVIEW

A pioneer in the development of high-speed plankton sampling gear is A. C. Hardy. He has devised two instruments, one known as the Hardy Plankton Recorder, the other as the Hardy Plankton Indicator. The latter is a simple, non-quantitative instrument designed for on-the-spot assays of plankton samples. It has been widely used by fishermen in the North Sea herring fishery and by scientists (Hardy 1936a; Barnes 1951).

The Hardy Plankton Recorder (Hardy 1936b, 1939) has proved to be a successful high-speed plankton sampler. It was first used during the Discovery Expedition to the Antarctic in 1925–27. It was designed to take a continuous sample over distances as great as several hundred miles. It has been operated from both research and commercial vessels. Only one recorder is towed at a time, ordinarily at a depth of about 10 meters and a vessel speed of 8 to 16 knots. The forward end of this collector is provided with a small opening, about 1¼ inches square, which may be reduced to ½ inch square or even less. The water, after entering the instrument, flows through a wide tunnel across which is stretched a band of silk or nylon gauze. The gauze band is slowly wound across the water tunnel into a chamber where it is stored in a bath of formalin. The spooling mechanism is geared to an external propeller that is actuated by the passing water, hence the spooling is in direct relation to the distance traveled. The recorder gives a continuous line of ecological observations across an area being investigated; furthermore, since the straining band is graduated into numbered divisions, it is possible to identify any portion of the sample as to approximate location of collection. This unique feature of the Hardy Plankton Recorder makes it particularly useful for certain kinds of ecological studies. Hardy Recorders are being used by us in a study of the relation between the distribution of plankton organisms and adult sardines. The most serious disadvantages of the instrument are (1) its lack of versatility in operation, since it is designed for towing at a single depth near the surface, and (2) the difficulty of identifying the organisms caught, since they are crushed when rolled up in the filtering band.

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A simple type of high-speed collector was employed by personnel of the South Pacific Fishery Investigations of the U. S. Fish and Wildlife Service from the purse seiner *Pearl Harbor*, during April to June, 1946 (Smith and Ahlstrom, 1948). The idea for the collector was suggested by the work of Hardy. The cruises were made off central California, primarily to explore for sardines with echo-ranging equipment. The collector consisted of three parts: a brass towing head, a cylindrical net, and a plankton bucket (ibid., fig. 11). The towing head, shaped somewhat like an inverted funnel, was 1 inch in diameter at the mouth, expanding to 2 inches before the point of attachment of the net; the cylindrical net was 2 inches in diameter by 10 inches long, and was constructed of No. 56xxx grit gauze; the plankton bucket was the more or less standard type used for limnological work.

Most samples were obtained by towing the net at 9 knots, for a period of 20 minutes. Not only did the collector tow well at this speed, but plankton organisms were taken in fair numbers and were in excellent condition. In all, 54 samples were obtained. The analyses of the samples, including the percentage composition (by volume) of the major constituents and the distribution of fish eggs and larvae, are discussed by Smith and Ahlstrom (1948).

The results from this initial high-speed collector were so encouraging that an experimental model of a high-speed volumetric plankton sampler was built (Ahlstrom and Smith, MS.). The collector consisted of four detachable parts: a weighted forward section, a metering device, a cylindrical net, and a metal plankton bucket. The forward section, constructed of bronze, was cylindrical except for a slight taper at the forward nose: the mouth opening was 1 inch in diameter with the inner bore widening gradually to 2 inches; this section provided weight (15 lbs.) and was equipped with diving vanes and multiple attachment points. The metering section, about 1 foot long, contained an impeller and worm gear in the main tube, with the gear train of the current meter underneath. It was provided with three tail fins, with the streamlined meter box acting as a fourth. All parts were made of bronze. The cylindrical net was fastened to the "metering" section of the sampler. Nets of several lengths (10 to 24 inches) and of several mesh sizes (No. 24xxx, 40xxx and 56xxx silk grit gauze) were tried and all worked effectively. The plankton bucket was of the type used with the Clarke-Bumpus net (1950). The device was used to collect more than 150 samples during two cruises off Baja California in 1948 (Ahlstrom and McHugh, MS.).

The Ahlstrom-Smith sampler had a number of good qualities. It was easy to operate, since it could be launched or retrieved with the same ease as a bathythermograph, and was towed on the bathythermograph cable. It had good towing qualities, keeping a steady course without yawing. The plankton was recovered in excellent condition. The metering device could be accurately calibrated, and gave consistent readings when in use at sea. The mouth opening preceded the cable. This is not difficult to arrange if the sampler is attached to the end of the cable. The disadvantages of the sampler were as follows: (1) at normal vessel cruising speed it could be towed only at shallow depths, perhaps not greater than 10 meters, (2) no record was obtained of the actual depth traversed by the sampler, and (3) it was not possible to use several samplers on the same cable at one time. This type of high-speed sampler is excellent for reconnaissance work.

To overcome these disadvantages, while retaining desirable features, Isaacs and associates developed the high-speed collectors described in this paper. The qualities that the investigators sought to incorporate in the high-speed sampler described in this paper are the following:

Good towing characteristics: The sampler has been so designed that bridles are not necessary, and the mouth opening precedes the towing wire, thus eliminating water disturbance in front of the sampler; the sampler keeps a steady horizontal position without yawing while being towed at 8 to 10 knots.

Simple method of attachment: A method of fastening to the towing cable has been devised that permits attachment at any desired position on the cable, and also permits the use of any desired number of samplers at one time (in order to sample several depth layers simultaneously).

Suitable depressing force: A suitable depressing force is needed to get samplers down to desired depths; an excellent depressor has been designed, that has proven useful with many types of oceanographic gear.

Quantitative measurement of water strained: A

measure of amount of water strained by each sampler has been accomplished by incorporating an impeller, gear train and recording device into the design of the sampler.

Record of depth sampled: A record of the depth traversed by a sampler has been made possible by incorporating a pressure-sensitive bellows with attached stylus. A permanent record of depth against flow is obtained on acetate film.

Plankton material should be recoverable in good condition: The high-speed sampler meets this requirement.

Rugged construction: High-speed gear must be ruggedly constructed to withstand the continuous vibration of the towing cable when hauled at high speed. A well designed sampler should operate for 100 hours or more before adjustments are needed. Ruggedness was a major consideration in the design of the Isaacs high-speed sampler.

Low cost: It is highly desirable that high-speed samplers be inexpensive, both in initial cost and maintenance. Our sampler is a fairly expensive instrument. However, the cost of the sampler could be considerably reduced if made in larger quantities. Also it is not necessary that every instrument be equipped with a depth-flow meter.

One desirable feature of the Hardy Plankton Recorder that we have not been able to incorporate into our high-speed sampler is a continuous record of plankton. Our sampler obtains an integrated sample over the distance hauled rather than a continuous line of observations.

DESCRIPTION OF HIGH-SPEED SAMPLER

The high-speed sampler is a streamlined metal tube containing a plankton filter and depth-flow meter (fig. 1). When assembled for operation, the sampler has an over-all length of 130 centimeters, a basic diameter of 7.6 cm. and a weight of 17.3 pounds (7.7 kg.). It is attached to a towing cable by means of a spherical brass clamp and socket.

The sampler is composed of three parts: an outer casing, a plankton filter, and a depth-flow meter.

The outer casing tapers from its basic diameter of 7.6 cm. to a mouth opening of approximately 2.5 cm. The anterior half of the casing is divided longitudinally to accommodate attachment to the towing cable some distance behind the mouth of the sampler. Three radially arranged stabilizing fins are attached to the rear section of the casing. A protective bumper at the back edge of the divided section protects both the towing cable and the tube. An experimental sampler which was not provided with the bumper almost severed the cable during a trial run, whereas samplers with the bumper have not injured the cable after many tows.

The plankton filter consists of two sections, the body or straining section, and a cod-end cup. The detachable straining section is made of Monel metal mesh having about 23 mesh openings to the centimeter (each opening 0.24 mm. across and 0.33 mm. on the diagonal). The straining section

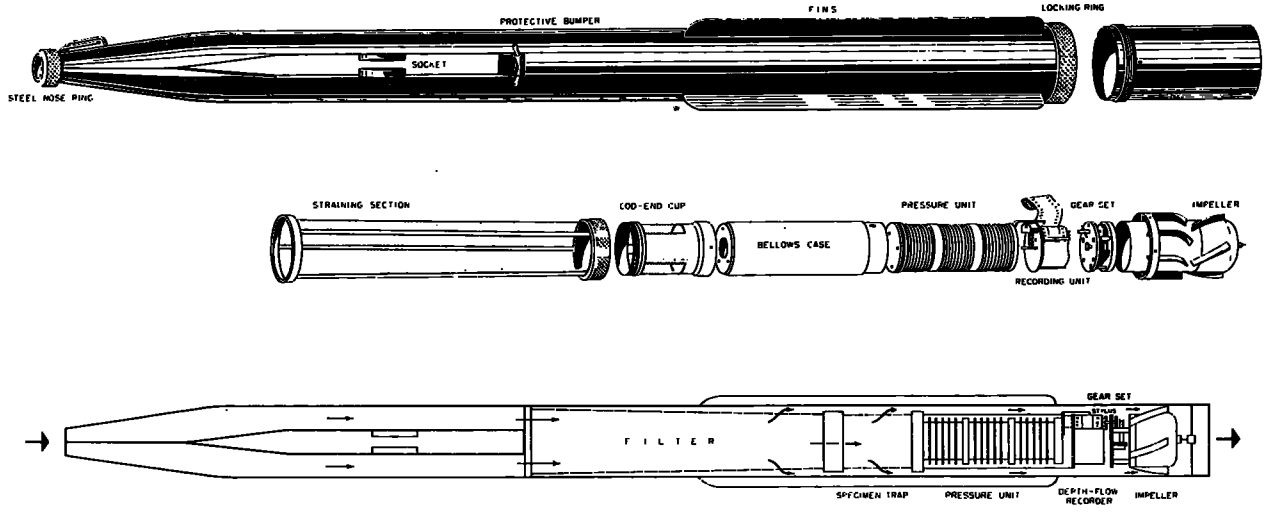

FIGURE 1.—Exploded schematic drawing of high-speed plankton sampler.

has an over-all length of approximately 36 cm.; it is supported by a brass ring at either end, and by three strengthening ribs. The cylindrical brass cod-end cup (specimen trap) is 10.5 cm. long by 5.2 cm. in diameter; two windows, approximately 5.0 cm. square, are cut out of the sides of the cup, and fitted with fine Monel metal screens (39 mesh openings to the centimeter). The cod-end cup is attached to the bellows case.

The plankton filter retains the plankton organisms in the water column entering the sampler. In present models, water is filtered at a rate of ⅛ to ¼ cubic meter per minute at 8 to 10 knots towing speed. The actual filtering rate is dependent, to some degree, on the extent of clogging of the filter by plankton organisms.

The depth-flow meter consists of three sections: a pressure unit with attached stylus, a metering unit (impeller and gear set), and a recording unit. The pressure unit makes use of bellows originally designed for the bathythermograph, which are available in different depth ranges. One type is effective to depths of 180 feet (approximately 55 meters), another to 450 feet (137 m.), and a third to depths of 900 feet (274 m.). The latter has not been used as yet with the present high-speed samplers. The bellows is housed in a brass tube. An L-shaped brass stylus is attached to the back end of the bellows.

The metering unit consists of an impeller and gear set enclosed in a brass housing. The impeller has a coaxially attached shaft which is supported at the ends in low friction bearings. Incorporated in the forward end of the shaft is a worm gear, which meshes with a gear in the gear set. The gear set is contained in a brass cylinder immediately forward of the impeller.

The recording unit is housed between the pressure unit and the gear set. It consists of a sprocket geared to the metering unit which advances a roll of 35-mm. clear acetate film. The stylus atached to the bellows produces a scratch on the 35-mm. film, recording depth of operation against quantity of water filtered. The film supply is sufficient for a one-hour tow at 10 knots when using one gear ratio, six hours when using another. After calibration, towing depths and quantity of water strained may be readily estimated by simple analysis of the record (calibration procedures are discussed in appendix II.).

TESTS

In May 1950, five high-speed samplers were tested during a regular cruise of the California Cooperative Oceanic Fisheries Investigations (cruise 5005, formerly numbered cruise 14). The tests took place in an area between Point Conception, Calif., and Point Descanso, Baja California. Standard 1-meter net hauls were made at 46 stations (Ahlstrom 1952). The high-speed samplers were towed between stations, most of which were spaced at 40-mile intervals.

Net hauls on station were taken with a standard plankton net of 1.0 meter in diameter at the mouth by approximately 5 meters in length, constructed of No. 30xxx grit gauze, a sturdy grade of Swiss bolting silk. The hauls were made obliquely from approximately 70 meters deep to the surface; a distance of approximately ½ mile was covered while making each tow.

Two series of high-speed hauls, each utilizing four samplers, were made when traveling between most stations. Locations of high-speed sampler hauls are shown in figure 2. The first series was begun immediately upon leaving a station. A depressor and three of the four samplers were attached and lowered at approximately half speed; after attachment of the fourth sampler the ship's speed was increased to normal cruising speed (approximately 10 knots), and an additional 150 to 180 meters of cable was payed out. The samplers were then towed for one hour, and retrieved.

SPACING OF SAMPLERS ON TOWING WIRE

The amount of towing cable that must be payed out to establish a sampler at a desired depth depends upon several factors, among which the following are probably the more important: amount and kind of depressing force; type and weight of the towing cable; speed of hauling; height of the boom above the water; number of samplers being hauled simultaneously.

It was possible to maintain three factors constant throughout the test operations. A ¼-inch rope-laid stainless steel towing cable was used for each test; the boom was maintained at a constant height (approximately 20 ft.) above the water; and four samplers in a series were used per tow. Only the remaining two factors could not be kept constant: (1) vessel speed of 10 knots was usually

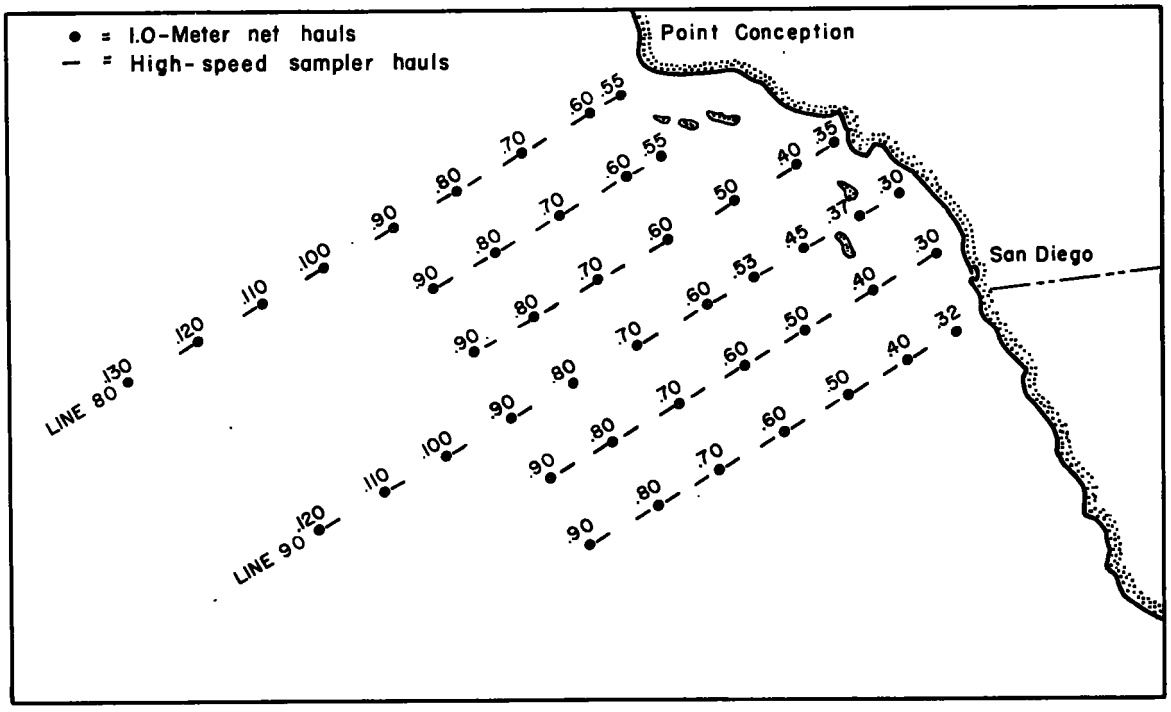

FIGURE 2.—Location of plankton hauls on cruise 5005.

maintained, but the speed varied somewhat with changing sea conditions and could not be considered constant; (2) owing to the loss of a depressor midway through the cruise, it was necessary to substitute a depressor with somewhat different depressing characteristics.

To determine the length of towing cable required to place a sampler at given depths, a single sampler was towed at normal cruising speed (10 knots) on the following lengths of towing cable: 15, 30, 50, 80, 130, 200, 300, and 450 meters. The sampler was placed approximately 6 meters above depressor. The data are summarized in table 1, and graphically presented in figure 3.

TABLE 1.—*Depths fished by a single high-speed sampler towed at a constant speed (10 knots) with selected lengths of towing cable*

Length of towing cable (meters)	Depth fished by sampler	Wire angle at vessel from vertical
	Meters	*Degrees*
15	6	----
30	11	65
50	16	72
80	19	76
130	25	78
200	33	80
300	39	81
450	48	82

The use of several samplers instead of one changed the curve slightly; the exact spacing of samplers on the cable to obtain desired towing depths of 10, 20, 30, and 40 meters below the surface was determined by trial and error. As shown in table 2 and figure 4, the spacing that placed the four samplers at desired depths of 10, 20, 30, and 40 meters was as follows: 10 m. of cable between the depressor and the first sampler, 15 m. between the first and second samplers, 45 m. between the second and third, 80 m. between the third and fourth, and 150 m. between the fourth sampler and the ship. These trials were made with the first depressor at regular vessel speed of 10 knots.

To sample the same depths, when using the second depressor, it was necessary to change the spacing, as shown in table 3, to the following: 5 meters between the depressor and first sampler, 20 m. between the first and second samplers, 45 m. between the second and third samplers,. 80 m. between the third and fourth samplers, and 180 m. between the fourth sampler and the ship. A fairly constant angle of 82° (from the vertical) was obtained with both depressors when the samplers were fishing at the desired depths and the ship was traveling at 10 knots (fig. 5).

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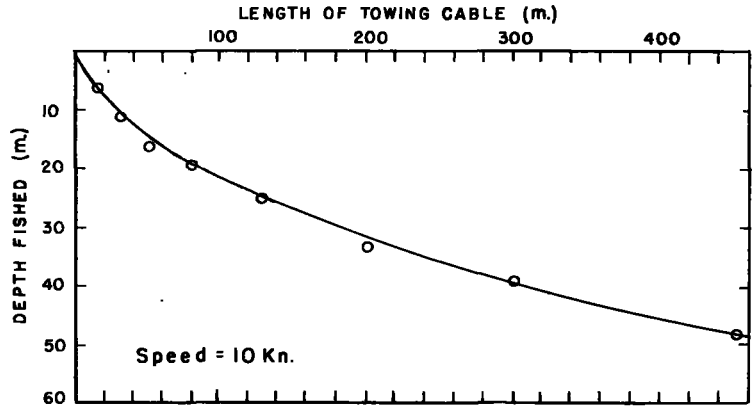

FIGURE 3.—Depths fished by a high-speed sampler with selected lengths of towing cable.

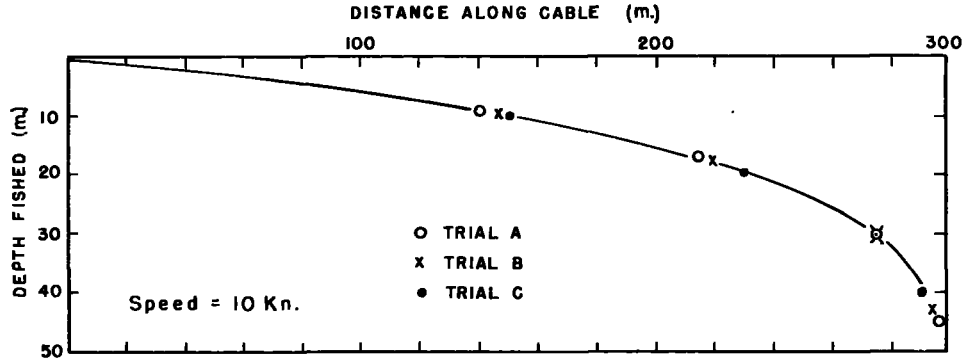

FIGURE 4.—Depths fished by four samplers at different spacings along towing cable.

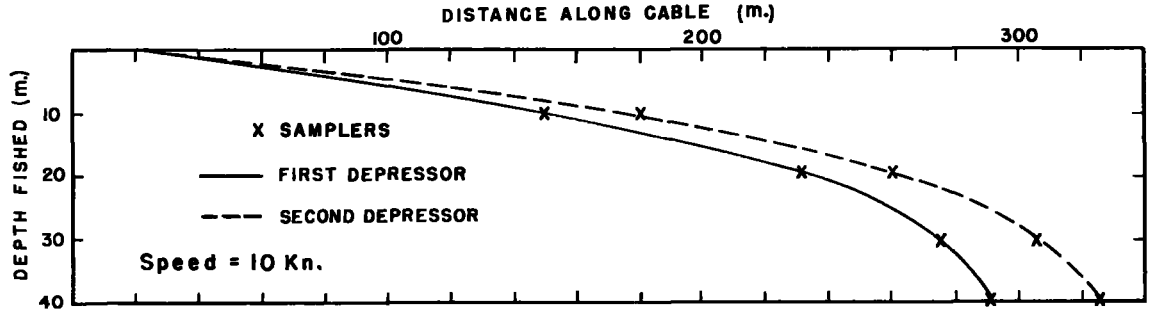

FIGURE 5.—Spacings required to place four samplers at depths of 10, 20, 30, and 40 meters when two different depressors were used.

TABLE 2.—*Depths fished by four samplers at different spacings along towing cable*

Sampler number	Trial A			Trial B			Trial C		
	Spacing between samplers	Length of towing cable	Depth fished	Spacing between samplers	Length of towing cable	Depth fished	Spacing between samplers	Length of towing cable	Depth fished
	Meters	*Meters*	*Meters*	*Meters*	*Meters*	*Meters*	*Meters*	*Meters*	*Meters*
		300			300			300	
1	3	297	45	6	294	43	10	290	40
2	22	275	30	19	275	30	15	275	30
3	60	215	17	55	220	18	45	230	20
4	75	140	9	73	147	9	80	150	10
	140			147			150		

TABLE 3.—*Spacing required to place four samplers at depths of 10, 20, 30, and 40 meters when two different depressors were used at cruising speed of 10 knots*

Sampler number	First depressor			Second depressor		
	Spacing between samplers	Length of towing cable	Depth fished	Spacing between samplers	Length of towing cable	Depth fished
	Meters	*Meters*	*Meters*	*Meters*	*Meters*	*Meters*
		300			330	
	10			5		
1		290	40		325	40
	15			20		
2		275	30		305	30
	45			45		
3		230	20		260	20
	80			80		
4		150	10		180	10
	150			180		

The three deeper samplers, as pointed out previously, were lowered and retrieved at half speed (5 knots). From an average of ten trials, using the first depressor, the following results were obtained: the total wire out was 150 m., the first sampler spaced 10 m. from the depressor, fished at 43 m.; the second sampler, 15 m. from the first, fished at 33 m.; and the third sampler, 45 m. from the second, fished at 13 m. (fig. 6). This shows the greater depth that can be attained at reduced vessel speed.

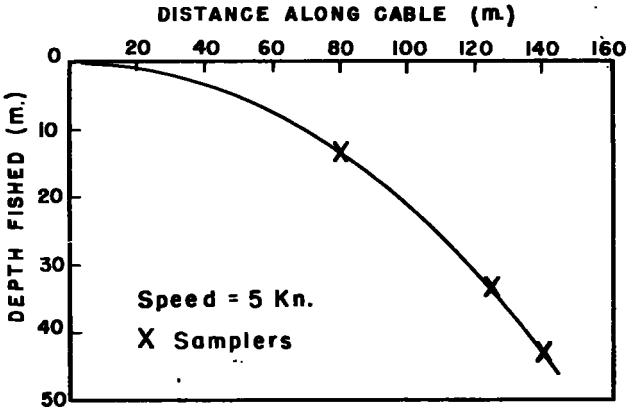

FIGURE 6.—Depths fished by three samplers towed on 150 meters of wire at ship's speed of 5 knots.

PLANKTON VOLUMES

Wet plankton volumes were determined for all samples obtained on cruise 5005. The plankton material obtained in 1-meter net hauls was standardized to the quantity in 1,000 cubic meters of water strained. This standard has been used in reporting all plankton volumes obtained on CCOFI cruises (Staff, South Pacific Fishery Investigations, 1952–56, Thrailkill, 1956).

The wet plankton volumes were determined for the individual catches obtained in high-speed samplers and standardized to the amount in 1,000 cubic meters of water strained. For comparability with standard net tows, the four plankton volumes of a series were averaged, and standardized to the amount in 1,000 cubic meters of water strained. The volumes of plankton in different parts of the area surveyed on cruise 5005, as determined by the two methods of collection, are shown in figure 7. Both methods revealed a similar outline of plankton distribution within the area. The largest individual volumes were taken by the standard 1-meter net; but a somewhat higher concentration of plankton throughout the entire area is shown in the catches of high-speed samplers. It should be noted that the two types of samplers are not entirely comparable for these reasons: (1) the standard net sampled a stratum from approximately 70 meters deep to the surface, while the high-speed samplers fished at four selected depths between 40 meters and the surface; (2) the mesh of the high-speed samplers was finer and hence retained a larger proportion of the smaller plankton material than the standard net.

The four levels sampled by high-speed samplers were found to differ in plankton density between day and night, as is shown in table 4. A similar volume of plankton was taken at all four levels during the night, but rather sharp stratification of plankton was noted during the daylight hauls, the density of plankton increasing with depth. Night hauls at 10 meters obtained a plankton volume three times greater than daylight hauls; at 20 meters twice as much plankton was taken; at 30 meters 1½ times; and at 40 meters 1¼ times as much was collected. At no level was as large a volume taken during daylight as at night. For all levels combined, the ratio of night to day was 1.75. The difference between night and day

TABLE 4.—*Comparison of plankton volumes taken at four selected depths by high-speed samplers (average plankton volume, in cc. per 1,000 m.³)*

Depth of sampler (meters)	All hauls	Day hauls	Night hauls	Night/day ratio
10	653	356	1,086	3
20	735	514	1,057	2
30	837	695	1,044	1.5
40	1,016	913	1,166	1.3
Average	810	619	1,088	1.75

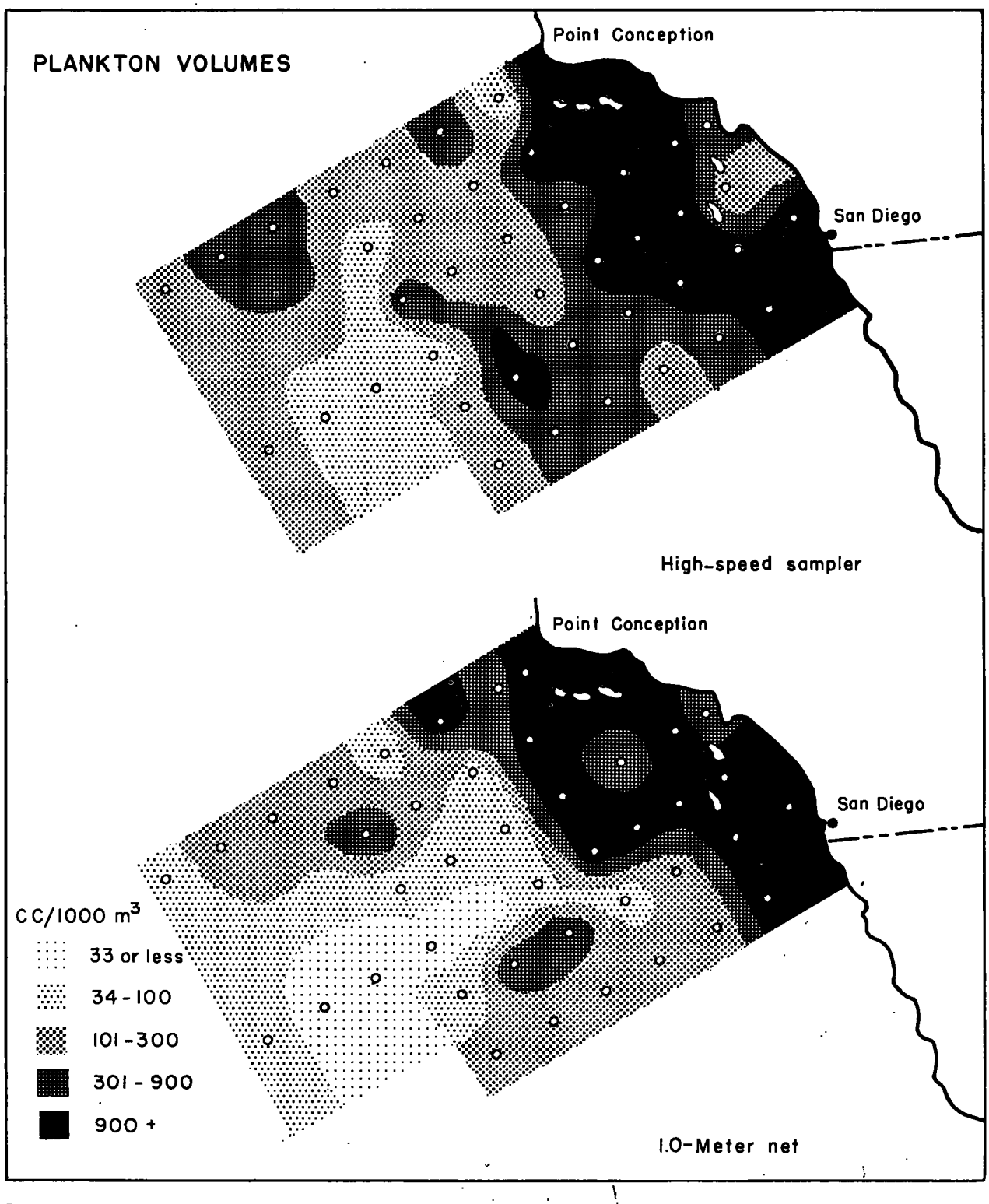

FIGURE 7.—Distribution of plankton volumes based on hauls made with high-speed samplers and with 1-meter net.

hauls in the levels sampled (0–40 m.) may be due to a downward migration of plankters out of the level by day, and an upward migration by night. Information of this type is not ordinarily obtained from routine hauls made with conventional nets.

Many plankton organisms tend to occur in swarms or patches. High-speed samplers obtain an average density relevant to greater distances (10 mi.) than is possible with conventional gear which samples a limited area only.

Because of the greater distance covered with high-speed samplers, it is possible to define average plankton abundance more precisely than has been possible in the past with conventional gear on similar cruise tracks.

SARDINE CATCHES

As has been indicated, the high-speed sampler facilitates the quantitative sampling of various eggs and larvae. The spawning and survival of the sardine in particular, in relation to oceanographic conditions, has been a major concern of the California Cooperative Oceanic Fisheries Investigations and is being studied on an extensive scale. The distribution and abundance of the eggs and larvae of the sardine, as well as those of the northern anchovy, jack mackerel, and lantern fish, found during cruise 5005, will be compared for the two types of gear.

Eggs.—A somewhat more extensive distribution of sardine eggs was obtained with the high-speed samplers than with conventional plankton nets, as shown in figure 8. Sardine eggs were taken at 10 stations with conventional plankton gear. They were present in one or both high-speed sampler hauls taken adjacent to these stations and, in addition, at four other stations.

The abundance of sardine eggs taken in the high-speed samplers was 3½ times greater than in the standard net hauls. Based on the high-speed samples, the estimated average number of sardine eggs spawned per day in this survey area was 642 billion eggs, as compared to 180 billion based on the standard net hauls.

Of particular interest is the sampling at and adjacent to station 97.40. At this station no sardine eggs were taken in the conventional net haul, but large numbers were taken in the high-speed sampler series made on either side of it. There can be little doubt that the sampling of sardine eggs with high-speed samplers was much more effective than with conventional gear when used to estimate the average density of eggs along cruise tracks.

Inasmuch as the high-speed samplers fished four different levels, the samples can be used to determine the level of occurrence of the largest concentrations of sardine eggs. The number of eggs (standard haul totals) taken at the different depth levels in 20 high-speed tows is shown in table 5.

TABLE 5.—*Depth distribution of sardine eggs as determined from high-speed sampler hauls*

Depth of sampler (meters)	Number of occurrences	Number of sardine eggs (standard haul totals)	Percent of total
10	16	2,741	39.9
20	13	1,541	22.4
30	14	1,350	19.6
40	13	1,246	18.1
Total		6,878	100.0

The largest number of sardine eggs collected, approximately 40 percent, were taken at the 10-meter level. The numbers taken at the 20-, 30-, and 40-meter levels were about equal. However, the depth distribution of the eggs varied greatly from series to series. The distribution between the samplers is shown in table 6 for the ten high-speed series in which most of the sardine eggs were taken.

TABLE 6.—*Depth distribution of sardine eggs in 10 high-speed sampler series*

Series taken adjacent to station numbered	Number of eggs taken (standard haul total)	Percentage of total taken at each level			
		10 meters	20 meters	30 meters	40 meters
		Percent	*Percent*	*Percent*	*Percent*
97.40a [1]	2,416	52	27	19	2
97.40b [1]	1,265	47	37	10	6
93.60	845	1	1	7	91
93.40a	676	33	16	37	14
87.60	312	32	36	29	3
90.60a	224	45	0	55	0
83.70	209	73	8	9	10
97.50	193	56	18	4	22
93.40b	161	27	0	40	33
90.60b	139	8	0	49	43

[1] When both high-speed sampler series taken adjacent to a station appear in this table, one of the series is designated a, the other b.

Larvae.—Sardine larvae, taken only in the lower half of the area surveyed, occurred mostly on the lines centering off San Diego. A somewhat wider distribution was indicated by collections taken with conventional gear than with high-speed samplers. Sardine larvae were taken at 12 sta-

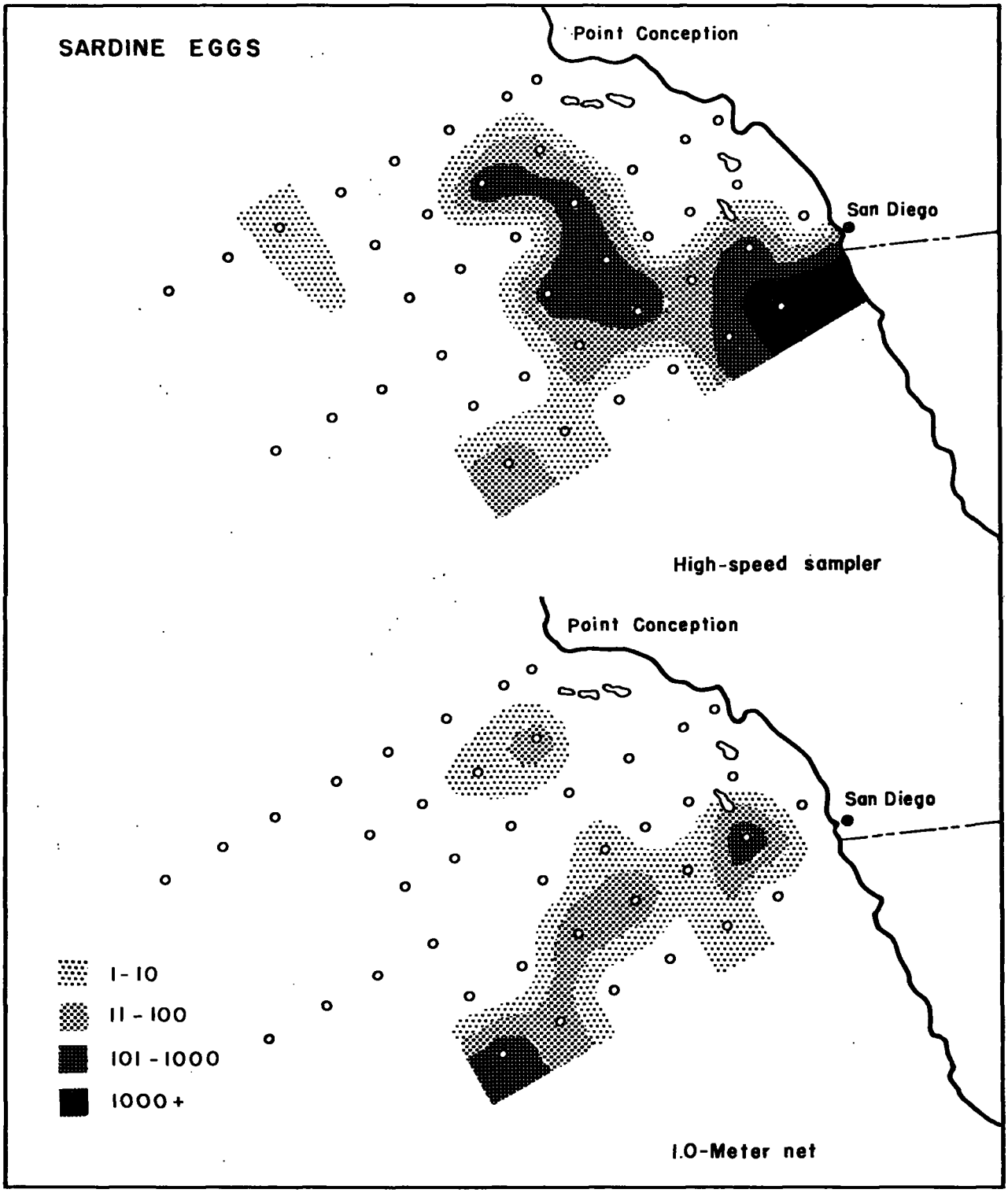

FIGURE 8.—Distribution of sardine eggs based on hauls made with high-speed samplers and with 1-meter net. The legend represents numbers per standard haul.

tions using conventional gear and adjacent to only 9 stations using high-speed samplers. The distributions obtained by both types of gear are shown in figure 9.

Census estimates of all sizes of sardine larvae in this area at the time of survey were similar for both types of gear: 477 billion for conventional gear as compared to 502 billion for the high-speed samplers. A comparison of the size of larvae taken by the two types of gear is shown in figure 10 and summarized in table 7. The smallest group size (2.5–5.0 mm.) and the largest group size (10.5 mm. and longer) were taken in slightly greater numbers by conventional gear, while larvae between 5.5 and 10.0 mm. long were taken in greater abundance by high-speed samplers.

TABLE 7.—*Abundance of sardine larvae, in billions, (census estimates) summarized by size group for 1-meter net hauls and high-speed sampler hauls*

Size of larvae (mm.)	High-speed sampler hauls	1-meter net hauls	Ratio, sampler/net
2.5–5.0	366	394	0.93
5.5–7.5	101	53	1.91
8.0–10.0	20	12	1.67
10.5 and larger	15	18	.83
Total	502	477	

These findings are, in part, contrary to expectation. It is known that the 1-meter net does not fully retain the smaller larvae, hence we would expect larger numbers of these sizes to be taken by the sampler. A possible explanation is that the 1-meter net hauls are influenced by local clumping of small sardine larvae, while the sampler catches are more representative of the mean density of these sizes.

The series of high-speed sampler hauls can be used to determine that depth within the 40-meter stratum at which sardine larvae occurred in greatest abundance. Numbers of larvae (standard haul totals) taken at the four depths sampled are tabulated in table 8. The largest number of larvae was taken at the 20-meter level. The concentration was 1.5 times as great as at the 10-meter level and nearly four times as great as at 30- and 40-meter depths. Approximately four-fifths of the larvae 8.0 mm. and longer were taken at the 20-meter level.

TABLE 8.—*Sardine larvae concentrations at four selected depths*

Depth of sampler (meters)	Number of larvae taken (standard haul totals)	Percent of total
10	274	29.8
20	422	45.9
30	116	12.6
40	107	11.7
Total	919	100.0

ANCHOVY CATCHES

Eggs.—Measuring only about 0.5 millimeters in their narrowest dimensions, anchovy eggs are not fully retained by our standard nets. In fact, a test conducted with a somewhat coarser mesh net than that now in use (No. 24xxx grit gauze with 0.9-mm. openings between threads when new, and shrinking to approximately 0.7 mm. after use) gave only about 1.5 percent as much retention as No. 40xxx grit gauze with pores of 0.40 mm. The net employed on cruise 5005 was constructed of No. 30xxx grit gauze, with 0.7-millimeter mesh openings when new, and approximately 0.55 mm. openings after use; this mesh retains only a small percentage of anchovy eggs. With the finer mesh used in high-speed samplers (openings 0.24 mm. across and 0.33 mm. on the diagonal) anchovy eggs were completely retained.

A census estimate of the abundance of anchovy eggs in the survey area gave 7,065 billion eggs, based on high-speed sampler hauls. The estimate based on net hauls was only 3.3 percent as large. Hence, the high-speed samplers proved effective in sampling anchovy spawning, while the conventional gear now in use is not effective for this purpose.

The depth distribution (within the upper 40-m. stratum) of anchovy eggs for hauls in which 100 or more eggs were obtained (standard number) is given in table 9. In the three hauls containing the largest number of eggs, the majority were taken below 20 meters. A portion of the eggs must have occurred below the levels fished by the high-speed samplers.

Larvae.—Anchovy larvae were taken at 10 stations with conventional gear, and adjacent to 13 stations with high-speed gear. The distribution obtained with the two types of equipment was similar; anchovy larvae occurred in a coastwise band about 125 miles wide.

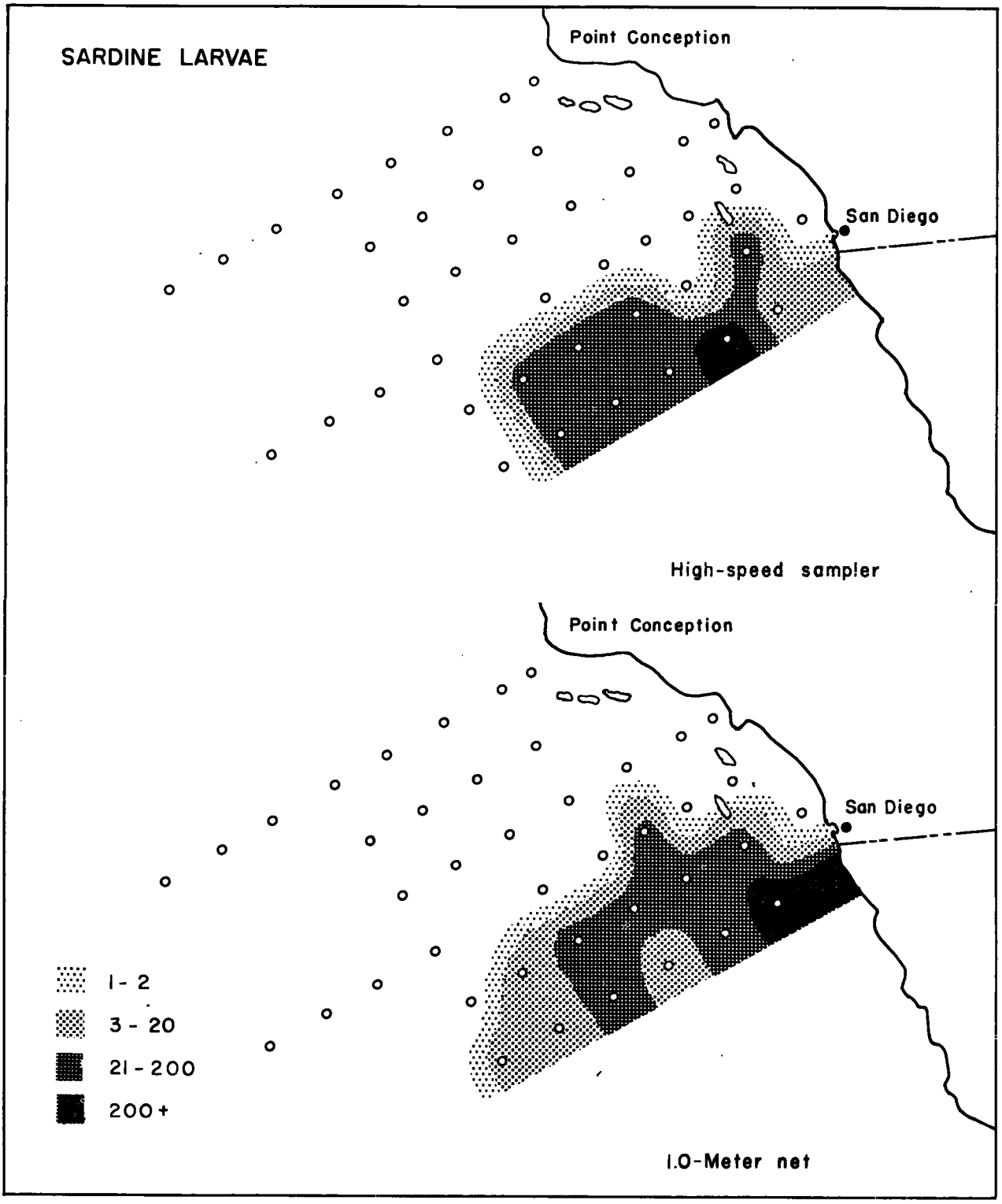

FIGURE 9.—Distribution of sardine larvae based on hauls made with high-speed samplers, and with 1-meter net. The legend represents numbers per standard haul.

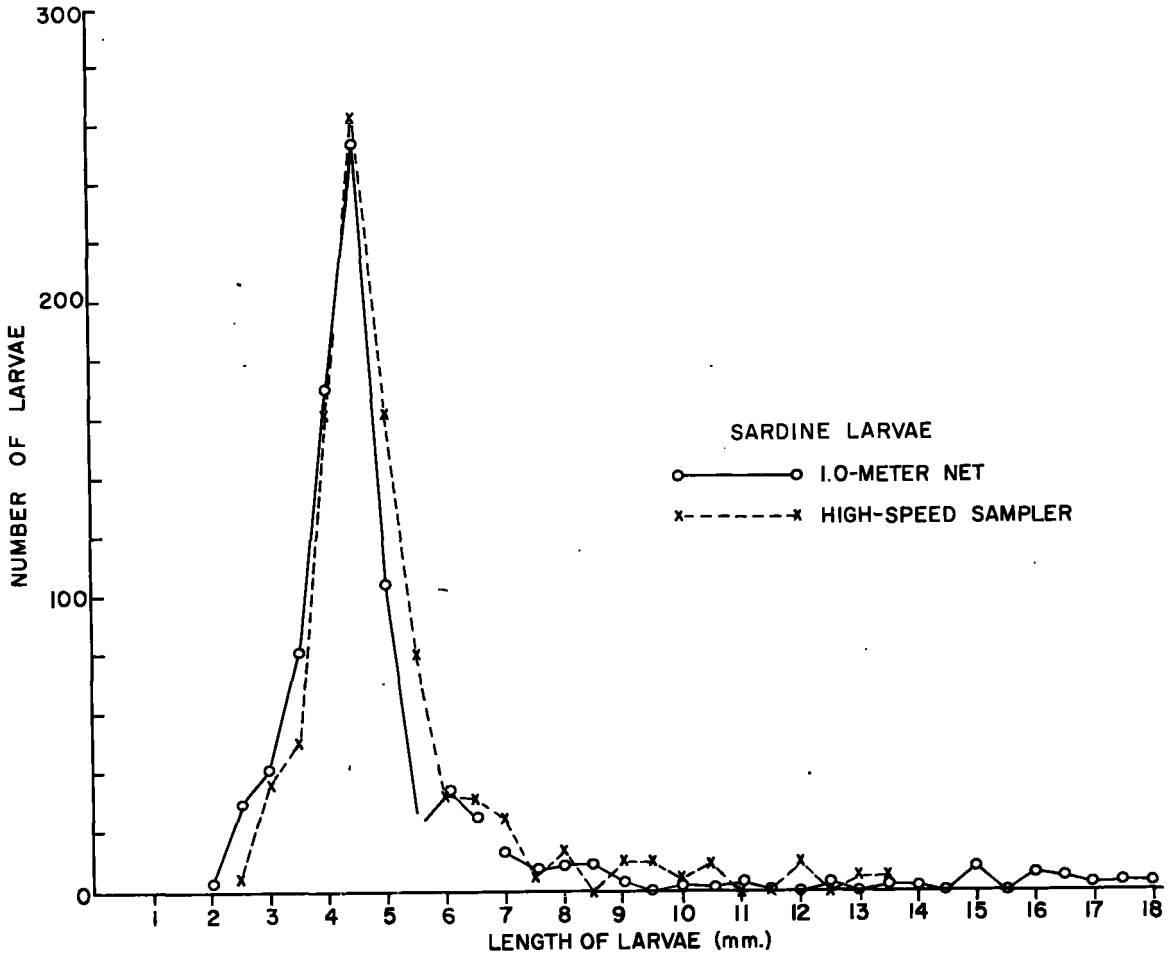

FIGURE 10.—Comparison of size composition of sardine larvae taken by high-speed sampler and 1-meter net.

TABLE 9.—*Depth distribution of anchovy eggs in 6 high-speed sampler series*

Series taken adjacent to station numbered	Number of eggs taken (standard haul total)	Percentage of total taken at each level			
		10 meters	20 meters	30 meters	40 meters
		Percent	*Percent*	*Percent*	*Percent*
93.50a [1]	15,200	2.1	2.4	56.7	38.8
93.50b [1]	8,432	3.3	2.5	8.7	85.5
93.40	1,076	3	3.3	37.1	56.5
93.30	201	60.7	39.3	0	0
90.37	183	91.8	0	8.2	0
97.50	113	8.8	37.2	35.4	18.6

[1] When both high-speed sampler series taken adjacent to a station appear in this table, one of the series is designated a, the other b.

Greater numbers of anchovy larvae were taken with high-speed samplers than with conventional gear. Census estimates of the number of anchovy larvae of all sizes in the area were more than three times as large when based on high-speed sampler collections as when based on standard net hauls: 2,156 billion as compared to 625 billion larvae. This reflects the larger numbers taken in individual hauls: nearly 2,900 anchovy larvae (standard number) were taken in one series of high-speed sampler hauls, while the largest number taken in a haul using conventional gear was 679. The size distribution of anchovy larvae taken by the two types of gear is shown in figure 11 and summarized in table 10.

TABLE 10.—*Abundance of anchovy larvae, in billions (census estimates), summarized by size group for 1-meter net hauls and high-speed sampler hauls*

Size of larvae (mm.)	High-speed sampler hauls	1-meter net hauls	Ratio, sampler/net
2.0–5.0	3,674	715	5.13
5.5–7.5	155	95	1.63
8.0–10.0	102	90	1.13
10.5–17.5	29	25	1.16
Total	3,960	925	

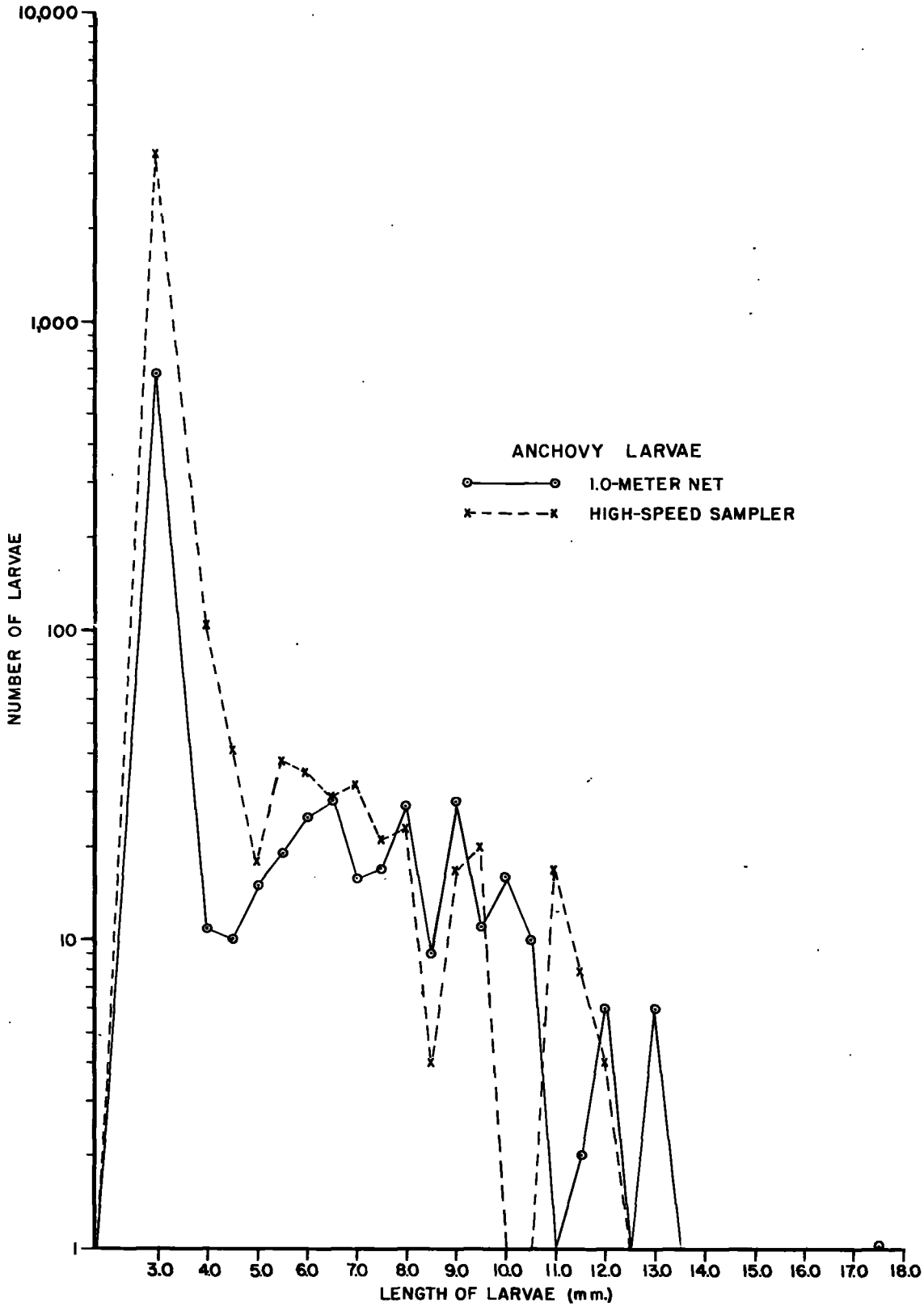

FIGURE 11.—Comparison of size composition of anchovy larvae taken by high-speed sampler and 1-meter net.

It is interesting to compare the numbers of larvae of different sizes taken by the two types of gear. More than five times as many of the smaller larvae, 2.0–5.0 mm. long, were taken in the high-speed sampler collections as in the net hauls. For larvae 5.5–7.5 mm. long, the ratio decreased to 1.63, and for larvae larger than 7.5 mm., the ratio was only slightly greater than 1. The much larger ratio of small larvae taken in high-speed sampler collections reflects, at least in part, the more complete retention of these sizes by the high-speed samplers. The Monel screen used in the high-speed samplers had pore openings of slightly less than one-fourth mm. wide, while the openings between meshes of 30xxx grit gauze used in the nets were slightly larger than one-half millimeter.

The largest concentrations of both anchovy eggs and larvae were taken at the 40-meter level in two adjacent hauls at station 93.50 representing the depth distribution at a particular locality under a specific set of conditions. In other studies of the depth distribution of anchovy eggs and larvae, eggs had not been taken in abundance as deep as 40 meters. However, at these stations there were probably many anchovy eggs and larvae below the depths reached by the lower sampler. The average depth distributions of anchovy eggs and larvae as determined from high-speed sampler hauls are summarized in table 11.

TABLE 11.—*Depth distribution of anchovy eggs and larvae as determined from high-speed sampler hauls*

Depth of sampler (meters)	Anchovy eggs		Anchovy larvae	
	Standard haul totals	Percent of total	Standard haul totals	Percent of total
10	941	3.7	210	2.7
20	741	2.9	2,393	30.7
30	9,845	39.0	1,820	23.3
40	13,742	54.4	3,377	43.3
Total	25,269	100.0	7,800	100.0

JACK-MACKEREL CATCHES

Eggs and larvae.—The eggs and larvae of the jack mackerel were more widely distributed than those of the sardine or anchovy, occurring throughout the area surveyed except near shore. The center of abundance was between 125 and 250 miles offshore. The distribution determined from high-speed samplers gives a more detailed picture than the distribution determined from net hauls (fig. 12).

Census estimates of the number of jack-mackerel larvae in the survey area at the time of the cruise gave 6,600 billion when based on high-speed sampler hauls, compared to 4,800 billion when based on standard net hauls. The difference may have resulted from better retention of larvae (3.0 mm. and smaller) by the high-speed sampler. Larvae more than 3.0 mm. in length are retained fully by both types of sampling gear.

Information on depth distribution of jack-mackerel eggs and larvae as determined from high-speed sampler series is summarized in table 12. Some material was probably below the nets in these series.

TABLE 12.—*Depth distribution of jack-mackerel eggs and larvae, based on high-speed sampler hauls*

Depth of sampler (meter)	Jack-mackerel eggs		Jack-mackerel larvae	
	Standard haul totals	Percent of total	Standard haul totals	Percent of total
10	16,580	42.5	3,471	20.2
20	9,060	23.2	6,227	36.2
30	6,900	17.7	4,297	25.0
40	6,510	16.7	3,205	18.6
Total	39,050	100.1	17,200	100.0

LANTERN FISH CATCHES

Larvae.—Larvae of the lantern fish *Lampanyctus leucopsarus* were taken throughout the survey area. They were obtained in all but two of the hauls made with conventional nets, and in 50 of the 59 series of hauls made with high-speed samplers. The distribution and abundance based on hauls made with high-speed samplers and with a 1-meter net is shown in figure 13.

Census estimates of the number of larvae of *L. leucopsarus* in the area at the time of cruise 5005 was 1,313 billion, based on high-speed sampler hauls, and 856 billion, based on 1-meter net hauls. Here again the difference may have been due to more complete retention of smaller larvae by the high-speed samplers.

There was an increase in abundance with depth, at least to the 40-meter level (table 13). Other studies made by the senior author have shown 40 meters to be the usual depth of greatest concentration, and some *Lampanyctus leucopsarus* larvae have been taken as deep as 100 meters. Hence, we may assume that larvae occurred below the level sampled by the high-speed nets.

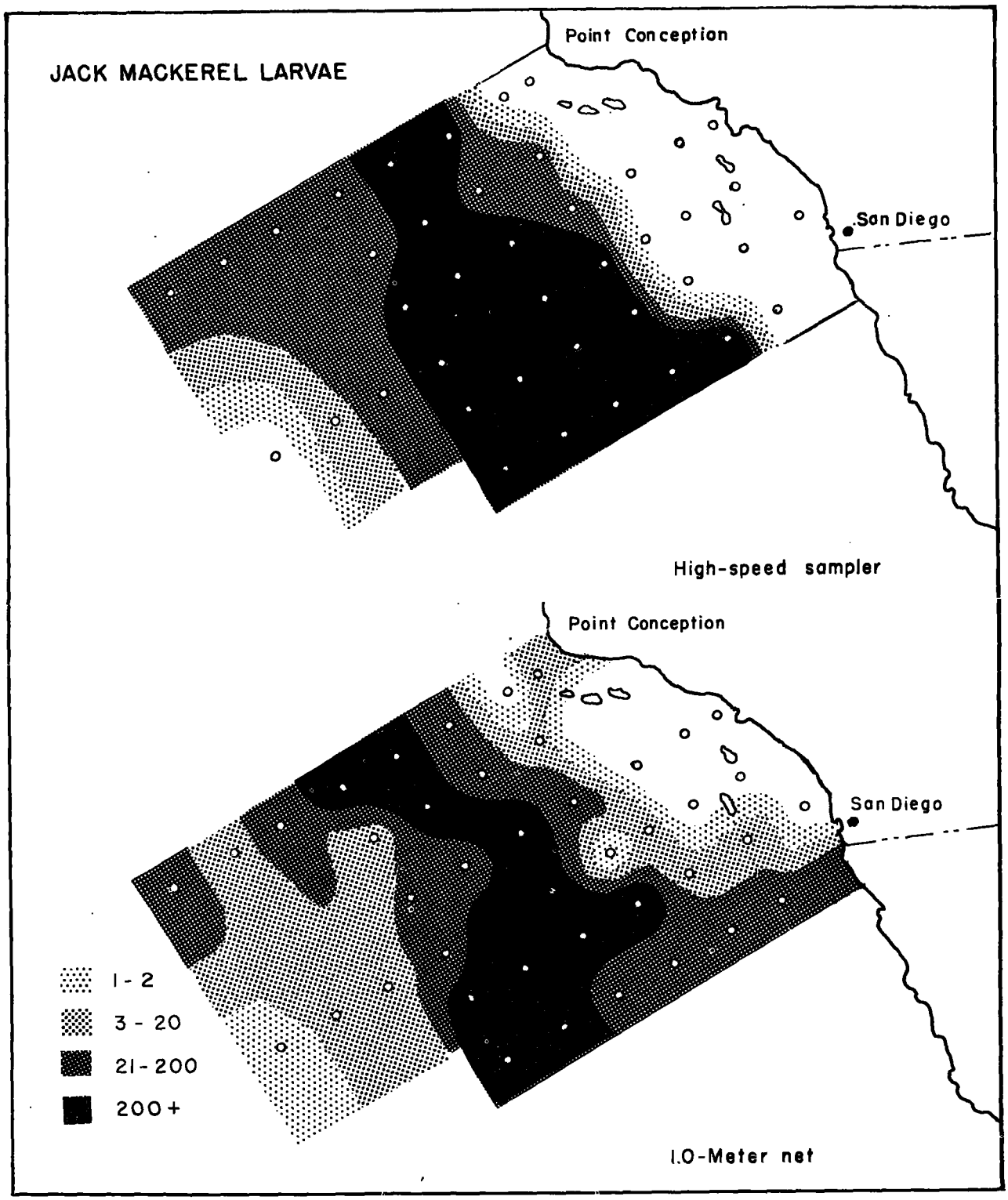

FIGURE 12.—Distribution of jack-mackerel larvae based on hauls made with high-speed samplers; and with 1-meter net. The legend represents numbers per standard haul.

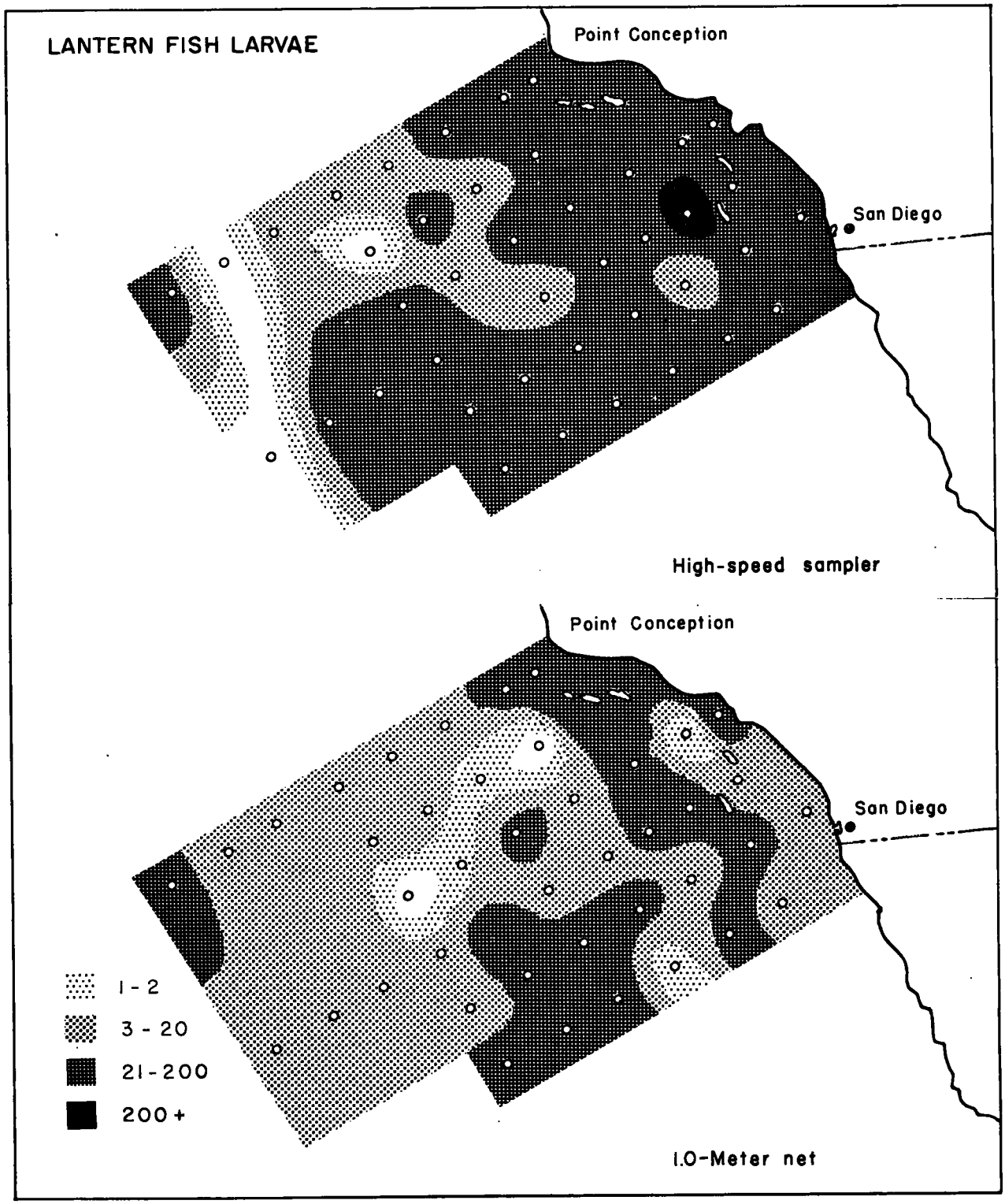

FIGURE 13.—Distribution of larvae of the lantern fish (*Lampanyctus leucopsarus*) based on hauls made with high-speed samplers and with 1-meter net. The legend is based on numbers per standard haul.

TABLE 13.—*Depth distribution of lantern fish larvae* (Lampanyctus leucopsarus), *based on high-speed sampler hauls*

Depth of sampler (meter)	Number of larvae taken (standard haul totals)	Percent of total
10	154	5.1
20	392	13.1
30	1,058	35.3
40	1,400	46.6
Total	3,004	100.1

OTHER FISH CATCHES

Small pelagic fish are occasionally taken at night in net hauls. Among those commonly caught are a number of species of lantern fish and some deep-sea smelts. Only a small fraction of the fish in the path of the net are caught, since most fish could easily avoid capture by the slow-moving standard gear. However, they have less chance of getting out of the path of the high-speed gear. This is clearly demonstrated by the fish taken during cruise 5005. Based on comparable volumes of water strained, approximately 30 times as many fish were taken in high-speed sampler hauls as with standard gear. This is a clear-cut demonstration of the greater efficiency of high-speed samplers as compared to standard nets in capturing the more agile organisms.

All fish taken with both types of gear were obtained between 8:00 p. m. and 4:00 a. m. probably as a result of the fish migrating upward for night feeding in the levels being sampled by our gear. The largest numbers were taken at 20 and 30 meters depth with high-speed samplers (table 14).

TABLE 14.—*Depths at which fish were taken in high-speed sampler hauls*

Depth of sampler (meter)	Number of fish taken (standard haul totals)	Percent of total
10	30	17.1
20	63	35.8
30	68	38.6
40	15	8.5
Total	176	100.0

The species of fish taken as juveniles or adults in both types of gear on cruise 5005 were as follows:

Myctophidae:
- *Ceratoscopelus townsendi*
- *Diaphus theta*
- *Diogenichthys atlanticus*
- *Hygophum reinhardti*
- *Lampanyctus leucopsarus*
- *Lampanyctus mexicanus*
- *Notolychnus valdiviae*

Gonostomatidae:
- *Vinciguerria lucetia*

Bathylagidae:
- *Bathylagus wesethi*
- *Leuroglossus stilbius*

EVALUATION

To sample organisms adequately, such as the larval stage of a fish, it is necessary to (1) delimit the range both horizontally and vertically; (2) obtain enough samples to estimate variation in density and (3) employ an instrument capable of quantitative measurement of water strained, retention of desired sizes (no loss of organisms through openings between meshes), capture of larger individuals in their relative proportion in the population, and in sufficient numbers for abundance and mortality estimates. The relative merits of high-speed samplers and of standard 1-meter plankton nets in fulfilling these requirements are evaluated in the following discussion.

Horizontal range.—Both types of gear seem to be equally effective in delimiting the horizontal distribution of plankton organisms. This was brought out in the discussion of the distribution of various fish eggs and larvae, as well as in figures and tables. These data are summarized in table 15. The high-speed sampler gave more information on the distribution of eggs, in the two species cited, than did the 1-meter net. The total occurrences for both eggs and larvae, however, are extremely close.

Vertical range.—High-speed samplers, used in a series, automatically give information on the distribution of organisms at the several depth zones sampled by the gear. Results of the previously discussed tests are summarized in table 16. From this information, it is obvious that the entire depth distribution of most species was not encompassed during cruise 5005 by these samplers. Hence, a somewhat deeper stratum should be sampled. It might be possible to sample as deeply as 60 meters using present equipment, but to exceed this would require changes in the depressing force and in the wire used. However, for the sardine and many other fish species, 60 meters probably would be deep enough for adequate quantitative sampling. For

some species, such as hake, this depth is not adequate.[2]

TABLE 15.—*Occurrences of fish eggs and larvae in 1-meter net hauls at stations as compared to occurrences in high-speed sampler hauls taken adjacent to stations*

Organism	1-meter net	High-speed sampler
Sardine eggs	10	14
Sardine larvae	12	9
Anchovy eggs	4	7
Anchovy larvae	10	13
Jack-mackerel larvae	34	28
Lampanyctus leucopsarus larvae	39	37
Total	109	108

TABLE 16.—*A summary of the depth distribution of eggs and larvae taken with high-speed samplers*

Organism	Percentage at each level				Total
	10 meters	20 meters	30 meters	40 meters	
Sardine eggs	39.9	22.4	19.6	18.1	100.0
Sardine larvae	29.8	45.9	12.6	11.7	100
Anchovy eggs	3.7	2.9	39	54.4	100
Anchovy larvae	2.7	30.7	23.3	43.3	100
Jack-mackerel eggs	42.5	23.2	17.7	16.7	100.1
Jack-mackerel larvae	20.2	36.2	25	18.6	100
Lampanyctus leucopsarus larvae	5.1	13.1	35.3	46.6	100.1

Conventional gear definitely has the advantage in this phase of sampling, since it is exceedingly versatile in depth sampling. Nets can be lowered to any desired depth, even to the deepest layers of the ocean; conventional gear can also be used in series to furnish data on depth distribution of organisms. However, with nets as large as 1.0 meter in diameter, as were used on cruise 5005, such series have been taken to establish depth distribution rather than for routine sampling. Once the depth distribution of an organism has been established, then oblique hauls can be made deep enough to encompass routinely this distribution.

Variation in density.—Obtaining enough samples of organisms to determine the variation in density with range is important because organisms are seldom found to be uniformly distributed. Usually there is considerable variation in abundance in various parts of their range. Because of these variations, it is difficult to sample an organism adequately with standard plankton gear. Strip samples, covering miles at a time, are far more representative of mean density; such samples automatically average-out much of the variation in abundance. This capability of the high-speed sampler, lacking in the spot sampler, is an important advantage and was the primary consideration prompting the development of this type of gear. The results obtained on cruise 5005 point up these advantages. Very large concentrations of sardine eggs, for example, that were missed entirely by standard net hauls were picked up by means of strip sampling.

Instrument requirements.—The performance of sampling gear can seriously limit the value of plankton collections. Four aspects of gear performance will be compared for the two types of plankton samplers.

An adequate means of measuring the quantity of water strained in making a haul is an essential requirement of an instrument used for quantitative sampling. The depth-flow mechanism of the high-speed sampler automatically records both water flow and depth; the Atlas current meter used with 1-meter nets gives a reliable record of water flow.

The high-speed sampler was constructed of finer meshed netting material than the 1-meter net now being employed on cruises of the California Cooperative Oceanic Fisheries Investigations. We did not have any serious clogging of the Monel screen of the high-speed samplers (on one test, clogging retarded flow by about 10 percent after 4 hours of continuous towing), yet retention of smaller-sized fish eggs and larvae was much better than with conventional gear. However, we are now experimenting with finer-meshed synthetic netting in 1-meter nets in order to increase retention without impairing the flow of water through the nets.

Large plankton organisms are often agile enough to dodge relatively slow-moving plankton nets. The high-speed sampler was designed to prevent dodging through its speed of operation and mode of attachment to the towing wire. The mouth opening of the sampler precedes the towing wire, consequently no part of the gear can act as a scare as do both the towing wire and the bridle of our standard plankton gear. Organisms capable of moving out of the path of a conventional net being hauled at 1 to 1½ knots may have little chance of dodging the high-speed sampler moving at 10 knots. The taking of approximately 30 times as many small pelagic fishes with high-speed gear as with conventional plankton nets (based on comparable volumes of water

[2] A newly designed depressor, given the model number 3x, permits operation to 300 meters with 3/8" and 1/2" towing cable (J. D. I.).

strained) accents the effectiveness of high-speed samplers in this field.

A limitation of high-speed samplers for certain purposes results from the rather small quantity of plankton collected. A group of 4 samplers hauled for 10 miles would collectively strain only about 40 cubic meters of water. This is less than one-tenth the quantity of water strained during a routine 1-meter net haul. The smaller quantity is adequate for measuring mean density of many plankton organisms, including fish eggs, but not for obtaining sufficient numbers of larvae, particularly of older stages, for mortality estimates.

The cost of constructing the Isaacs high-speed sampler may place a limitation on its widespread use. As one way of reducing the cost of equipment, it is practicable to use only one instrument with a depth-flow meter in a string of 4 or 5 samplers towed simultaneously. On cruise 5005, the three upper high-speed samplers were equipped with plankton filters of the same mesh size. Due to the time required for attaching and retrieving the samplers, the upper sampler was hauled only 83.6 percent as long, on the average, as the sampler at 30 meters, while the sampler at 20 meters was hauled 94.1 percent as long. A comparison of the volumes of water strained by the three samplers showed that the upper one strained on the average 83.2 percent as much as the sampler at 30 meters, and the 20-meter sampler strained 93.5 percent as much. We conclude from these comparisons that a fairly accurate estimate of volume of water strained by either of the upper samplers could have been obtained by using the volume of water strained by the net at 30 meters, adjusted for difference in time of hauling.

APPENDIX I: OPERATING INSTRUCTIONS

Preparing film.—Film used in the high-speed sampler is 35 mm. perforated clear No. 3 Safety Leader film. The film which is obtained in bulk must be cut into appropriate lengths (approximately 2½ ft.). To prepare the film for use, roll on a slotted brass rod (⅛" in diameter) just tight enough that the roll will come off the rod without difficulty. Wrap with a rubber band, applying sufficient tension to prevent unrolling, but not enough for tension lines to bake into the film. After the film is properly banded, remove from the rod.

The film is baked in order to set it in a tight roll, which assures that the film will automatically rewind during use. It should be baked for 4 hours at a temperature of 220° F. in a thermostatically-controlled oven.

After baking, the film is cooled to room temperature, and then rerolled. This is done so that the point of maximum tension will be on the outside of the roll, ensuring that the film will rewind on itself when in use.

Handling of samplers.—We have found from experience that careful instructions for assembling the samplers, and attaching and removing them from the towing cable may prevent costly repairs or even loss of the equipment.

Assembling.—Load the sampler with film starting the film around the film sprocket and marking the zero trace. Attach the straining section of the plankton filter to the cod-end cup. Attach the metering unit and tighten the stylus screw. Insert complete unit in the outer casing and secure.

Placing samplers on towing cable.—Attach and lower the depressor (illustrated in fig. 14) into the water with ship at half speed. Place the ball clamp on the towing cable and tighten (fig. 15). Remove the nose ring from the sampler and push the slotted nose over the wire, above or below the cable clamp. Pull the cable clamp into the cable-clamp seat and replace the nose ring. Lower the sampler the desired amount and attach (fig. 16) the second sampler in the same manner, and so on.

Removing samplers from towing cable.—The procedure for removing samplers from the towing cable is just the reverse of the preceding description. When samplers break water, they assume the mouth-up vertical position of pre-lowering, thus preventing loss of any part of the sample.

Disassembling.—Remove outer casing while keeping sampler upright to prevent loss of sample. Play a jet of salt water along the outside of the plankton filter to dislodge any adhering plankton. Detach the straining section of the filter and concentrate sample further by patting salt water on the outside of the mesh of the cod-end cup. Pour sample into a suitable container, label, and add preservative. Detach the metering unit. Remove film by slicing down through the film with a knife blade, and label (fig. 17). Wash plankton filter and metering unit with fresh water. Reload film, and reassemble sampler.

At no time during assembling or disassembling should force be used on the high-speed sampler. Gentle tapping or rocking motions will dislodge any stubborn sections without damaging the instrument. Should any section consistently stick, silicone stopcock grease can be used to overcome the tendency.

APPENDIX II: CALIBRATION

The method of standardizing hauls would require a lengthy explanation and hence would be out of place in this paper which is concerned with performance and not the technical aspects of quantitative sampling. The method of standardizing regular plankton hauls is discussed by Ahlstrom (1948), and a modification of this method was used in standardizing the high-speed sampler hauls.

The following procedures were used for obtaining depth flow calibrations:

Depth calibration.—The depth calibration was done at sea during calm weather. Instead of a

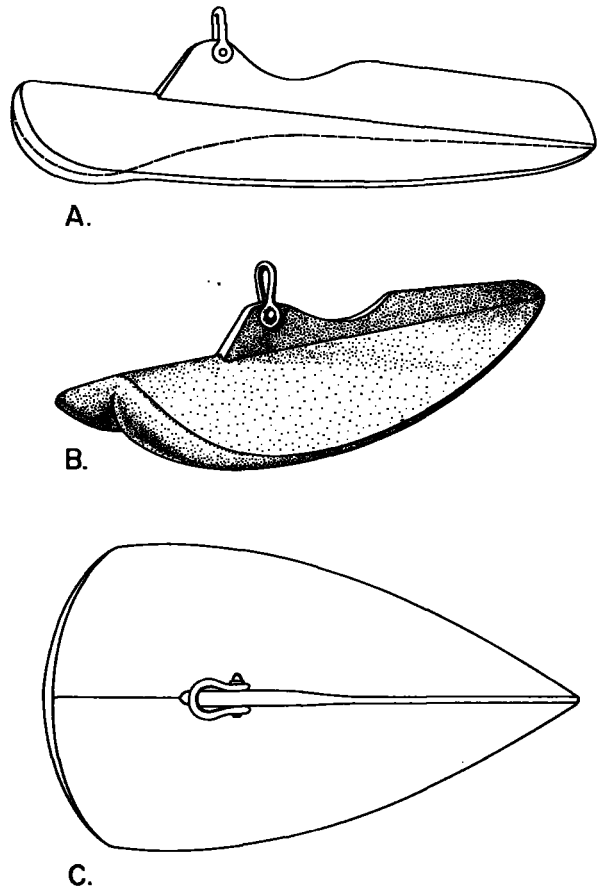

FIGURE 14.—Three views of depressor.

depressor, an ordinary 100-lb. weight was attached to the end of the towing cable. The sampler being calibrated for depth was attached about 10 meters above the weight. It was properly loaded with film and lowered to the water surface, at which time the meter wheel of the winch was set at zero. The sampler was then successively lowered to a number of depths. After each lowering the metering unit was removed, the depth scratched above the trace on the film, the sprocket turned about one-half a revolution, and the unit reassembled for the next lowering. Two kinds of pressure elements have been used, one type effective to approximately 55 meters, the other to approximately 137 meters. For the shallower element, lowerings were made to 10, 20, 30, 40, 50, and 60 meters, respectively. For the deeper element, lowerings were made to 10, 20, 30, 40, 50, 60, 70, 80, 100, 120, 130, and 140 meters. At the completion of a calibration the traces were measured and graphed against depth as determined by wire out, and a line was fitted to the points. Typical depth calibration graphs for the two types of pressure elements are shown in figure 18.

Flow calibration.—Flow calibration presented more of a problem. Several methods were tried before a satisfactory one was found. The most difficult problem was to find a suitable method for measuring the volume of water that passed through the sampler during the tests. Several preliminary methods did not achieve a desirable degree of either accuracy or consistency (repeatability) of results. These included rough and ready methods of either weighing or collecting and measuring the water passing through the sampler. Finally, a water meter was installed in front of the sampler in the calibration system. By this means it was possible to measure accurately the quantity and rate of flow of water passing through the sampler during each trial.

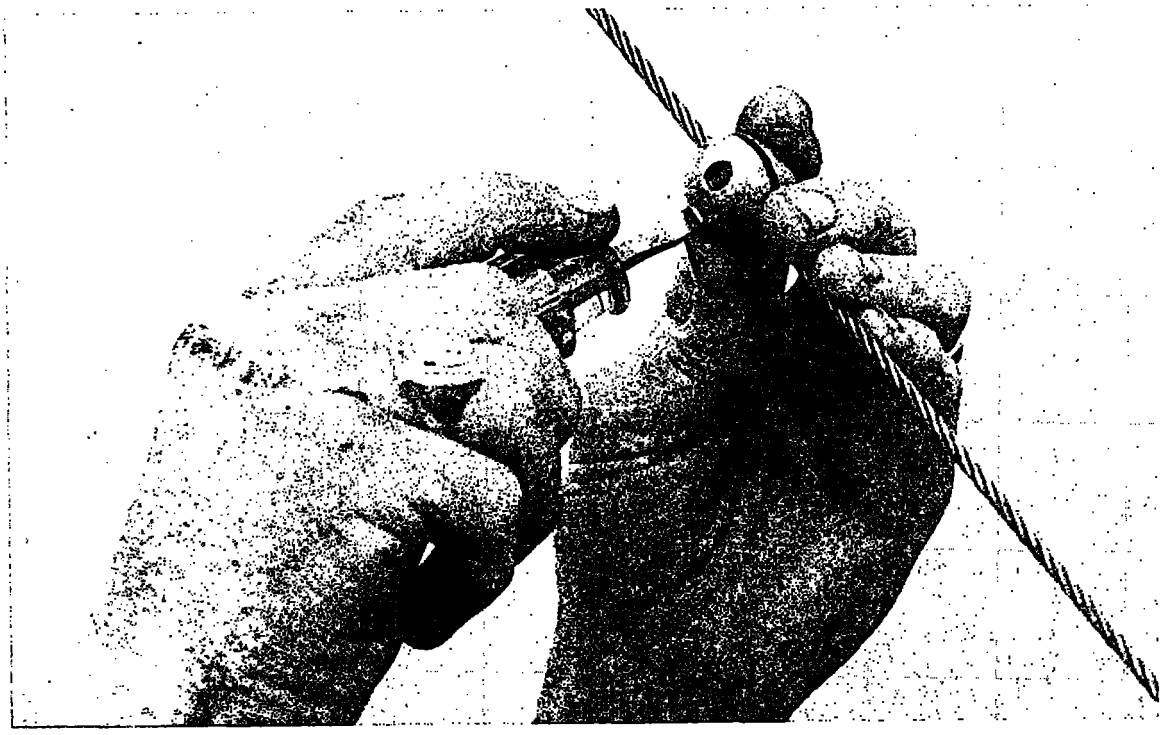

FIGURE 15.—Fastening ball clamp to towing cable.

FIGURE 16.—Fastening sampler to towing cable.

NOTE:—The samplers after attachment to the towing cable, hang vertically with the mouth up. When lowered into the water, they orient themselves and assume a horizontal fishing position.

FIGURE 17.—Removal of film from sampler.

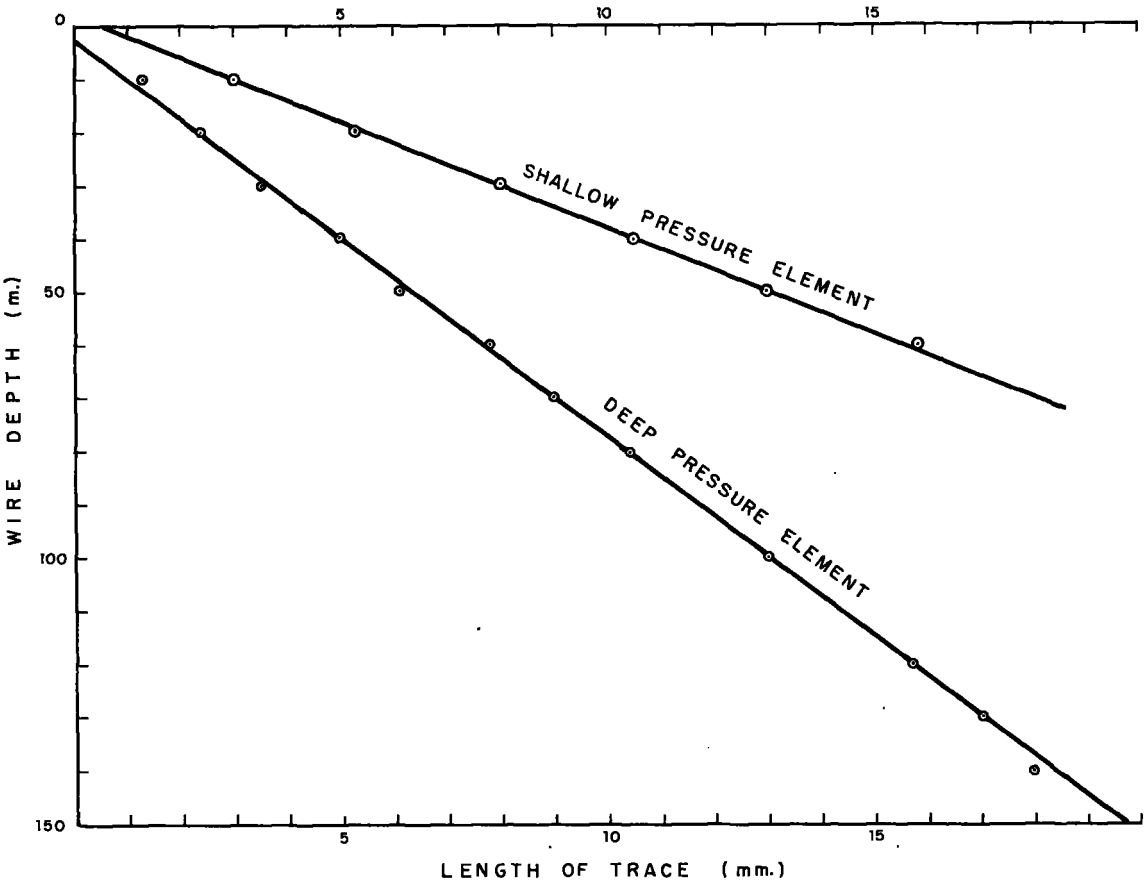

FIGURE 18.—Typical depth-calibration curves for the two types of pressure elements used.

The calibration tests were conducted in a pool. There are four important elements in the calibration system: (1) Housing for attaching essential portion of high-speed sampler to the calibration system; (2) metering device (a calibrated water meter) measuring flow; (3) water source; and (4) flow rate valve (for controlling volume of water entering system per unit of time).

Housing.—Inasmuch as the casings used with high-speed samplers at sea could not be employed conveniently during calibration tests, a cylindrical casing was substituted (fig. 19). It had a bonnet at its forward end for convenient attachment to a water meter.

Water meter.—The water meter employed had openings of 1½ inches diameter (3.8 cm.) at attachment points. It was calibrated, before use, by the Engineering Department of the San Diego Municipal Water Company (fig. 19).

Water source.—The water source was a submersible pump that drew water from the pool in which the calibration tests were made. A 1½-inch hose connected the pump to the calibration setup. The submersible pump used with this operation gave an even, steady flow of water through the calibration tube.

Valve.—A manually operated valve was used to control the rate of flow of water entering the system. In calibrating the flow-meter, it was desirable to obtain rates of flow that would bracket those obtained when in use at sea. The flow-meter being calibrated is shown in figure 20.

Because the flow-meter is directly geared to a sprocket over which is led the clear acetate film, when the flow-meter is actuated by water passing through the sampler, a trace is obtained on the film. The length of the trace is determined by two factors, the volume of water and rate of flow. In calibrating the flow unit, identical volumes of water were used on all trials, but the rate of flow was varied. A range of flow rates from 3.1 to 10.0 cubic feet per minute (0.088 to 0.283

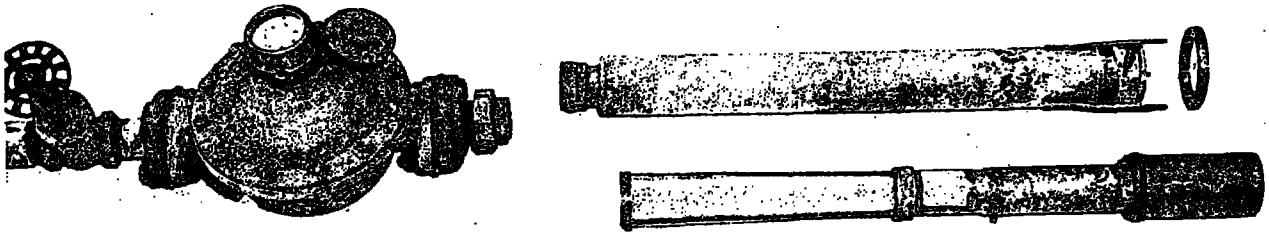

FIGURE 19.—Disassembled flow calibration units.

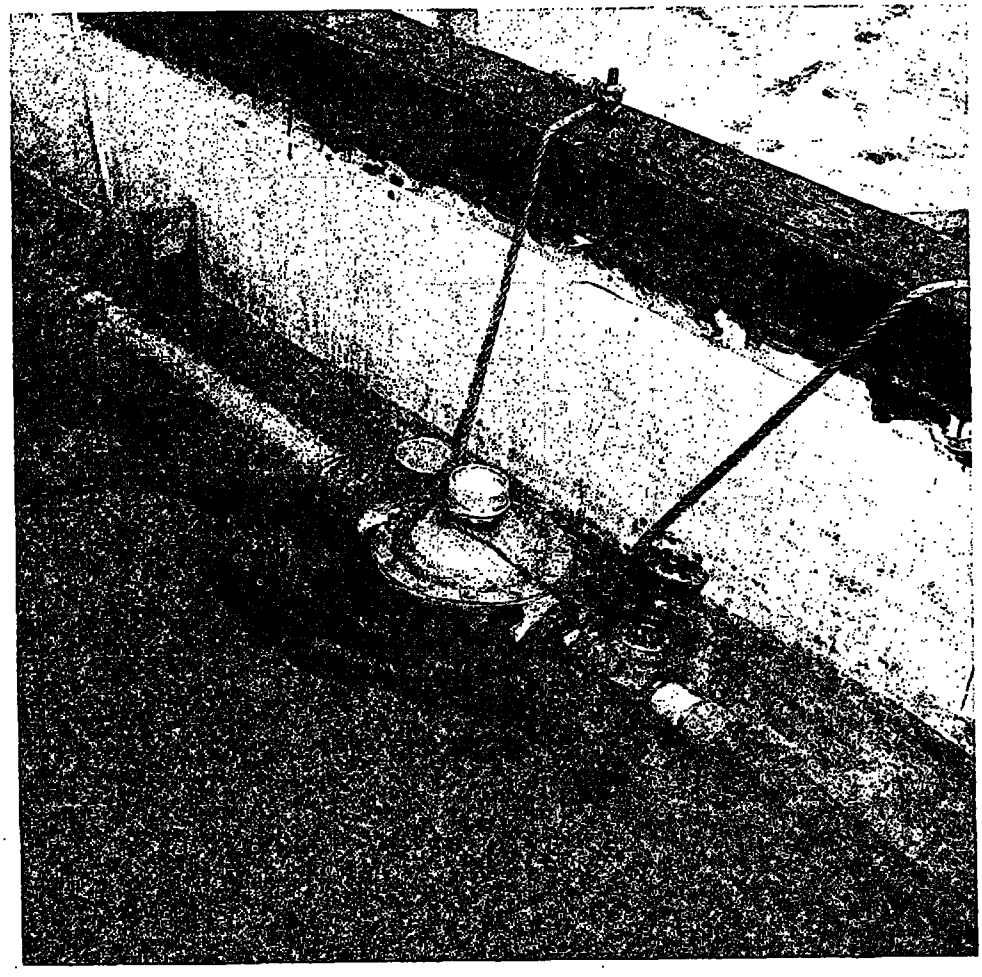

FIGURE 20.—Flow calibration setup in pool.

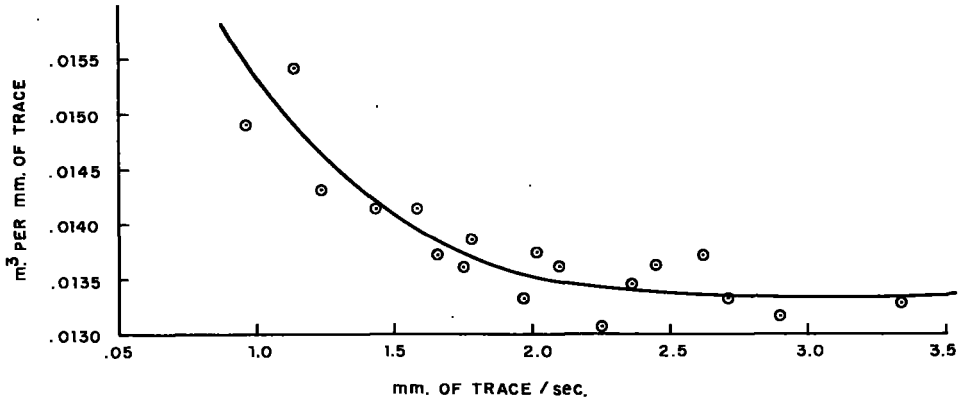

FIGURE 21.—A typical flow calibration.

m.³/min.) was used. (The water meter used in the calibration tests recorded in ft.³). The data obtained during calibration tests of one of the flow-meters are given in table 17 and graphically illustrated in figure 21.

TABLE 17.—*Typical flow calibration using a constant volume of water (40 ft.³ or 1.133 m.³) and various rates of flow*

Time in seconds	Length of trace (mm.)	Millimeters trace per seconds	Cubic meters per millimeter trace
255	85.1	0.334	0.0133
297	86.0	.290	.0132
313	84.9	.271	.0133
315	82.5	.262	.0137
340	83.2	.245	.0136
356	84.1	.236	.0135
386	86.7	.225	.0131
395	83.2	.210	.0136
409	82.4	.202	.0137
430	84.9	.197	.0133
456	81.7	.179	.0139
475	83.1	.175	.0136
496	82.5	.166	.0137
503	80.0	.159	.0142
555	80.0	.144	.0142
638	79.1	.124	.0143
643	73.5	.114	.0154
780	76.0	.097	.0149

Note on flow calibration.—The following considerations were helpful in choosing the range of 3.1 to 10.0 cubic feet per minute:

The normal cruising speed of the survey vessels was 10 knots; hence the vessel would cover 1 nautical mile in 6 minutes. Assuming that the high-speed samples strained while being towed 1 nautical mile, a cylinder of water 1 mile long by 2.54 centimeters in diameter (diameter at mouth opening), it would strain 0.94 cubic meters of water or 0.157 cubic meters per minute. (This is equivalent to 5.5 ft.³/min.).

Inasmuch as the collector has a 1-inch or 2.54-centimeter opening at the inlet and a 3-inch or 7.62-centimeter opening at the outlet, it was anticipated (and preliminary tests had confirmed) that the sampler would strain a somewhat greater quantity of water than the above-calculated cylinder.

However, it was also anticipated that there would be considerable variation in the volume of water strained from haul to haul, due to varying degrees of clogging of the fine-meshed net.

The flow rates at sea, measured by length of film trace per second of hauling, fell within the anticipated range of flow rates used in calibration.

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EXPERIMENTAL EXPLOITATION OF FISH POPULATIONS

BY RALPH P. SILLIMAN AND JAMES S. GUTSELL

with the technical assistance of

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ABSTRACT

Four laboratory populations of guppies were grown in small aquariums under controlled light, temperature, and food supply. Two of the populations were selected by lot as controls; the other two were used as experimental populations for application of various fishing pressures.

Successive application of fishing rates of 25, 10, 50, and 75 percent per triweekly period produced major changes in the experimental populations not duplicated in the controls. The general effect of exploitation was to produce a decrease in the size of the population, the amount of the decrease varying upward with the exploitation rate, until at the 75-percent rate the test populations were extinguished. Abundance and size composition of the stocks followed classical conceptions derived on theoretical grounds.

Equilibrium yield was found to be related to fishing rate in the manner of a humped curve, with maximal yield at fishing rates between 30 and 40 percent, when the populations were at approximately one-third their asymptotic weight. The yield of fish flesh at the maximum represented about one-fifth the weight of the food consumed.

The conventional fishery measures—catch, catch per unit of effort, and average fish length—were calculated and were found to yield a large amount of information about population size and results of changes in rate of exploitation.

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EXPERIMENTAL EXPLOITATION OF FISH POPULATIONS

By RALPH P. SILLIMAN and JAMES S. GUTSELL, *Fishery Research Biologists*

In fishery investigations, interest centers about the catching rate, or rate of exploitation, since this rate is one, and often the only one of the factors affecting the fishery, which is under the control of man. Indeed, a large part of all fishery research has been directed toward the problem of finding the consequences of various fishing rates, and in particular of locating the rate which will provide the maximum sustained yield of fish for use as food. Most of the approaches to this problem have been ecological, consisting in the observation of the fish in their natural environment, and their reaction to changes in fishing and in environment. The well-known contributions of Baranov (1918), Russel (1931), Graham (1935), Thompson and Bell (1934), and Ricker (1948) use observations of this type, coupled with relatively simple mathematical models. Use of such observations is greatly complicated by the fact that population changes due to natural causes often mask those due to fishing.

More recently the maximum-yield problem has been approached through the technique of complex mathematical models, such as those developed by Beverton and Holt (1956). This approach, too, is difficult when the various recruitment, growth, and mortality rates affecting the populations not only vary but have their variations dependent on population characteristics. As noted by Schaefer (1943), "The problem is much more complex when the mortality or recruitment rates are not uniform, and leads, in general, to no simple solution."

The laboratory experiment as an approach to the maximum-yield problem has not to our knowledge been used previously for fish populations. For insects, the laboratory reactions of populations to removals have been studied by Nicholson (1954) and Watt (1955), using sheep blowflies and flour beetles, respectively. Although these experiments produced an abundance of useful information, it seems likely that the great differentiation of larval from adult insect forms caused the reactions to be somewhat different from those of fish populations, where in most exploited species the adult form is assumed at a very early age. An experiment utilizing two laboratory populations of the guppy, *Lebistes reticulatus*, was started by Silliman (1948) but was terminated before it had produced any results relating to exploitation.

The experiments reported herein represent a resumption of the work of Silliman (1948), who listed as reasons for choosing the guppy as an experimental animal, its small size, rapid reproductive and growth rates, and hardiness. Primary objectives of the work were to learn as much as possible about the reaction of fish populations to different rates of exploitation, to discover the relation between equilibrium yield and exploitation rate, and to establish principles of exploitation which would be applicable to commercially utilized fish populations. An additional objective was to find how many of the known facts regarding population changes would be revealed by the conventional measures of total catch, catch per unit of effort, and mean length of fish in the catch.

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Thanks are also due Arnold G. Golding, who made the fish measurements. Finally, we wish to acknowledge the contribution of Dr. Stanislas F. Snieszko, Director of the Microbiological Laboratory, Fish and Wildlife Service, Leetown, W. Va., whose sympathetic cooperation made the experiments possible.

PLAN OF THE EXPERIMENT

The experiment involved four aquarium tanks and their guppy populations, two of which were to be test populations exploited at selected rates and the other two of which were to serve as controls. The size of the aquariums, amount and type of food, etc., were based on previous experience of Silliman (1948). Experimental procedure was decided upon before work was begun, and consisted in starting the four populations at well below their asymptotic levels and allowing growth to asymptotic size before starting exploitation of the test populations (the plan was later changed to save time by starting exploitation at a population level somewhat below the asymptotic level). The two control populations (chosen by lot) were to be maintained under the same conditions as the test populations, with the exception of removals.

The intent was to make the experiment resemble as closely as possible a commercial fishery. For this reason the "fishing" was done in such a manner as to permit the escape of small fish, as occurs with net selection in an actual fishery. Also "refuges" were provided for newly born fish, comparable to the nursery grounds of many exploited populations. Removals were made triweekly, bearing the same relation in a time sense to the approximate 3-week guppy brood interval as does an annual fishing season to an annually spawning fish.

Finally, plans for exploitation included continuation of each selected fishing rate until equilibrium at that rate, or extinction of the populations, had occurred. In practice, the limitations of time required the interpretation of "equilibrium" to mean the lack of substantial changes in the magnitude and size composition of the catch and population, rather than the observation of the populations at each exploitation rate over a period long enough for the attainment of absolute equilibrium.

MAINTENANCE AND EXPLOITATION PROCEDURES AND EQUIPMENT

The four aquariums (designated *A*, *B*, *C*, and *D*) were placed in a concrete trough upon which was built a plywood box enclosing all units to form a lightproof enclosure. The box was painted a flat black inside and out. All heating and cooling apparatus, the bulbs of recording thermometers, and the aquariums were kept in a water bath approximately 9 cm. in depth. This water bath was constantly circulated by an electric stirrer and was covered with a layer of oil to reduce evaporation. The units were placed as shown on the accompanying diagram (fig. 1).

The aquariums were each 44 by 24 by 22.3 cm. and were filled with water to the depth of 17 cm. (volume of about 17 liters). A small electric air pump operated standard aquarium activated-charcoal filters (8 by 8 by 10 cm.) and stone aerators for each tank. In addition, each tank contained a refuge as a means of protection for the young fish; this was in the corner (fig. 1), closed in by a fence consisting of solid glass rods 3 mm. in diameter with 1.5-mm. spacing. Each aquarium was covered with a plastic screen to keep the fish from jumping out.

Once each week (usually on Friday) all populations were removed from the aquariums, and the water was filtered and the equipment cleaned. The water from each aquarium was filtered first through a silk cloth (20 standard mesh) and then through analytical filter paper. All units (filters, etc.) in the aquariums were thoroughly washed in running water. Two liters of water were replaced by an equal amount of new water each week.

At the time of cleaning the aquariums each population was separated in groups of mature males, mature females, immatures, and fry. Fry were distinguished from immatures by grading through a wire basket (2.5-mm. mesh). The males were classed as mature when the black spots on each side were prominent or when the typical male color was observed. The change from immature to adult females was determined by size and form.

After separation by sex and stage of maturity, all fish except the fry were weighed. Each population (or half of it if the amount was too large) was poured into a plastic household strainer 5 cm. in diameter with 1-mm. mesh (a plastic funnel 10 cm. high was used to keep the guppies from jumping out); the excess water from the strainer was removed by blotting the bottom on filter paper until practically no moisture showed on the paper; and the fish were then poured into a previously balanced pan holding about 75 ml. of water and were weighed on a torsion balance.

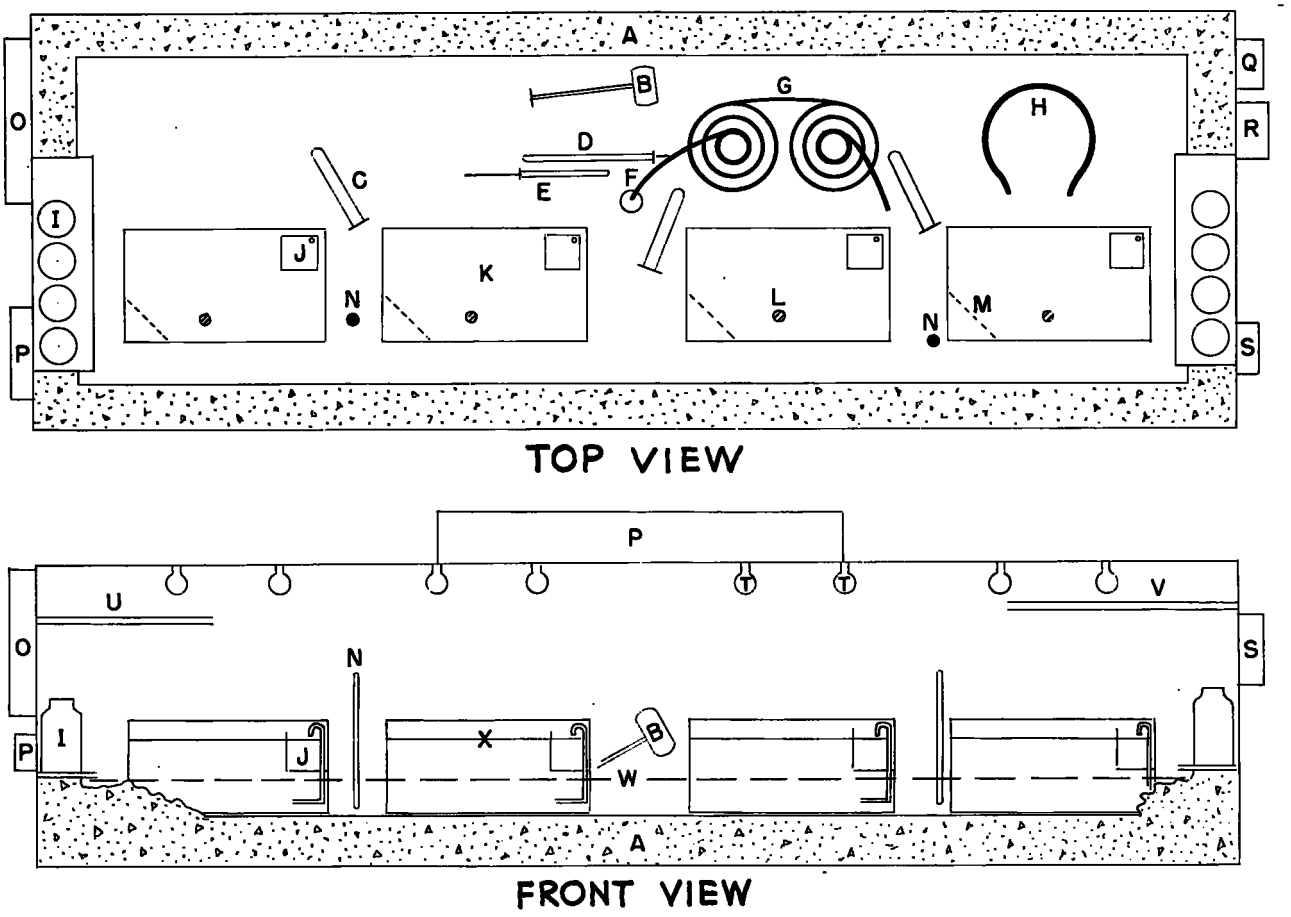

FIGURE 1.—Experimental apparatus: *A*, concrete tank with sides 4 inches thick; *B*, stirrer; *C*, submerged aquarium heater; *D*, bulb of thermoregulator; *E*, bulb of temperature recorder; *F*, outlet for cold-water coil; *G*, cold-water coils (water 54° C., continuous flow); *H*, heating unit; *I*, brine-shrimp (*Artemia*) hatching jars; *J*, filter (plastic containing activated charcoal); *K*, aquariums; *L*, aerators; *M*, refuges to harbor fry (1.5-mm. spacing); *N*, thermometers, laboratory glass; *O*, thermometer (7-day recording); *P*, air vent; *Q* and *R*, temperature control and switch; *S*, automatic time switch; *T*, lights (two 25-watt bulbs over each aquarium); *U*, cold-water inlet; *V*, air line; *W*, water-bath level; *X*, water line in aquariums.

When it was necessary to divide the population into two parts, the second half was drained and weighed with the first.

The cropping or removal of fish in the test populations was carried out at the end of each 3 weeks. Removals were made after the weighing, before the fish were returned to the aquariums. Fish were netted from a container one at a time, with removals corresponding to the exploitation rate being applied. Thus, at the 25-percent rate, each fourth fish was removed. To avoid bias, removals were started at successive croppings with fish No. 1, No. 2, No. 3, and No. 4, after which the cycle was repeated. The fry, having previously been separated from the rest of the populations, were not included in the removals. All fish removed were preserved in 5-percent formalin.

All four populations were fed frozen *Daphnia*, dry food, and brine shrimp (*Artemia*). The dry food was a standard commercial aquarium food, coarse grade. Two lots of this food were used, one for the first 99 weeks, the second for weeks 100 to 174. The second lot differed from the first only in the addition of aureomycin and vitamin B_{12}.

The Brine shrimp were prepared by placing one-fourth level teaspoon (approximately 1.2 ml.) of the eggs in 750 ml. of saline solution. This solution was prepared the previous day by putting one level tablespoon of common rock salt into each 750 ml. of water. The four individual hatching jars of shrimp eggs were kept at about 24° C. for

48 hours, after which time the hatched shrimp were syphoned off through a fine-mesh silk cloth and rinsed into the aquariums.

Near the end of the experiment, duplicate hatches of brine shrimp were produced for weighing to determine the amount being fed. Hatches of nauplii produced in the usual way were filtered from the salt water with several types of filters (bolting cloth; Gooch crucible with asbestos; sintered glass crucible, coarse; stainless-steel crucible, coarse). After being washed with distilled water to remove salt, the nauplii were placed in an oven at 60° C. for 10 to 12 hours, vacuum dried at 60° C. for 4 hours, and weighed. The average of the weighings was 0.125 mg.

Food was placed in each aquarium according to the following weekly schedule:

Day of week	*Amount per feeding of—* *Daphnia (gram)*	*Brine shrimp (milligram)*	*Dry food (gram)*
Sunday	-----	------	0. 1
Monday through Friday	1. 0	0. 125	. 1
Saturday	-----	. 125	. 1
Total amount per week	5. 0	0. 750	0. 7

Such minor variations from the above schedule as occurred were the same for all four aquariums.

A temperature regulator was installed in connection with electrical heaters (fig. 1) for the purpose of keeping the aquarium temperatures at 75° F. with a variation of ±2° F. This equipment did not function properly, however, and large variations in temperature occurred, as set forth later in the report. These variations were the same for all four aquariums, owing to the circulation of the water bath containing them.

Light was maintained practically constant by having the aquariums in a light-tight box, which was opened only during feeding, cleaning, or other need. The two 25-watt incandescent lamps above each aquarium were turned on 12 hours a day (6 a. m. to 6 p. m.) by means of an electrical time switch.

NARRATIVE OF EXPERIMENT

The first 5 weeks of experimentation were occupied with attempts to maintain populations of inferior stock, all of which died. During the sixth week new stock was obtained, and the populations grew satisfactorily. Thus the experiments reported herein started with week No. 6, May 6–12, 1951 (a list of week numbers is given in table 1). Two stocks were secured and were divided among the aquariums in such a way that aquariums *A* and *C* had stocks from one source and *B* and *D* from the other. Populations *A* and *C* were started with 5 males and 3 females each; populations *B* and *D* with 5 fish of each sex.

TABLE 1.—*List of week numbers used in table and graph designations*

Week No.	Beginning Month	Day	Year	Week No.	Beginning Month	Day	Year	Week No.	Beginning Month	Day	Year
1	Apr.	1	1951	59	May	11	1952	117	June	21	1953
2		8		60		18		118		28	
3		15		61		25		119	July	5	
4		22		62	June	1		120		12	
5		29		63		8		121		19	
6	May	6		64		15		122		26	
7		13		65		22		123	Aug.	2	
8		20		66		29		124		9	
9		27		67	July	6		125		16	
10	June	3		68		13		126		23	
11		10		69		20		127		30	
12		17		70		27		128	Sep.	6	
13		24		71	Aug.	3		129		13	
14	July	1		72		10		130		20	
15		8		73		17		131		27	
16		15		74		24		132	Oct.	4	
17		22		75		31		133		11	
18		29		76	Sep.	7		134		18	
19	Aug.	5		77		14		135		25	
20		12		78		21		136	Nov.	1	
21		19		79		28		137		8	
22		26		80	Oct.	5		138		15	
23	Sep.	2		81		12		139		22	
24		9		82		19		140		29	
25		16		83		26		141	Dec.	6	
26		23		84	Nov.	2		142		13	
27		30		85		9		143		20	
28	Oct.	7		86		16		144		27	
29		14		87		23		135	Jan.	3	1954
30		21		88		30		146		10	
31		28		89	Dec.	7		147		17	
32	Nov.	4		90		14		148		24	
33		11		91		21		149		31	
34		18		92		28		150	Feb.	7	
35		25		93	Jan.	4	1953	151		14	
36	Dec.	2		94		11		152		21	
37		9		95		18		153		28	
38		16		96		25		154	Mar.	7	
39		23		97	Feb.	1		155		14	
40		30		98		8		156		21	
41	Jan.	6	1952	99		15		157		28	
42		13		100		22		158	Apr.	4	
43		20		101	Mar.	1		159		11	
44		27		102		8		160		18	
45	Feb.	3		103		15		161		25	
46		10		104		22		162	May	2	
47		17		105		29		163		9	
48		24		106	Apr.	5		164		16	
49	Mar.	2		107		12		165		23	
50		9		108		19		166		30	
51		16		109		26		167	June	6	
52		23		110	May	3		168		13	
53		30		111		10		169		20	
54	Apr.	6		112		17		170		27	
55		13		113		24		171	July	4	
56		20		114		31		172		11	
57		27		115	June	7		173		18	
58	May	4		116		14		174		25	

All four populations were allowed to grow without interference, under the conditions of food, light, temperature, and space as set forth above until week 40, when cropping of populations *A* and *B* was begun at the rate of 25 percent per 3-week period. Maintenance of populations *C* and

D was continued without change; thus *C* became the control for *A*, and *D* for *B*. The cropping of *A* and *B* was changed to 10 percent at week 79, to 50 percent at week 121, and finally to 75 percent at week 151.

Under the final high rate, populations *A* and *B* declined steadily until population *B* became extinct at week 170. The remaining three populations were maintained until week 174, when population *A* contained only one fish. At this time all three populations were killed, and the experiment therefore ended, the terminal date being July 31, 1954. Changes occurring in number and weight of the four populations during the experiment are portrayed in graphs, figures 2 and 3.

It is noteworthy that the two unexploited populations, after their initial growth, fluctuated about an asymptotic level and did not enter into a long-term decline. This is in contradistinction to the results of Shoemaker (1947) whose 13 laboratory populations of guppies began to decline sharply after the 75th week, reaching a final average weight after 137 weeks, about one-fifth the peak level. He concluded that such fluctuations in abundance were characteristic of populations containing a predator (adult) and prey

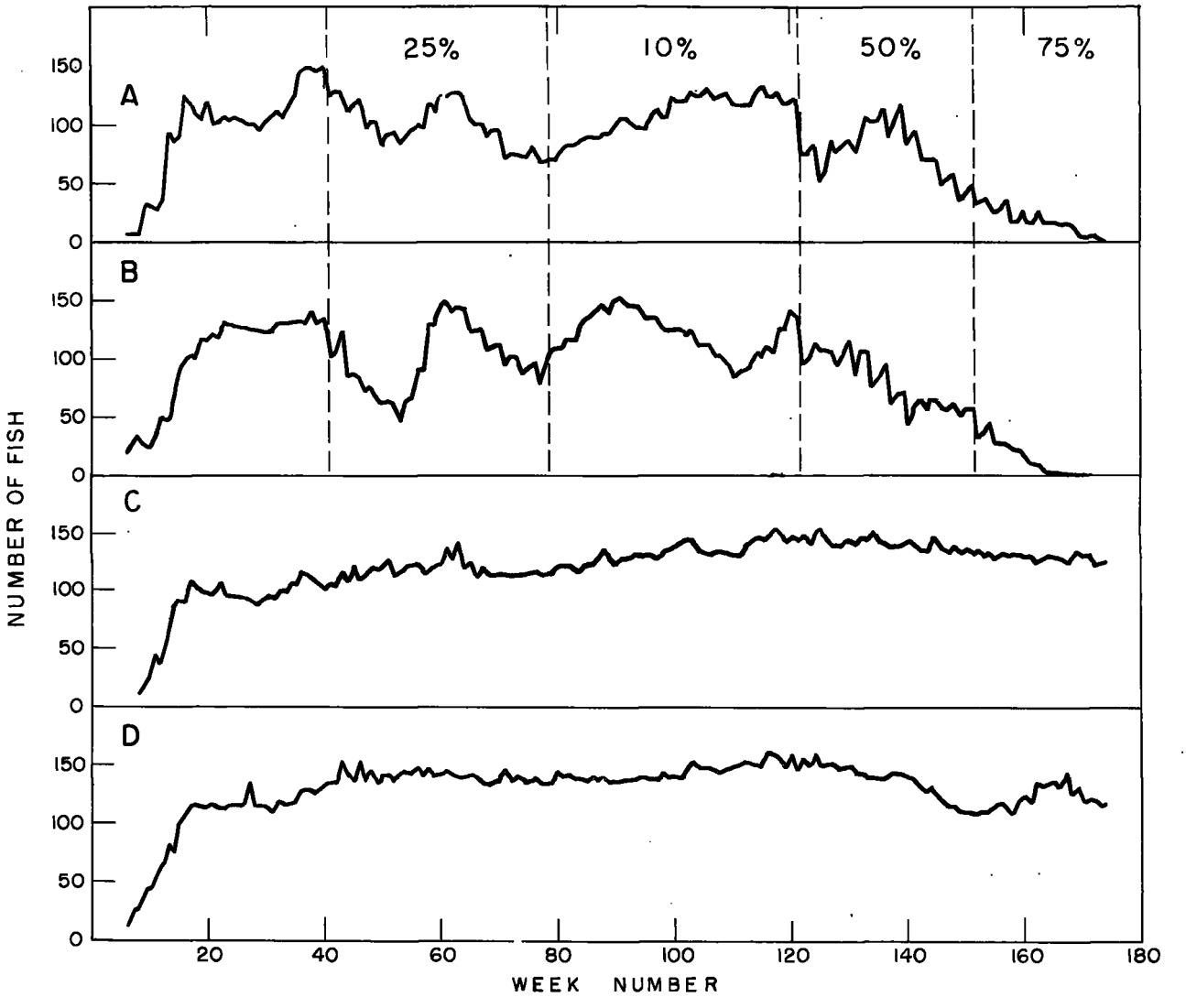

FIGURE 2.—Weekly population numbers during course of experiment. Percentages in upper two panels are triweekly exploitation rates.

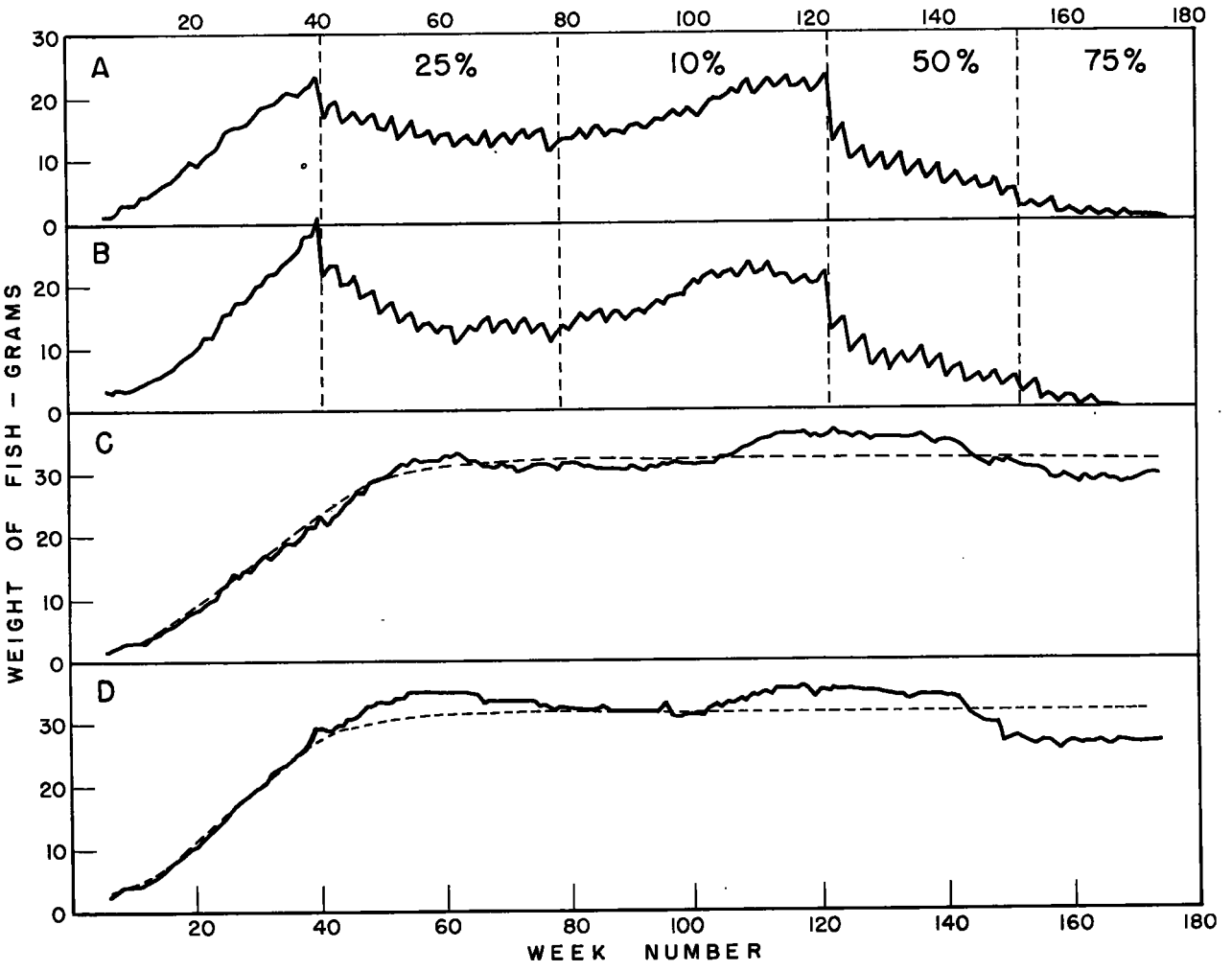

FIGURE 3.—Weekly population weights during course of experiment. Percentages in upper two panels are triweekly exploitation rates. Broken-line curves in lower two panels are logistic fits.

(juvenile) component, but certainly the experiments reported herein do not evidence fluctuations of the magnitude observed by Shoemaker. It seems possible that Shoemaker's fluctuations resulted from the method of feeding, in which an excess of food was offered at all times, and from the lack of special refuges for newborn fish. Such a situation could well lead to more unstable populations than one in which the amount of available food was fixed and refuges were available, as in the present experiments.

The number of generations of observation (44) required to obtain the information reported herein is impressive. This is equivalent to 44 years in an actual fishery even in the unlikely instance that variables other than fishing are controlled as fully as in the laboratory populations. It points up the lengthy observations needed as a reliable basis for management of commercial fisheries.

GROWTH OF POPULATIONS

Growth in weight (fig. 3) proved to be much more regular than growth in numbers (fig. 2). This undoubtedly resulted from the disturbance of numbers by the newly born broods of fry; because of their insignificant weight these broods disturbed total weight of the populations very little. Each of the four populations increased in weight almost without interruption until week 40, when cropping of populations *A* and *B* was begun. Growth of populations *C* and *D* continued until peaks were reached at weeks 62 and 58, respectively. During the remainder of the experiment the total weights fluctuated considerably but gave

every indication of varying about a mean value, which would of course be the asymptotic population level.

Attempts were made to fit a number of types of growth curves, including the modified exponential (Sherman and Morrison, 1950), the Gompertz, and the logistic. Of these the logistic provided the most satisfactory fit to the observations. In making the fit, the asymptotic weight was taken as the mean for weeks 56 through 174: 32.1 grams for population *C* and 32.0 grams for population *D*. This correspondence, incidentally, seems remarkable for two populations with different genetic origins, and confirms the findings of other investigators (e. g., Spear and Glude, 1957) that within species environmental characteristics such as temperature and food supply can be more important than heredity as influences on growth. Constants of the curves were determined by the method of Spurr and Arnold (1948), fitting to the empirical weights for weeks 6 through 55. Deviations of the observational data from the fitted curves (fig. 3) indicated periodic fluctuations of about 65 weeks duration superimposed upon the basic growth pattern. These are similar for the two control populations, although the initial peak deviates more from the logistic curve in population *D* than in population *C*. The deviations are ascribable partly to changes in temperature, as will be discussed later.

CHANGES DURING EXPLOITATION

Changes in Number

The initial reaction to the imposition of a 25-percent triweekly exploitation rate to populations *A* and *B* was the expected decrease in total population numbers (tables 2 and 3, figs. 4 and 5). This decrease is contrasted with the continuing upward trend of the control populations *C* and *D*, clearly demonstrating that the decrease was the result of exploitation. In both *A* and *B* the decrease was composed of an immediate reduction in the accumulated stock of adults followed by an initial reduction in the number of juveniles. The space and food thus made available apparently caused an improved survival rate, resulting in a new influx of juveniles and a peak of population numbers at about week 60. A further adjustment between juveniles and adults then took place, resulting in a relatively stable ratio starting with week 73.

Decreasing the exploitation rate to 10 percent caused the numbers of both adults and juveniles to increase in *A* and *B*. The history of the two populations after week 91 differs, however. In *A* the increase in adults continued throughout the 10-percent exploitation period, while the juveniles declined (presumably as the result of competition from the greater number of adults; cf. Park 1941) after week 100. In *B* the decline of juveniles started earlier (week 91) and was followed by a sharp increase beginning with week 109. Also, there was a decline in adult numbers after week 106. No firm hypothesis for these differences between *A* and *B* is offered, although they may result from genetic differences in reproductive rate and ability to secure food.

Changes under the 50-percent rate resemble those occurring under the 25-percent rate, the same initial decline in adults followed by an influx of juveniles being present. As anticipated, the final level for adults is much lower than under either the 10-percent or the 25-percent rate.

The 75-percent rate proved to be catastrophic for the test populations. Even though the amount of food and space per individual fish was great, this could not increase survival sufficiently to offset the loss of progeny resulting from the rapid reduction in mature adults. Both *A* and *B* proceeded steadily to extinction.

In general, the test populations demonstrated violent changes in population size and composition, coinciding with changes in exploitation rate, and not found in the control populations. It seems certain, therefore, that the changes did result from the experimental removal of fish at the stated rates.

The "natural deaths" (figs. 4 and 5) consist of dead fish found in the aquariums. Since most of the mortality occurs through cannibalism, these dead fish represent only a small fraction of the total mortality. However, it is of some interest that the rate of occurrence of dead fish increased during the latter part of the experiment in the two control populations, as the proportion of old fish became greater; apparently senility played some part in these deaths. In the test populations fish were cropped off so fast that there was no opportunity for an accumulation of older individuals.

The graphs of catch (figs. 4 and 5, center panels) verify some established principles of fishery ex-

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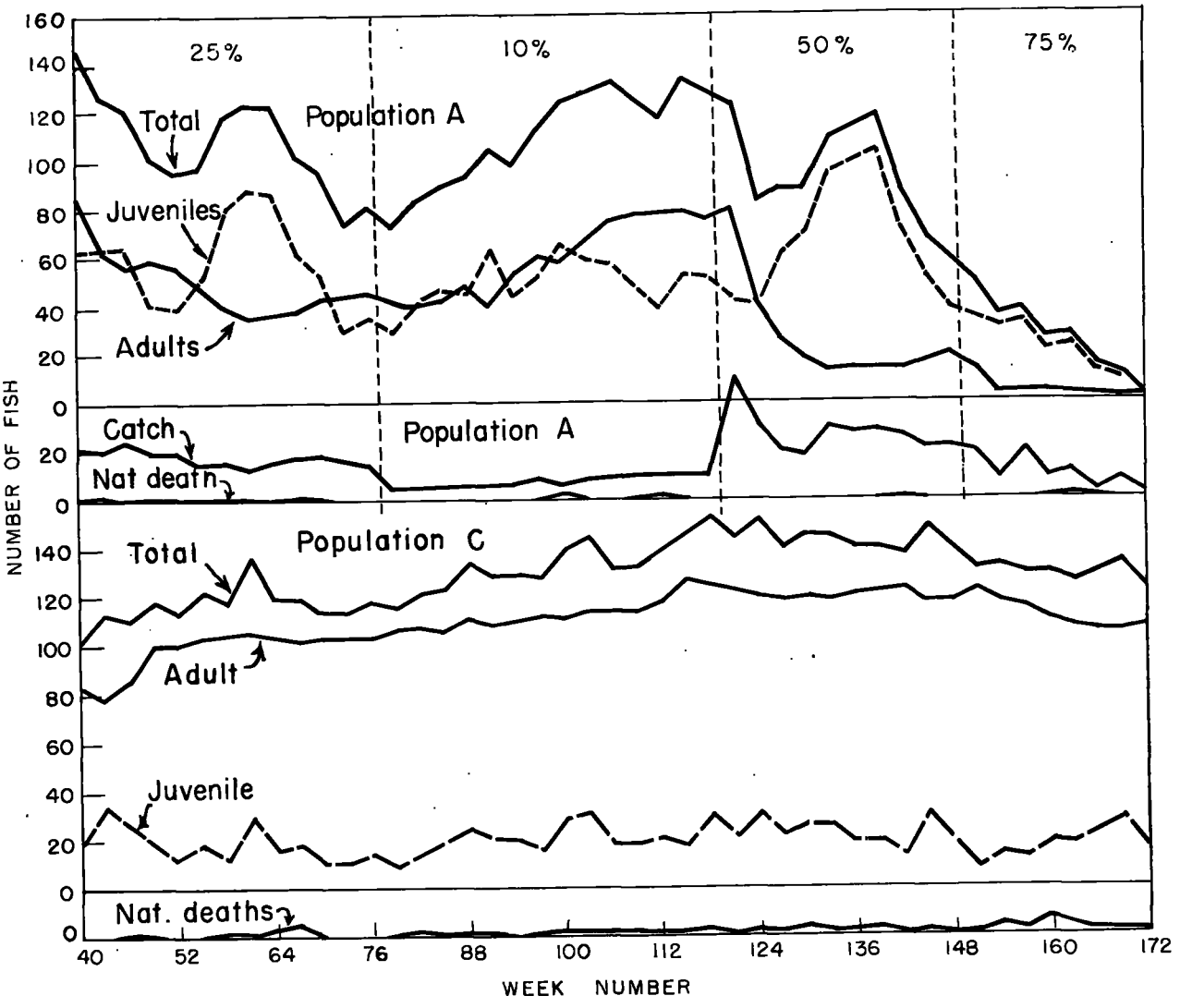

FIGURE 4.—Triweekly population, catch, and mortality numbers during exploitation period in populations *A* (test) and *C* (control).. Percentages in upper two panels are triweekly exploitation rates.

ploitation: (*a*) At such low levels of exploitation as 10 percent, the catch is stable but below what the stock is capable of producing; (*b*) increase of the rate from 10 percent to 50 percent produces a large temporary increase in catch, followed by a decrease and stabilization at a level lower than the initial, but higher than that at the 10-percent rate; (*c*) at the 75-percent rate both catch and stock decline steadily—this is true "overfishing."

Changes in Weight

As mentioned above, population weights are much less disturbed by the entrance and mortality of new broods of young fish, and therefore are less subject to violent fluctuations, than population numbers. For our purposes this is fortunate, for commercial-catch statistics are usually expressed in weights rather than in numbers of fish. The data on weights of the experimental populations (table 4, fig. 6), although less detailed than the data on numbers, are thus of particular interest for the examination of trends, and for comparison with commercial-fishery data. It is noteworthy that the weight curves (fig. 6) for comparable populations (*A* with *B*, *C* with *D*) correspond much more closely than the number curves (figs. 4 and 5). This lends support to the theory expressed above that the differences in the number

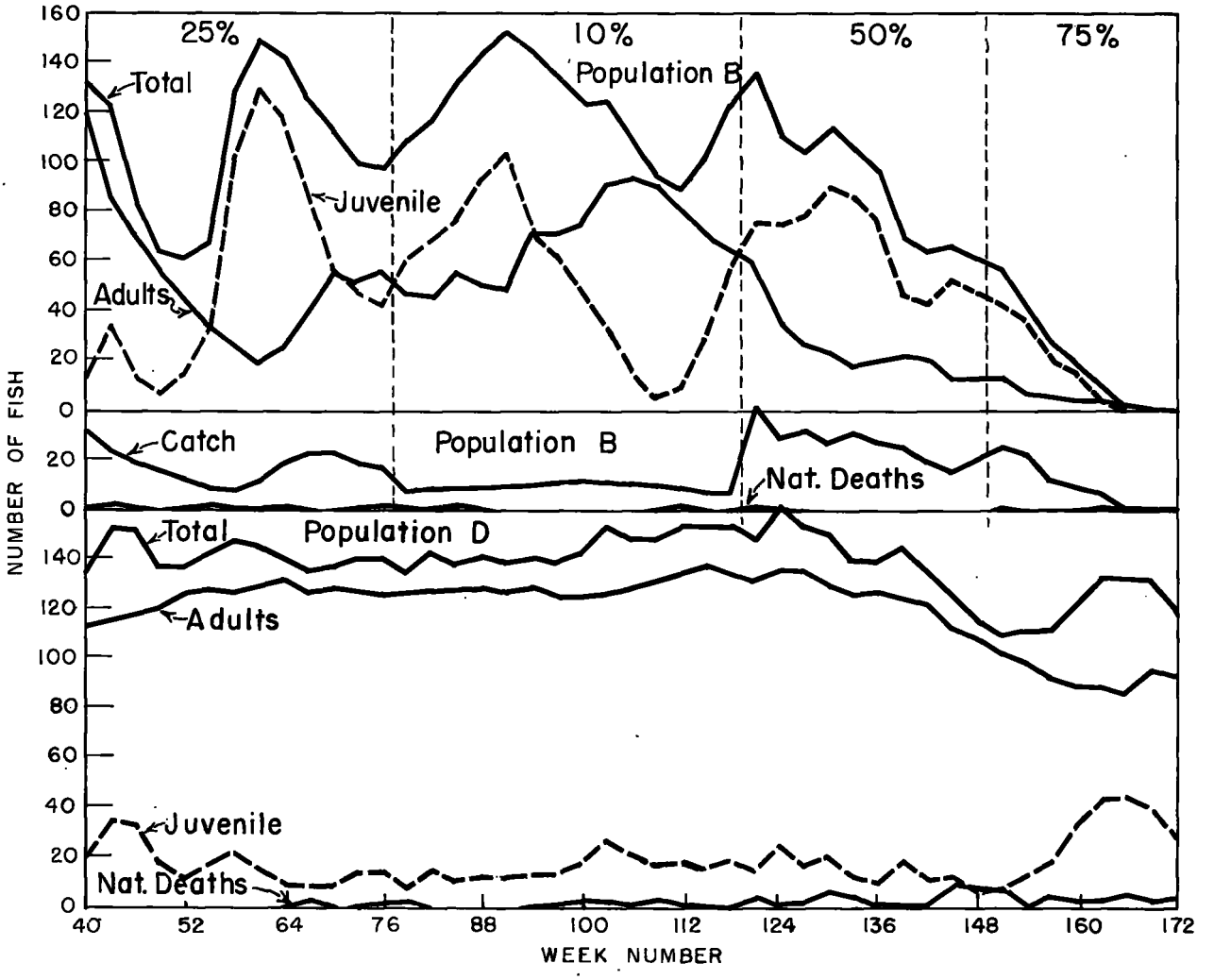

FIGURE 5.—Triweekly population, catch, and mortality numbers during exploitation period in populations *B* (test) and *D* (control). Percentages in upper two panels are triweekly exploitation rates.

curves for populations *A* and *B*, particularly during the 10-percent exploitation rate, may result from inherited differences in fecundity, which change the numbers substantially but the weights insignificantly.

It is instructive to compare the graphs of catch and total weight at the 50-percent rate with the graphs of "total landings" and "catch per skate" (a measure of total weight) in Thompson and Bell (1934, p. 37). Although Thompson and Bell's theoretical graphs were constructed with an assumed constant recruitment which obviously did not prevail in the guppy populations, the correspondence of the graphs is nevertheless remarkable. It shows that the experimental populations behaved as might be anticipated on the basis of a rather simple mathematical formulation. This was true even though the change in fishing rates ("number of skates") of the halibut example was such as to cause the final catch to be lower than the initial, whereas the reverse was true for the guppy experiment.

Changes in Sex Composition

Since the sex of mature fish could be readily determined by inspection, sex-composition data were available for the duration of the experiment. The percentage of males (table 5, fig. 7) indicates a marked tendency for a greater proportion of males in the exploited (*A* and *B*) populations as

TABLE 2.—*Triweekly data on population composition and catch under exploitation in test* (A) *and control* (C) *populations*

[Numbers listed are before removals at the indicated percentage rates. Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment]

Exploitation rate and week No.	Population A									Population C							
	Juvenile			Adult			Grand total	Catch	Natural deaths	Juvenile			Adult			Grand total	Natural deaths
	Fry	Immature	Total	Male	Female	Total				Fry	Immature	Total	Male	Female	Total		
25 percent																	
40	(1)	(1)	64	47	38	85	149	22	1	(1)	(1)	19	37	46	83	102	0
43	(1)	(1)	64	36	27	63	127	21	2	(1)	(1)	35	34	45	79	114	0
46	21	45	66	35	21	56	122	25	0	(1)	(1)	25	39	47	86	111	1
49	18	24	42	38	21	59	101	20	1	9	9	18	43	57	100	118	0
52	16	23	39	33	23	56	95	20	1	4	9	13	44	57	101	114	0
55	39	9	48	28	21	49	97	15	1	11	8	19	47	57	104	123	0
58	53	25	78	21	19	40	118	16	1	7	6	13	47	58	105	118	2
61	69	20	89	18	17	35	124	13	0	24	7	31	48	58	106	137	0
64	61	26	87	20	16	36	123	16	0	13	3	16	45	59	104	120	4
67	29	35	64	21	17	38	102	18	2	14	4	18	46	56	102	120	6
70	20	33	53	24	19	43	96	19	0	5	6	11	48	56	104	115	1
73	8	21	29	27	18	45	74	16	0	4	7	11	47	56	103	114	0
76	23	12	35	22	24	46	81	15	0	7	7	14	48	56	104	118	0
10 percent																	
79	26	5	31	22	20	42	73	5	0	4	5	9	48	59	107	116	0
82	34	9	43	22	18	40	83	5	0	9	5	14	50	58	108	122	2
85	29	18	47	25	17	42	89	6	0	10	8	18	48	58	106	124	1
88	23	22	45	30	18	48	93	7	0	20	4	24	48	63	111	135	1
91	34	30	64	26	15	41	105	7	0	13	7	20	46	63	109	129	1
94	24	20	44	30	24	54	98	7	0	13	7	20	49	61	110	130	0
97	25	27	52	31	30	61	113	9	0	6	10	16	51	61	112	128	2
100	44	22	66	30	28	58	124	7	2	18	11	29	53	58	111	140	2
103	34	26	60	39	29	68	128	9	0	24	7	31	54	60	114	145	1
106	33	24	57	43	32	75	132	9	0	6	12	18	54	60	114	132	2
109	21	27	48	46	32	78	126	11	0	2	16	18	58	57	115	133	2
112	13	26	39	49	30	79	118	11	1	10	11	21	61	57	118	139	1
115	30	24	54	49	30	79	133	11	0	14	4	18	63	64	127	145	1
118	32	21	53	46	30	76	129	10	0	27	3	30	60	64	124	154	4
50 percent																	
121	26	17	43	47	33	80	123	49	0	14	8	22	58	54	122	144	1
124	20	19	39	19	24	43	82	31	0	24	7	31	58	63	121	152	3
127	47	15	62	10	16	26	88	21	0	11	10	21	54	65	119	140	3
130	50	21	71	5	13	18	89	19	0	17	9	26	56	64	120	146	5
133	48	47	95	5	8	13	108	30	0	15	11	26	55	64	119	145	2
136	58	42	100	8	6	14	114	28	0	5	14	19	55	66	121	140	2
139	61	44	105	7	7	14	119	29	0	8	11	19	58	64	122	141	3
142	33	41	74	7	7	14	88	27	1	6	8	14	60	64	124	138	0
145	26	25	51	9	9	18	69	22	0	25	7	32	57	61	118	150	2
148	14	25	39	12	9	21	60	23	0	13	7	20	57	62	119	139	1
75 percent																	
151	24	12	36	9	6	15	51	21	0	7	2	9	57	66	123	132	2
154	23	9	32	1	3	4	36	9	0	9	6	15	55	63	118	133	5
157	12	22	34	1	3	4	38	20	0	8	6	14	56	60	116	130	3
160	13	8	21	3	2	5	26	9	0	14	5	19	55	56	111	130	7
163	12	12	24	2	2	4	28	12	2	14	5	19	53	55	108	127	4
166	11	2	13	1	2	3	16	3	0	17	7	24	52	54	106	130	2
169	0	10	10	0	2	2	12	9	0	20	9	29	53	53	106	135	2
172	0	0	0	2	1	3	3	2	0	7	8	15	55	53	108	123	1

[1] Not listed separately; included in "total."

TABLE 3.—*Triweekly data on population composition and catch under exploitation in test* (B) *and control* (D) *populations*

[Numbers listed are before removals at the indicated percentage rates. Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment]

Exploitation rate and week No.	Population *B*									Population *D*							
	Juvenile			Adult			Grand total	Catch	Natural deaths	Juvenile			Adult			Grand total	Natural deaths
	Fry	Immature	Total	Male	Female	Total				Fry	Immature	Total	Male	Female	Total		
25 percent																	
40	(1)	(1)	13	47	74	121	134	32	0	(1)	(1)	21	53	60	113	134	0
43	(1)	(1)	35	35	53	88	123	24	2	(1)	(1)	36	55	61	116	152	0
46	5	9	14	26	44	70	84	19	0	(1)	(1)	34	57	61	118	152	1
49	2	5	7	22	34	56	63	15	0	5	12	17	59	61	120	137	0
52	13	2	15	19	27	46	61	13	0	5	6	11	61	65	126	137	0
55	32	1	33	15	19	34	67	9	2	11	5	16	62	66	128	144	0
58	95	8	103	12	14	26	129	8	0	15	6	21	62	65	127	148	0
61	103	28	131	8	11	19	150	11	0	14	2	16	62	68	130	146	0
64	73	45	118	17	8	25	143	18	1	7	2	8	63	69	132	141	0
67	33	53	86	29	10	39	125	23	0	6	3	9	57	69	126	135	3
70	19	39	58	34	21	55	113	23	0	4	5	9	59	69	128	137	0
73	22	26	48	32	20	52	100	19	0	9	5	14	59	68	127	141	0
76	32	10	42	30	26	56	98	17	1	9	6	15	56	70	126	141	1
10 percent																	
79	45	17	62	25	22	47	109	7	0	1	7	8	55	72	127	135	1
82	45	26	71	25	21	46	117	8	0	8	7	15	56	72	128	143	0
85	43	34	77	31	25	56	133	9	1	4	6	10	56	72	128	138	0
88	54	40	94	28	23	51	145	9	0	5	7	12	57	72	129	141	0
91	58	46	104	29	20	49	153	10	0	6	6	12	56	71	127	139	1
94	41	32	73	45	27	72	145	10	0	6	7	13	57	71	128	141	0
97	24	39	63	45	27	72	135	11	0	7	7	14	55	70	125	139	2
100	2	46	48	47	29	76	124	12	0	8	9	17	52	73	125	142	3
103	13	21	34	54	37	91	125	11	0	15	12	27	54	72	126	153	2
106	9	8	17	53	41	94	111	10	0	10	11	21	55	73	128	149	1
109	3	2	5	50	41	91	96	10	0	7	10	17	55	77	132	149	4
112	8	1	9	46	35	81	90	9	1	13	6	19	56	79	135	154	0
115	30	0	30	42	30	72	102	7	0	9	7	16	56	81	137	153	1
118	56	3	59	37	28	65	124	7	0	12	7	19	56	79	135	154	0
50 percent																	
121	53	23	76	34	25	59	135	41	1	7	9	16	55	77	132	148	4
124	52	24	76	22	13	35	111	29	0	14	11	25	56	80	136	161	1
127	41	37	78	16	11	27	105	32	0	7	10	17	54	82	136	153	3
130	59	31	90	16	8	24	114	27	0	10	11	21	51	79	130	151	7
133	43	44	87	11	7	18	105	31	0	0	13	13	48	79	127	140	5
136	39	37	76	12	8	20	96	28	0	2	9	11	49	79	128	139	1
139	19	29	48	10	12	22	70	26	0	11	8	19	47	79	126	145	1
142	26	18	44	11	9	20	64	19	0	7	5	12	44	79	123	135	2
145	35	18	53	6	7	13	66	16	0	8	5	13	34	79	113	126	10
148	22	26	48	5	8	13	61	20	0	2	5	7	32	77	109	116	7
75 percent																	
151	24	20	44	9	5	14	58	26	1	5	3	8	30	72	102	110	9
154	13	24	37	4	3	7	44	23	0	10	3	13	29	70	99	112	1
157	11	10	21	3	3	6	27	12	1	17	2	19	25	68	93	112	5
160	7	9	16	3	1	4	20	9	1	30	4	34	24	66	90	124	3
163	0	5	5	2	2	4	9	7	2	31	13	44	25	64	89	133	4
166	0	0	0	1	1	2	2	1	0	29	16	45	26	61	87	132	6
169	0	0	0	1	0	1	1	1	0	22	19	41	27	63	90	131	3
172	0	0	0	0	0	0	0	0	0	10	17	27	30	64	94	121	4

[1] Not listed separately; included in "total."

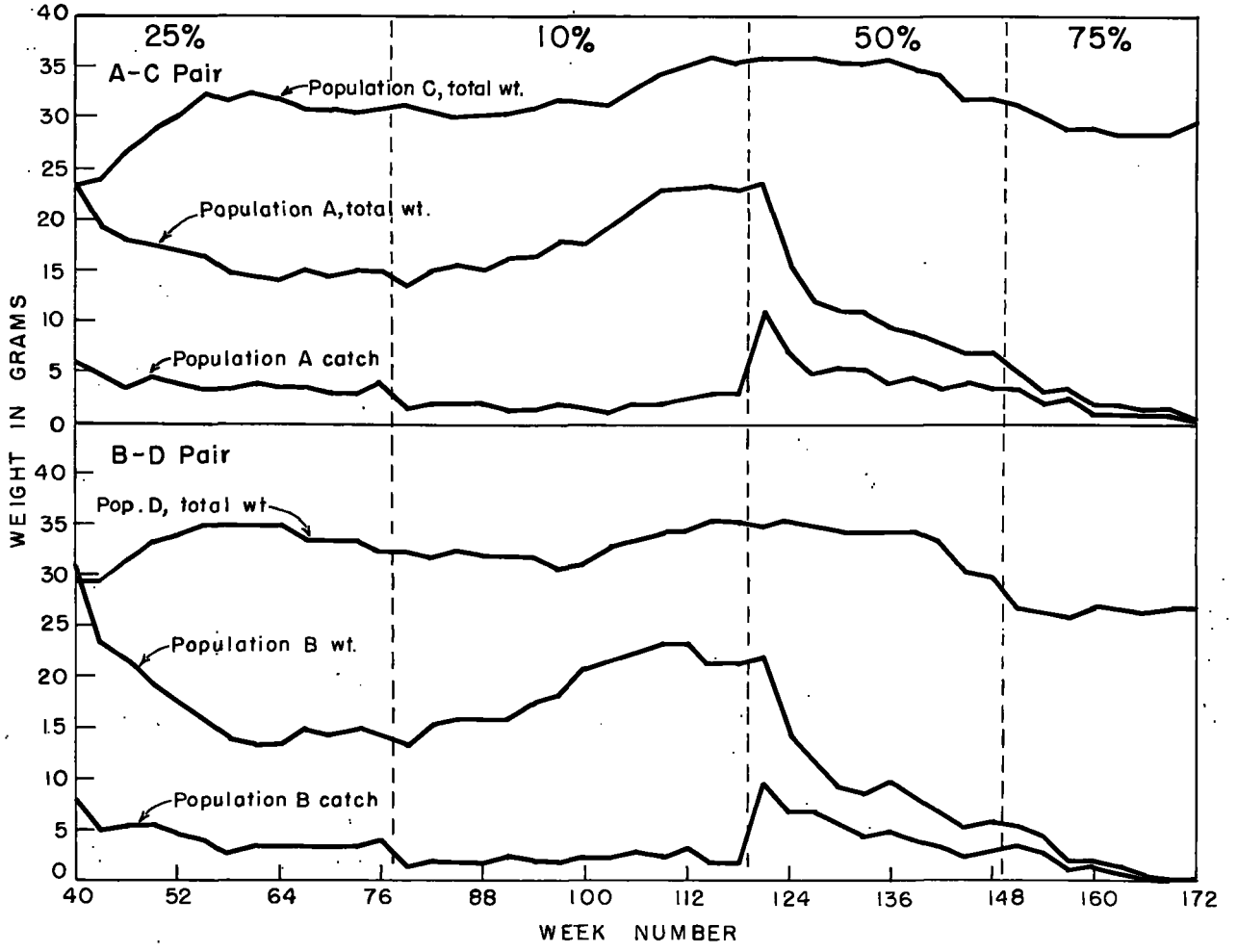

FIGURE 6.—Triweekly population and catch weights during exploitation period. Test populations (*A* and *B*) paneled with their respective controls (*C* and *D*). Percentages shown are triweekly exploitation rates.

compared with the controls (*C* and *D*). Because of the random method of selecting the fish for removals (described under Maintenance and Exploitation Procedures and Equipment) this could not have resulted from selective "fishing." Since it is possible to recognize males as mature at a somewhat earlier age than females, the apparent preponderance of males in the exploited populations may result merely from the younger average age in these populations as compared with the unexploited controls (figs. 4 and 5).

The control population *C* exhibited a strong tendency to stabilize at a 50–50 sex ratio, with only minor departures from this after week 97. In control population *D*, however, there was a decline in percentage of males with apparent stabilization at about 30 percent. This seems not to have affected the ability of the stock to maintain itself, since comparable (*C* and *D*) population sizes remained close to identity with respect both to numbers (fig. 2) and to weight (fig. 3).

The above findings are at variance with those of Breder and Coates (1932), who observed a stabilized sex composition of one-third males in three different laboratory populations of guppies. They attached considerable significance to this proportion, believing it to be characteristic of artificial populations of the species. In a later work, Breder and Coates (1936) found that the average proportion of males in the three populations after 4 years was still one-third, although this varied considerably from winter to

TABLE 4.—*Triweekly population and catch weights*

[In grams. Percentages listed are triweekly exploitation rates, and weights listed are before removals at these rates]

Rate and week No.	Population A		Population B		Population C	Population D
	Total weight	Catch weight	Total weight	Catch weight	Total weight	Total weight
25 percent						
40	23.3	6.0	30.8	8.0	23.3	29.3
43	19.7	4.9	23.5	5.0	24.0	29.6
46	18.0	3.7	22.0	5.6	26.8	31.5
49	17.6	4.4	19.6	5.6	29.1	33.4
52	16.9	4.1	17.5	4.5	30.5	34.0
55	16.3	3.5	16.0	4.0	32.3	35.2
58	15.1	3.5	14.2	3.1	31.8	35.2
61	14.7	3.8	13.6	3.5	32.3	35.0
64	14.0	3.3	13.3	3.5	32.2	35.0
67	14.8	3.3	14.8	3.7	30.9	33.4
70	14.7	2.8	14.7	3.6	31.1	33.5
73	15.0	3.0	14.8	3.4	30.6	33.3
76	14.9	3.9	14.1	3.8	31.0	32.6
10 percent						
79	13.3	1.4	13.3	1.5	31.5	32.5
82	14.9	2.1	15.6	1.9	31.1	32.2
85	15.5	1.9	16.2	1.9	30.6	32.3
88	15.0	2.0	16.1	2.1	30.5	32.2
91	16.1	1.7	16.2	2.3	30.7	31.9
94	16.6	1.5	17.5	2.2	30.9	32.1
97	18.0	1.9	18.6	1.9	31.8	31.2
100	17.5	1.7	20.9	2.3	31.6	31.5
103	19.4	1.2	22.0	2.4	31.6	32.8
106	21.2	2.0	22.6	2.8	32.8	33.4
109	23.0	2.0	23.6	2.7	34.5	34.6
112	23.2	2.6	23.7	3.3	35.4	34.7
115	23.5	2.9	21.4	1.9	35.8	35.7
118	22.9	3.0	21.5	2.2	35.3	35.6
50 percent						
121	23.5	11.2	21.9	10.2	35.9	35.0
124	15.3	7.0	14.9	7.0	35.8	35.7
127	11.9	5.2	12.1	6.8	36.0	35.2
130	11.2	5.7	9.4	5.3	35.5	34.4
133	11.1	5.6	9.2	4.3	35.4	34.3
136	9.6	4.2	10.0	4.8	35.9	34.5
139	9.0	4.3	8.5	4.2	34.9	34.3
142	8.1	3.5	6.9	3.5	34.4	33.5
145	7.2	3.9	5.4	2.6	31.9	30.6
148	7.0	3.5	6.2	2.8	31.8	29.9
75 percent						
151	5.2	3.4	5.3	3.7	31.5	26.9
154	3.0	2.1	4.5	2.9	30.3	26.5
157	3.3	2.4	2.0	1.2	29.2	26.2
160	1.9	1.2	2.2	1.7	29.0	26.8
163	1.8	1.2	1.3	1.1	28.5	26.7
166	1.3	.9	.5	.3	28.4	26.7
169	1.4	1.0	.2	.2	28.6	27.0
172	.6	.2	.0	.0	29.4	27.0

summer in accordance with the length of daylight. This seasonal variation was eliminated in the present experiments by the use of controlled artificial light, but the reason for the difference in average ratio between these populations and those of Breder and Coates, and for the difference between populations *C* and *D* of the present experiment, is obscure. Genetic differences seem to offer the most probable explanation.

Shoemaker (1947) found an apparent 50–50 sex ratio at birth in his laboratory populations of guppies, although the survival rate of males was considerably less than that of females, leading in a year to a population with about one-fifth males. Here again the source of this contrast with the present experiments is unknown.

TABLE 5.—*Percentage of male fish in mature portion of experimental populations during exploitation period*

Week No.	Percentage male for population				Week No.	Percentage male for population			
	A	*B*	*C*	*D*		*A*	*B*	*C*	*D*
40	55	39	44	47	109	59	55	50	42
43	57	40	43	47	112	62	57	52	41
46	62	37	45	48	115	62	58	50	41
49	64	39	43	49	118	60	57	48	41
52	59	41	44	48	121	59	58	48	42
55	57	44	45	48	124	44	63	48	41
58	52	46	45	49	127	38	59	45	40
61	51	42	45	48	130	28	67	47	39
64	50	68	43	48	133	38	61	46	38
67	55	74	45	45	136	57	60	45	48
70	56	62	46	46	139	50	45	48	37
73	60	62	46	46	142	50	55	48	36
76	48	54	46	44	145	50	46	48	30
79	52	53	45	43	148	57	38	48	29
82	55	54	46	44	151	60	64	46	29
85	60	55	45	44	154	25	57	47	29
88	62	55	43	44	157	25	50	48	27
91	63	59	42	44	160	60	75	50	27
94	56	62	45	44	163	50	50	49	28
97	51	62	46	44	166	33	50	49	30
100	52	62	48	42	169	0	100	50	30
103	57	59	47	43	172	67	0	51	32
106	57	56	47	43					

Change Due to Temperature

Malfunctioning of the thermostatic devices used in the experiment resulted in considerable variations in temperature of the water bath in which the aquariums were kept (table 6, fig. 8). Occasional violent fluctuations within the range 65°–91° F. were of short duration, but even the triweekly means were not constant.

TABLE 6.—*Triweekly mean and extreme water-bath temperatures (for week listed and previous two weeks)*

Week No.	Temperature ° F.			Week No.	Temperature ° F.		
	Minimum	Maximum	Mean		Minimum	Maximum	Mean
40	70.5	79.0	75.3	109	68.5	78.5	72.4
43	68.0	78.0	74.7	112	68.5	78.0	71.0
46	71.5	78.5	75.1	115	68.0	82.0	72.8
49	71.0	80.0	76.0	118	70.0	80.5	72.9
52	69.0	81.0	76.6	121	72.0	79.5	72.6
55	67.5	91.0	74.0	124	71.5	80.5	72.4
58	68.5	80.5	74.1	127	71.5	80.5	72.9
61	70.0	79.0	74.3	130	70.0	85.0	75.3
64	67.5	83.5	76.1	133	71.0	85.0	76.3
67	72.0	79.5	75.0	136	70.5	85.0	73.9
70	74.5	77.5	74.7	139	70.5	83.5	73.8
73	74.5	77.5	74.6	142	67.5	83.5	74.8
76	74.5	79.5	75.9	145	65.5	87.5	74.5
79	73.0	77.5	75.2	148	66.5	84.5	76.2
82	72.0	79.5	75.5	151	69.0	87.5	75.0
85	69.0	79.5	76.6	154	69.0	85.5	74.9
88	69.5	80.0	76.0	157	68.5	87.0	76.5
91	66.5	79.0	75.5	160	68.5	87.5	76.8
94	67.5	78.0	74.9	163	70.0	87.0	78.7
97	67.0	77.5	73.8	166	69.5	85.0	75.4
100	68.5	78.5	75.3	169	72.5	86.5	75.5
103	68.5	78.5	75.2	172	72.5	78.0	74.5
106	68.5	79.5	73.2				

To determine whether this temperature fluctuation had an effect on population size, the rectilinear correlation coefficients were calculated for the regression of population *C* and *D* mean weights on triweekly mean temperatures starting

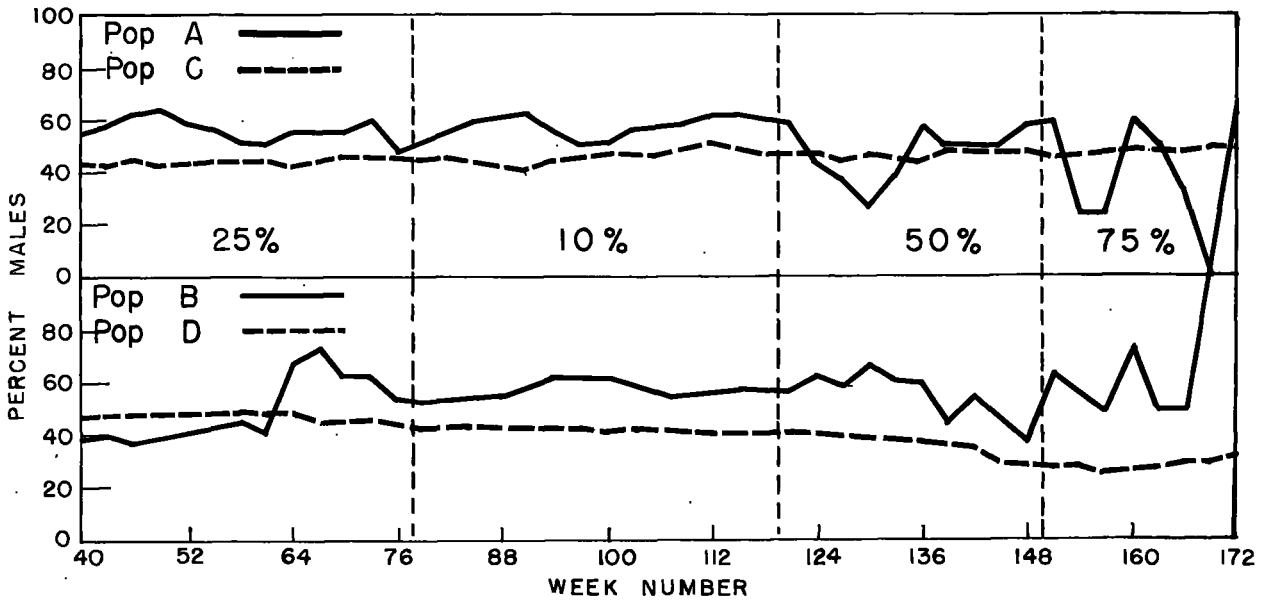

FIGURE 7.—Percentage of male fish in mature portion of experimental populations during the exploitation period. Percentages shown are triweekly exploitation rates.

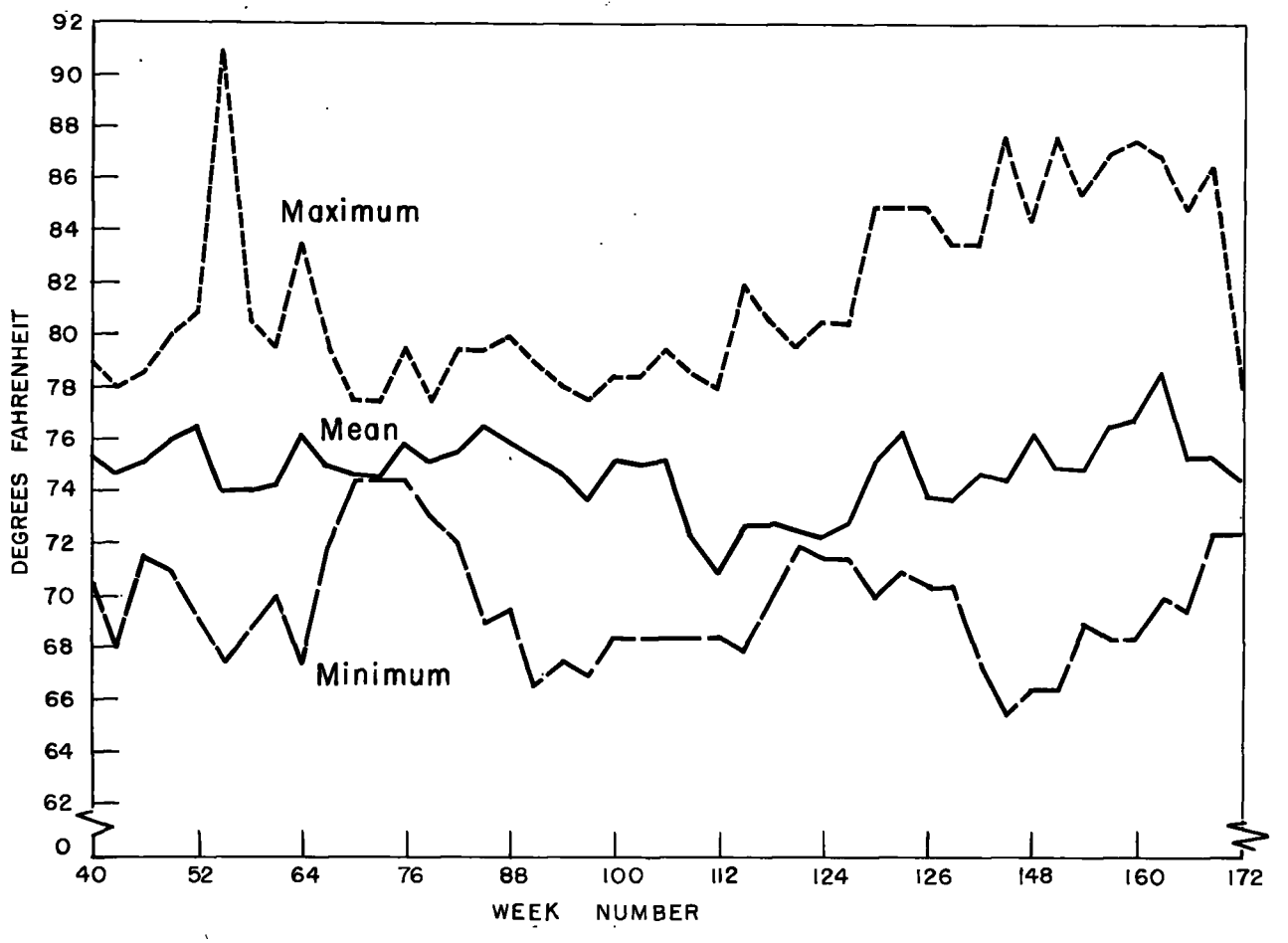

FIGURE 8.—Triweekly mean and extreme water-bath temperatures (for week listed and previous two weeks).

with week 40. The values, −0.5629 for C and −0.5316 for D, with values of P both less than .01, indicated a significant negative correlation of population size with temperature. Apparently continued temperatures much above 72° F. have an inhibiting effect on survival and growth (Gibson and Hirst, 1955, observed maximal growth of guppies in fresh water at 23° C. or 73° F.), reproductive rate, or some combination of these variables. A similar effect was observed by Shoemaker (1947), whose laboratory populations of guppies experienced a temperature range almost identical to that reported above. He suggested that reduced oxygen at the higher temperatures might be partially responsible.

The correlation between temperature and population size is rather mild, the squared coefficients indicating only about 30 percent of the fluctuations associated with temperature. The major portion of the periodic changes in size of the control populations must be ascribed to some factor as yet unknown. Similarity of the temperature correlations for the two populations does suggest that the electrically stirred water bath was efficient in maintaining uniform temperatures among all four aquariums.

EQUILIBRIUM YIELDS

Definition of Equilibrium

A rigorous definition of "equilibrium" in an exploited population would require that all vital rates, recruitment, growth, fishing mortality, natural mortality, be constant or fluctuate in a perfectly regular manner. In such a population the season-to-season age, size, and sex composition would be absolutely unvarying, and the yield would of course be constant. It is extremely unlikely that such a condition would ever obtain in any natural population, even if the fishing rates were held constant, for fluctuations would be imposed by changes in such aspects of the environment as food supply and temperature. Even under laboratory conditions it is hardly possible to control every known source of variation, and there are probably some that are unknown. Thus only by observations over a very long period of time could average values for the "equilibrium" constants be obtained.

In the present experiment it has been necessary to forego such long-term observations. Even as performed the work required over 3 years to observe the effects of 4 exploitation rates, with continuing and increasing risk of interruption by accidental experimental failure. It was felt that a close approximation to equilibrium conditions would obtain when a given exploitation rate had been maintained long enough so that there were no longer significant unidirectional changes in population composition. Observation of such a condition for a period of 6 weeks was the criterion for changing to another exploitation rate. Histograms (figs. 9 and 10) of the populations divided

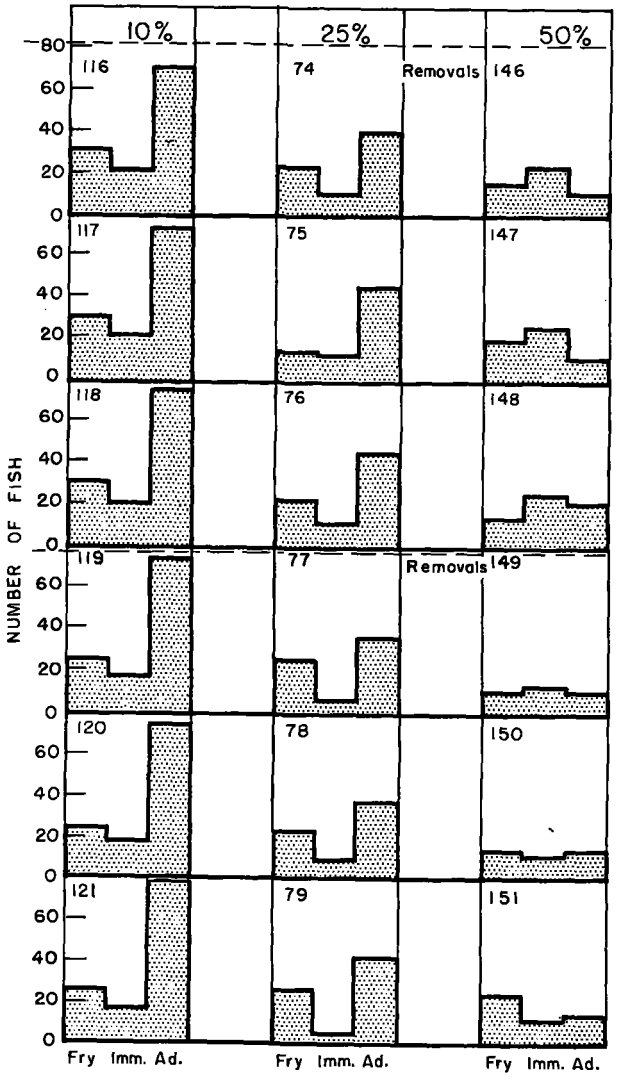

FIGURE 9.—Histograms of composition of population A during "equilibrium" period at each triweekly percentage exploitation rate. Week numbers given in each panel. "Removals" refers to cropping at point indicated by broken line.

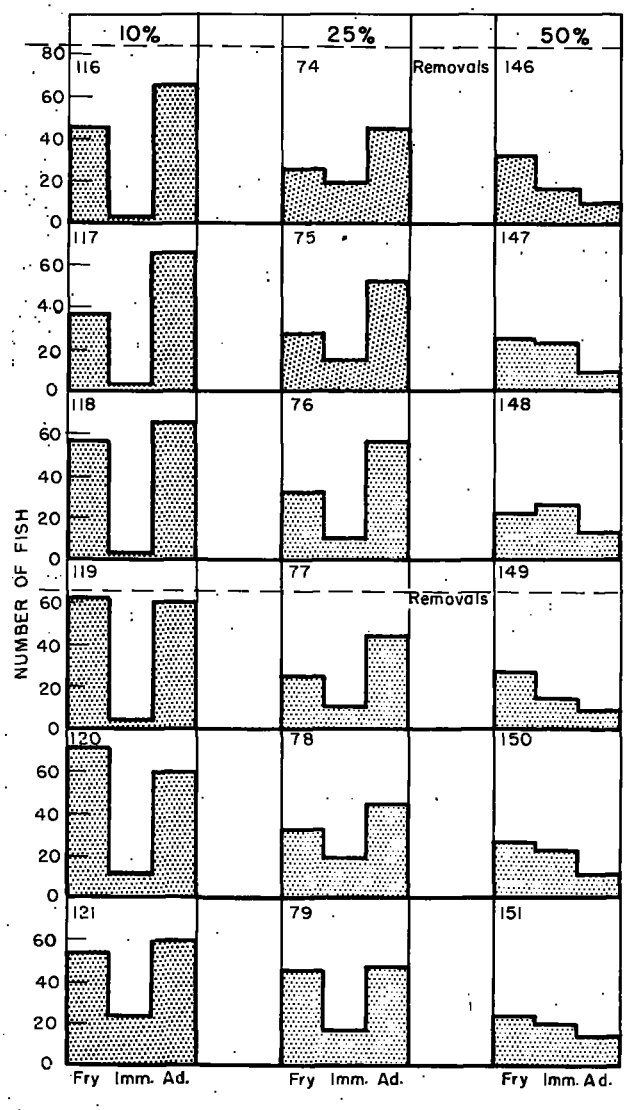

FIGURE 10.—Histograms of composition of population *B* during "equilibrium" period at each triweekly percentage exploitation rate. Week numbers given in each panel. "Removals" refers to cropping at point indicated by broken line.

into the categories "fry," "immature," and "adult" (as defined under Maintenance and Exploitation Procedures and Equipment) for the 6-weeks period preceding each change in exploitation rate indicate reasonable conformance to the criterion, but it is possible to question the establishment of equilibrium at the 50-percent rate. If, in fact, equilibrium did not exist at this level, the continued application of that rate would result in extinction just as occurred under the 75-percent rate. The presumed effects of this on the yield curves will be discussed below.

Whatever question may be raised as to the closeness of the approximation to equilibrium yields obtained by application of the "6-week" criterion, it remains true that the test of this or any analytical procedure lies in the consistency of the results. The reader may judge this for himself in the data presented below.

Relation Between Rate of Exploitation and Yield

Comparison of yields of the two test populations (fig. 11) shows that they are almost identical at each exploitation rate. Application of the *t* test indicates no significant difference (*P* approximately 0.2) and averaging of the yield data was therefore justified. The resulting mean yields (fig. 11) gave a more consistent representation of the relation between exploitation rate and yield than did the data for the individual populations.

The empirical relation between rate of exploitation and yield (table 7, fig. 12) is reminiscent of a parabola, but considerable experimentation did not reveal it to conform to any simple mathematical formula.[1] A difficulty arose in locating the second intersection with the *x* axis. Since the populations were extinguished at the 75-percent rate, it was known that yield there was zero. It is possible, however, that the point of zero yield might be reached anywhere between the 50- and the 75-percent rate. Thus the intersection has been bracketed but not located (and is so indicated in fig. 12).

By transforming percentage exploitation rates to instantaneous (Ricker 1948) rates (table 7, fig. 13) the yield curve derived herein may be com-

TABLE 7.—*Equilibrium yield, mean of populations A and B, as related to triweekly and instantaneous exploitation rates, and to population mass*

Exploitation rates		Population mass	Yield per 3 weeks
Triweekly (percent)	Instantaneous		
		Grams	*Grams*
10	0.11	21.5	2.50
25	.29	13.1	3.52
50	.69	5.0	3.20
75	1.39	0	0

[1] Dr. M. B. Schaefer has shown that if equilibrium yield be divided by instantaneous rate of exploitation, and this ratio plotted against instantaneous rate of exploitation, a relatively simple curve will result. Such a curve could be fitted by a polynomial, but for the purposes of this report the calculation does not seem justified. Extrapolation of a curve fitted by eye indicates population extinction at a weekly exploitation rate of about 59 percent.

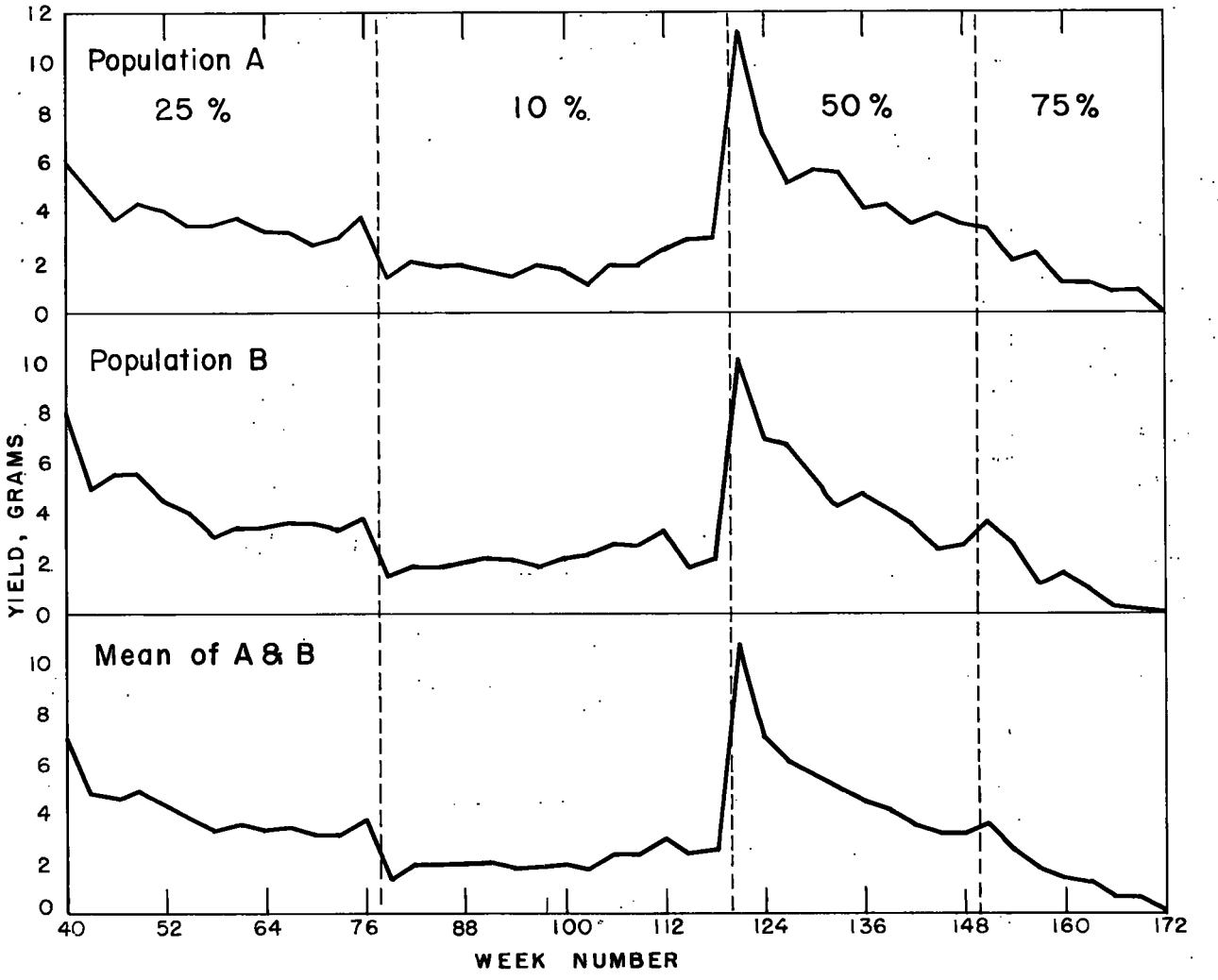

FIGURE 11.—Yield in weight of test populations under exploitation. Percentages in upper panel are triweekly exploitation rates.

pared with those of Beverton and Holt (1956, fig. IX: 22) which relate theoretical annual yield of North Sea haddock populations to the instantaneous fishing rate (F). In these curves, account has been taken of the dependence of both recruitment and growth on population density, making the mathematical models involved closely similar to natural populations. This similarity is validated by the close resemblance of Beverton and Holt's curve "s" to the guppy-yield curve, a resemblance the more remarkable when one considers the tremendous differences between the aquarium populations of guppies and the North Sea populations of haddock. We have here an example of the interplay of hypothesis and experiment characteristic of scientific research.

If yield is compared with mass of population (table 7, fig. 14) the results are comparable to the derivative form of the Verhulst-Pearl logistic, as discussed by Schaefer (1954). In this curve the second intersection of the x axis was taken to be the mean asymptotic level of the two control populations (C and D) under the assumption that this level would prevail in the test populations under zero exploitation. Comparison of the mass (weight) curves of the test and control populations (A with C, B with D, fig. 3) during the pre-exploitation period (weeks 6–10) lends support to this assumption.

It is obvious that the guppy curve does not conform to the logistic, since it departs from symmetry more than could be attributed to random

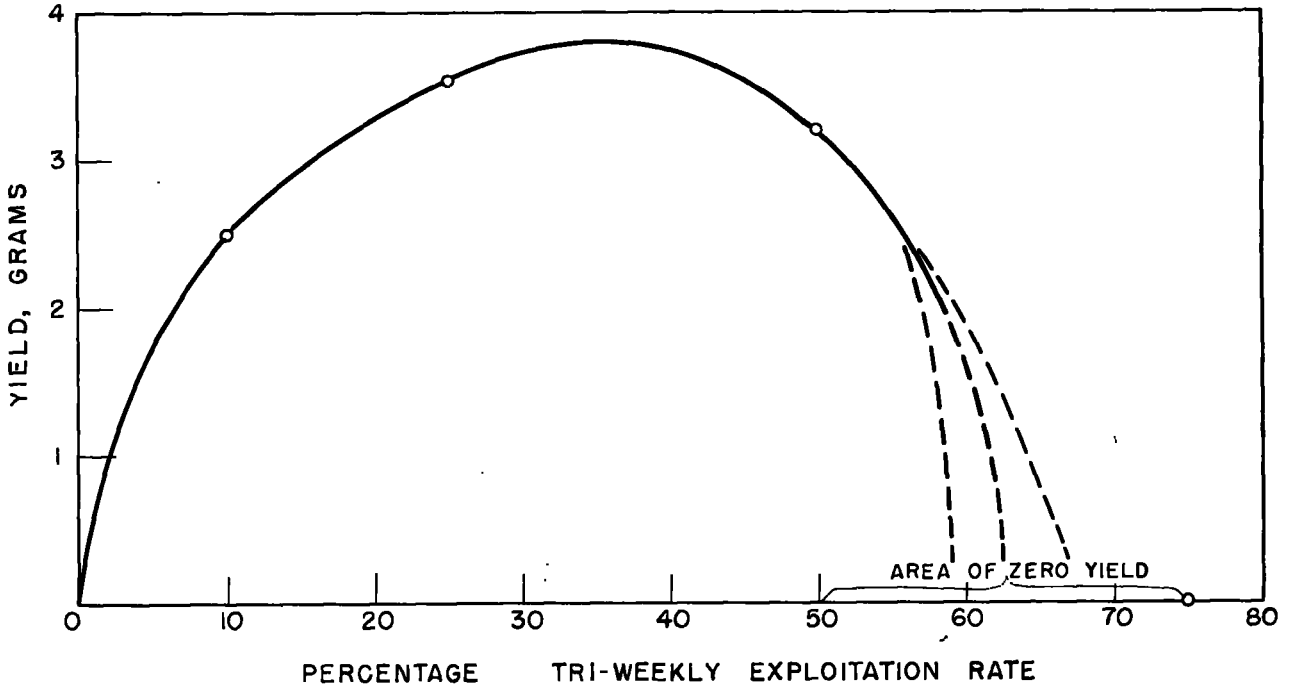

FIGURE 12.—Relation between triweekly rate of exploitation and the equilibrium yield in weight, mean of populations *A* and *B*.

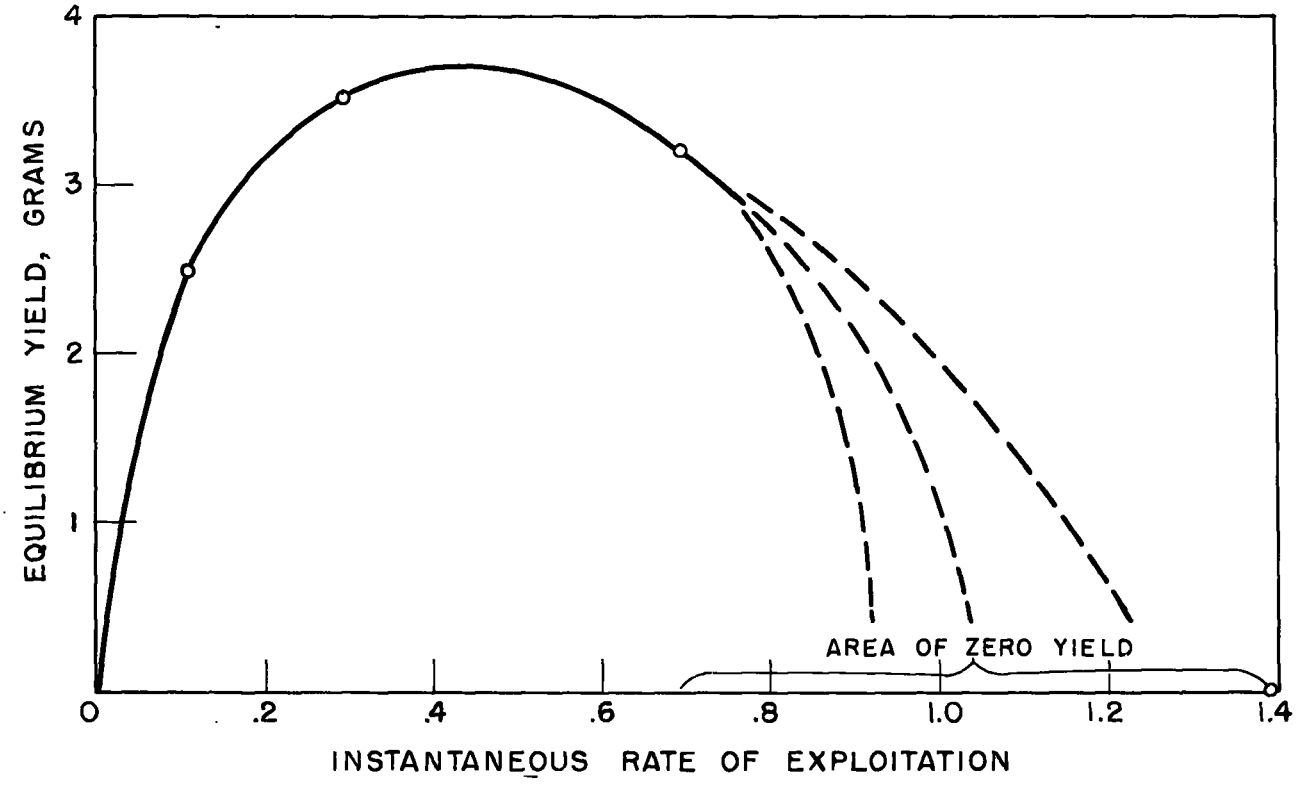

FIGURE 13.—Relation between instantaneous rate of exploitation and equilibrium yield, mean of populations *A* and *B*

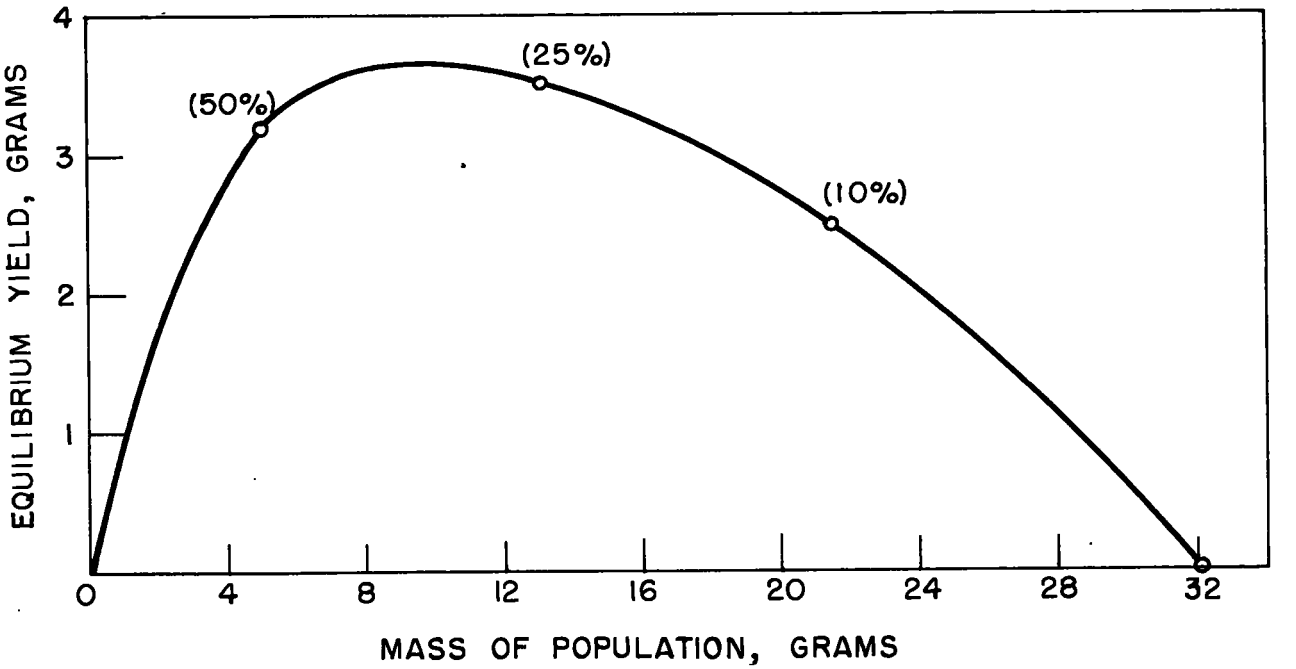

FIGURE 14.—Relation between mass of population and equilibrium yield, mean of populations *A* and *B*. Percentages in parentheses are triweekly exploitation rates.

variation or experimental error. It does, however, have enough features in common with the logistic to lend support to Schaefer's basic theory regarding the effect of changes in fishing intensity on fished stocks. He himself points out "that in at least some populations of fishes, the curve is actually somewhat asymmetrical."

It is pertinent to note here that the equilibrium-yield-on-mass curve of the population under exploitation, even if symmetrical, cannot be expected to conform to the derivative of the initial population-growth curve. The reason for this lies in the fact that the growing population has a different composition with respect to size, age, and maturity than the mature population under equilibrium conditions.

In general, all three of the treatments of the equilibrium-yield data discussed above have verified the contention of Sette (1943b) that "A population has its maximum increase when it is neither at its maximum, nor minimum, size, but when middling in size; and that is the level at which the most individuals can be regularly removed and still be fully replenished by the population's inherent tendency to grow." The empirical curves indicate that the maximum equilibrium yield for the guppy populations would occur at triweekly exploitation rates between 30 and 40 percent, with population mass at between 8 and 12 grams. If, as indicated above to be possible, 50 percent rather than 75 percent represents the real extinction rate, the maximum-yield findings would be the same although the curves would be more asymmetrical than shown here.

It is of interest to calculate the rate of food conversion at the maximum equilibrium yield. The maximum of the empirical yield curves depends somewhat on the subjective fitting by inspection, but the maximum observed yield was 3.5 grams per 3-week period. The amount of food consumed per such period (as detailed under Maintenance and Exploitation Procedures and Equipment) was 17.1 grams. The indicated efficiency of food conversion is thus 20 percent. Modern hatchery practice yields "conversion ratios" (pounds of food per pound of fish produced) of 2.35 to 4.95 for salmon (Burrows et al., 1952), equivalent to efficiencies of 42 and 20 percent, respectively. Data of Markus (1932) indicate an efficiency of 23 percent for largemouth bass. The results for the guppy populations are thus close to those recorded for other species.

Comparison of the efficiencies of food conversion at the three nonlethal exploitation rates indicates

that exploitation rates in the range of 25 to 50 percent are most efficient, converting about 20 percent of the food consumed into available fish flesh. Efficiency for the 10-percent exploitation rate was only 15 percent.

INFORMATION FROM CONVENTIONAL MEASURES

Catch Per Unit of Effort

In most commercial-fishery investigations, direct data on population size are not available. Because knowledge of this statistic leads to calculation of rate of exploitation, and to observation of the effects of varying exploitation rates, it is highly desired by fishery administrators. In the experimental populations, therefore, it is of interest to see how closely the calculated catch per unit of effort reflects the known population sizes.

In calculating catch per unit, it was assumed that the amount of effort was directly proportional to the annual percentage exploitation rate applied, as would be true in a fishery where there were no competition between units of gear. Thus the 10-percent exploitation rate was equated to 1 unit of gear, 25 percent to 2.5 units, 50 percent to 5, and 75 percent to 7.5. Division of the known catches (table 4) by the assumed effort units completed the calculation. In this type of calculation catch per unit is by definition proportional to stock size, and would be exactly one-tenth the population weight, were the percentage exploitation rates applied on a weight basis. Since the rates were applied on the basis of numbers, some divergence between expected and actual weight caught per unit is possible.

The empirical curve of catch per unit of effort (table 8, fig. 15) shows that this measure does correspond to one-tenth the population weight, except during the period of the 10-percent exploitation rate, where there appears to have been a selection against the larger fish. In view of the method of selecting the fish for cropping, this is difficult to understand, and no explanation is offered. Nevertheless, the catch per unit of effort gives a good description of the major changes in population weight. In practical fisheries there are many sources of error in measuring both catch and effort, and the experiment can, of course, shed no light on these.

TABLE 8.—*Triweekly catch, effort, catch per unit of effort, and population size of exploited populations*

[Effort units explained in text]

Week No.	Effort (units)	Population A		Population B		Population A+B	
		Catch (grams)	Catch/unit (grams)	Catch (grams)	Catch/unit (grams)	Catch (grams)	Catch/unit (grams)
40	2.5	6.0	2.40	8.0	3.20	14.0	2.80
43	2.5	4.9	1.96	5.0	2.00	9.9	1.98
46	2.5	3.7	1.48	5.6	2.24	9.3	1.86
49	2.5	4.4	1.76	5.6	2.24	10.0	2.00
52	2.5	4.1	1.64	4.5	1.80	8.6	1.72
55	2.5	3.5	1.40	4.0	1.60	7.5	1.50
58	2.5	3.5	1.40	3.1	1.24	6.6	1.32
61	2.5	3.8	1.52	3.5	1.40	7.3	1.46
64	2.5	3.3	1.32	3.5	1.40	6.8	1.36
67	2.5	3.3	1.32	3.7	1.48	7.0	1.40
70	2.5	2.8	1.12	3.6	1.44	6.4	1.28
73	2.5	3.0	1.20	3.4	1.36	6.4	1.28
76	2.5	3.9	1.56	3.8	1.52	7.7	1.54
79	1.0	1.4	1.40	1.5	1.50	2.9	1.45
82	1.0	2.1	2.10	1.0	1.90	4.0	2.00
85	1.0	1.9	1.90	1.9	1.90	3.8	1.90
88	1.0	2.0	2.00	2.1	2.10	4.1	2.05
91	1.0	1.7	1.70	2.3	2.30	4.0	2.00
94	1.0	1.5	1.50	2.2	2.20	3.7	1.85
97	1.0	1.9	1.90	1.9	1.90	3.8	1.90
100	1.0	1.7	1.70	2.3	2.30	4.0	2.00
103	1.0	1.2	1.20	2.4	2.40	3.6	1.80
106	1.0	2.0	2.00	2.8	2.80	4.8	2.40
109	1.0	2.0	2.00	2.7	2.70	4.7	2.35
112	1.0	2.6	2.60	3.3	3.30	5.9	2.95
115	1.0	2.9	2.90	1.9	1.90	4.8	2.40
118	1.0	3.0	3.00	2.2	2.20	5.2	2.60
121	5.0	11.2	2.24	10.2	2.04	21.4	2.14
124	5.0	7.0	1.40	7.0	1.40	14.0	1.40
127	5.0	5.2	1.04	6.8	1.36	12.0	1.20
130	5.0	5.7	1.14	5.3	1.06	11.0	1.10
133	5.0	5.6	1.12	4.3	.86	9.9	.99
136	5.0	4.2	.84	4.8	.96	9.0	.90
139	5.0	4.3	.86	4.2	.84	8.5	.85
142	5.0	3.5	.70	3.5	.70	7.0	.70
145	5.0	3.9	.78	2.6	.52	6.5	.65
148	5.0	3.5	.70	2.8	.56	6.3	.63
151	7.5	3.4	.45	3.7	.49	7.1	.47
154	7.5	2.1	.28	2.9	.39	5.0	.33
157	7.5	2.4	.32	1.2	.16	3.6	.24
160	7.5	1.2	.16	1.7	.23	2.9	.19
163	7.5	1.2	.16	1.1	.15	2.3	.15
166	7.5	.9	.12	.3	.04	1.2	.08
169	7.5	1.0	.13	.2	.03	1.2	.08
172	7.5	.2	.03	0	0	.2	.01

Size Composition of the Catch

Because of the convenience with which fish sampled from the commercial catch can be measured, length composition of the catch is probably the second (next to catch per unit of effort) most common type of observation available to fishery biologists and administrators. Size-composition data have been widely used in fishery administration, and such data were gathered during the present experiment to determine the extent to which they reflect changes in population size and other population characteristics related to exploitation.

All fish removed during the cropping procedure were measured, and the length frequencies were compiled. The numbers of fish involved were too small to permit detailed analysis of the distributions, such as accurate location of modes or fitting of normal curves, but the mean lengths at each

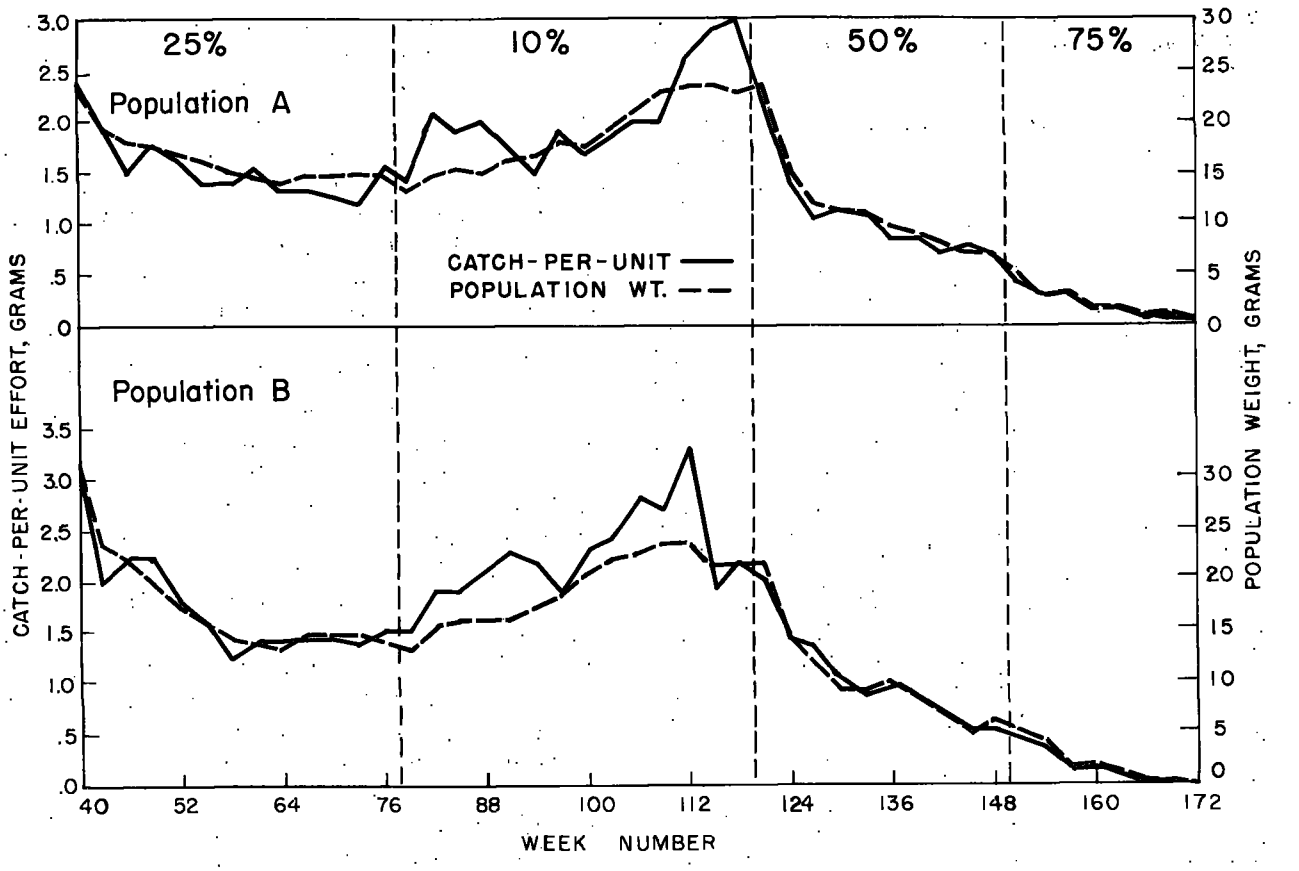

FIGURE 15.—Triweekly catch per unit of effort and population size of exploited populations. Percentages in top pane indicate triweekly exploitation rates.

cropping were calculated (table 9). With the exception of the last few weeks of the experiment, when numbers measured were too small (under 10 fish) to give reliable results, the changes in mean length (fig. 16) roughly paralleled those in population size (fig. 15). This is in accordance with expectation, since stocks that are "fished down" will normally consist of smaller fish than those that are at or near asymptotic abundance.

Catch, Catch Per Unit, and Size

A pertinent question is: "What could the intelligent fishery administrator have learned about the populations under exploitation, from a study of conventional fishery data?" In an attempt to answer this, the three series—catch, catch per unit of effort, and average length of individual fish in the catch—were brought together for examination (fig. 17). Data from the two exploited populations were combined in order to eliminate some of the variability not related to exploitation rates, inasmuch as previous comparisons had revealed the series for populations *A* and *B* to be similar in their essential features.

The start of a virgin fishery at the 25-percent exploitation rate was followed by the inevitable decline in both catch and catch per unit, reflecting a real decline in population size (fig. 15). After week 58, however, relative stability prevailed and indicated that the stocks could stand the drain of the fishery being imposed upon them. The decrease in catch at the 10-percent rate might have "been viewed with alarm" were not the catch per unit and average-length measures available. These, however, showed that the population was actually increasing in mass and in average size of individual fish. Data from the previous history of the fishery (25-percent rate) would indicate that the 10-percent exploitation rate did not utilize the full productivity of the stocks.

The sharp decline in catch, catch per unit, and average length after imposition of the 50-percent

TABLE 9.—*Number and mean length of fish cropped, by individual croppings, populations* A *and* B, *and mean of the two*

Week No.	Population *A*		Population *B*		Population *A* and *B*	
	No.	Mean length	No.	Mean length	No.	Mean length
		Mm.		*Mm.*		*Mm.*
40	22	28.5	32	27.6	54	28.0
43	21	26.3	24	25.9	45	26.6
46	25	23.6	19	28.3	44	25.7
49	20	25.4	15	31.3	35	28.0
52	20	24.5	13	28.7	33	26.2
55	15	26.3	9	32.2	24	28.5
58	16	24.3	8	30.1	24	26.3
61	13	27.5	11	27.0	24	27.3
64	16	24.1	18	24.0	34	24.1
67	18	23.2	23	22.4	41	22.8
70	19	23.0	23	23.1	42	23.1
73	16	24.3	19	25.0	35	24.6
76	15	26.0	17	26.2	32	26.2
79	5	28.0	7	24.8	12	26.2
82	5	30.8	8	26.8	13	28.4
85	6	27.4	9	26.0	15	26.6
88	7	26.1	8	27.0	15	26.6
91	7	25.0	10	25.9	17	25.5
94	7	25.8	10	26.0	17	25.9
97	9	26.0	11	24.3	20	25.1
100	7	26.8	12	25.0	19	25.7
103	9	22.0	11	26.6	20	25.0
106	9	25.7	10	27.6	19	26.7
109	11	24.0	10	28.1	21	26.0
112	11	25.6	9	30.5	20	27.8
115	11	27.2	7	27.2	18	27.3
118	10	28.1	7	28.8	17	28.4
121	49	26.4	41	25.9	90	26.3
124	31	25.5	29	25.5	60	25.5
127	21	25.3	32	24.1	53	24.6
130	19	23.7	27	23.7	46	23.8
133	30	23.3	31	22.0	61	22.7
136	27	22.2	30	23.9	57	23.1
139	29	22.1	26	23.0	55	22.6
142	27	22.3	19	24.1	46	23.1
145	22	23.2	16	21.8	38	22.7
148	23	22.3	20	21.1	43	21.8
151	21	23.1	26	22.1	47	22.6
154	9	22.7	23	20.8	32	21.4
157	20	20.9	12	20.6	32	20.8
160	9	20.7	9	23.6	18	22.2
163	11	19.5	7	22.8	18	20.8
166	3	26.0	1	25.0	4	25.8
169	9	21.3	1	24.0	10	21.6
172	2	22.5	0	0.0	2	22.5

rate most resembles the situations that have caused alarm among those concerned with real fisheries. Inspection of the equilibrium-yield curve (fig. 12) indicates that the 50-percent rate was indeed somewhat past the point of maximum return. If the history of the catch under the 25-percent rate were available, it would have become obvious at about week 142 that nothing was being gained by the additional fishing effort being put forth, and the fishery could have been cut back to an intermediate level in an attempt to secure a better yield at less cost. If the fishery had been started at the 50-percent level, the data would be difficult to interpret, but such a situation is unlikely among actual fisheries, which practically always start small and gradually increase. The value of obtaining as complete biological data as possible from the inception of a new fishery is sharply pointed up.

Finally, it is of interest to know whether the doom of the stocks at the 75-percent rate could have been foreseen. Certainly, if the previous history of the three measures were available, it would have become quickly apparent that the additional effort was not only depressing population size and average fish length, but was actually decreasing the catch. Under such circumstances, even the most optimistic fishing industry could probably be convinced of the need to retrench.

PRINCIPLES OF EXPLOITATION

Fishery biologists may think we presume a great deal when we venture to generalize for full-scale commercial fisheries from observations on our laboratory populations of guppies. True, the differences are immense between the vast, diffuse marine populations which form the object of most of our large fisheries, and the self-contained populations of guppies in their tiny laboratory tanks. They seem no greater, however, than the differences between laboratory populations of mice or guinea pigs and populations of human beings; the results of experimentation on the former have often been successfully applied to the latter, particularly in fields such as pathology, where experiments with human beings could not be carried out. With due caution, therefore, we offer certain applications of our findings to problems of commercial-fishery conservation. Before doing so, however, we may well enumerate the points of similarity and difference between our laboratory fish populations and the populations of marine fish upon which commercial fisheries depend.

It was set forth in describing the procedures and apparatus of the experiments that these were deliberately arranged to make them resemble as much as possible commercial fisheries. The following points of similarity to an idealized marine fishery may be listed:

1. The individual populations were fully interbreeding and self-reproducing.

2. There was a finite upper limit to population imposed by the food supply, which was held constant.

3. There was competition for food, both between individuals of the same size and between juveniles and adults.

4. Through cannibalism, the survival rates were dependent on population density.

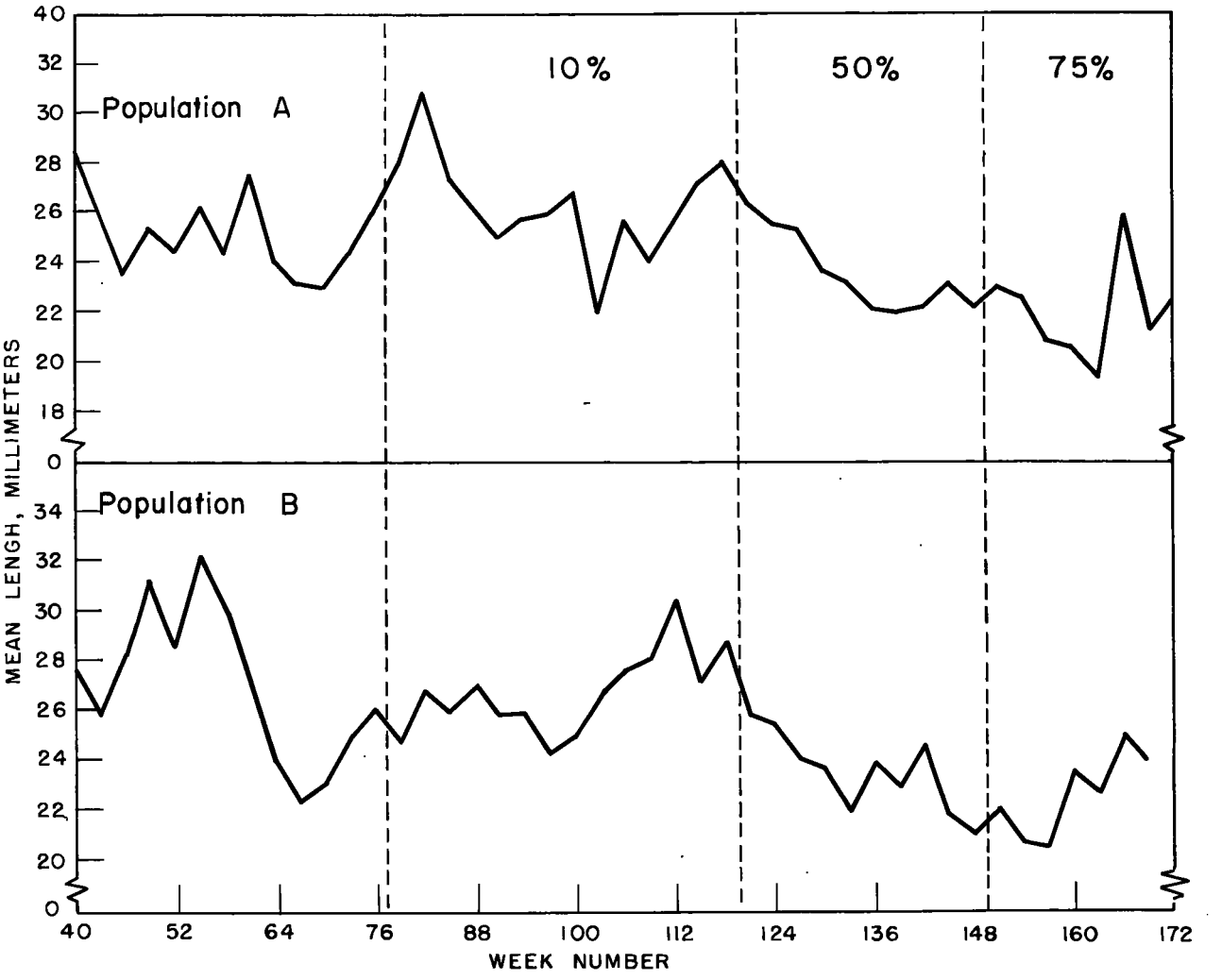

FIGURE 16.—Mean lengths of cropped fish under exploitation, by individual croppings. Percentages in top panel indicate triweekly exploitation rates.

5. The youngest juveniles were protected in a separate nursery area.

6. The "fishing" was done at intervals roughly equivalent to the reproductive period of the fish.

7. The "fishery" was selective, permitting the smallest juveniles to escape.

8. All catchable-sized fish were equally vulnerable to capture.

The chief differences (other than control of the environment) between laboratory and natural populations are:

1. The obvious differences in size and number of fish, and size of the environment.

2. The lack, in some cases, of an approach to infinite divisibility, such that a single fish may represent a substantial proportion of population size and number.

3. The low fecundity of the guppy as compared with most marine and anadromous fishes.

4. The lack of an independent population of predatory organisms such as preys on the stocks of many marine fishes.

5. Presence of an exploitation rate high enough to extinguish the population, which probably would not be economically feasible in most real fisheries.

The first category of differences is inherent in any small representation of a large thing, such as a ship model or a hydraulic model of a dam. Much research has been accomplished with such models.

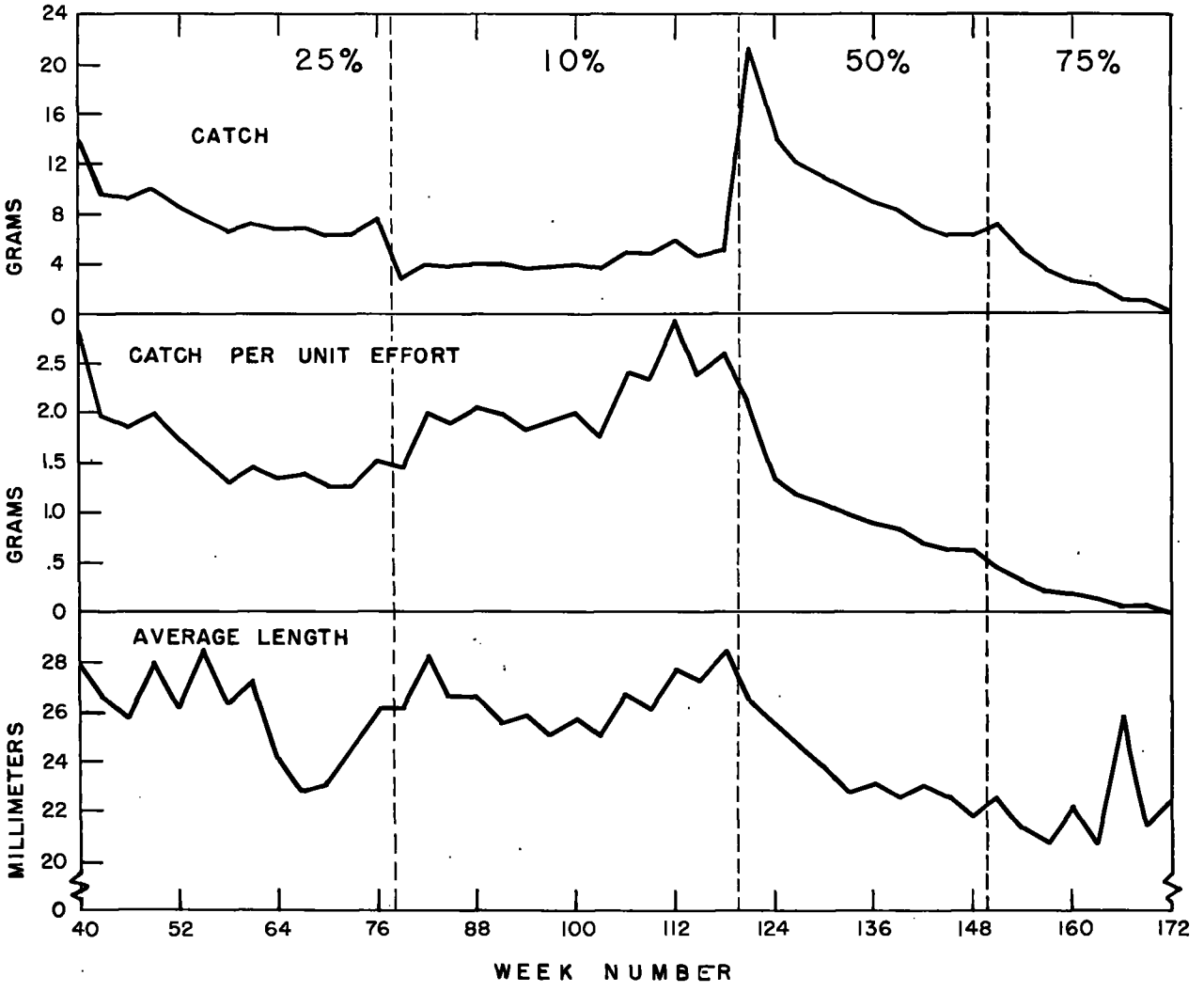

FIGURE 17.—Catch, catch per unit of effort, and average length for combined populations *A* and *B*. Percentages in top panel indicate triweekly exploitation rates.

however, and if the data are properly analyzed, valuable information is produced.

Lack of infinite divisibility presents difficulties chiefly in the roughness of data, such as the inconsistent average lengths obtained near the end of the experiments for the exploited populations. Inaccuracies resulting from this source should not be serious.

Low fecundity might be expected to present one of the most important sources of difficulty in applying the guppy results to commercial-fishery problems. Broods obtained from individual females by Silliman (1948) averaged about 20 fish each, as compared with the many thousands of eggs produced by marine species. Since the guppy is a live-bearer, however, the newborn young fish is a viable free-swimming organism, with considerably better chances of survival than the pelagic egg of marine species.

It would be difficult to say what larval size in marine fish is comparable in viability to the newborn guppy, but the tremendous mortalities suffered by marine pelagic eggs and larvae are notable. For instance, in the Pacific sardine, which is thought to lay 100,000 or more eggs per season, only about 100 larvae survive from 100,000 eggs after 40 days (Ahlstrom 1954); in the Atlantic mackerel, with a production of "several hundred thousand" eggs per season, only four 50-millimeter larvae survived from each 1 million

eggs laid (Sette 1943a).[2] Thus the effective fecundity of the guppy in contributing to recruitment of the catchable stock may be as great as that of marine species. Indeed, the well-known inverse relation between egg number and degree of parental care (of which live-bearing is one form) may well provide just such an adjustment. A corollary implication of this relation is that the high fecundity and low survival rate of marine species probably make them much more inclined to violent fluctuations in recruitment (and thus abundance) than the guppy populations.

It is difficult to estimate the consequences of the absence of an independent predatory population. Certainly in marine fisheries the responses of populations to fishing pressures must be modified to some extent by the ever-present predation of larger fish, of sharks, or of seals and other marine mammals, as the case may be. In one manner of looking at the problem, this can be considered as another element of the controlled environment in the laboratory populations; the independent predation has been held constant at a value of zero.

One principle of exploitation, already established theoretically, has been verified by the present experiments: that even a low rate of exploitation causes some change in population size. Thus the equilibrium mass of the populations exploited at the 10-percent rate was about one-third less than the asymtotic mass of the unexploited control populations. It is demonstrated that a finding of simple reduction in population size, is not in itself a cause for alarm or retrenchment.

A second principle of exploitation is that fish populations up to a certain level of exploitation are resilient, responding to removals with increased survival and growth rates. This is brought out strikingly in the saw-tooth curves of population mass (fig. 2 and 3), each tooth representing the reduction due to removals, and the recovery therefrom. The effect of resiliency in restoring a population to a higher level of abundance after reduction in exploitation rates, is brought out by the increase in mass of both exploited populations to an equilibrium level about 50 percent greater than that prevailing under the 25-percent exploitation rate, after reduction of the rate to 10 percent. An instance of resilience in an actual marine-fish population was provided when stocks of North Sea trawl fish recovered significantly during the reduced fishing intensity of World War II (Margetts and Holt, 1948).

A principle complementary to that of resiliency is that if a population of the type considered here is continuously subjected to a rate of fishing greater than the maximum rate of replacement of which the population is capable (at a very low population level) it will continue to decline until extinction. Only about 20 reproductive periods were required to extinguish the guppy populations at the 75-percent exploitation rate, although it is true they had already been considerably reduced by application of the 50-percent rate. One needs to keep in mind here that many natural fish populations probably could stand fishing rates considerably in excess of 75 percent, and that in practical fisheries fishing usually becomes economically infeasible before the extinction rate is reached.

Perhaps the most important principle of exploitation is that there exists for each population, somewhere between zero and lethal exploitation rates, a rate of exploitation at which the maximum equilibrium yield will be produced. This is not a new idea, of course, but the laboratory experiments have provided verification and demonstration of it. Results reported above indicate that for laboratory populations under the controlled conditions imposed, with a constant supply of food, the maximum return is obtained under exploitation rates of 30 to 40 percent per reproductive period, when population mass is at about one-third its asymptotic level.

In commercial fisheries where the stocks might reasonably be expected to have reactions similar in some degree to those of the laboratory populations, and where catch and fishing effort are the only data available, the above findings may serve as a very rough guide to exploitation. If the population size is proportional to catch per unit of effort (Schaefer 1954) or can be derived from it (Ricker, 1940, 1944), fishing rates which reduce the size to not less than one-third to one-half its maximum value, when accompanied by an increase in catch, can tentatively be considered satisfactory pending estimation of the yield curve for the fishery in question; higher fishing rates should be

[2] The year class from which these data were obtained was a poor one, and the indicated survival rate probably below normal; the rate, however, does give an indication of the tremendous mortalities suffered in the marine environment.

permitted only with caution. It follows without saying that such a rough rule of thumb should be used only when supplementary biological data are lacking. Every effort should be made to obtain information on growth, survival, fishing, and reproductive rates, on fecundity, on age composition of the stock and age at maturity and on the relation of these variables to size of stock and conditions of the environment, so that management of the fishery can be placed on a solid scientific foundation.

In sum, the experimental populations have provided chiefly verification and demonstration of existing theories of exploitation rather than providing new ones. They have shown that the theoretical principles expounded by outstanding fishery biologists of recent decades are not simply the obscure results of abstruse mathematical formulations, but represent the visible, measurable reactions of living organisms to mortality imposed by man. If this report provides some illumination to those fishery biologists who are interested in the effect of exploitation on fish populations, and who think quantitatively but not necessarily mathematically, it will have served its purpose.

SUMMARY

1. Four laboratory populations of guppies were grown in small aquariums, under conditions of space, light, temperature, and food controlled as closely as possible.

2. Two of the populations were selected by lot for the exploitation tests; the other two were maintained without exploitation under identical conditions, as experimental controls.

3. Populations were maintained for a period of 168 weeks, during the last 128 of which the test populations were exploited.

4. Initial growth of the populations followed the logistic curve; asymptotic mass levels of about 32 grams were reached by the control populations in about 50 weeks.

5. Successive exploitation rates of 25, 10, 50, and 75 percent per reproductive period (3 weeks) were imposed on the two test populations.

6. Major changes in number during exploitation were similar for the two test populations. The 25-percent rate caused an initial decrease in the number of adults, followed by an increase in the number of juveniles. At the 10-percent rate there was an increase in the number of adults, followed by a decrease in the number of juveniles. Changes at the 50-percent rate were similar to those at the 25, but more extensive. At 75 percent there was rapid decline of both juveniles and adults to extinction.

7. Changes in weight resembled those in number, but fluctuations were less violent. The changes in weight of catch after the increase from 10- to 50-percent exploitation followed classical conceptions derived on theoretical grounds.

8. The proportion of males was greater in the test than in the control populations; the final apparent stabilization was at 50 percent for one control population and 30 percent for the other.

9. Comparison of control-population size with temperature fluctuations due to imperfect thermostatic control revealed a significant negative correlation accounting for about 30 percent of the fluctuations in population size.

10. Equilibrium yield, defined as the average yield during a period of 6 weeks without significant unidirectional changes in population composition, was related to fishing rate in a manner that indicated maximal yield at fishing rates between 30 and 40 percent, when the populations were at approximately one-third their asymptotic level.

11. The maximum actual yield realized represented the conversion into fish flesh of about 20 percent of the food consumed.

12. Examination of three conventional fishery measures, catch, catch per unit of effort, and average fish length, showed that these could yield a considerable amount of valuable information on population size and results of changes in rate of exploitation. Catch per unit closely, and average length roughly, followed changes in size of population.

13. The laboratory population experiments verified and demonstrated the following principles of exploitation:

a. Any exploitation of a population, however mild, reduces its abundance somewhat.

b. Below a certain level of exploitation fish populations are resilient, increasing their survival and/or growth rates to compensate for the fish removed.

c. It is possible, at least with some populations, to raise exploitation rates to the point at which they will cause extinction of the population.

d. Somewhere between no exploitation and excessive exploitation, there lies a level at which the maximum equilibrium yield can be obtained.

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APPENDIX

TABLES OF WEEKLY DATA AND LENGTH FREQUENCIES

TABLE A–1.—*Weekly population and removal numbers and weights, population* A

[Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment.]

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
6			5	3	8							1.5	
7			5	3	8							1.6	
8			5	3	8							2.1	
9	(1)	25	5	3	33							2.9	
10	(1)	21	5	3	29							2.8	
11	(1)	20	5	3	28							3.6	
12	(1)	29	5	3	37		1			1		4.3	
13	(1)	88	5	3	96		2			2		4.6	
14	(1)	79	5	3	87		1			1		5.2	
15	(1)	83	5	3	91							6.0	
16	(1)	115	6	3	124		1			1		6.7	
17	(1)	110	6	3	119		3			3		7.1	
18	(1)	100	6	3	109							8.0	
19	(1)	93	10	3	106		2			2		9.3	
20	(1)	108	10	3	121							9.8	
21	(1)	89	10	2	101				1	1		9.7	
22	(1)	88	13	2	103		2			2		10.7	
23	(1)	92	13	2	107							11.5	
24	(1)	89	13	2	104							12.2	
25	(1)	70	33	2	105							14.3	
26	(1)	67	34	2	103		1			1		14.9	
27	(1)	64	35	2	101							15.4	
28	(1)	63	36	2	101							15.7	
29	(1)	59	35	2	96		1	1		2		16.2	
30	(1)	63	38	2	103							17.1	
31	(1)	63	40	4	107							18.7	
32	(1)	65	44	4	113							18.4	
33	(1)	59	45	4	108		1			1		19.0	
34	(1)	65	47	4	116							20.1	
35	(1)	75	47	5	127			1		1		20.9	
36	(1)	94	47	5	146							20.4	
37	(1)	66	49	35	150							20.5	
38	(1)	68	49	31	148							21.4	
39	(1)	60	49	38	147							22.1	
40	(1)	64	47	38	149			1		1	22	23.3	6.0
41	(1)	63	35	26	124				1	1		16.3	
42	(1)	66	36	26	128				1	1		18.4	
43	(1)	64	36	27	127						21	19.7	4.9
44	(1)	67	27	19	113							15.9	
45	(1)	64	32	21	117							17.0	
46	21	45	35	21	122						25	18.0	3.7
47	17	32	30	18	97							15.8	
48	17	31	35	19	102							16.9	
49	18	24	38	21	101			1		[2] 1	20	17.6	4.4
50	13	18	31	21	83			1		1		14.9	
51	22	15	31	24	92							15.2	
52	16	23	33	23	95						20	16.9	4.1
53	24	14	26	21	85							13.7	
54	31	10	28	21	90			1		1		15.1	
55	39	9	28	21	97						15	16.3	3.5
56	40	21	19	20	100							14.0	
57	32	26	21	19	98				1	1		14.3	
58	53	25	21	19	118						16	15.1	3.5
59	60	20	13	17	110							12.8	
60	74	20	14	17	125							13.8	
61	69	20	18	17	124						13	14.7	3.8
62	80	19	16	12	127							12.3	
63	76	21	18	13	128							13.3	
64	61	26	20	16	123						16	14.0	3.3
65	38	40	14	12	104			1		1		12.4	
66	32	35	17	17	101							13.1	
67	29	35	21	17	102	1				1	18	14.8	3.3
68	26	25	21	17	89							12.4	
69	29	29	21	17	96							13.7	
70	20	33	24	19	96						19	14.7	2.8
71	15	25	18	13	71							12.9	
72	11	23	24	18	76							13.9	
73	8	21	27	18	74						16	15.0	3.0
74	23	10	19	21	73							13.3	
75	14	13	21	24	72							14.4	
76	23	12	22	24	81						15	14.9	3.9
77	26	6	19	18	69							11.5	
78	23	9	19	18	69							12.7	
79	26	5	22	20	73						5	13.3	1.4
80	26	7	19	17	72							13.3	
81	34	9	19	18	80							14.2	
82	34	9	22	18	83						5	14.9	2.1
83	32	11	23	16	82							13.6	
84	26	19	24	16	85							14.9	
85	29	18	25	17	89						6	15.5	1.9
86	31	20	23	15	89							14.2	
87	23	22	26	18	89							15.0	

See footnotes at end of table.

TABLE A–1.—*Weekly population and removal numbers and weights, population* A—Continued

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
88	23	22	30	18	93						7	15.0	2.0
89	26	20	25	21	92							14.7	
90	30	29	26	15	100							15.4	
91	34	30	26	15	105						7	16.1	1.7
92	29	27	26	24	106							14.8	
93	28	17	31	24	100							15.6	
94	24	20	30	24	98						7	16.6	1.5
95	21	20	30	26	97							16.3	
96	21	25	31	28	105							16.8	
97	25	27	31	30	113						9	18.0	1.9
98	30	24	26	27	107							17.2	
99	26	26	28	28	108			1		1		18.4	
100	44	22	30	28	124				1	1	7	17.5	1.7
101	31	25	35	30	121							17.1	
102	29	25	38	29	121							18.3	
103	34	26	39	29	128						9	19.4	1.2
104	36	19	38	31	124							19.4	
105	36	18	40	31	125							20.2	
106	33	24	43	32	132						9	21.2	2.0
107	24	22	45	32	123							20.5	
108	22	24	46	32	124							22.0	
109	21	27	46	32	126						11	23.0	2.0
110	24	22	45	28	119				1	1		20.5	
111	13	25	48	30	116							22.0	
112	13	26	49	30	118						11	23.2	2.6
113	19	29	44	26	118							21.6	
114	27	27	46	27	127							22.5	
115	30	24	49	30	133						11	23.5	2.9
116	32	22	44	27	125							21.6	
117	31	22	46	27	126							22.0	
118	32	21	46	30	129						10	22.9	3.0
119	26	18	43	32	119							21.1	
120	25	19	43	32	119							22.1	
121	26	17	47	33	123						49	23.5	11.2
122	27	7	19	21	74							12.9	
123	19	14	19	24	76							14.3	
124	20	19	19	24	82						31	15.3	7.0
125	18	8	10	16	52							10.0	
126	19	15	10	16	60							11.2	
127	47	15	10	16	88						21	11.9	6.2
128	51	10	4	12	77							8.3	
129	54	14	4	12	84							9.6	
130	50	21	5	13	89						19	11.2	5.7
131	30	35	3	8	76							8.2	
132	31	46	4	8	89							9.7	
133	48	47	5	8	108						30	11.1	5.6
134	58	36	3	4	101							7.1	
135	51	40	5	6	102							8.5	
136	58	42	8	6	114						28	9.6	4.2
137	51	24	5	7	87							6.9	
138	63	27	7	7	104							7.9	
139	61	44	7	7	119						29	9.0	4.3
140	39	39	2	5	85			1		1		6.2	
141	42	41	4	6	93							7.2	
142	33	41	7	7	88						27	8.1	3.5
143	40	20	6	4	70							5.7	
144	29	26	7	8	70							6.4	
145	26	25	9	9	69						22	7.2	3.9
146	15	23	6	5	49							5.1	
147	20	26	6	5	57							5.7	
148	14	25	12	9	60						23	7.0	3.5
149	11	13	6	4	34							4.2	
150	14	11	8	6	39							4.8	
151	24	12	9	6	51						21	5.2	3.4
152	25	4	1	3	33							2.0	
153	24	6	1	3	34							2.4	
154	23	9	1	3	36						9	3.0	2.1
155	7	16	1	2	26							2.0	
156	5	21	1	2	29							2.5	
157	12	22	1	3	38						20	3.3	2.4
158	12	5	0	1	18							1.1	
159	12	3	2	1	18							1.3	
160	13	8	3	2	26						9	1.9	1.2
161	9	6	1	1	17	1				1		1.1	
162	9	5	1	1	16		1			1		1.2	
163	12	12	2	2	28						12	1.8	1.2
164	11	3	1	1	16							.8	
165	11	2	1	2	16							1.1	
166	11	2	1	2	16						3	1.3	.9
167	3	8	0	2	13							.7	
168	3	8	0	2	13							1.2	
169	0	10	0	2	12						9	1.4	1.0
170	0	3	0	0	3							.4	
171	0	3	0	0	3							.5	
172	0	0	2	1	3						2	.6	.2
173	0	0	0	1	1							.3	
174	0	0	0	1	1							.4	

[1] Not listed separately; included in "immature".
[2] Includes one fish of unknown sex.

TABLE A–2.—*Weekly population and removal numbers and weights, population* B

[Categories "fry" and "immature" defined in text section, Maintenance and Exploitation Procedures and Equipment]

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
6	(1)	10	5	5	20		1			1		3.5	
7	(1)	19	5	4	28							2.9	
8	(1)	27	5	4	36		1			1		3.3	
9	(1)	19	5	3	27		1		1	2		3.3	
10	(1)	15	5	3	23							3.5	
11	(1)	30	5	3	38							3.8	
12	(1)	43	5	3	51							4.6	
13	(1)	40	5	3	48		1			1		4.8	
14	(1)	48	5	3	56		1			1		5.4	
15	(1)	74	6	3	83		2			2		6.0	
16	(1)	89	6	3	98		1			1		6.7	
17	(1)	94	6	3	103		3			3		7.2	
18	(1)	92	6	3	101							8.0	
19	(1)	108	6	3	117							9.0	
20	(1)	107	6	3	116							9.5	
21	(1)	112	6	3	121							10.3	
22	(1)	108	8	3	119							11.9	
23	(1)	120	8	3	131							12.2	
24	(1)	118	8	3	129							13.6	
25	(1)	112	13	3	128			1		1		15.9	
26	(1)	110	15	3	128		1	1		2		15.9	
27	(1)	102	20	3	125							17.6	
28	(1)	98	22	3	123							17.5	
29	(1)	98	22	3	123							18.5	
30	(1)	92	27	3	122							19.9	
31	(1)	93	27	3	123							20.5	
32	(1)	95	32	4	131							22.2	
33	(1)	92	35	3	130							21.9	
34	(1)	91	36	4	131							22.8	
35	(1)	87	40	4	131							24.2	
36	(1)	88	40	4	132							24.9	
37	(1)	51	42	38	131							26.2	
38	(1)	86	45	10	141							28.0	
39	(1)	34	45	51	130							27.8	
40	(1)	13	47	74	134						32	30.8	8.0
41	(1)	8	35	59	102							22.2	
42	(1)	17	35	54	106				2	2		23.6	
43	(1)	35	35	53	123						24	23.5	5.0
44	(1)	21	25	40	86							19.8	
45	(1)	20	25	42	87							20.7	
46	5	9	26	44	84						19	22.0	5.6
47	11	6	21	34	72							18.0	
48	17	5	22	34	78							18.8	
49	2	5	22	34	63						15	19.6	5.6
50	16	6	18	22	62							15.6	
51	16	2	18	28	64							16.8	
52	13	2	19	27	61						13	17.5	4.5
53	11	1	15	19	46							14.2	
54	28	1	15	19	63	2				2		15.3	
55	32	1	15	19	67						9	16.0	4.0
56	57	7	12	13	89							13.0	
57	58	7	12	13	90							14.0	
58	95	8	12	14	129						8	14.2	3.1
59	91	20	7	12	130							12.5	
60	99	28	8	11	146							13.6	
61	103	28	8	11	150						11	13.6	3.5
62	98	29	6	8	141			1		1		11.1	
63	84	43	10	7	144							12.5	
64	73	45	17	8	143						18	13.3	3.5
65	34	62	18	10	124							12.8	
66	37	53	24	10	124							13.8	
67	33	53	29	10	125						23	14.8	3.7
68	26	43	28	10	107							12.7	
69	28	43	30	10	111							14.0	
70	19	39	34	21	113						23	14.7	3.6
71	19	30	28	19	96							12.7	
72	24	30	29	19	102							13.8	
73	22	26	32	20	100						19	14.8	3.4
74	25	19	27	18	89							12.4	
75	27	15	27	25	94	1				1		13.7	
76	32	10	30	26	98						17	14.1	3.8
77	25	10	24	20	79							11.1	
78	32	18	24	20	94							12.4	
79	45	17	25	22	109						7	13.3	1.5
80	48	19	24	19	110							13.0	
81	45	19	25	21	110							14.2	
82	45	26	25	21	117						8	15.6	1.9
83	51	15	28	23	117							14.6	
84	41	32	30	25	128							15.6	
85	43	34	31	25	133					[2]1	9	16.2	1.9
86	50	35	28	23	136							14.2	
87	50	42	28	22	142							15.3	
88	54	40	28	23	145						9	16.1	2.1
89	64	33	27	16	140							14.7	
90	59	45	29	18	151							15.3	
91	58	46	29	20	153						10	16.2	2.3
92	51	44	31	20	146							15.6	

See footnotes at end of table.

TABLE A–2.—*Weekly population and removal numbers and weights, population* B—Continued

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
93	56	33	37	20	146							16.3	
94	41	32	45	27	145						10	17.5	2.2
95	30	36	44	25	135							17.0	
96	26	38	44	26	134							17.9	
97	24	39	45	27	135						11	18.6	1.9
98	11	47	42	24	124							18.3	
99	2	48	46	28	124							20.0	
100	2	46	47	29	124						12	20.9	2.3
101	13	30	47	35	125							20.0	
102	7	27	50	35	119							21.3	
103	13	21	54	37	125						11	22.0	2.4
104	11	13	53	36	113							20.9	
105	9	13	53	36	111							21.8	
106	9	8	53	41	111						10	22.6	2.8
107	8	3	49	41	101							21.2	
108	10	3	49	41	103							22.3	
109	3	2	50	41	96						10	23.6	2.7
110	3	2	46	35	86							21.6	
111	6	1	46	35	88				1	1		22.6	
112	8	1	46	35	90						9	23.7	3.3
113	21	0	42	31	94							21.2	
114	32	0	42	30	104							21.3	
115	30	0	42	30	102						7	21.4	1.9
116	45	1	37	28	111							20.2	
117	36	3	37	28	104							21.1	
118	56	3	37	28	124						7	21.5	2.2
119	62	4	34	25	125							20.0	
120	71	11	34	25	141		1			1		20.7	
121	53	23	34	25	135						41	21.9	10.2
122	48	13	21	13	95							12.9	
123	47	20	22	13	102							14.1	
124	52	24	22	13	111						29	14.9	7.0
125	55	32	12	7	106							9.5	
126	50	31	15	11	107							11.0	
127	41	37	16	11	105						32	12.1	6.8
128	53	22	10	7	92							7.1	
129	55	28	11	8	102							7.9	
130	59	31	16	8	114						27	9.4	5.3
131	45	28	8	5	86							6.0	
132	62	29	9	6	106							7.4	
133	43	44	11	7	105						31	9.2	4.3
134	29	34	9	5	77							7.0	
135	29	38	9	8	84							8.7	
136	39	37	12	8	96						28	10.0	4.8
137	22	27	7	5	61							6.0	
138	26	30	8	5	69							7.1	
139	19	29	10	12	70						26	8.5	4.2
140	14	20	6	4	44							5.2	
141	27	19	7	6	59							6.3	
142	26	18	11	9	64						19	6.9	3.5
143	32	11	5	5	53							3.9	
144	40	14	5	7	66							4.6	
145	35	18	6	7	66						16	5.4	2.6
146	32	16	5	4	57							4.2	
147	25	23	5	4	57							5.0	
148	22	26	5	8	61						20	6.2	2.8
149	27	14	7	2	50							3.4	
150	26	22	8	3	59							4.5	
151	24	20	9	5	58		1			1	26	5.3	3.7
152	16	10	3	3	32							2.3	
153	8	23	3	3	37							3.3	
154	13	24	4	3	44						23	4.5	2.9
155	20	4	2	2	28							1.6	
156	18	5	3	2	28							1.9	
157	11	10	3	3	27				1	1	12	2.0	1.2
158	11	9	1	1	22							1.2	
159	7	12	1	1	21							1.8	
160	7	9	3	1	20		1			1	9	2.2	1.7
161	0	9	1	0	10	1				1		.7	
162	0	7	2	0	9		1			1		1.0	
163	0	5	2	2	9						7	1.3	1.1
164	0	2	0	0	2							.3	
165	0	2	0	0	2							.4	
166	0	0	1	1	2						1	.5	.3
167	0	0	1	0	1							.2	
168	0	0	1	0	1							.2	
169	0	0	1	0	1						1	.2	.2

[1] Not listed separately; included in "Immature."
[2] Includes one fish of unknown sex.

TABLE A-3.—*Weekly population numbers and weights, population* C

[Categories "fry" and "immature" defined in text section Maintenance and Exploitation Procedures and Equipment]

Week No.	Number of fish					Number natural deaths					Weight, grams
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
6	(1)	1	5	3	9						1.5
7	(1)	4	5	4	13						2.1
8	(1)	1	5	4	10		1			1	2.7
9	(1)	10	5	4	19		2			2	3.2
10	(1)	18	5	4	27						3.1
11	(1)	36	5	3	44		9			9	3.0
12	(1)	28	5	3	36		1			1	3.2
13	(1)	51	5	3	59						4.0
14	(1)	76	5	3	84						4.4
15	(1)	83	5	3	91		1			1	4.9
16	(1)	81	5	4	90		1			1	5.6
17	(1)	101	5	3	109						6.2
18	(1)	94	4	3	101		1			1	6.3
19	(1)	92	4	3	99		1			1	7.4
20	(1)	90	4	3	97		2			2	8.0
21	(1)	91	4	3	98						8.5
22	(1)	97	7	3	107						9.4
23	(1)	85	8	3	96						9.9
24	(1)	83	9	3	95						11.5
25	(1)	75	16	3	94		2			2	12.3
26	(1)	75	16	3	94						13.8
27	(1)	68	19	3	90		1			1	13.5
28	(1)	63	22	3	88		1			1	14.6
29	(1)	67	21	3	91		1	1		2	14.3
30	(1)	68	24	3	95						15.3
31	(1)	65	25	3	93		1			1	16.9
32	(1)	67	29	3	99						16.7
33	(1)	61	34	3	98						17.5
34	(1)	66	35	5	106						18.7
35	(1)	68	32	5	105			1		1	18.9
36	(1)	75	33	6	114		1			1	19.2
37	(1)	45	36	32	113						19.9
38	(1)	52	35	22	109						21.5
39	(1)	28	36	42	106						21.5
40	(1)	19	37	46	102						23.3
41	(1)	23	37	46	106						21.9
42	(1)	24	35	45	104						22.8
43	(1)	35	34	45	114						24.0
44	(1)	30	35	44	109			1		1	24.9
45	(1)	38	36	47	121						26.0
46	(1)	25	39	47	111						26.8
47	10	19	40	47	116						27.0
48	16	14	41	49	120						28.7
49	9	9	43	57	118						29.1
50	12	11	42	57	122						29.3
51	18	10	43	57	128						29.7
52	4	9	44	57	114						30.5
53	5	12	44	57	118						31.4
54	9	9	46	57	121						31.4
55	11	8	47	57	123						32.3
56	11	9	47	57	124						31.6
57	2	6	47	60	115			1		1	32.0
58	7	6	47	58	118				1	1	31.8
59	10	6	47	58	121						31.9
60	11	7	47	58	123						32.3
61	24	7	48	58	137						32.3
62	14	7	48	58	127						33.0
63	28	6	49	58	141				1	1	32.6
64	13	3	45	59	120			3		3	32.2
65	13	6	45	60	124						32.0
66	6	3	46	58	113	1		1	2	4	31.0
67	14	4	46	56	120				2	2	30.9
68	5	7	46	56	114						30.8
69	6	6	46	56	114			1		1	31.3
70	5	6	48	56	115						31.1
71	5	5	47	56	113						31.1
72	6	4	48	56	114						30.0
73	4	7	47	56	114						30.6
74	8	3	48	56	115						30.8
75	8	5	48	56	117						31.1
76	7	7	48	56	118						31.0
77	4	5	47	58	114						30.8
78	1	7	48	58	114						30.7
79	4	5	48	59	116						31.5
80	9	2	50	60	121						31.4
81	8	4	50	59	121						31.4
82	9	5	50	58	122	1			1	2	31.1
83	6	4	49	58	117						31.0
84	10	4	48	58	120			1		1	30.3
85	10	8	48	58	124						30.6
86	12	5	47	61	126			1		1	30.5
87	14	5	48	61	128						30.3
88	20	4	48	63	135						30.5
89	11	5	48	63	127						30.4
90	5	9	47	61	122			1		1	31.2
91	13	7	46	63	129						30.7
92	12	7	47	61	127						30.4

See footnotes at end of table.

TABLE A–3.—*Weekly population numbers and weights, population* C—Continued

Week No.	Number of fish					Number natural deaths					Weight, grams
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
93	14	7	49	61	131						31.0
94	13	7	49	61	130						30.9
95	12	7	50	61	130						31.5
96	4	10	53	60	127				1	1	31.7
97	6	10	51	61	128			1		1	31.8
98	10	10	52	61	133						31.5
99	15	11	49	61	136			2		2	31.5
100	18	11	53	58	140						31.6
101	20	9	52	60	141						31.6
102	26	7	55	60	148						31.6
103	24	7	54	60	145			1		1	31.6
104	11	10	56	59	136					[2] 1	32.6
105	11	9	56	58	134				1	1	32.7
106	6	12	54	60	132						32.8
107	5	14	56	60	135				1	1	33.7
108	5	14	57	59	135				1	1	33.8
109	2	16	58	57	133						34.5
110	2	14	59	57	132						34.9
111	3	11	61	57	132			1		1	35.5
112	10	11	61	57	139						35.4
113	13	11	61	58	143						35.8
114	16	10	62	58	146	1				1	36.0
115	14	4	63	64	145						35.8
116	17	4	62	64	147						36.1
117	23	3	62	65	153			1		1	36.6
118	27	3	60	64	154			2	1	3	35.3
119	17	5	60	64	146						35.9
120	21	5	59	64	149			1		1	35.6
121	14	8	58	64	144						35.9
122	20	7	60	64	151						37.1
123	16	6	59	63	144				2	2	35.8
124	24	7	58	63	152			1		1	35.8
125	26	9	56	63	154			2		2	35.6
126	17	10	56	65	148						35.8
127	11	10	54	65	140			1		1	36.0
128	9	12	54	65	140			1	1	2	35.1
129	9	10	56	64	139				1	1	35.5
130	17	9	56	64	146			2		2	35.5
131	12	9	56	64	141						35.4
132	20	9	56	63	148				1	1	35.3
133	15	11	55	64	145			1		1	35.4
134	15	16	55	65	151			1		1	35.6
135	9	15	55	64	143				1	1	35.6
136	5	14	55	66	140						35.9
137	7	13	55	64	139			1	2	3	34.8
138	7	13	56	64	140						34.7
139	8	11	58	64	141						34.9
140	13	9	59	65	146						34.9
141	9	10	58	65	142						34.8
142	6	8	60	64	138						34.4
143	6	8	59	62	135			1		1	33.6
144	10	7	58	61	136						32.4
145	25	7	57	61	150			1		1	31.9
146	15	6	57	61	139				1	1	31.4
147	11	6	57	61	135						31.2
148	13	7	57	62	139						31.8
149	8	4	57	65	134						31.4
150	11	4	57	66	138						31.9
151	7	2	57	66	132				2	2	31.5
152	10	4	57	64	135				2	2	30.8
153	8	4	56	63	131			1	1	2	30.4
154	9	6	55	63	133			1		1	30.3
155	4	7	55	63	129						30.5
156	8	6	56	62	132				1	1	30.2
157	8	6	56	60	130				2	2	29.2
158	11	6	56	58	131				2	[2] 3	29.2
159	11	6	56	58	131				1	1	29.5
160	14	5	55	56	130			1	2	3	29.0
161	18	5	54	55	132		1		1	2	28.2
162	14	2	53	57	126						28.8
163	14	5	53	55	127				2	2	28.5
164	14	9	53	55	131						28.6
165	15	7	52	56	130			1		1	28.8
166	17	7	52	54	130				1	1	28.4
167	14	8	51	54	127			1		1	28.6
168	11	10	51	54	126				1	1	28.0
169	20	9	53	53	135						28.6
170	16	10	53	52	131					[2] 1	28.7
171	17	9	54	52	132						29.0
172	7	8	55	53	123						29.4
173	9	9	55	51	124				1	1	29.4
174	12	8	55	51	126						29.4

[1] Not listed separately; included in "immature."
[2] Includes one fish of unknown sex.

TABLE A–4.—*Weekly population numbers and weights, population* D

[Categories "fry" and "immature" defined in text section, Maintenance and Exploitation Procedures and Equipment]

Week No.	Number of fish					Number natural deaths					Weight (grams)
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
6	(1)	0	5	5	10						3.1
7	(1)	16	5	5	26		1			1	3.2
8	(1)	17	5	5	27						3.8
9	(1)	33	4	5	42						4.1
10	(1)	35	4	4	43						3.9
11	(1)	50	4	3	57		1		1	2	3.9
12	(1)	58	4	3	65						4.8
13	(1)	76	4	3	83						5.8
14	(1)	70	5	3	78						6.0
15	(1)	87	8	3	98						7.0
16	(1)	95	9	3	107						7.9
17	(1)	102	10	3	115						8.4
18	(1)	100	10	3	113						9.3
19	(1)	100	10	3	113		1			1	10.3
20	(1)	101	10	3	114						10.7
21	(1)	101	10	3	114						11.5
22	(1)	97	13	3	113						13.0
23	(1)	98	13	3	114						13.3
24	(1)	100	13	3	116						14.5
25	(1)	92	20	3	115						15.9
26	(1)	89	25	3	117						17.0
27	(1)	100	32	3	135						18.6
28	(1)	78	34	3	115						18.7
29	(1)	78	33	3	114			1		1	19.9
30	(1)	77	34	3	114						20.0
31	(1)	72	34	3	109		2			2	21.2
32	(1)	76	41	3	120						22.7
33	(1)	72	42	3	117		1			1	23.2
34	(1)	69	46	3	118						23.7
35	(1)	65	50	4	119						24.5
36	(1)	75	50	4	129						25.4
37	(1)	36	53	40	129						26.1
38	(1)	29	51	48	128						27.6
39	(1)	25	52	53	130						29.6
40	(1)	21	53	60	134						29.3
41	(1)	25	51	60	136						28.8
42	(1)	22	54	60	136						29.5
43	(1)	36	55	61	152						29.6
44	(1)	27	55	61	143						30.9
45	(1)	18	55	61	134	1				1	31.0
46	(1)	34	57	61	152						31.5
47	5	15	56	61	137						32.8
48	13	12	59	61	145						33.2
49	5	12	59	61	137						33.4
50	9	10	59	63	141						33.5
51	10	7	60	65	142						33.6
52	5	6	61	65	137						34.0
53	11	5	62	65	143						34.0
54	12	6	62	65	145						35.0
55	11	5	62	66	144						35.2
56	16	6	62	66	150						35.0
57	6	6	62	66	140						35.2
58	15	6	62	65	148						35.2
59	7	5	63	66	141						35.1
60	10	2	63	67	142						34.9
61	14	2	62	68	146						35.0
62	10	2	63	68	143						34.9
63	7	3	63	68	141						34.9
64	7	2	63	69	141						35.0
65	10	3	61	69	143						34.6
66	14	3	57	69	143			3		3	33.2
67	6	3	57	69	135						33.4
68	3	4	57	69	133						33.4
69	8	4	56	69	137						33.4
70	4	5	59	69	137						33.5
71	14	5	59	69	147						33.4
72	7	5	58	69	139						33.4
73	9	5	59	68	141						33.3
74	6	5	58	69	138						33.4
75	6	5	57	69	137						32.7
76	9	6	56	70	141			1		1	32.6
77	5	4	55	71	135			1		1	32.2
78	4	5	55	71	135						32.3
79	1	7	55	72	135						32.5
80	10	8	55	72	145						32.4
81	6	6	57	72	141						32.3
82	8	7	56	72	143						32.2
83	7	5	56	72	140						32.2
84	6	5	56	72	139						32.1
85	4	6	56	72	138						32.3
86	8	6	56	72	142						32.1
87	3	7	56	72	138						32.1
88	5	7	57	72	141						32.2
89	3	4	55	74	136			1		1	32.0
90	5	5	56	72	138						31.5
91	6	6	56	71	139						31.9
92	6	6	56	71	139						31.9

See footnotes at end of table.

TABLE A-4.—*Weekly population numbers and weights, population* D—Continued

Week No.	Number of fish					Number natural deaths					Weight (grams)
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
93	6	7	56	71	140						32.1
94	6	7	57	71	141						32.1
95	5	7	57	72	141						32.9
96	7	7	56	70	140				2	2	31.3
97	7	7	55	70	139						31.2
98	9	8	55	73	145						31.6
99	8	9	52	73	142			3		3	31.3
100	8	9	52	73	142						31.5
101	4	10	54	72	140				1	1	31.6
102	7	12	54	72	145	1				1	32.5
103	15	12	54	72	153						32.8
104	12	11	54	73	150						32.6
105	10	12	54	73	149						33.5
106	10	11	55	73	149			1		1	33.4
107	6	11	57	73	147				1	1	34.0
108	6	10	57	73	146			1		1	33.7
109	7	10	55	77	149			2		2	34.6
110	9	9	55	77	150						34.5
111	10	7	55	79	151						34.9
112	13	6	56	79	154						34.7
113	12	5	57	79	153						35.3
114	11	5	56	79	151			1		1	35.5
115	9	7	56	81	153						35.7
116	18	7	56	81	162						35.4
117	16	7	55	81	159						36.0
118	12	7	56	79	154						35.6
119	8	8	56	77	149				3	3	34.5
120	17	10	56	77	160						34.9
121	7	9	55	77	148			1		1	35.0
122	11	13	56	77	157						35.6
123	6	10	56	80	152			1		1	35.7
124	14	11	56	80	161						35.7
125	7	11	54	80	152			2		2	35.4
126	7	10	54	82	153						35.5
127	7	10	54	82	153			1		1	35.2
128	8	8	52	81	149			2	1	3	34.8
129	8	12	50	80	150			1	1	2	34.5
130	10	11	51	79	151				2	2	34.4
131	6	10	51	79	146				1	1	34.3
132	5	11	49	79	144			1	1	2	33.9
133	0	13	48	79	140			2		2	34.3
134	1	12	48	79	140					[2] 1	33.6
135	2	12	48	78	140						34.0
136	2	9	49	79	139						34.5
137	8	10	47	79	144			1		1	34.5
138	10	10	47	78	145						34.5
139	11	8	47	79	145						34.3
140	9	7	47	79	142						34.1
141	8	5	46	80	139						34.0
142	7	5	44	79	135		1		1	2	33.5
143	5	3	41	80	129			2	1	3	32.7
144	12	5	36	80	133			4		4	30.8
145	8	5	34	79	126			2	1	3	30.6
146	6	5	32	78	121			2	2	4	30.0
147	3	5	31	78	117			1	1	2	29.8
148	2	5	32	77	116				1	1	29.9
149	4	5	31	72	112				5	[2] 6	27.2
150	5	5	29	73	112			1		1	27.8
151	5	3	30	72	110				2	2	26.9
152	4	4	30	72	110						27.2
153	9	3	29	71	112				1	1	26.5
154	10	3	29	70	112						26.5
155	15	3	28	70	116			1		1	27.0
156	21	2	27	70	120			1	1	2	27.0
157	17	2	25	68	112			1	1	2	26.2
158	17	2	25	66	110			1	1	2	26.2
159	27	5	24	66	122					[2] 1	26.8
160	30	4	24	66	124						26.8
161	23	7	24	66	120			1		1	26.5
162	36	12	25	65	138			1	1	2	26.8
163	31	13	25	64	133				1	1	26.7
164	34	13	28	63	136			1		1	27.0
165	36	12	28	62	138				2	2	26.5
166	29	16	26	61	132			1	2	3	26.7
167	32	24	26	60	142				2	2	27.0
168	16	21	27	60	124						26.8
169	22	19	27	63	131		1			1	27.0
170	13	18	28	63	122				1	1	27.0
171	11	20	29	62	122			1	1	2	27.1
172	10	17	30	64	121			1		1	27.0
173	4	18	29	65	116				1	1	26.9
174	4	19	29	65	117						27.2

[1] Not listed separately; included in Immature.
[2] Includes one fish of unknown sex.

TABLE A–5.—*Temperature record, water bath, all populations*

[Data are for period from count time of previous week, taken as noon of count day, to count time at week listed, from thermograph records]

Week No.	Temperature			Week No.	Temperature			Week No.	Temperature		
	Average	Minimum	Maximum		Average	Minimum	Maximum		Average	Minimum	Maximum
6	74.8	72.5	77.0	63	77.2	72.0	79.5	120	73.1	72.0	79.5
7	75.5	73.5	77.5	64	77.4	67.5	83.5	121	72.4	72.0	73.5
8	74.1	73.0	77.5	65	75.6	72.0	79.5	122	72.4	72.0	73.0
9	75.0	72.5	77.0	66	74.9	73.0	79.0	123	72.3	72.0	72.5
10	75.8	71.5	79.0	67	74.6	74.0	77.0	124	72.5	71.5	80.5
11	75.2	73.5	76.5	68	74.7	74.5	77.5	125	73.0	71.5	80.5
12	75.1	73.0	76.6	69	74.7	74.5	75.0	126	72.2	71.5	79.5
13	77.8	74.5	79.0	70	74.7	74.5	75.0	127	73.5	71.5	75.5
14	77.4	75.0	78.5	71	74.4	74.5	76.0	128	75.4	72.0	84.0
15	76.8	73.0	79.0	72	74.8	74.5	77.5	129	75.0	70.0	83.0
16	78.5	76.5	80.5	73	74.7	74.5	77.0	130	75.6	70.0	85.0
17	77.2	75.5	80.0	74	75.7	74.5	78.5	131	77.0	72.0	84.0
18	78.8	76.0	80.0	75	75.2	74.5	78.5	132	76.9	71.5	85.0
19	75.3	72.0	76.0	76	76.9	74.5	79.5	133	74.9	71.0	82.0
20	78.6	75.0	80.0	77	75.4	74.5	77.5	134	76.5	71.0	85.0
21	79.3	77.0	81.5	78	75.3	74.0	77.0	135	73.5	70.5	82.0
22	76.3	74.0	79.0	79	75.0	73.0	76.5	136	71.6	70.5	76.5
23	78.2	76.0	81.0	80	75.2	73.0	79.5	137	73.9	70.5	83.0
24	76.8	74.0	81.0	81	75.4	72.0	79.0	138	76.3	70.5	83.5
25	76.6	74.0	80.0	82	75.9	72.0	79.0	139	71.3	70.5	77.0
26	75.6	73.0	78.5	83	75.8	71.0	79.5	140	72.3	71.0	77.5
27	74.6	73.0	76.5	84	77.8	73.5	79.5	141	76.2	67.5	83.5
28	75.4	73.5	78.5	85	76.1	69.0	78.5	142	75.9	70.5	83.5
29	74.6	73.5	75.5	86	74.5	69.5	78.5	143	73.8	69.5	83.0
30	74.8	73.0	76.0	87	76.6	70.0	80.0	144	77.6	72.5	87.5
31	75.2	74.0	76.5	88	77.0	71.5	79.0	145	72.0	65.5	78.0
32	74.1	72.5	75.5	89	76.3	67.5	79.0	146	76.7	72.5	82.5
33	76.9	72.0	79.5	90	74.3	66.5	77.5	147	78.1	70.0	84.5
34	75.5	72.0	78.5	91	75.9	68.5	78.0	148	73.8	66.5	83.0
35	75.2	72.0	80.0	92	74.9	67.5	78.0	149	76.1	68.0	86.0
36	73.8	71.5	77.0	93	75.4	69.0	77.0	150	73.6	66.5	84.5
37	76.2	73.0	78.5	94	74.4	68.0	77.0	151	75.2	69.0	87.5
38	73.6	70.5	74.5	95	74.3	67.5	77.5	152	73.8	70.0	82.0
39	77.2	71.5	79.0	96	73.4	67.0	76.0	153	75.2	69.5	85.5
40	75.2	72.0	78.0	97	73.7	67.5	76.0	154	75.6	69.0	83.5
41	73.0	68.0	76.5	98	75.2	68.5	77.5	155	74.2	71.5	84.0
42	75.2	72.5	77.5	99	75.4	69.0	77.5	156	77.3	71.5	87.0
43	75.8	73.5	78.0	100	75.4	69.0	78.5	157	77.9	68.5	85.0
44	74.8	72.5	77.5	101	74.7	68.5	78.5	158	77.4	69.0	87.5
45	76.2	73.0	78.5	102	76.2	69.0	78.5	159	77.0	70.5	86.0
46	74.4	71.5	77.0	103	74.6	68.5	78.5	160	75.9	68.5	84.0
47	73.8	71.0	75.5	104	74.6	68.5	79.5	161	77.8	70.5	87.0
48	77.3	73.5	80.0	105	72.5	68.5	77.0	162	77.4	70.0	85.5
49	76.8	74.0	78.0	106	72.6	68.5	78.0	163	80.8	71.5	84.5
50	77.4	74.0	79.5	107	71.8	68.5	78.0	164	78.0	69.5	85.0
51	77.7	74.0	79.5	108	73.1	68.5	78.5	165	74.8	70.0	82.0
52	74.7	69.0	81.0	109	72.2	68.5	78.0	166	73.5	70.0	81.0
53	72.6	68.0	77.0	110	70.2	68.5	77.5	167	75.1	72.5	83.0
54	74.4	67.5	79.0	111	70.4	68.5	77.5	168	75.6	72.5	86.5
55	74.9	68.0	91.0	112	72.5	70.5	78.0	169	75.9	73.0	83.5
56	72.7	68.5	78.5	113	72.2	70.0	78.5	170	74.5	73.0	76.5
57	74.4	69.0	79.5	114	73.7	68.0	82.0	171	74.3	72.5	78.0
58	75.1	69.0	80.5	115	72.5	68.5	80.5	172	74.7	72.5	78.0
59	75.3	72.0	79.5	116	75.2	70.0	80.5	173	73.8	72.5	78.5
60	74.3	70.0	79.0	117	71.2	70.0	73.5	174	74.0	72.5	76.5
61	73.3	70.5	76.0	118	72.3	72.0	72.5				
62	73.7	69.5	77.0	119	72.4	72.0	77.0				

TABLE A–6.—*Length frequencies (total length) of fish removed, population* A

Length, mm.	Number of fish for week No.—																						
	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109
11																								
12																								
13																								
14																								
15					1																			
16			1		1							1												
17					3													2						
18				2			1		2	1	2		1											1
19		1	2						1	6	2	1	1									1		
20		2	3	1			3		3	2	1		2				1	1	1			1	1	2
21		1	1	1				1		2	1	1	1			2	1					2		1
22	2	1	6	2	2	2	3	2		1	4	5	2				1	2		2	1	1		1
23	2	2	2	4	2	3	1	2	3		4	3	1	2			1		1	1	1		2	1
24	1	3	1	4	2	3	2	2	1	2	1	1			1	2				1	1		3	1
25	3	5	3		2	3	1	1	3	1	1	1			1				2	1	1	2		2
26	1		1	1	1												1		1	1				
27	1		2																	1	1	1		
28				1			1	1	1		1		1				1					1		
29	1	1		1	3		1				1									1				
30	2		1		1								2						1				1	
31	1						1			1			2	2									1	
32	3		1			3						1		1	1				1					1
33	4	2						1	1													1		
34		1										1			1							1		
35		1					1					1	1			1								1
36				1	1		1				1									1				
37	1			1														1						
38			1																					
39						1				1					1									
40										1						1		1						
41					1								1											
42						1	1																	
43									1								1							
44		1		1																				

Length, mm.	Number of fish for week No.—																						
	112	115	118	121	124	127	130	133	136	139	142	145	148	151	154	157	160	163	166	169	172	174
11	1																					
12																						
13																						
14																						
15						1	1								2		1					
16							1		1			1	1			1	2	1				
17					1		2		1	4		1	2	1	1	1	1	3				
18				1	3		1		5	4	1	4	1	2		2		3				
19		1		1	4	3	3	2	2	3	5	1	2	1	1	2	1			3		
20				1		1	2	7	1	3	5				1	6				3		
21	1			2	2	1	1	3	2	1	3	1	2	3		4		2		1		
22			1	6	3	1		8	3	4	1		4	4		1		1			1	
23	2	1		7	1	3	1	3	3	2	4	5	6	2	1		1				1	
24	1	2	1	5	2	1	1	2	1	2	2	1		3	1		2		1			
25	1	3		9	3	4	1	1	4	1	2	3	1	2		2			1			
26	1		2	3	1				3	2	1	2	1	1						1		
27		1	2	1	2						1		1									
28			1	1				1		1		1									1	1
29	1			1			1					1							1			
30	1			1		2					1							1				
31			1		1	1	1						2									
32				1	1	1		1														
33				1	3						1				1		1					
34	1		1	1			1							1								
35		2		1			1									1						
36	1		1		2									1								
37				3	1					1												
38		1																				
39				1	1	1		1							1							
40									1													
41										1												
42				1				1														
43				1		1																
44												1										

TABLE A–7.—*Length frequencies (total length) of fish removed, population* B

Length, mm.	Number of fish for week No.—																						
	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109
14																								
15										1														
16			1		1																			
17														1		1				1				
18			1						2		3								1					
19								1		3							1	1				1		
20							1	1	4	4	2		2						2		2			
21								1	2	5	3	2	1	2		1		1			1			
22			1					1	2	4	5	4	1		1	1		1		1	2			
23	1	3	1					3	3	2	2	3	1		1	1	1	1		1	2		3	1
24	4	4		2	2	1	1				3	3	1		1	1				4	2	3		1
25	5	3		1	3		1		1		1		2	1			1	2	2			1	1	2
26	3	1	5	1	1		1			1	2	1		1	2		1		1	1		2		
27	4	2		1				1	1	1		1	2			1				1		1	2	1
28	3	3				2					3	1						1		1			1	1
29	5	3					1		1	1			2	1	1		1	1	1	1				1
30	3	3				2					1	1	1	1			1		1		1		1	
31	3	2	1									1		1	1		1					1		2
32			4	1	1							1	1					1	1			1		
33			2	3	1											2								
34			2	2	1										1	1	1				1			
35				2	1													1	1			1	2	
36			1	1			1															1		
37					1	2		1																
38					1	2															1			1
39			1			1							1											
40								1	1		1													
41									1															
42							1																	
43	1							1		1														
44																								
45																								
46																								

Length, mm.	Number of fish for week No.—																					
	112	115	118	121	124	127	130	133	136	139	142	145	148	151	154	157	160	163	166	169	172	174
14								1														
15													3									
16				1		1						2			1							
17				3	1	2	1	5	1	2		3		1		3						
18				3	1	1	5	2			2		1		1	3						
19		1		3	3	3	1	1		3	1	1	6	3	6	1						
20	2			3	3	4	1	1	1	4	1	1	3	6	8		1	1				
21	1			2	3	4	4	1	10	3	3	1		3	4		4	2				
22			1		2	2	2	6	2	1	2	1		2				1				
23	1	1		1	2	3	4	4	4	2	2	1	2	7	1		1					
24	1	2	1	2	1	2	1	2	4	3	1	1	2			2	1			1		
25		2	1	4	3		2	4	2	1	1	2		1	1	2	1	2	1			
26	2		1	6	1	2	2	1	2	1			1	2		1		1				
27				1	1	2	1			2		2	1									
28					1	1				1	3											
29								2														
30				1	1	1				2	1											
31		1								1												
32	1										1											
33				1				1	3			1										
34	1		1	2	1																	
35	1		1	3																		
36			1		1	1					1			1								
37	1			2	1		1		1								1					
38	1			1	2								1									
39		1				1	1								1							
40																						
41				1		1																
42				1		1																
43					1																	
44																						
45																						
46							1															

TABLE A–8.—*Length frequencies (total length) of fish in control populations remaining at end of experiment*

Length, mm.	Number of fish for—		Length, mm.	Number of fish for—		Length, mm.	Number of fish for—	
	Population C	Population D		Population C	Population D		Population C	Population D
9	4	0	22	10	9	35	3	5
10	4	2	23	11	5	36	4	1
11	1	0	24	18	8	37	3	3
12	1	1	25	11	7	38	1	1
13	0	0	26	7	4	39	2	0
14	1	0	27	3	3	40	3	0
15	0	0	28	0	7	41	1	1
16	0	0	29	0	4	42	0	0
17	1	1	30	6	8	43	0	0
18	0	3	31	6	4	44	0	0
19	1	4	32	7	7	45	0	0
20	0	6	33	5	13	46	1	0
21	3	3	34	8	7			

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ANALYSIS OF CATCH STATISTICS OF THE HAWAIIAN SKIPJACK FISHERY

By Daniel T. Yamashita

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ABSTRACT

The catch statistics of the Hawaiian skipjack fishery and its associated live-bait fishery for the period 1900 through 1953 are brought together from all available records.

The various facets of the live-bait fishery, the only important one in the central Pacific, the methods of data collection for the skipjack and live-bait fisheries, and the completeness and accuracy of the catch records, are analyzed. Skipjack records in terms of weight caught were nearly complete for 1945 through 1953, as an estimated 94 percent of the catch was reported compared with an estimate of only two-thirds to three-fourths of the catch in earlier records. The bait-catch records for 1946 through 1953 were approximately 75 percent complete.

A description of the 1953 fishing fleet and the essential specifications of the sampans in the Territory of Hawaii, information which may be useful in evaluating future changes in catch per unit of effort, are presented.

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ANALYSIS OF CATCH STATISTICS OF THE HAWAIIAN SKIPJACK FISHERY

By DANIEL T. YAMASHITA, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

The skipjack or aku, *Katsuwonus pelamis* (Linnaeus), is widely distributed over the world, occurring in most tropical and subtropical seas. It supports the largest fishery in Hawaii, both in weight and value of fish taken. The Pacific Oceanic Fishery Investigations (POFI) of the United States Fish and Wildlife Service has studied the Hawaiian fishery and the general biology of the skipjack in this region as a part of its general program of research on the tuna resources of the central Pacific.

This report presents and analyzes the available catch statistics for the Hawaiian skipjack fishery and associated live-bait fishery for the period 1900–1953. It includes historical data necessary to an interpretation of the statistics, and also provides a description of the 1953 fishing fleet, which may be helpful in evaluating future changes in catch per unit of effort. It supplements a previous report by June (1951), in which he described the methods used in the skipjack fishery.

The basic statistics used in this report, unless otherwise stated, have been collected by the Hawaiian Division of Fish and Game, and some have been published in the form of biennial reports and monthly catch reports. The collection of such data is done routinely for fish of all species caught in Hawaiian waters.

I am particularly indebted to Vernon E. Brock, Director of the Hawaiian Division of Fish and Game, for making the catch records available for this analysis, and to Yoshio Yamaguchi and Tamotsu Shimizu for their generous help with this study.

THE SKIPJACK FISHERY

From a modest beginning, when the fish were dried or sold on the fresh market, the Hawaiian skipjack fishery has developed into one of the important industries of Hawaii, with most of the fish now being canned. The present Honolulu cannery was established in 1917 and incorporated in 1922 as the Hawaiian Tuna Packers, Ltd. The Nawiliwili Canning Co., Ltd., began operation in 1951 at Nawiliwili, Kauai, but the cannery closed in 1954. At present, the Honolulu cannery and the fresh market are able to utilize all of the skipjack landed, which annually amounts to about 50 to 70 percent by weight of the total fish taken in the Territory.

The available statistics on these landings are presented in figure 1 and tables 1 and 2. These data show landings of less than a million pounds in 1900 and 1903, an annual average of about 5 million pounds from 1928 to 1936, and a pre-World War II peak of more than 13 million pounds in 1940. After the war the landings built up, with minor interruptions, from a low of less than a million pounds in 1944 to a peak of 12.9 million pounds in 1951, which was followed by a poor catch in 1952 and another good year in 1953.

TABLE 1.—*Weight and value of Hawaiian skipjack* (Katsuwonus pelamis) *landed before and during early period of World War II*

[Landings: in thousands of pounds; price: per pound]

Year	Market		Cannery		Total landings	Average price/pound
	Landings	Price	Landings	Price		
1900	422	$0.100			422	$0.100
1903	761	.041			761	.041
1928 [1]	2,878	.069	1,547	$0.020	4,425	.052
1929 [1]	2,964	.071	374	.026	3,338	.066
1930 [1]	3,918	.053	2,319	.023	6,237	.042
1931 [1]					6,123	
1932 [1]					3,162	.058
1933 [1]	2,892	.046	2,669	.020	5,561	.034
1934 [1]	2,982	.047	4,942	.023	7,924	.032
1935 [1]	4,873	.044			4,873	.044
1936 [1]	4,674	.038	[2] 989	[2] .037	5,663	.038
1936 [3]			2,071	.036	2,071	.036
1937	403	.053	12,384	.038	12,787	.039
1938	494	.054	9,228	.040	9,722	.041
1939	407	.058	8,198	.040	8,605	.041
1940	2,112	.036	11,308	.040	13,420	.039
1941	1,050	.040	2,602	.040	3,652	.040
1942					10	.278

[1] Fiscal year ending June 30.
[2] January to June 1936.
[3] July to December 1936.

NOTE.—Approved for publication April 4, 1957. Fishery Bulletin 134.

TABLE 2.—*Weight and value of Hawaiian skipjack* (Katsuwonus pelamis) *landed March 1944 to December 1953*

[Based on catch records of the Hawaiian Division of Fish and Game]

Year	January	February	March	April	May	June	July
1944:							
Pounds sold			41,668	68,914	132,524	76,751	35,882
Price/pound			$0.293	$0.278	$0.242	$0.258	$0.273
1945:							
Pounds sold	71,065	74,278	84,747	99,384	160,199	135,327	532,071
Price/pound	$0.272	$0.250	$0.251	$0.251	$0.262	$0.270	$0.253
1946:							
Pounds sold	206,952	249,643	108,119	245,018	612,493	981,592	743,267
Price/pound	$0.240	$0.275	$0.276	$0.274	$0.262	$0.157	$0.154
1947:							
Pounds sold	441,911	163,975	232,612	267,894	316,017	620,835	1,108,642
Price/pound	$0.205	$0.263	$0.272	$0.256	$0.226	$0.146	$0.139
1948: [1]							
Pounds sold	672,053	439,680	236,582	344,552	568,140	1,136,811	2,034,804
Price/pound	$0.172	$0.168	$0.194	$0.187	$0.192	$0.155	$0.145
Pounds caught	602,142 (678,841)	395,448 (444,121)	233,327 (238,972)	335,862 (348,032)	534,758 (573,879)	999,302 (1,148,294)	2,038,345
1949:							
Pounds sold	68,413	116,327	120,615	235,465	1,016,826	2,255,535	1,690,860
Price/pound	$0.319	$0.261	$0.309	$0.304	$0.138	$0.119	$0.124
Pounds caught	68,683	116,625	121,717	236,392	1,020,457	2,260,284	1,696,565
1950:							
Pounds sold	154,562	141,213	186,494	399,497	579,600	982,714	1,942,838
Price/pound	$0.211	$0.204	$0.228	$0.190	$0.152	$0.140	$0.126
Pounds caught	157,066	141,932	187,740	400,973	581,851	985,410	1,948,585
1951: [2]							
Pounds sold	87,123	86,392	94,178	525,796	2,287,977	2,577,022	2,312,616
Price/pound	$0.238	$0.238	$0.379	$0.182	$0.132	$0.128	$0.127
Pounds caught	87,489	87,583	97,094	529,374	2,295,651	2,584,710	2,323,489
1952:							
Pounds sold	28,771	89,606	55,721	384,925	573,965	814,238	1,649,956
Price/pound	$0.276	$0.273	$0.352	$0.186	$0.165	$0.141	$0.133
Pounds caught	29,054	89,958	55,867	387,141	577,992	818,345	1,654,397
1953:							
Pounds sold	195,193	203,203	575,884	862,125	1,236,649	2,237,334	1,507,242
Price/pound	$0.248	$0.204	$0.148	$0.134	$0.128	$0.125	$0.125
Pounds caught	200,197	204,139	576,345	863,700	1,239,585	2,241,430	1,509,773
Weighted average price/pound	$0.211	$0.224	$0.226	$0.196	$0.160	$0.136	$0.137

Year	August	September	October	November	December	Total catch	Weighted average price/pound
1944:							
Pounds sold	59,233	99,016	123,744	33,921	62,359	734,012	
Price/pound	$0.254	$0.254	$0.259	$0.231	$0.278		$0.259
1945:							
Pounds sold	760,035	663,842	662,358	436,738	227,258	3,907,302	
Price/pound	$0.282	$0.275	$0.253	$0.255	$0.264		0.264
1946:							
Pounds sold	720,829	589,146	655,367	400,981	116,844	5,630,251	
Price/pound	$0.136	$0.147	$0.141	$0.237	$0.326		0.187
1947:							
Pounds sold	634,219	507,044	373,019	465,272	460,096	5,591,536	
Price/pound	$0.146	$0.145	$0.160	$0.178	$0.179		0.174
1948: [1]							
Pounds sold	1,290,683	878,024	422,843	234,227	78,552	8,336,951	
Price/pound	$0.144	$0.152	$0.175	$0.225	$0.253		0.162
Pounds caught	1,296,645	879,362	423,636	234,840	78,974	8,052,641 (8,383,941)	
1949:							
Pounds sold	2,421,441	1,035,291	490,509	255,122	157,605	9,864,009	
Price/pound	$0.121	$0.129	$0.153	$0.186	$0.178		0.138
Pounds caught	2,426,601	1,038,151	491,960	258,735	158,516	9,894,686	
1950:							
Pounds sold	1,801,779	1,174,012	1,020,678	706,048	391,867	9,481,302	
Price/pound	$0.136	$0.133	$0.134	$0.132	$0.153		0.142
Pounds caught	1,805,031	1,176,794	1,022,590	708,271	395,179	9,511,422	
1951: [2]							
Pounds sold	2,672,960	1,384,488	410,181	247,062	188,489	12,874,274	
Price/pound	$0.125	$0.117	$0.136	$0.164	$0.189		0.134
Pounds caught	2,683,270	1,387,647	411,595	248,094	190,313	12,926,309	
1952:							
Pounds sold	1,751,162	983,537	574,324	109,792	248,022	7,264,019	
Price/pound	$0.129	$0.134	$0.136	$0.202	$0.214		0.146
Pounds caught	1,758,153	986,554	575,603	110,138	248,649	7,291,851	
1953:							
Pounds sold	2,138,806	1,278,507	1,196,400	217,364	381,830	12,030,537	
Price/pound	$0.123	$0.129	$0.132	$0.161	$0.144		0.132
Pounds caught	2,142,181	1,281,278	1,199,164	218,077	383,537	12,059,406	
Weighted average price/pound	$0.138	$0.145	$0.157	$0.190	$0.194		0.154

[1] Summarized late reports for pounds caught not available for January through June 1948. Adjusted catches, in parentheses, based on weight sold; future references to total catches for 1948 will be based on these figures.

[2] Published monthly catch statistics changed from pounds sold to pounds caught in November 1951.

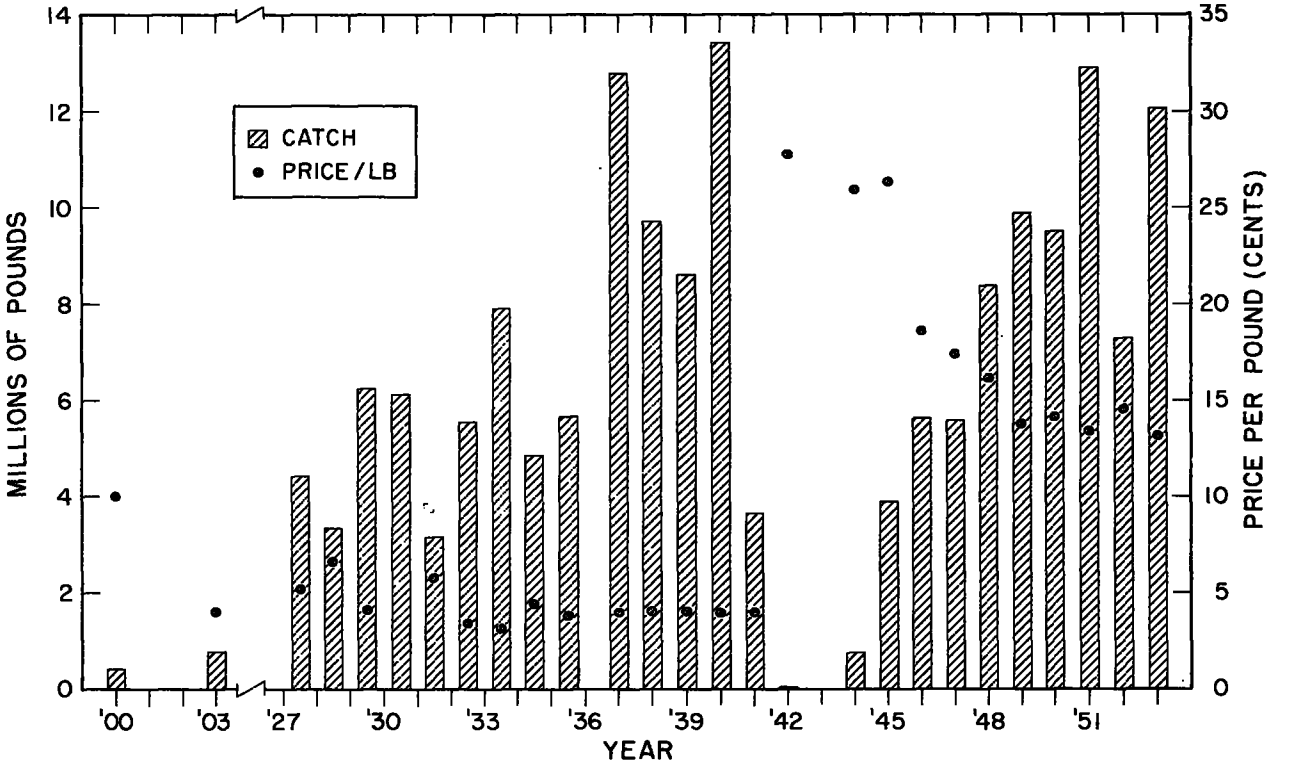

FIGURE 1.—Annual Hawaiian skipjack catch (weight sold) and price per pound for all available years, 1900–1953. The data for 1928–36 are by fiscal years (July to June); data for 1937–53 are by calendar years.

The number of boats (sampans) engaged in the local fishery has varied only slightly in recent years. There were 26 boats actively fishing for skipjack in 1953 as compared with 32 in 1948 (June 1951). This apparent decrease during the 5-year period may have resulted from a change in the interpretation of what constitutes a skipjack vessel. Many of the smaller craft that fish for skipjack on a part-time basis may not have been included in the 1953 records. Between 1948 and 1953 only 2 new sampans joined the fleet, but 2 of the older boats (not included in the total count) were wrecked and lost during 1953.

The size and design of the sampans are essentially as described by June (1951). The boats range from 58.3 to 80.5 feet in registered length and generally are of wooden construction—only two have steel hulls. All are equipped with diesel engines and are driven by a single screw. A major change in recent years has been the replacement of some of the older engines with new high-speed engines rated up to 450 horsepower. As fishing is usually done close to port and the catch is landed within a few hours of capture, the sampans do not have mechanical refrigeration systems but some carry ice. The basic specifications and distribution, by islands, of the 26 full-time skipjack boats operating in 1953 are given in appendix table 1, page 272.

The usual sequence of operations of a Hawaiian skipjack sampan is to catch bait on 1 or more days, depart for the fishing grounds early in the morning, fish, then return to port and unload the catch that night. If sufficient bait remains, the boat may depart the next day for the fishing grounds; if not, the operational sequence is repeated.

CATCH STATISTICS

Methods of Collection

The systematic collection of fishery statistics in Hawaii has evolved from occasional surveys through a stage of regular but relatively incomplete coverage to the present system, which endeavors to record the complete commercial production in the Territory.

The first statistics on the Hawaiian fishery, for 1900 and 1903, were believed to be complete by Cobb (1902, 1905), who collected them. In 1925,

the legislature enacted a law requiring catch reports of fish dealers in the ports of Honolulu and Hilo. These reports, estimated to be two-thirds to three-fourths complete (Hawaii Commissioners of Agriculture and Forestry, 1946), were used in the compiling of the 1928 to 1942 catch records. It is probable that even after this legislation the reporting of catch data was still somewhat erratic, and that in the late 1920's and early 1930's the portion of the total catch reported may have been even smaller than this estimate.

In 1945 the 1925 law was amended to require catch reports from all fish dealers in the Territory; furthermore, a new law enacted in the same year required all owners or agents of licensed fishing craft to report their catches. Although this amendment was not passed until 1945, fish catch statistics from the major islands have been available since 1943. However, the catches for the period January 1943 through February 1944 were reported only in terms of the combined weight of all species landed.

The skipjack-catch report form has gone through a number of revisions since its introduction in March 1944. The initial form applied to all types of fishing on a monthly basis, whereas the present form provides for detailed information on individual fishing trips and is issued for skipjack reporting only (see appendix figs. 1–5, pp. 273-277). The catch statistics were compiled manually until 1947, when the punch-card method using IBM machines was introduced. This change has resulted in the preparation of more complete skipjack statistics since 1948.

In addition to the regular catch reports, interviews on 2 or 3 days a week with captains of the sampans were started in July 1949 (see appendix fig. 6, for a sample of the interview form). These interviews have been continued, during the summer months primarily, in order to obtain a better estimate of the catch per unit of effort of both skipjack and bait. The system was further modified in June 1953 by placing interview sheets on boats with the more cooperative captains who agreed to fill them in routinely. These sheets are collected and checked for additional information.

Completeness and Accuracy

It is apparent from the review of collection methods that the statistics for the Hawaiian skipjack fishery have been collected in a variety of ways and with varying degrees of completeness and accuracy. An evaluation of the more recent catch statistics requires consideration both of the routine followed in the fishery (p. 255) and of the methods by which the statistics are reported.

The skipjack are sold to the cannery on a weight basis, and it is the responsibility of the fishermen or their agents to report the exact weight sold and the price received, together with an estimate of the total weight and number of skipjack caught. The total weight caught must be estimated, since the fish used for home consumption are usually not weighed, nor are those fish weighed that spoiled before they reached the cannery. As the amount caught totals only about 1 percent more than the weight sold, errors in the estimate of total weight are relatively unimportant. The number of fish caught is calculated from an estimate of the average weight of the fish and the total weight of the catch. These reports are required of all persons possessing commercial fishing licenses; however, reports are required only for productive trips.

An important source of error in the catch statistics results from the occasional failure of fishermen to report their catches. An estimate of the unreported catches has been derived from a comparison of interview records and catch reports for 1952. The unproductive trips, which are often reported in the interview records but are not included in the catch reports, have been omitted from this analysis.

To evaluate the accuracy of the skipjack catch records, the extent of agreement between the interview records and the catch reports was determined by comparing the dates and sizes of skipjack catches and the dates and sizes of the bait-fish catches in each. The localities of catch for skipjack and bait were occasionally used as criteria of agreement. Bait-catch localities were usually in agreement in the two sets of reports, but oftentimes discrepancies arose in the reporting of the localities of skipjack catches (see p. 258). Based on the extent of agreement between them, the interview and the catch records were classified into five categories.

The first category is that in which an interview record matches a catch report for a given catch. An interview record was considered to match a catch report when (1) the date of catch as determined by interview was not more than 2 days before the reported date of landing; (2) the bait

catch given in the interview was made on the same day, in the same locality, and in about the same quantity as in the catch report; and (3) the estimated catch in the interview was within 75 percent of the reported catch.

The second category, in which more than 1 day's catch as determined by interviews is included in a single catch report, occurred occasionally when skipjack were caught on successive days without rebaiting. Reports falling in this category were recognized by (1) agreement in size and location of bait catch; (2) agreement (within 75 percent) between the sum of two or more consecutive interview estimates of skipjack catches and the total in the catch report; and (3) correspondence in date (within 2 days) between the last interview and the catch report.

The third category, in which catches listed in catch reports are much higher than those listed in the interview records, occurred in a few instances. Such catches were regarded as suspiciously high if the catches from individual trips of other boats operating during the same period of time were known to be small. In these instances it is believed that the catches shown on the interview records were combined into one catch report with other catches not covered by interviews. The part of the catch probably corresponding to that estimated in the interview was calculated by applying the ratio of weighed to estimated catch for the appropriate month (table 3, col. 8).

The fourth category includes interview records that were definitely not included in the catch reports. They were recognized when a check of all catch reports precluded the possibility of placing them in any one of the first three categories.

The fifth category includes the few instances in which the catch reported is not within 75 percent of the estimated catch from interviews and there is no evidence that would permit classifying the catch reports as category 3. Only 2.8 percent of the reports fell in this category, and these interview and catch records were eliminated from further consideration. Categories 3 and 5 were differentiated by determining whether the catch reports could have included catches not covered by the interview records. If there was any possibility, judging by the available records, of additional catches having been included in the catch report, the reports were placed in category 3.

From the comparison of catch reports and interview records the percentage of trips and the percentage of catch reported have been estimated for these different categories and are summarized in table 3. The trips for which there were interviews, exclusive of unproductive trips and those falling in category 5, have been listed in column 1. Column 2 lists the catches reported separately (category 1), and column 3 the catches reported in combined form (categories 2 and 3). Column 4 shows the percentage of trips reported

TABLE 3.—*Comparison of interview records and catch reports for the Hawaiian skipjack* (Katsuwonus pelamis) *fishery, 1952*

Month	Trips					Catch (in pounds)						
	1	2	3	4	5	6	7	8	9	10	11	12
	Number of trips interviewed [1]	Catch reports, category 1	Catch reports, categories 2 and 3	Percent of trips separately reported	Percent of all trips reported	Estimated catch shown on interview record, category 1	Weighed catch shown on catch report, category 1	Ratio of weighed/estimated catch	Catch shown on interview records, categories 1, 2, 3, and 4	Computed catch all trips interviewed [2]	Catch shown on catch reports, categories, 1, 2, 3, and 4	Percent of catch reported [3]
May	7	5	0	71.4	71.4	20,900	21,489	1.033	25,100	25,928	21,489	82.9
June	26	22	0	84.6	84.6	98,200	104,179	1.061	101,400	107,585	104,179	96.8
July	39	24	6	61.5	76.9	98,500	103,522	1.051	155,090	163,000	145,086	89.0
August	50	36	11	72.0	94.0	313,600	321,674	1.026	409,400	420,044	403,354	96.0
September	40	32	6	80.0	95.0	201,720	219,585	1.089	238,870	260,129	251,080	96.5
October	40	28	7	70.0	87.5	76,850	81,526	1.061	99,450	105,516	92,654	87.8
November	7	4	2	57.1	85.7	9,000	10,873	1.208	11,500	13,892	12,379	89.1
Total	209	151	32			818,670	862,848		1,040,810	1,097,014	1,030,221	
Average				72.2	87.6			1.054				93.9

[1] Exclusive of unproductive trips and category 5.
[2] Column 8×column 9.
[3] Column 11÷column 10.

separately and column 5 the percentage of trips reported both separately and in combined form. On the average, 87.6 percent of the trips recorded by interview were reported in the catch reports; only 72.2 percent were reported as separate trips.

In order to estimate the total catch from the reported catch, it was necessary first to establish the relation between the fisherman's estimate of his catch and the true weight of the catch (table 3, cols. 6, 7, and 8). The results show that the weighed catch averages 1.054 times the estimated catch reported in the interview records since the tendency of the fishermen is to underestimate their catch. The total catch estimated by the fishermen in all interviews (col. 9) has been multiplied by the monthly ratios (col. 8) to obtain a computed total catch that should have been reported for all trips covered by interviews (col. 10). Column 11 includes the total catch from all catch reports that correspond to the interviews (col. 9). The percentage of catch reported (col. 12) averaged 93.9 percent of the probable total catch. This value is somewhat higher than that for percentage of trips reported (87.6 percent), and suggests that the fishermen tended to overlook the small catches in their catch reports. If it is assumed that the percentage by weight reported has been constant for the years 1945 to 1953, then the total annual catch may be estimated as shown in table 4.

A peak catch of 13.7 million pounds was estimated for 1951. If we assume that the prewar peak of 1940 was only three-fourths complete and actually totaled 17.9 million pounds instead of the reported 13.4 million, then the fishery has yet to attain the level of the prewar catches.

TABLE 4.—*Reported and estimated annual skipjack catch, 1937–53*

Year [1]	Reported catch (pounds) [2]	Estimated catch (millions of pounds)
1937	12,787,261	17.0
1938	9,722,150	13.0
1939	8,604,768	11.5
1940	13,420,333	17.9
1945	3,907,302	4.6
1946	5,630,251	6.0
1947	5,591,536	6.0
1948	8,336,951	8.9
1949	9,864,009	10.5
1950	9,481,302	10.1
1951	12,874,274	13.7
1952	7,264,019	7.7
1953	12,030,537	12.8

[1] Reports assumed to be 75 percent complete for years 1937–40 (Hawaii Commissioners of Agriculture and Forestry, 1946) and 93.9 percent complete for 1945–53. No adequate data available for the war years, 1941–44.
[2] Based on weight sold, from Hawaiian Division of Fish and Game records.

Another questionable aspect of the catch records is related to the reporting of the localities in which the catches were made. In the interviews the location was given by distance and direction from some reference point on land, and in the catch reports the location was identified by an area number as shown in fisheries chart No. 2 supplied by the Hawaiian Division of Fish and Game (fig. 2). Although the method of reporting differed between the interviews and the catch reports, gross disagreements in catch localities were readily detected by comparing corresponding reports from the two sources.

With reference to the designated fishing locality, interview records and catch reports were separated into two groups: those showing agreement as to catch locality and those not showing agreement as to catch locality. The reports were considered in agreement if there was general correspondence as to location and distance of the catch from a reference point on land. In spite of rather liberal treatment, the number in agreement was only about 45 percent; in many cases the same catch was reported from opposite ends of an island or even from different islands. Thus, assuming that the true catch locality was given when the two reports were in agreement, and that a fictitious locality was given when there was disagreement between the reports, less than one-half of all reports show the true source of the catch. Hence, any short-term study (within a year) on the localities of skipjack catch should be made in terms of general rather than specific areas if results are to be of value. However, errors in the comparison of specific areas over a period of years should be less important.

Value and Weight of the Landings

The price received by fishermen for skipjack for many years before World War II was about 4 cents a pound, but it jumped to 28 cents when landings were seriously curtailed by the war. The increase in landings after the war was accompanied by a decrease in price, which in 1949 leveled off at about 14 cents a pound (table 2). This is an average of the price paid by the cannery, about 12 cents, and the higher prices received in the fresh fish market, particularly in seasons of low landings. The gross annual receipts to the fishermen were about a million dollars or more from 1945 on and reached a peak of $1.7 million in 1951.

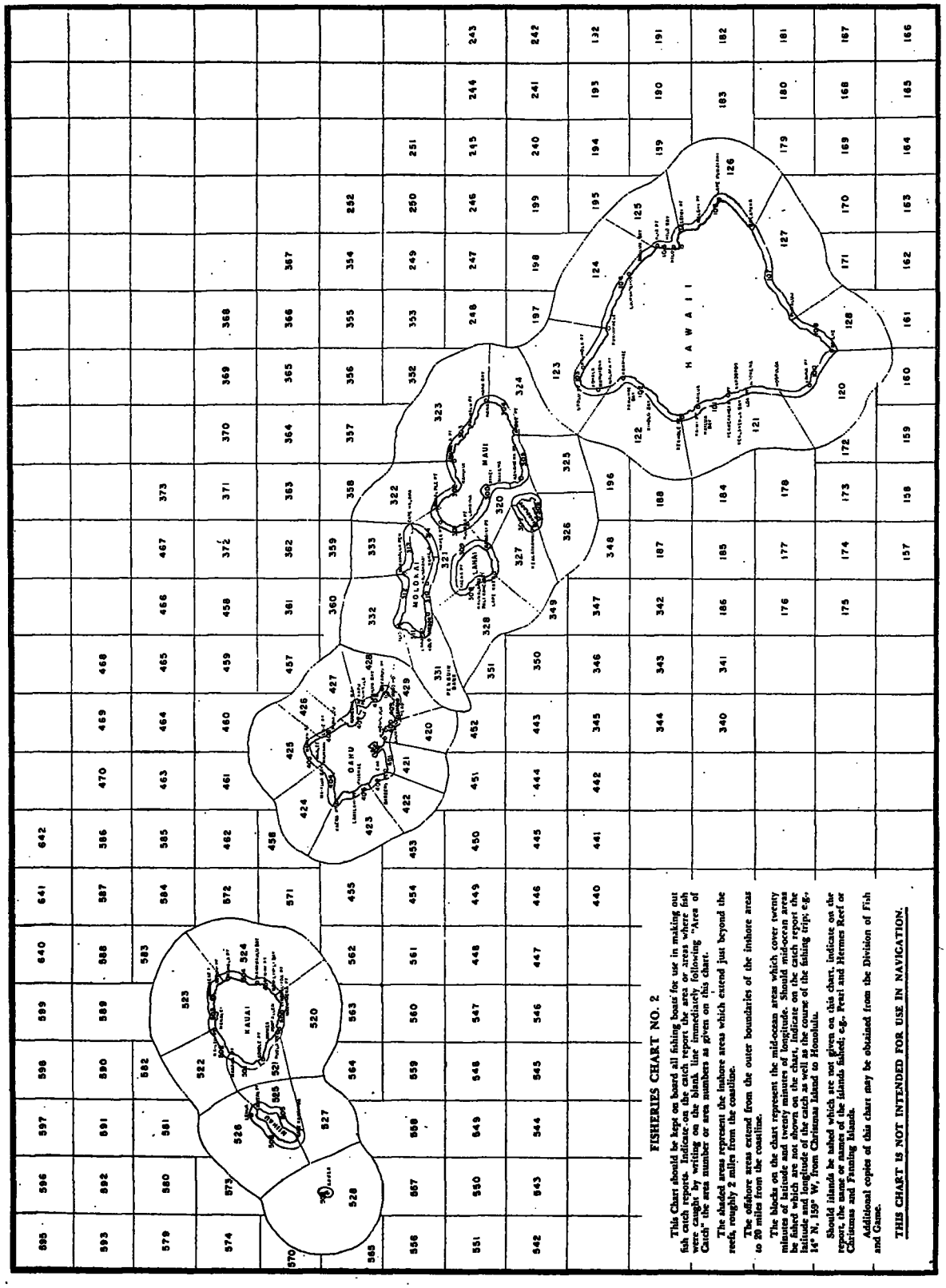

FIGURE 2.—Hawaiian Division of Fish and Game fisheries chart No. 2, showing the statistical areas established for Hawaiian waters.

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From 1928 through 1936 the catch totals were summarized only by fiscal years, but in subsequent years they are available for calendar and fiscal years. In some years the published reports do not designate whether the fish went to the market or to the cannery. In fiscal year 1936, the cannery reported its purchases for the period January through June 1936, but not for July through December 1935. The 1941 catch was low, partly because of the curtailment of fishing resulting from prewar naval maneuvers and wartime restrictions and partly because of the failure of some of the boats to operate during the first 6 months of the year owing to a controversy over the price of fish. None of these factors were serious enough to have distorted the general trend of increasing landings during the period ending in 1940.

Because of a change in the method of collecting data on the skipjack fishery, the postwar (World War II) catch statistics are much more complete than the records from 1928 through 1942. Some variations occur in the published figures, however, because from March 1944 to October 1951 the skipjack catch statistics were published in terms of weight sold, and in November 1951 this was changed to weight caught. Table 2 provides a comparison of the amount caught and the amount sold for the years 1948 to 1953 as compiled from both published and unpublished records of the Hawaiian Division of Fish and Game.

These statistics show an upward trend in the catch from 1944 to 1951, which appears to have been due partly to a changing fleet and partly to a change in relative abundance or availability of skipjack. There was a gradual increase in the number of vessels in operation from 1944 until the beginning of 1947, when about 26 vessels were engaged in full-time skipjack fishing. However, 10 of these sampans did not fish during the first 6 months of 1947 because of a disagreement over prices, and thus the first full year of fishing was 1948. The number of vessels in the fleet has remained nearly constant since the beginning of 1948.

Seasonal Variations in the Catch

The exploitation of skipjack in Hawaiian waters is highly seasonal and the bulk of the catch is landed during the months of May, June, July, August, and September (table 2). The average monthly landings reported for the years 1948 to 1953 are shown in figure 3. The reasons for this large seasonal influx of skipjack into the fishery remain obscure, but food and spawning may influence the movement into the fishery.

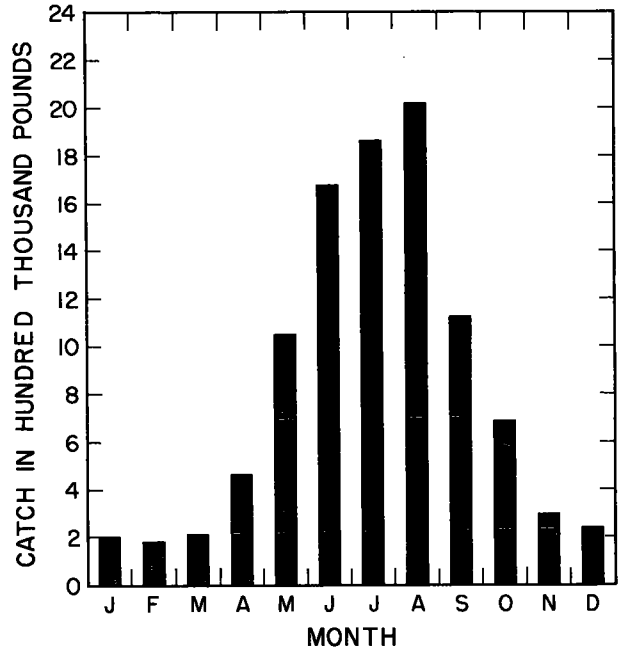

FIGURE 3.—Average monthly skipjack catch, 1948–53, based on records of the Hawaiian Division of Fish and Game.

King and Hida (1954) found that slightly more plankton, and consequently more tuna food, occurs in Hawaiian waters during the summer than in winter. It does not appear plausible, however, that a slight change in the food supply could cause such a marked seasonal fluctuation in the skipjack catch.

On the other hand, fishes are known to undertake long migrations in response to the spawning urge. From an examination of skipjack ovaries in different months of the year, Brock (1954) found indications "that the spawning period probably extended from late February, March, or April to the first part of September," coincidental with the months of high skipjack landings. He also noticed that the fully ripe or spent fish were rarely found in the catches, indicating that they may be unavailable to the fishery when in this condition, and he found evidence that individual fish spawn repeatedly during one spawning season.

POFI investigations on larval tunas (Matsumoto 1958) support Brock's conclusion that skip-

jack spawn during the summer. Matsumoto found that in plankton samples obtained in August, during a cruise in Hawaiian waters, 164 of the 326 identified tuna larvae were skipjack. The dominant size group was less than 6 mm. in length, indicating that spawning could not have been far off either in time or space.

Experiences of skipjack fishermen with spawning fish are also of interest. They have observed that "spawning schools," encountered infrequently during the height of the season, are never fished successfully and, hence, are abandoned for more readily biting schools. The schools are considered to be spawning because they are often seen in a cloud of what is thought to be milt in the water.

If the seasonal abundance of skipjack in the Hawaiian fishery is attributed to a spawning migration, the actual biological or oceanographic conditions causing this movement are not evident at the present time.

Size and Number of Fish in the Catch

The average weight and total number of skipjack caught (table 5) were computed from the catch records for each month from 1948 through 1953. A comparison of the data for those years showed that skipjack were taken in the greatest numbers and that the fish had the highest average weights during the 2 best years, 1951 and 1953 (fig. 4). The variation in number of fish landed between the fair years of 1949 and 1950 and the poor year of 1952 is relatively less than the variation in the total weight of fish landed, suggesting that skipjack may have been equally abundant during these years and that the difference in total catch was largely due to differences in the size of the fish.

The success of fishing, and with it the magnitude of the total catch in weight, is controlled, other things being equal, by a combination of two factors: the absolute numbers of fish available and the size of the fish. The good catches of 1951 and 1953 were due to the presence of large numbers of large fish, whereas the 1952 catch was poor because the skipjack were both few and small. A lesser abundance of fish may be compensated for within limits by the presence of larger fish, e. g., the third largest catch in weight, for the years under consideration, was recorded in 1949, but this year ranked last in the total number of

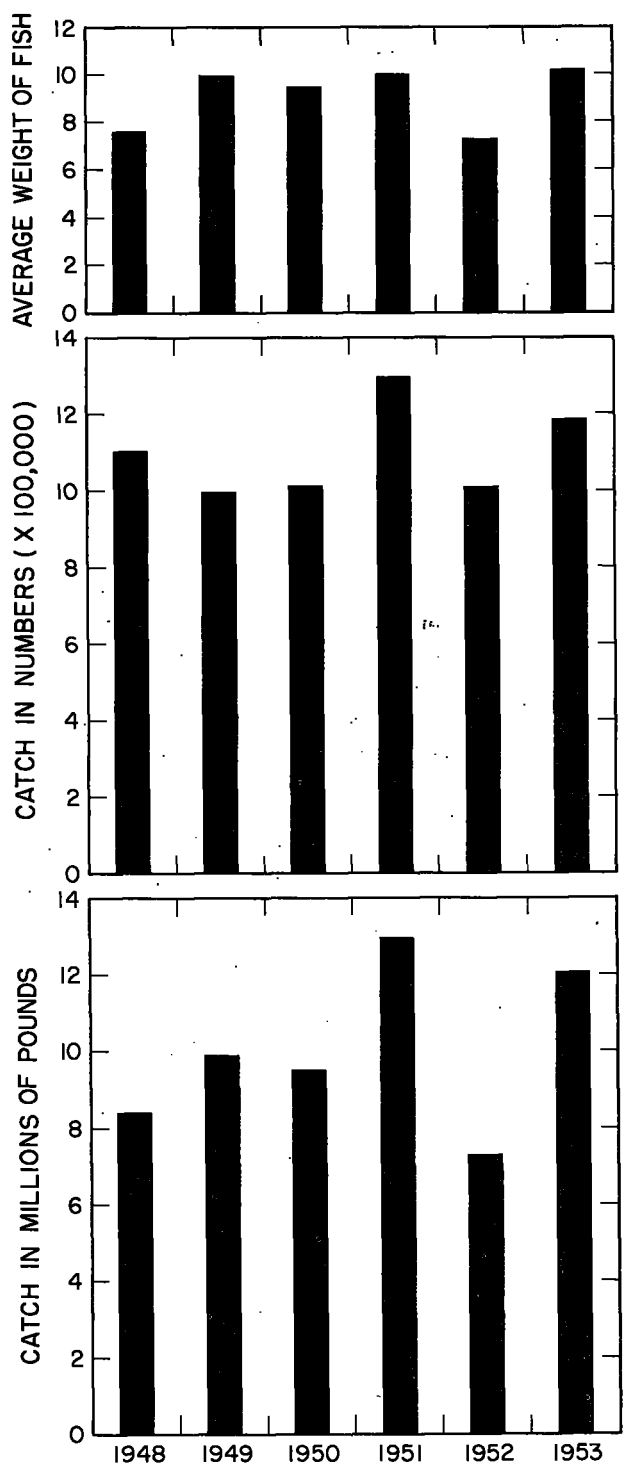

FIGURE 4.—Skipjack catch by average weight and number of fish taken and total catch, 1948–53, based on records of the Hawaiian Division of Fish and Game.

TABLE 5.—*Number and average weight of skipjack landings, by month and year, 1948–53*

[From Hawaiian Division of Fish and Game records; weight in pounds]

Month	1948		1949		1950		1951		1952		1953		Weighted average—	
	Number landed	Average weight	Number landed	Average weight	Number landed	Average weight	Number landed	Average weight	Number landed	Average weight	Number landed	Average weight	Number landed	Weight
January	[1] 66,384	10.226	10,562	6.503	27,344	5.744	11,916	7.342	4,233	6.863	14,902	13.434	24,372	9.024
February	[1] 43,851	10.128	14,121	8.259	21,115	6.722	8,680	10.090	11,527	7.804	26,142	7.809	21,341	8.645
March	[1] 56,454	4.233	15,921	7.645	39,350	4.771	15,281	6.354	7,963	7.016	55,831	10.323	31,672	6.697
April	[1] 78,705	4.422	36,446	6.486	53,179	7.540	61,879	8.555	58,782	6.586	105,278	8.204	66,174	7.014
May	[1] 84,295	6.808	93,758	10.884	80,757	7.205	160,625	14.292	82,230	7.029	128,414	9.653	112,570	9.982
June	[1] 224,583	5.113	160,897	14.048	105,912	9.304	198,916	12.994	101,230	8.084	157,238	14.255	157,348	10.580
July	199,897	10.197	136,194	12.457	117,832	16.537	360,622	6.443	224,538	7.368	190,580	7.922	183,362	9.085
August	130,029	9.972	225,793	10.747	159,610	11.309	232,177	11.557	269,325	6.528	190,823	11.226	197,458	10.028
September	128,336	6.852	137,997	7.523	191,629	6.141	129,978	10.676	113,934	8.659	137,935	9.289	137,358	8.037
October	49,038	8.639	92,231	5.334	100,996	10.125	61,848	6.655	93,412	6.162	106,384	11.272	85,595	8.185
November	30,061	7.812	46,796	5.529	59,554	11.893	32,721	7.582	14,213	7.749	22,339	9.762	35,332	8.645
December	10,922	7.231	23,246	6.819	51,543	7.667	22,411	8.492	25,560	9.728	50,247	7.633	30,590	7.912
Total number	1,102,555	.....	993,962	.....	1,008,821	.....	1,297,054	.....	1,006,947	.....	1,186,113	.....	1,083,172	.....
Weighted average weight	.....	7.604	.....	9.955	.....	9.428	.....	9.966	.....	7.242	.....	10.167	.....	9.107

[1] Calculated from the adjusted total catch.

fish caught. Large catches in weight may also be obtained when large numbers of small fish are caught, however, the chances of a large catch in weight are far greater under the former condition, because the number of fish that can be caught with a given effort is somewhat independent of size for fish averaging less than 20 pounds. One report (Hawaii Commissioners of Agriculture and Forestry, 1952) states that the maximum efficiency can be realized in live-bait fishing by working skipjack schools that average between 15 to 20 pounds per fish. Fishing usually lasts 10 to 15 minutes for any one school or for a single pass at a school, hence a larger total weight can result from a "small number-larger size" combination than from a "large number-smaller size" combination.

Catch by Areas

The fishing of distant offshore grounds by the local fishery is restricted principally by the high bait mortality, the limited range of the sampans, and the lack of refrigeration for the catches. Of these three factors, live-bait mortality must be considered of primary importance. A 100-percent bait mortality even before reaching the fishing grounds is not an uncommon occurrence; consequently, much of the skipjack fishing is done close to the baiting areas.

The skipjack catch by areas, as reported by the fishermen for the years 1948 through 1953, was compiled according to the scheme of area designations used on fisheries chart No. 2 of the Hawaiian Division of Fish and Game (fig. 2). The analysis was made despite discrepancies in the reports of localities of catch, as discussed earlier, for it was felt that although there may be errors in the comparison between the small individual areas (20 square miles) within a year, the errors should be negligible over a number of years and between larger, combined areas.

The localities of capture were divided into 3 major zones: Inshore, within 2 miles of land; coastal, 2 to 20 miles; and offshore, beyond 20 miles. The major portion of the catch (about 75 percent) was caught in the coastal zone, as was shown by Royce and Otsu (1955), and the remaining 25 percent of the catch came almost entirely from the offshore zone; the inshore zone contributed an insignificant amount to the total annual catch (fig. 5).[1]

Examination of skipjack catches with respect to distance offshore shows that, except for 1952, catches from the coastal zone remained fairly constant for the years 1948 to 1953, and ranged from 5.3 million to 8 million pounds. Figure 5 suggests that a total of 8 million pounds per year may be the maximum catch that can be harvested from this zone with the present fishing intensity, as implied by the successful years of 1951 and 1953 when 7.7 million and 8.0 million pounds were caught. If this assumption is correct, any in-

[1] There are some discrepancies in the figures between the total catch and the totals of the three zones because of the rounding off of the catches into thousands of pounds and the omission of some catches from unidentified areas.

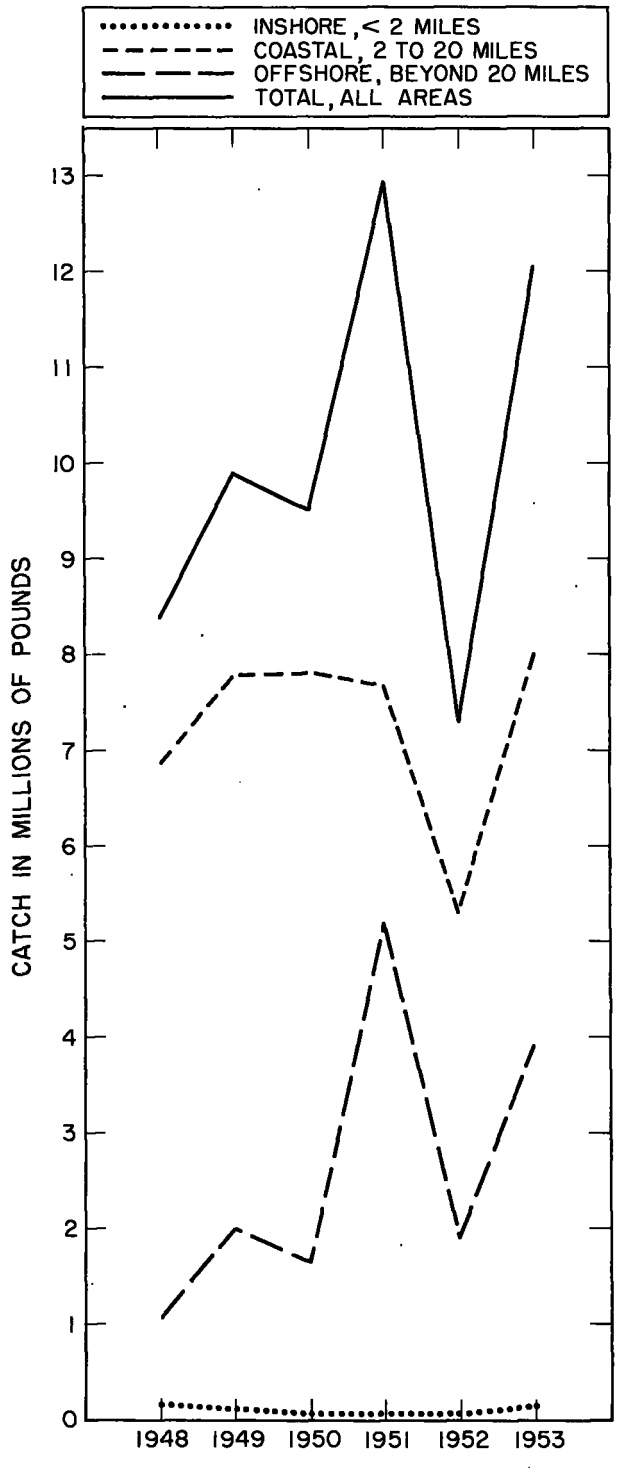

FIGURE 5.—Skipjack catch by zones and total catch from all areas.

crease in the total annual landings must come from increased catches in the offshore zone.

In general, catches from the offshore zone are closely correlated with the catches from all areas (fig. 5). In the record year of 1951, 40 percent of the total catch was taken in the more distant zone and in 1953, 32 percent, whereas during other years not more than 26 percent of the total catch was taken there.

About 90 percent of the annual catch from the offshore zone is obtained from areas between Oahu and Kauai (fig. 6, solid area) and around Oahu, Molokai, and Maui (fig. 6, hatched areas). This distribution of the catch is probably associated with the fact that the majority of the sampans in the fishing fleet are based on Oahu and Maui.

The offshore zone was subdivided into three major regions: Kauai Channel, Oahu-Molokai-Maui, and all other areas, in order to ascertain, if possible, which were the principal localities associated with the major fluctuations in annual catch (fig. 7). The total catch in the offshore zone closely parallels the catch from the region around Oahu-Molokai-Maui. Thus, it appears that the success of a fishing year depends to a large extent on the landings from this particular region.

According to the catch reports, the coastal zone around Oahu was the most productive in the Hawaiian fishery. The skipjack catch from each of the statistical areas (fig. 2, Nos. 420–429) within this zone have ranged from 99,000 to 1 million pounds per year. This apparent concentration of skipjack is probably related in part to the distribution of the fishing fleet on Oahu and in part to the location of the major baiting grounds.

An examination of all areas in the Hawaiian fishery averaging over 100,000 pounds of skipjack per year showed that (1) the best summer catches were made in areas 422 through 427, area 455 off Oahu, and area 125 off Hilo, Hawaii; (2) consistent catches without any pronounced increase during the summer months were made in areas 331, 332, 328, and 428 between Oahu and the Molokai-Lanai area, and area 122 off Kawaihae Bay, Hawaii; and (3) winter landings were relatively higher from the protected lee of the islands, especially areas 328 off Lanai, 423 off Waianae, Oahu, and 122 off Kawaihae Bay.

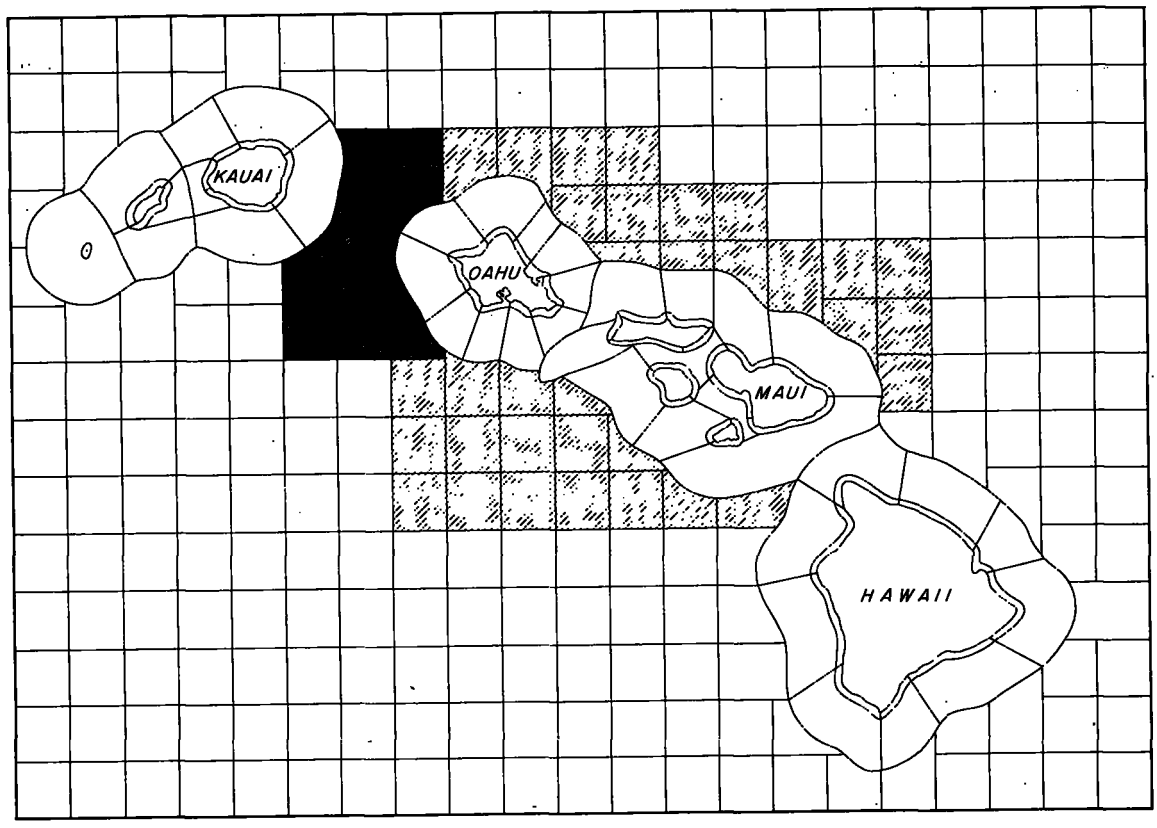

FIGURE 6.—The major offshore fishing zones between Oahu and Kauai (solid area) and around Oahu, Molokai, and Maui (hatched areas), Hawaiian Islands.

During the poor skipjack season of 1952, catches from the coastal zone showed a decline for Oahu and an increase for Kauai. The increase in the catch from Kauai, however, was insufficient to offset the drop in the catch from Oahu, resulting in a net decrease in the catch from all coastal zones. There was also a decrease in catch from the offshore zone, but the catch was still higher than the previous lows from the same zone for 1948 and 1950 when the annual landings amounted to 8.4 million and 9.5 million pounds, respectively, as compared with 7.3 million pounds for 1952. There were 3 productive areas (averaging over 400,000 pounds per year) during the poor year of 1952 that showed an increase in catch over the same areas for the best postwar year, 1951. These localities were all within 20 miles of land: area 125 off Hilo, and areas 331 and 328 southwest of Molokai and Lanai.

The region that shows the most promise of potentially greater productivity is in the offshore zone north of Oahu, Molokai, and Maui, but still within the range of the fishing fleet. The present catches are probably not indicative of the abundance of skipjack in these northern waters because of the low effort expended there, related to generally unfavorable weather conditions. The catch records over the 6-year period show good catches for 1 or 2 years, with no catch reported during other years. The areas to the south of Oahu (fig. 2, Nos. 351, 451–453) have shown evidence of increased production during the last 2 or 3 years.

With the type of vessel in use at present in the skipjack fishery, the most promising immediate prospect of increasing the catch is to exert more effort in the offshore zones, especially around Oahu, Molokai, Maui, and Lanai. The exploitation of these areas might be most feasible during the usual offseason period, when fish are not abundant in the coastal zones.

INDEX OF RELATIVE ABUNDANCE

A general measure of the catch per unit of effort in the skipjack fishery on an annual basis can best

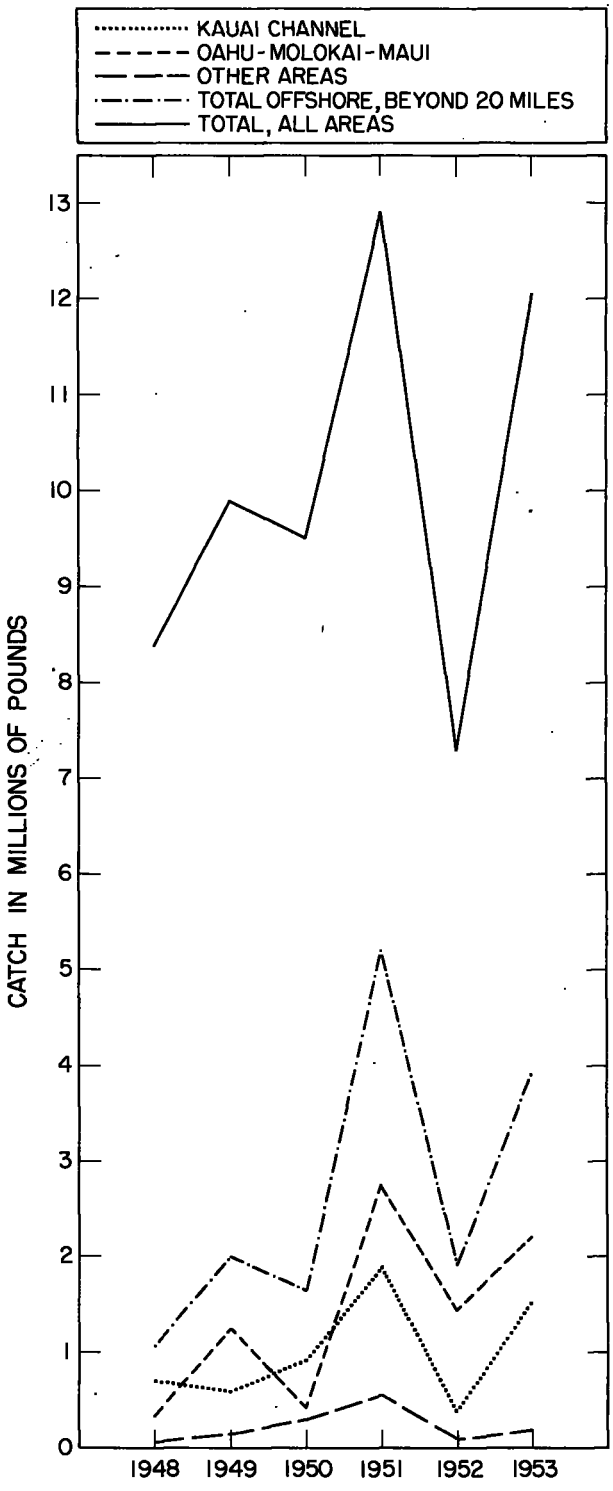

FIGURE 7.—Skipjack catch from the three major divisions of the offshore zone; from all areas beyond 20 miles; and the total catch from all areas: inshore, coastal, and offshore.

be obtained from the reports of the individual fishing trips turned in by the fishermen. A critical examination of the catch reports is necessary, however, to separate the effort expended in catching bait from the actual fishing effort.

In order to obtain some index of relative skipjack abundance, the average catch per productive fishing trip (1 day's fishing) was calculated for one sampan for a number of years and compared with the average catch for a number of other sampans for the same years. Unfortunately, as previously mentioned, the completely unproductive trips could not be accounted for in the analysis due to inadequate records.

Six sampans, A, B, C, D, E, and F, were originally selected for analysis on the basis of reliable catch reports turned in, as determined by comparison of catch and interview data. Two additional sampans, G and H, were included because their catch records showed that the number of trips reported was comparable to the number reported by the others, although their reports could not be verified for reliability, since no interview records were available. All of these vessels were based on Oahu and were representative of the local fishing fleet insofar as size of vessel was concerned.

The original catch records were examined for the years 1948 to 1953, and the average catch per trip was selected as the catch per unit of effort. The criterion used in the selection of the catches was agreement between bait-catch date and fish-landing date, both of which appear on each report sheet (appendix figs. 3 and 4, pp. 275-6). Catches used in this analysis were those in which (1) the landing date and bait-catch date were identical, (2) the landing date immediately followed a baiting date, or (3) the landing date immediately followed another landing date that was preceded by a baiting period during which bait was caught in sufficient quantities for two or three successive fishing trips.

A comparison of the skipjack catch of the selected vessels shows that, as expected, the best individual catches were made during the months of highest total catch for the fishery, and the larger vessels generally made the best catches (table 6). The relation between catches by boats and years, as shown by both the catch of individual boats and the average catch of the eight vessels (table 7), suggests a situation in the fishery different from

that indicated by the total landings. All of the selected vessels with the exception of one (G) enjoyed their most productive trips during 1951, but the catches of only four of the vessels (A, B, D, and H) showed that 1952 was an unusually poor year. Furthermore, even during the relatively good year of 1953, one of the boats (F) made its smallest catch of the period.

TABLE 6.—*Average catch of skipjack per trip of eight vessels, by season, 1948–53*

[Trip=1 day's fishing]

Vessel	Registered length (feet)	Average catch (in pounds) during—		
		Offseason [1]	Preseason and postseason [2]	Main season [3]
A	68	3,252	4,936	7,405
B	67	2,224	3,832	7,316
C	80	3,841	6,507	11,704
D	62	2,773	3,497	5,701
E	77	2,971	5,768	8,409
F	74	3,080	4,706	7,614
G	60	2,010	3,037	6,653
H	70	2,411	3,476	5,468

[1] January–March and November–December.
[2] April–May and September–October.
[3] June–August.

TABLE 7.—*Average catch of skipjack per trip of eight vessels, by years, 1948–53*

[Trip=1 day's fishing]

Vessel	Average catch (in pounds) in—						
	1948	1949	1950	1951	1952	1953	All years [1]
A	5,037	7,494	4,550	9,705	4,450	6,068	6,070
B	4,261	5,903	4,641	7,436	3,683	4,681	5,142
C	6,106	8,197	6,871	10,174	7,104	10,053	8,161
D	3,411	4,284	3,931	6,077	3,391	4,229	4,230
E	5,257	8,259	5,014	10,894	5,265	6,312	6,767
F	.....	6,747	6,110	9,883	4,771	4,724	6,319
G	2,954	4,064	3,797	4,968	3,174	5,624	4,159
H	3,701	5,132	3,647	6,279	2,928	3,938	4,259
Average, all vessels [1]	4,393	6,235	4,878	8,348	4,440	5,788	5,696

[1] Based on total catches and corresponding number of trips.

The average skipjack catches of the eight vessels (based on a total of about 500 trips per year) were compared with the total annual landings (fig. 8), for the period 1948 to 1953. The chief difference between the two curves based on these data is the reversal in rank for the catches of 1949 and 1953. According to the catch-per-trip data, skipjack were in greater abundance in 1949 than in 1953; however, the records indicate a longer fishing season in 1953, and a corresponding larger catch that year. The total catch amounted to 12.1 million pounds in 1953, as compared with 9.9

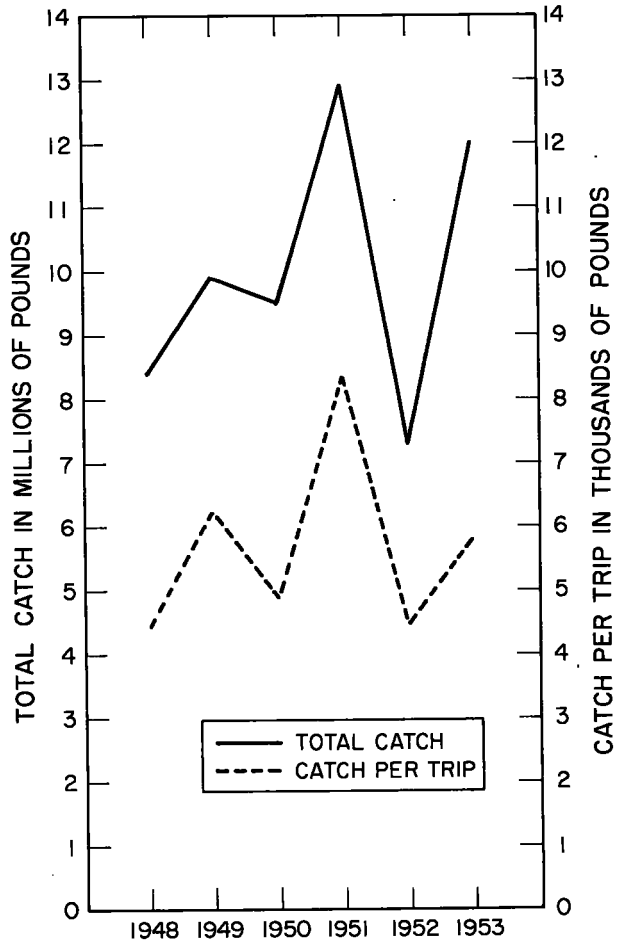

FIGURE 8.—Comparison between total annual landings and average catch per trip of eight sampans, 1948–53.

million pounds in 1949. Since the average weight of fish taken was about the same in both years, the relative abundance of skipjack may have been greater in 1949 than in 1953.

PREDICTING THE CATCH

An examination of the catch by months for the postwar years has produced some evidence of a correlation between the catch in certain early months of the year and in the main season. There is also an indication that the total catch of skipjack in any one year is associated with the size of the year-class 2 or 3 years earlier.

Employing a correlation analysis and the catch records (weight sold) for 8 years, 1946 to 1953,[2]

[2] 1946 and 1947 were not comparable with the more recent years with respect to the number of vessels in the fleet, and during 1953 a greater amount of effort was expended; nevertheless, the catch records for these years were included in this analysis to increase the number of observations.

the following comparisons were made: (1) First 3 months with remainder of the year, (2) April with May through September, (3) April with May through December, (4) April with the remaining 11 months (January to March and May to December) of the year, (5) first 6 months with last 6 months of the year, and (6) last 3 months (October to December) with the subsequent year. In all comparisons except the first, which gave a nonsignificant negative correlation, the results showed nonsignificant positive correlations. The highest correlation value ($r=0.667$, $P=$ca. 0.06) resulted from the comparison of catches for April and the remaining 11 months of the year; this apparent relation, admittedly tenuous, is worthy of closer study when more data are available.

Brock (1954, p. 95), in his analysis of skipjack length frequencies, states that,

> If it is assumed that these modal groups [40–50 cm., 68–72 cm., 79–80 cm.] represent year-classes, the following interpretation of the length frequency data may be made: At some age, perhaps 1 or 2 years, an age group or year-class is first taken in significant amounts by the fishermen during the summer fishing. By the second summer, this age group, at a length of 70 to 75 centimeters, is again taken and, as a matter of fact, is the size group most eagerly sought by the fishermen. This year-class appears again in the catch during the third summer but cannot be traced thereafter with any certainty from the available data.

The comparison between length frequencies of Hawaiian skipjack (Brock 1954, fig. 1) and the annual catch in weight indicates that larger catches are made when the greater percentage of the catch consists of the 68- to 72-cm. size group. Assuming that the seasonal abundance of skipjack in the local fishery is associated with spawning, and that the 68- to 72-cm. size fish are in their second or third year, the abundance of fish for every other year or every third year should be significantly correlated, neglecting, of course, the possibilities of catastrophic larval mortality and any oceanographic changes affecting the return of the spawning stock.

The correlation coefficient resulting from a test of the hypothesis that the annual catches of skipjack (1946–53) from every other year are positively related showed some correlation but was not statistically significant ($r=0.518$, $P>0.05$), and the comparison of the catches from every third year showed no correlation ($r=0.029$).

The possibility of making worthwhile predictions of seasonal or annual catches from preseason data seems doubtful at the present time, although it should be reexamined when a longer time series of catch data is available. The chief hope of prediction probably lies in relating fluctuations in the availability of skipjack with fluctuations in the physical, chemical, or biological properties of the environment.

THE BAIT FISHERY

The local skipjack fishery is primarily dependent on the live-bait supply, and the crew of a sampan may spend up to 50 percent of its time fishing for bait. Baiting, both day and night, may continue for 2 or 3 days before a sufficient supply can be accumulated for 1 day's fishing. Two species are of major importance in the local live-bait fishery: the anchovy or nehu, *Stolephorus purpureus* Fowler and the silverside or iao, *Pranesus insularum* (Jordan and Evermann). The nehu makes up about 92 percent of the catch; the iao most of the remainder. The postwar records show that the annual bait production has averaged about 36,000 buckets,[3] with a maximum of about 42,000 buckets caught under the present fishing intensity (table 8).

[3] A bucket is approximately equal to 7 pounds of fish.

TABLE 8.—*Bait-fish catch, by buckets, 1946–53*

[1 bucket=7 pounds of fish; data from Hawaiian Division of Fish and Game]

Locality	1946	1947	1948	1949	1950	1951	1952	1953
Anchovy (nehu):								
Oahu	16,728	21,690	23,868	27,246	22,360	18,646	14,744	21,470
Maui	6,804	5,448	10,974	7,344	[1] 10,066	[1] 9,537	[1] 6,056	[1] 8,890
Hawaii	1,410	1,470	3,708	2,664	1,671	3,292	3,103	3,718
Kauai	72	534	762	108	526	1,213	1,031	1,614
Molokai	204	150	468	288	738	582	602	76
Lanai			36					
Other			24				10	36
Total	25,218	29,292	39,840	37,650	[1] 35,361	[1] 33,270	[1] 25,546	[1] 35,804
Other bait fish (all islands)	642	1,458	2,196	1,908	[1] 4,277	[1] 7,221	[1] 4,261	[1] 1,878
Grand total	25,860	30,750	42,036	39,558	[1] 39,638	[1] 40,491	[1] 29,807	[1] 37,682

[1] Adjusted bait catch (see pp. 268 and 269).

CATCH STATISTICS

Methods of Collection

Since July 1947 the method of reporting has been based on a system whereby the fishermen turn in a combined skipjack and bait report for each successful fishing trip (but not necessarily for each baiting operation), noting the following information on bait: Date of catch, locality, amount of bait caught, and amount used. These reports are edited, coded, and transferred to punch cards which are in turn transcribed to IBM summary sheets. Unlike the commercial fish catch, the bait catches are not published for circulation; therefore the annual catches by islands must be obtained from IBM record sheets or other summarized records. The interview records have also been a source of information concerning bait catches since July 1949.

Completeness and Accuracy

In order to estimate the proportion of the bait catch reported, an analysis similar to that made on the skipjack catch was followed by comparing interview records and catch reports (table 9). The procedure was slightly modified under the assumption that the catches as reported in the interview records were reasonably accurate (1) because the optimum capacity of the bait boxes was known, and (2) because of the close proximity of the bait-catch date to the interview date.

Interview records (table 9, col. 1) were first compared with corresponding catch reports (col. 2) to determine the accuracy of the catch reports (col. 3). All bait catches as reported in interview records (col. 4) were then checked against all reported catches (col. 5) in order to compute the percentage of the catch reported (col. 6). The reported catch included all the corresponding catches (col. 2) plus the few instances in which the amount of bait caught, as reported in the catch records, was not the original amount caught, but the amount left over from a previous trip. In such instances, the original amount caught was usually not reported, and errors such as this could be detected only by the comparison of interview records and catch reports. All duplicated or partially duplicated catches that could be recognized by an examination of a sequence of catch reports were omitted from this analysis.

Comparison of columns 3 and 6 in table 9 shows that the fishermen made a fairly accurate bait-catch report when they turned in the reports, but frequently they failed to make the bait reports. Analysis showed that each individual bait report may be 91 percent complete, but that only about 75 percent of the total catch was actually accounted for.

There were other irregularities, too. Examination of the summary records showed an apparent marked increase in bait catch reported for Maui waters from 1950 to 1953. This increase coincided with the introduction of a new record form during the summer of 1950. The new forms were very similar to the old except for the changing of the unit of bait measurement from box [4] to bucket (appendix figs. 3 and 4, pp. 275–6). Many of the bait catches from Maui during this period

[4] One box is equivalent to 6 buckets of bait.

TABLE 9.—*Comparison of interview records and catch reports for the bait fishery, 1952*

[Catch, by buckets]

Month	1 Bait catches shown on selected interview records	2 Bait catches shown on catch reports corresponding to interview records in col. 1	3 Percent of bait catch reported in catch reports	4 Bait catch shown on all interview records	5 Bait catch shown on all catch reports corresponding to interview records in col. 4	6 Percent of total catch reported
May	93.5	84.0	89.8	148.5	84.0	56.6
June	509.0	467.0	91.7	585.0	473.0	80.8
July	523.0	494.0	94.4	798.0	504.0	63.2
August	757.5	694.0	91.6	800.5	713.0	89.1
September	742.0	665.0	89.6	835.0	683.0	81.8
October	632.0	567.0	89.7	858.0	599.0	69.8
November	66.0	56.0	84.8	146.0	56.0	38.4
Total	3,323.0	3,027.0		4,171.0	3,112.0	
Average			91.1			74.6

were recorded on the old form, primarily because the Maui vessels were slow to change to the new form. It is believed, however, that most of the vessels, though they used the old form, actually recorded their catches in buckets in compliance with the new regulations. For instance, entries such as 25 boxes of bait for a fishing trip on a sampan with only 6 bait boxes were numerous during this period. However, if these statistics, as recorded in the IBM summary sheets, are converted to buckets (6 buckets per box) in order to make comparisons with recent years, the totals appear unreasonable.

For this study, all the bait caught from Maui waters during the period from 1950 through 1953 was considered in terms of buckets regardless of whether or not it was reported as boxes and regardless of the form used. This could lead to an underestimation of the catch, because some of the vessels may actually have meant boxes, particularly when using the old form. There is little possibility of this adjustment affecting that portion of the bait reported from Maui by non-Maui sampans (primarily those from Oahu), because they quickly adopted the new form. Some underestimation of the catches by Maui vessels must remain, but the general level of the catches they reported was usually larger than 6 (the number of bait boxes on board), suggesting that they were complying with the new regulations although using the old form.

BAITING AREAS

The distribution of bait catch by islands (table 8) shows that Oahu and Maui are the major sources of nehu, as averages of 64 and 25 percent, respectively, of the total catch were reported from these two islands. The important baiting grounds on Oahu are Kaneohe Bay, Pearl Harbor, and Honolulu Harbor, and the bulk of the catch comes from the first two localities. The catch from Pearl Harbor varies according to the extent of the restrictions placed upon the fishery by the United States Navy and is usually less than that taken from Kaneohe Bay. On Maui, about 86 percent of the nehu catch is obtained from Maalaea Bay and the Kihei region. The islands of Hawaii, Kauai, and Molokai contribute lesser amounts to the fishery, largely because of the limited extent of the baiting grounds.

On Oahu, the island supporting the most intensive bait fishery, the annual catch has fluctuated between 15,000 and 27,000 buckets during the period 1946 to 1953. The increase in the catch in 1947 (see table 8) may have been due in part to an increase in the number of sampans operating during the latter part of the year. The slight increase during the following year (1948) was also probably related to the larger number of boats in operation throughout the year. Since the number of vessels remained fairly constant after 1947, the years 1948 to 1953 may be considered comparable insofar as fishing effort for bait is concerned. The considerable increase in the 1949 bait catch may be attributed to the partial lifting of restrictions in Pearl Harbor, making more baiting grounds available to the fishermen. The island of Kauai has shown a general increase in bait catches compared to earlier years, and so has Molokai, except for the year 1953.

The fluctuation in the bait catch on the different islands, aside from availability and abundance, may be due in part to the geographical position of the major islands. The island of Hawaii with only two principal baiting grounds (Kawaihae-Kona region and Hilo Harbor) may be considered as a separate area, whose bait resources are utilized mainly by its own sampans. The islands of Kauai, Oahu, Molokai, and Maui may be grouped together because of the practices followed by the sampans based there. Sampans from Oahu, because of their central location, may bait in Kauai, Molokai, or Maui, as well as Oahu. The sampan stationed in Kauai, on the other hand, may bait in Kauai and Oahu but probably would not exploit the baiting grounds in the more distant island of Maui to any appreciable extent. Likewise, the boats from Maui may bait in Maui, Oahu, or Molokai but will do little baiting, if any, in Kauai, and although Maui is closer to Hawaii than to Oahu, the Maui sampans will favor Oahu because the opportunities of catching bait and possibly unloading their skipjack catches are better there than in Hawaii. Hence, the bait catch from the island of Hawaii has remained constant because of the more or less isolated nature of its fishery, whereas the catches from Kauai and Molokai may have been affected by the amount of effort directed to these islands, depending on the abundance of bait in the major baiting grounds of Oahu and Maui.

SIGNIFICANCE OF BAIT PRODUCTION

On the basis of the foregoing information on bait statistics and the analysis of the completeness of the reported catch, the maximum annual yield of bait may be reestimated to be closer to 50,000 or 60,000 buckets (table 10) than to the reported catch of 42,000. Since it has been found from previous studies that there is about 30 percent mortality of bait associated with the initial period of capture (Hawaii Commissioners of Agriculture and Forestry, 1952) and the reported amount of bait caught may be only 75 percent complete, the total annual bait catch as reported may be roughly comparable to the amount actually utilized in the fishery.

TABLE 10.—*Reported and estimated annual bait catch, 1946–53*

[Reports assumed to be 74.6 percent complete; in thousands of buckets]

Year	Reported catch	Estimated catch
1946	25.9	34.7
1947	30.8	41.3
1948	42.0	56.3
1949	39.6	53.1
1950	39.6	53.1
1951	40.5	54.3
1952	29.8	39.9
1953	37.7	50.5

TABLE 11.—*Relation between live-bait and skipjack catches, 1946–53*

[1 bucket=7 pounds of fish]

Year	Bait catch (buckets)	Skipjack (pounds)	
		Sold	Catch per bucket
1946	25,860	5,630,251	217.7
1947	30,750	5,591,536	181.8
1948	42,036	8,336,951	198.3
1949	39,558	9,864,009	249.4
1950	39,638	9,481,302	239.2
1951	40,491	12,874,274	318.0
1952	29,807	7,264,019	243.7
1953	37,682	12,030,537	319.3

The availability of bait may, in certain years, be a limiting factor in the skipjack fishery. A comparison of the annual bait and skipjack catches (table 11) shows that the catch of skipjack per bucket of bait was higher for 1951 and 1953 than for any of the other years. Apparently, these 2 years represented periods of maximum efficiency with respect to utilization of bait; furthermore, the interviews with fishermen indicated that bait was a limiting factor during these years. During 1947 and 1948, when bait efficiency was low, the amount of bait probably had little effect on production.

An evaluation of the effect of variations in the bait supply is difficult, however, because of numerous other factors affecting the annual skipjack landings. The fish may be equally abundant in different years, but their vulnerability due to biting readiness (slow or fast biting) may differ; thus, more bait may be needed to catch an equal amount of fish in one year than in another. Also, the fish may differ in size between years; thus, the predominance of smaller fish in the fishery would require the use of more bait to catch an equal weight of fish. But, regardless of the efficiency in the utilization of bait, the possibilities of obtaining larger skipjack catches at the present time are more favorable when more live bait is available. Brock [5] has discussed the monthly variations in the weight of skipjack caught per bucket of bait used, and showed that larger catches are obtained during the summer months, when the bulk of the annual catch is landed.

SUMMARY

1. All existing catch records of the Hawaiian skipjack fishery for the period 1900 to 1953 have been brought together in this report. The annual skipjack catch for the more recent years, 1948 to 1953, ranged from 7 million to 13 million pounds, and accounted for 50 to 70 percent by weight of all fish landed in the local commercial fishery.

2. Comparison of interview and catch records indicated that the 1945–53 skipjack catch statistics were approximately 94 percent complete.

3. Because of the variation in size composition of the catch, the apparent relative abundance of skipjack depends on whether the total weight or the total number of fish in the catch is used. In order of decreasing catch by weight, the years may be arranged as follows: 1951, 1953, 1949, 1950, 1948, and 1952. In terms of catch by number of fish, the order becomes 1951, 1953, 1948, 1950, 1952, and 1949.

4. Because of the convenience to the sampans of fishing close to home ports and to baiting grounds, about 75 percent of the skipjack catch

[5] Mimeographed statement "Explanation of tables and figures concerned with use of bait for the years 1950 to 1954," Hawaii Commissioners of Agriculture and Forestry, Division of Fish and Game, Honolulu.

during 1948 to 1953 was taken within 20 miles of land. The catch within this coastal zone has remained relatively constant from year to year (with the exception of 1952); large increases in the annual catch have been the result of increased catches from the offshore zone.

5. The average skipjack catch in weight per trip was used as a possible index of relative abundance and the catch in decreasing order may be arranged as follows: 1951, 1949, 1953, 1950, 1952, and 1948.

6. Attempted predictions of the yearly skipjack catch based on past catch statistics alone are of little value, partly because of the relative shortness of the period under observation. More reliable predictions may be possible in the future when the relation between fish stocks and environment can be ascertained.

7. The expansion of the Hawaiian skipjack fishery has been restricted primarily by the shortage of bait. The principal bait used is nehu (*Stolephorus purpureus*), an anchovy, and the main sources of supply are the inshore waters of Oahu and Maui.

8. An examination of interview records and catch reports indicated that only 75 percent of the total bait catch was reported. In view of the high bait mortality (about 30 percent), the reported bait catch, averaging about 36,000 buckets (252,000 pounds) a year, may be a close approximation of the amount actually used in fishing.

9. The skipjack catch per bucket of bait (7 pounds) ranged from a low of 182 pounds in 1947 to a high of 319 pounds in 1953.

10. Specifications of each full-time skipjack sampan in the Territory of Hawaii for 1953 are presented in the appendix to aid in evaluating future changes in catch that may be related to changes in vessel design.

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APPENDIX

In respect to information listed in the following table, the basic specifications of the full-time Hawaiian skipjack sampans fishing in 1953 were taken primarily from the files of the United States Customs, Marine Division, unless otherwise stated. The various registered measurements, as defined in Merchant Vessels of the United States (United States Treasury, 1952) are as follows:

Registered length "is the length measured on the top of the tonnage deck from the fore part of the outer planking or plating at the bow to the after part of the sternpost of screw steamers and to the after part of the rudderpost of other vessels. The registered length is not usually the same as the overall length nor the load-water-line length."

Registered breadth "is the breadth at its widest part measured from the outer side of the planking or plating on one side to the corresponding point on the opposite side."

Registered depth "is the depth measured from the inner side of the tonnage deck, amidships, to the bottom of the hold. The depth is not the draft of a vessel."

APPENDIX TABLE 1.—*Basic specifications of the full-time Hawaiian skipjack boats (sampans) fishing in 1953*

[All boats with single screw, diesel engine(s)]

Name of boat	Official number	Island	Tonnage		Registered dimensions			Type of hull	Date built	Number in crew	Engine	Horsepower	Bait boxes [1]		
			Gross	Net	Length (ft.)	Breadth (ft.)	Depth (ft.)						Number	Average effective volume (gal.)	Type of circulation
Amberjack	252808	Maui	61	41	70.0	16.0	7.3	Steel	1947	15	General Motors	330	6	1,085	Forced.
America Maru	231965	Oahu	54	33	71.5	14.8	8.8	Wood	1930	10	Gray Marine	330	6	685	Open flow.
Bluefin	238180	do	31	19	66.1	13.1	5.9	do	1927	10	do	225	6	558	Do.
Bonito	239892	do	37	19	67.7	13.8	6.7	do	1940	10	Atlas Imperial [2]	155	6	580	Do.
Broadbill	238206	do	36	11	66.8	12.8	6.0	do	1926	10	General Motors	300	6	614	Do.
Buccaneer	253735	do	68	40	69.4	16.9	7.8	Steel	1947	12	do	330	6	1,232	Forced.
Constance C	238251	do	44	21	60.5	13.2	7.2	Wood	1930	9	Gray Marine [2]	230	6	736	Open flow.
Corsair	257593	Hawaii	51	34	65.0	15.2	7.2	do	1949	12	Atlas Imperial	160	6	1,000	Do.
Darling Dot	254011	Oahu	77	52	80.5	16.9	6.8	do	1947	14	do	250	6	1,297	Do.
Dolphin	239501	Maui	33	17	66.8	12.7	7.3	do	1928	8	Gray Marine [2]	110	6	688	Do.
Electa	237448	Oahu	47	23	72.1	13.5	7.7	do	1938	11	Union	150	6	854	Do.
Helena II [3]	239190	Maui	29	13	65.8	12.3	6.2	do	1928	11	Gray Marine	225	6	575	Do.
Kiyo Maru [4]	238307	Oahu	27	18	58.3	11.8	5.6	do	1937	7	Union	150	6	600	Do.
Marlin	238043	do	44	18	70.0	13.5	5.9	do	1935	11	Caterpillar [2]	275	6	670	Do.
Maui Maru [5]	239364	Maui	29	14	67.3	13.0	5.7	do	1929	9	Gray Marine	165	6	577	Do.
Momi	238185	Oahu	31	15	61.9	12.5	5.5	do	1934	8	Caterpillar	115	6	574	Do.
Neptune	237230	do	46	20	71.5	13.6	6.6	do	1938	10	Atlas Imperial	250	6	839	Do.
Olympic	252822	Maui	38	25	66.8	14.5	6.0	do	1947	10	Gray Marine	450	6	708	Do.
Orion	251045	Oahu	51	23	76.6	16.2	6.7	do	1946	12	Caterpillar [3]	400	6	1,064	Do.
Sailfish	230892	do	51	35	74.4	15.1	6.5	do	1931	10	Atlas Imperial	160	6	1,135	Do.
Skipjack	238265	Hawaii	39	19	71.9	13.9	6.3	do	1928	11	Caterpillar [2]	165	6	785	Do.
Sooty Tern	253367	Maui	45	31	72.8	14.9	6.2	do	1947	13	Gray Marine [2]	330	6	1,127	Do.
S. T. Uruma [6]	252940	Oahu	47	32	72.3	15.7	5.1	do	1947	13	Atlas Imperial	250	6	891	Do.
Sunfish	238284	do	32	15	69.8	12.6	5.8	do	1926	10	Gray Marine [2]	225	6	664	Do.
Tradewind	260364	Kauai	54	34	72.6	15.5	7.3	do	1950	11	Atlas Imperial	200	6	873	Do.
Yellowfin	238314	Oahu	33	17	59.3	12.6	5.9	do	1928	10	Gray Marine	225	6	576	Do.

[1] From unpublished report "Measurements of bait tanks on Territory of Hawaii aku boats" by A. L. Tester, 1949.
[2] From files of the Hawaiian Division of Fish and Game.
[3] Changed to *Ooji* in 1954.
[4] Changed to *Holokahana II* in 1954.
[5] Changed to *Helena II* in 1955.
[6] Changed to *Kilohana* in 1954.

TERRITORY OF HAWAII
BOARD OF COMMISSIONERS OF AGRICULTURE AND FORESTRY

MONTHLY STATEMENT OF FISH CATCH

(One copy must be filed for each boat operated)

Report for month of..... 194.... Name of Operator.....

Commercial ☐ Address.....

Sport - - - ☐ .....

License No..... Approx. No. of Hours Boat was Operated:.....

Boat F. G. No..... Gallons of Gasoline Used in Boats:.....

Gallons of Gasoline Used in Motor Vehicles:.....

DESCRIPTION OF BOAT

Type	Motor: Inboard	Motor: Outboard	Horse Power	Length	Beam	Draft

DISTRICT WHERE FISH CAUGHT:.....

Variety	Weight Caught	No. Lbs. Sold	Price Per Lb.	Total Money Rec'd	Variety	Weight Caught	No. Lbs. Sold	Price Per Lb.	Total Money Rec'd
Ahi					Ulua				
Aku					Weke				
Akule or Hahalalu					Lobster				
A'u					Crabs				
Mahimahi					Opihi				
Moi					Squid				
Sea Mullet					Turtle				
Pond Mullet					Others (List Below) –				
Opakapaka									
Opelu									
TOTAL					TOTAL				

The above statement is true and correct to the best of my knowledge.

Date:..... .....
(Signature)

Witness:.....
(Game Warden)

District:.....

APPENDIX FIGURE 1.—Fish-catch report form; introduced in March 1944 as standard form for reporting all types of fishing.

DIVISION OF FISH AND GAME

FISH CATCH REPORT

Sheet No..... Date.....19.....

Name of Licensee..... Lic. No.....

Name of Boat..... F. and G. No.....

Area of Catch..... Fishing Gear.....

(SEE ZONE MAP)

	SPECIES CAUGHT	NO. CAUGHT	LBS. CAUGHT	LBS. SOLD	VALUE	
TUNAS	Aku					
	Ahi					
	Ahipalaha					
	Bluefin					
	Big Eye					
	Kawakawa					
A'U	Striped					
	Black					
	Broadbill					
	Au Lepe					
	Mahimahi					
	Ono					
	Hapuupuu					
	Kahala					
	Kalekale					
	Omilu					
	Opakapaka					
	Uku					
	Ulaula					
	Ulua					
	Weke-ula					
	Awa					
	Akule					
	Hahalalu					
	Amaama (Sea)					
	Kala					
	Kumu					
	Moi					
	Oio					
	Papai					
	Ula					
	Weke					
	Opelu					
	Iheihe					

BAIT FISH	NEHU	IAO	OTHERS	OPELU (KAAU)
No. of Boxes.....				
Area Taken.....				

The above statement is true and correct to the best of my knowledge.

Signature..... District:.....

THIS COPY FOR DIVISION OF FISH AND GAME

APPENDIX FIGURE 2.—Fish-catch report form; introduced in July 1945 as standard form for reporting all types of fishing.

TERRITORY OF HAWAII
BOARD OF COMMISSIONERS OF AGRICULTURE AND FORESTRY
DIVISION OF FISH AND GAME

FISH CATCH REPORT

Name of Licensee..... License No.....

Name of Boat..... FG No.....

Type of Fishing..... ☐ Fishing Gear..... ☐

FORM C-1 S-B 81645-200 BKS-3-49

Area of Catch..... ☐ (See Fisheries Chart No. 2) Date of Landing..... Mo. ..... Day 19.....

	SPECIES CAUGHT		No. CAUGHT	LBS. CAUGHT	LBS. SOLD	VALUE*
TUNAS 001	Aku (Skipjack)	002				
	Ahi (Yellowfin) (Shibi)	003				
	Ahipalaha (Albacore) (Tombo-shibi)	004				
	Bluefin	005				
	Big-eyed (Menpachi-shibi)	006				
	Kawakawa	007				
SWORD-FISHES (A'U) 008	Striped Marlin	009				
	Black Marlin	010				
	Broadbill Swordfish	011				
	Au lepe (Sailfish)	012				
Mahimahi		013				
Ono		014				

BAIT REPORT

BAIT FISH		DATE TAKEN	LOCALITY TAKEN	QUANTITY TAKEN	QUANTITY USED
Nehu	01			boxes†	boxes†
Iao	02			boxes†	boxes†
Opelu	20			fish	fish
Sardines	07				pounds

* Value represents the amount of money received by the fisherman for total pounds of fish sold. Do not record price per pound.
† One box of livebait is approximately equivalent to 6 buckets of livebait.

The above reports are true, correct, and complete to the best of my knowledge and belief.

Signature..... Port of Landing..... ☐
Licensee or Authorized Agent

Island.....

THIS COPY FOR DIVISION OF FISH AND GAME

APPENDIX FIGURE 3.—Fish-catch report form; introduced in July 1947 as standard form for reporting live-bait (skipjack) and flagline (longline) fishing.

TERRITORY OF HAWAII
BOARD OF COMMISSIONERS OF AGRICULTURE AND FORESTRY
DIVISION OF FISH AND GAME

FISH CATCH REPORT

Name of Permittee..... Boat Permit No.....

Name of Boat..... FG No.....

Type of Fishing..... Fishing Gear.....

FORM C-1 S-B 93859 10M SETS-7-51

Area of Catch..... (See Fisheries Chart*No. 2)

Date of Landing..... ..... 19..... Mo. Day

	SPECIES CAUGHT		No. CAUGHT	LBS. CAUGHT	LBS. SOLD	VALUE*
TUNAS 001	Aku (Skipjack)	002				
	Ahi (Yellowfin) (Shibi)	003				
	Ahipalaha (Albacore) (Tombo-shibi)	004				
	Japanese Bluefin (Black Tuna) (Maguro)	005				
	Big-eye (Menpachi-shibi) ("Bluefin")	006				
	Kawakawa	007				
SWORDFISHES (A'U) 008	Striped Marlin	009				
	Black Marlin	010				
	Short-nose Marlin	107				
	Silver Marlin	108				
	Broadbill Swordfish	011				
	Au lepe (Sailfish)	012				
Mahimahi		013				
Ono		014				

BAIT REPORT

BAIT FISH		DATE TAKEN	TIME TAKEN† DAY	TIME TAKEN† NIGHT	LOCALITY TAKEN	QUANTITY TAKEN	QUANTITY USED
Nehu	41					buckets	buckets
Iao	42					buckets	buckets
Opelu	20					fish	fish
Sardines	07						pounds

* Value represents the amount of money received by the fisherman for total pounds of fish sold. Do not record price per pound.
† Check one to indicate whether baiting was done at day or at night. Applies to livebaiting only.

The above reports are true, correct, and complete to the best of my knowledge and belief.

Signature..... Port of Landing.....
Permittee or Authorized Agent

Island.....

THIS COPY FOR DIVISION OF FISH AND GAME

APPENDIX FIGURE 4.—Fish-catch report form; introduced in July 1950 as standard form for reporting live-bait (skipjack) and flagline (longline) fishing.

BOARD OF COMMISSIONERS OF AGRICULTURE AND FORESTRY

AKU CATCH REPORT

DIVISION OF FISH AND GAME TERRITORY OF HAWAII

C-4

Name of Permittee..... Boat Permit No..... Month..... 19.....

Name of Boat..... F.G. No..... Type Fishing.....

Day of Landing	Area of Catch	Port of Landing	AKU (Skipjack) 002		AHI (Yellowfin) 003			MAHIMAHI 013			KAWAKAWA 007			OTHERS				OTHERS			
			Lbs. Caught	Value*	No. Caught	Lbs. Caught	Value*	No. Caught	Lbs. Caught	Value*	No. Caught	Lbs. Caught	Value*	Species Caught	No	Lbs. Caught	Value*	Species Caught	No.	Lbs. Caught	Value*

BAIT REPORT

Date Taken	Locality Taken		Time Taken †		SPECIES TAKEN			Quantity Taken in Buckets	Quantity Died in Buckets	Quantity Used in Buckets	Quantity Left Over in Buckets
			Day	Night	Nehu 41	Iao 42	Other (Give Name) ‡				

The reports contained hereon are true, correct, and complete to the best of my knowledge and belief.

Signature .....
Permittee or Authorized Agent

* "Value" represents monies received.

† Check one to indicate whether baiting was done day or night.

‡ Check either nehu or iao—write out name of bait fish if other than nehu or iao.

APPENDIX FIGURE 5.—Presently used fish-catch report form; introduced in July 1954 as standard form for reporting live-bait (skipjack) fishing only.

DIVISION OF FISH AND GAME
Board of Agriculture and Forestry
Territory of Hawaii

AKU BOAT INTERVIEW SHEET

(Confidential)

Interview Date..... (MONTH DAY YEAR)

Catch Date..... (MONTH DAY YEAR) Boat..... Captain.....

Time Began to Scout for Fish.....

First School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Second School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Third School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Fourth School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Fifth School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Sixth School Fished: From.....to..... Total Wt.....Av. Wt.....
Catch Locality ..... Am't. of Bait Used.....

Schools Sighted Not Fished

TIME	LOCALITY	ESTIMATED SIZE OF SCHOOL	ESTIMATED AV. WT. OF FISH

Finished for Day ..... Number of Fishermen on Boat.....

BAIT FISHING

	DATE	SPECIES	%	AMOUNT CAUGHT IN BUCKETS	CATCH LOCALITY	TIME SPENT TO CATCH BAIT
Day Bait.....						
Night Bait.....						

Amount of Bait Died.....
(IF POSSIBLE GIVE SPECIES AND AMOUNT BY PERCENT)

Amount of Bait Left.....
(IF POSSIBLE GIVE SPECIES AND AMOUNT BY PERCENT)

Remarks (Sufficient bait for day's fishing, schools fished for but no fish caught, etc.):.....

.....

.....

CONFIDENTIAL

APPENDIX FIGURE 6.—Skipjack interview record form.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

UPTAKE AND ACCUMULATION OF RADIOACTIVE ZINC BY MARINE PLANKTON, FISH, AND SHELLFISH

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AND THOMAS J. PRICE

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ABSTRACT

Zinc concentrations in sea water and in shellfish samples, collected from inshore waters along the Atlantic and Gulf of Mexico coasts are reported. Oysters, clams, and scallops concentrate large amounts of this trace metal, the oysters containing the greatest amounts. Radioactive zinc added to the water was rapidly taken up in great amounts by shellfish. Considerable accumulation of the nuclide takes place in the gills of these mollusks, with high concentrations in the kidneys of scallops, and considerable amounts in the hepatopancreas.

Nitzschia closterium, a marine phytoplankton, took up large amounts of zinc 65 and apparently concentrates zinc, thus allowing its transfer to marine animals. Marine fish quickly take zinc into the body from the digestive tract. Much of the incoming zinc appears to be excreted rather promptly. A rapid uptake of radioactive zinc from an oral dose took place in the kidney, liver, and other internal organs, but the loss of the nuclide was also rapid. A slow and long-continued accumulation took place in bone, integument, and muscle tissues. Although there was immediate loss of contained radioactive zinc when marine fish were returned to flowing sea water, a small percentage remained with only very slight loss over many days.

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UPTAKE AND ACCUMULATION OF RADIOACTIVE ZINC BY MARINE PLANKTON, FISH, AND SHELLFISH

By Walter A. Chipman, Theodore R. Rice, and Thomas J. Price, *Fishery Research Biologists*, Bureau of Commercial Fisheries

In a study by the National Academy of Sciences, the Committee on the Effects of Atomic Radiation on Oceanography and Fisheries (1956, p. 73) state that they have "considered three aspects of the atomic energy program that directly involve the oceans and, therefore, the marine sciences: Weapons tests over or in the sea, disposal of radioactive wastes from nuclear power plants, and the use of radioactive substances in increasing our understanding of the oceans and of the creatures that live in the sea."

It was in anticipation of this third aspect of the atomic-energy program that the series of studies, of which the present is a part, was undertaken. The principal object of this study is not radioactivity and its effects on living things. It is rather to understand the role of trace elements in the metabolism of marine organisms and particularly the role of the very scarce element in sea water, zinc. The radioisotope zinc 65 was used because it permits the employment of the exact and sensitive radioactive-tracer techniques recently developed.

MATERIALS AND METHODS

In recent years chemical methods for the estimation of zinc have been greatly improved. It was thus possible to review the earlier values reported for marine and brackish waters and for the organisms living in these environments. Also, labeling the zinc of sea water with Zn^{65} of high specific activity (considered as the amount of radioactive element per unit weight of the element present) made possible the studies of the rate of incorporation and the accumulation of zinc by marine organisms without appreciably increasing the zinc concentrations to which the organisms were exposed. The detection of Zn^{65} at great dilution, the use of methods of isotopic dilution, and the rate of change of the isotopic concentrations in the various tissues through the use of radioisotope techniques made possible the studies of the zinc uptake and distribution in various types of marine life. These studies, although not too meaningful in explaining precisely the role of zinc in the metabolism of marine plankton, fish, and shellfish, serve as a necessary and a good starting point for future investigations into the nature of the biological systems in which zinc plays a metabolic role.

The species of phytoplankton used was *Nitzschia closterium* maintained in unialgal and bacteria-free culture in the laboratory. Sea water enriched with nutrient chemicals was employed as the culture medium, prepared as previously described (Rice 1953). The marine shellfish included oysters *Crassostrea virginica* Gmelin, hard-shell clams *Venus mercenaria* Linnaeus, and bay scallops *Pecten irradians* Lamarck, collected in the vicinity of the laboratory and held in tanks of flowing sea water. The species of marine fish used, croakers *Micropogon undulatus* Linnaeus, and pinfish *Lagodon rhomboides* Linnaeus, were taken in a small trawl and held in a salt-water tank at the laboratory. The croakers ranged from 5 to 8 inches in length, but were selected to give a uniform size in the tests. The pinfish were from 3½ to 5 inches long.

Chemical estimations of zinc in sea water were made from samples carefully collected in pyrex bottles. A few shellfish samples were tested with freshly collected specimens. Those from distant points were of organisms preserved in alcohol. Care was taken in all instances to avoid metal contamination. The shellfish samples were vacuum dried at 70° C. and aliquots of the dried tissues ashed at 600° C. The ash was dissolved in a small amount of 50-percent HCl and made to a fixed volume with water. Two hundred fifty milliliters of the sea water or aliquots of the dissolved ash were shaken with dithizone and the

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zinc extracted at *p*H 5.5 as zinc dithizonate in carbon tetrachloride following the procedures outlined by Vallee and Gibson (1948). Estimations of the zinc contents were made according to the colorimetric procedures recommended by these authors. The dithizone was purified by the method suggested by Hoch and Vallee (1952).

Except for that used in two series of observations with marine fish, Zn^{65} was cyclotron produced and carrier free obtained in the form of the chloride in acid solution. The disintegration rates reported are based on relative counting of the samples and of dilutions of the original shipment using the concentration stated by the supplier corrected for radiological decay. Most of the measurements were made of liquids with a glass dip-type Geiger-Müller counting tube. In some tests, however, a well-type scintillation crystal was used.

CHEMICAL ESTIMATIONS OF THE ZINC CONTENT OF SEA WATER AND SHELLFISH

Each week for 1 year water samples were taken at the dock at the laboratory at Beaufort, N. C., and analyzed for zinc content. It was determined that there was no significant difference in samples taken at high tide and low tide at this location. The complete range in zinc content was from 1.2 γ to 19.6 γ per liter; the latter, however, was observed when a great amount of fresh water was present following a hurricane. The monthly averages (table 1) show a seasonal pattern with the lowest values for zinc content occurring during the winter months.

Samples of oysters were obtained for measurement of their contained zinc from localities along the Atlantic and Gulf coasts, and samples of clams and scallops were collected from the vicinity of the laboratory at Beaufort. At the time of sampling of the shellfish, sea water also was taken for analysis. The results of the measurements of the oysters and water in which they were living are given in table 2.

TABLE 1.—*Average of weekly observations of the zinc content of the sea water at Beaufort, N. C.*

Month	Zinc in micrograms (γ) per liter	Month	Zinc in micrograms (γ) per liter
November	9.7	May	13.2
December	2.8	June	14.1
January	3.5	July	12.4
February	5.4	August	[1] 14.6
March	5.0	September	12.1
April	12.1	October	11.6

[1] Before hurricane, 12.5; after hurricane, 19.6.

TABLE 2.—*Zinc content of oysters and the surrounding sea water*

[Winter and early spring samples]

Locality	Zinc in oysters (micrograms per gram of fresh tissue)	Zinc in sea water (micrograms per gram)
Milford, Conn	3174	0.0188
Upper Chesapeake Bay	2933	.0240
Lower Chesapeake Bay:		
York River, Va	1295	
James River, Va	1484	.0079
Chincoteague Bay, Md	778	
Beaufort, N. C	1171	.0046
Brunswick, Ga	313	.0011
Gulf of Mexico:		
Pensacola, Fla	600	.0008
Galveston, Tex	391	[1]

[1] Trace.

It is apparent that the area around Milford, Conn., and the upper Chesapeake Bay have a high concentration of zinc. This undoubtedly is related to runoff and pollution, for both of these areas have metal industries of considerable magnitude close by. The inshore waters of the Gulf of Mexico are relatively low in zinc content.

The oysters collected in Long Island Sound near Milford and those from the upper Chesapeake Bay contained more zinc than the others. However, relative to the zinc available in the water, these oysters had a lower concentration factor than those from areas of the Gulf where the zinc content of the water was low. In any case, the oysters were found to concentrate zinc in their bodies thousands of times over the concentration of the surrounding sea water.

In order to compare the zinc content of the tissues of the different shellfish, samples of oysters, scallops, and hard-shell clams were collected from an area not far from the laboratory. In a sample of 25 oysters, the zinc content ranged from 3.70 γ to 6.66 γ per mg. of dried meats. The zinc in this group averaged 5.09 γ per mg. Three groups of 25 scallops each were analyzed for their zinc content, and 19 were tested individually. The zinc content of individual scallops ranged from 0.61 γ to 1.43 γ per mg. of dried tissues, and the average for all groups was 1.04 γ per mg. A sample of 20 hard-shell clams from the area averaged 2.62 γ per mg. of dried meats. It appears that oysters have greater amounts of zinc

in their bodies than clams and scallops, and that scallops are relatively low in zinc content.

The distribution of zinc in the organs and tissues of oysters and scallops was determined on composite samples of the dissected parts of a number of animals. Only the mantle, gills, labial palps, and adductor muscle of the oysters were separated from the remainder of the body. The oysters had considerable stored glycogen and little gonad tissue at the time of year the tests were made. The zinc content of the oysters as a whole was measured at 5.50 γ per mg. of dried tissue. The results of the measurements with oysters are given in table 3. The tissue distribution of zinc

TABLE 3.—*Distribution of zinc in the oyster*

[Based on dried tissue]

Tissue	Zinc content (micrograms per milligram)
Mantle	6.91
Gills	8.02
Labial palps	9.58
Adductor muscle	.61
Remainder	6.69

in scallops was determined in experiments using zinc^{65} and are reported later. The adductor muscle was low in zinc, whereas the labial palps and gills were relatively high.

OBSERVATIONS ON MARINE PHYTOPLANKTON

Toxicity of Zinc

Low concentrations of zinc have been reported to be toxic to higher plants. Since it was desired to study phytoplankton growth in cultures containing added zinc, it was necessary to know that the added element was not above the toxic level for the species used.

Zinc sulfate was added to sea-water culture medium in which the marine diatom *Nitzschia* was grown to give concentrations of 100, 250, 500, 750, and 1,000 γ of zinc per liter. Control cultures were grown in medium without added zinc, the zinc content of which was measured as 15 γ per liter. The lowest concentration used which reduced the division rate of the *Nitzschia* cells below that of the controls was 250 γ per liter. This value is approximately 10 times the highest zinc concentration found in the sea-water samples collected along the Atlantic and Gulf coasts. It seems unlikely that concentrations of zinc in nature would limit phytoplankton growth unless pollution with this element were very great.

Uptake of Radioactive Zinc

To study the uptake of radioactive zinc at sea-water concentrations of the element, a culture containing 43×10^7 *Nitzschia* cells per liter was prepared and enough carrier-free Zn^{65} added to give a concentration of 27 μc (microcuries) per liter. The culture was placed in a cabinet with continuous light from daylight-type fluorescent bulbs giving 800 foot-candles. Aliquot volumes of the culture suspension were removed periodically and filtered, and the radioactivity of the filtrate was determined. The cells removed all but a trace of the Zn^{65} from the medium within 24 hours, 80 percent of it within the first hour. In another experiment, run in a similar manner but in which the cells were not dividing since they were kept in the dark for 48 hours prior to and also during the test, they took up 87 percent of the Zn^{65} from the sea-water medium in 24 hours.

In both experiments the available zinc in the medium entered the cells very rapidly. If the availability of the zinc had been maintained, it is likely that the uptake would have continued and much greater amounts would have been taken by the cells. If the uptake of the Zn^{65} resulted from exchange of zinc between that in the cells and that in the sea water, the same specific activity would be expected inside the cells at isotopic equilibrium as outside. Since the specific activity of the Zn^{65} was very high in the sea water, the observed uptake, if due to exchange, would indicate a very great concentration of zinc in the cells.

If one assumes that the nondividing cells kept in the dark were in isotopic equilibrium with the sea-water medium as regards zinc, and that the difference in the weight per unit volume of the cells and that of the sea water were insignificant, one can estimate a concentration factor for zinc based on the reduction during the 24 hours.

The Zn^{65} of the medium was reduced to 13 percent of its original concentration. To reduce it this amount, it would have been necessary to add 6.7 volumes of nonradioactive water to each volume present, or 6.7 λ (microliters) for each λ present. This would be the equivalent of 6.7×10^9 cubic microns added per each λ present. From

measurements of *Nitzschia* cells, it was determined that a cell had a volume of 375 cubic microns. With a population of 43×10^7 cells per liter, there would be 430 cells per λ, or about 13.1×10^4 cubic microns of nonradioactive cells per λ. The cells therefore had approximately 50,000 times the zinc of the sea water per unit of volume. It should be mentioned that it is likely that less zinc was taken by the cells in this test than would have been if the availability of zinc had been maintained.

To observe the effect of added zinc on its uptake by *Nitzschia* cells, cultures were prepared with sufficient zinc added to give total concentrations of 100 γ, 1,000 γ, and 5,000 γ per liter. To each were added 45 μc of Zn^{65} per liter. Periodically, aliquots were removed, the cells filtered, and radiological measurements made of the filtrate. Based on the labeling of the total zinc with Zn^{65}, giving a known specific activity, the amounts of zinc entering the cells at the different concentrations can be calculated.

The zinc very rapidly entered the cells, much of it within the first hour (table 4). When considerable amounts were present, more was taken by the cells. The cells in the medium having 100 γ of zinc per liter continued their divisions and growth. At the end of 96 hours, the cell population had increased from 7.2×10^7 to 70×10^7 cells per liter. Those in medium containing 1,000 γ and 5,000 γ per liter did not divide. The presence of 5,000 γ of zinc per liter was sufficient to damage the cells, as indicated by a decrease in their zinc content after 48 hours. Because of the great uptake, there was a marked change in the availability, particularly in the culture containing the lowest concentration. It seems likely that more would have been taken by the cells if greater amounts were still available. The amount of zinc per cell at the end of 96 hours was as follows:

Zinc in a liter culture initially	*Zinc per cell after 96 hours*
100 γ	1.4×10^{-6} γ
1,000 γ	96×10^{-6} γ
5,000 γ	361×10^{-6} γ

Realizing that individual *Nitzschia* cells are small in volume and in weight, it is apparent that they can take up tremendous amounts of zinc if available in the sea water, more being taken when the amount present is increased. It is evident that, if Zn^{65} is present in the sea water, the isotope will be accumulated by the phytoplankton.

TABLE 4.—*Uptake of zinc by* Nitzschia *cells from sea water to which was added different amounts of zinc*

[Initial cell population: 7.2×10^7 per liter]

Time in hours	Gammas (micrograms) of zinc in cells of liter culture		
	Culture containing 100 γ/liter	Culture containing 1,000 γ/liter	Culture containing 5,000 γ/liter
1	56	380	1,000
6	67	450	1,250
24	86	600	2,500
48	91	680	2,550
66	96	700	2,200
96	[1] 98	[1] 700	[2] 2,000

[1] Cell increase ten fold.
[2] No increase in cell numbers.

Zinc Requirements for Cell Division

Certain amino acids and their salts have the ability to form nonionic chelates in which polyvalent ions are tightly bound. Such materials have proved useful in determining the nutrient requirements of planktonic algae. One of these, a sodium salt of ethylene-diamine-tetraacetic acid (EDTA) was employed to chelate the zinc in experiments with the *Nitzschia* cells. The addition of EDTA to cultures to which had been added Zn^{65} prevented the uptake of the isotope by the cells, no detectable change in 24 hours in the radioactivity of the medium occurring. It is apparent that the zinc of the sea water in such combination is not available to the cells.

In an experiment in which the *Nitzschia* cells were suspended in culture medium containing 30 μc of Zn^{65} and 0.05 grams of EDTA per liter, the population increased from 0.18×10^7 to 213×10^7 cells per liter in a period of 15 days. The cells had divided an average of 10 times in these cultures in which the available zinc was virtually zero. Also, any zinc leaving the cells would become unavailable to them. During the 15 days, a small amount of the Zn^{65} did leave the sea water, indicating that chelation of the zinc was not complete. However, even though the specific activity of the Zn^{65} was high, cell division proceeded with only extremely small amounts of available zinc.

Loss of Radioactive Zinc

Nitzschia cells, which had been made radioactive by growing in a culture to which had been added Zn^{65}, were filtered from this medium and resuspended in sea water. At intervals, aliquots of the suspension were filtered and the radioactivity

of the filtrate measured. The radioactive zinc lost from the cells during 48 hours was extremely slight, barely measurable.

If the zinc within the cells is exchangeable, the addition of EDTA to the sea water in which the radioactive cells were suspended would chelate the zinc once it left the cells and prevent its return. When this was done, the radioactive zinc entered the sea water and increased in amount with time until 89 percent of that originally in the cells had entered the medium within a period of 48 hours.

Another method of observing the loss of radioisotopes from phytoplankton is to wash the radioactive cells after collecting them on a filter and observe the changes in the radioactivity of the washing medium. The radioisotope leaving the cells is not available for reentry into the cells.

Nitzschia cells containing Zn^{65} were filter-washed with distilled water and with sea-water medium. In some tests, carrier zinc was added to the sea-water washing medium. There was a loss of contained Zn^{65} from the cells to the sea-water medium, the loss being greater when the zinc content of the washing medium was increased (table 5). Very little Zn^{65} was washed from the cells by distilled water. Larger quantities left the cells when the specific activity of the washing medium was lowered from the added zinc. These experiments demonstrate that much of the contained Zn^{65} of *Nitzschia* cells was exchangeable.

TABLE 5.—*Loss of zinc ^{65} from* Nitzschia *cells filter-washed with distilled water and with culture medium containing different amounts of added zinc*

Washing medium	Percentage lost from cells
Distilled water	2.80
Culture medium	14.64
Culture medium + 0.1 γ zinc	15.42
Culture medium + 1.0 γ zinc	30.55
Culture medium + 10.0 γ zinc	34.27
Culture medium + 100.0 γ zinc	42.28

Extraction of Zinc From Phytoplankton Cells

Aliquots of a *Nitzschia* culture to which had been added radioactive zinc were centrifuged. To the different tubes containing the separated radioactive cells were added either 10-percent trichloracetic acid (TCA), hot distilled water, ethyl ether, or 95-percent ethyl alcohol, and the packed cells were resuspended. Extraction with TCA was allowed to take place for 1 hour while that with the other reagents continued for 24 hours. At the end of the extraction time, the cells were filtered and the radioactivity of the filtrate measured.

Nearly all the Zn^{65} of the cells was extracted with TCA (98.4 percent). Ethyl ether removed 7.4 percent; hot distilled water, 4.5 percent; and ethyl alcohol, 1.4 percent.

OBSERVATIONS ON SHELLFISH

Uptake of Radioactive Zinc by Oysters

When shellfish were placed in sea water to which had been added Zn^{65}, there was considerable radioactivity associated with their shells. It was observed that this uptake of radioactivity by oyster shell soon reached an apparent steady state. When the radioactive shells were placed in sea water, the isotope rapidly left the shells with an approach to a new equilibrium between the radioactivity of the shells and the surrounding sea water. Since the Zn^{65} added to the sea water was carrier free and sea water contains but little zinc, it is likely that considerable amounts of the Zn^{65} were adsorbed to the surface of the shells.

In one series of tests, oysters were kept in sea water to which had been added carrier-free Zn^{65} to give a concentration of about 0.01 μc per ml. and, after a given time, were all opened and the radioactivity of their tissues measured. In other tests some of the oysters were removed at intervals and their tissues analyzed. In all tests, however, the oysters were subjected to decreasing amounts of Zn^{65}. The radioactivity of the sea water in which the animals were held was determined at intervals, and whenever the oysters were sampled. The results of two tests are shown in table 6.

TABLE 6.—*Uptake of zinc 65 by oysters immersed in sea water containing the isotope*

[Average of 15 oysters. Zinc 65 concentrations reported in millimicrocuries (mμc)]

Hours of exposure	Zinc 65 content of oysters (mμc/gm. fresh tissue)	Zinc 65 content of sea water (mμc/ml.)	
		Initially	At end
Test 1:			
5	210.2	10.6	5.2
24	263.6	8.1	3.0
48	243.5	8.3	4.9
Test 2:			
42	137.1	9.7	3.8
66	376.2	9.7	2.5
90	508.8	9.7	1.8
114	366.3	9.7	
138	311.9	9.7	1.5

The Zn^{65} very quickly decreased in the sea water and very rapidly increased in the tissues of the oysters. It seems apparent that the isotope entered almost immediately. There was very little increase with time as the experiments progressed. This might be explained as due to experimental conditions since the oysters were subjected to decreasing concentrations of Zn^{65} in the water. An apparent steady state would be observed if the availability of the Zn^{65} were maintained. If this had been done, it is likely that the isotope in the tissues would have reached a high concentration since the radioactive zinc added was carrier free. However, with a high specific activity in the sea water, it was quite impossible to have an insignificant decrease in the Zn^{65} of the water in which the oysters were immersed. Despite the fact that an apparent steady state could not be reached in the experiments, the results indicate that oyster tissues contain very large amounts of zinc. Experiments using Zn^{65} with added zinc carrier are reported later in experiments with separated gills.

Uptake and Exchange by Separated Oyster Gills

A number of experiments were made of the uptake of radioactivity by the separated gills of the oyster when immersed in sea water containing Zn^{65}. In some the effects of added zinc were ascertained, while in others, exchange phenomena were demonstrated. In all instances there was a very rapid uptake of the Zn^{65} when this isotope was added to the sea water in carrier-free solutions. Even with added zinc, reducing the specific activity of the Zn^{65} in the sea water, the uptake was usually quite rapid and great, indicating that the oyster tissues contained very large amounts of zinc.

As an example of the uptake of radioactive zinc, the results of measurements made in one experiment are presented in table 7. In this test the gills of an oyster were immersed in 25 ml. of sea water to which had been added 2.5 γ of zinc. Radioactive zinc was added, and the radioactivity of the sea water was measured at intervals. The Zn^{65} entered the tissues very rapidly at first and less rapidly as the test was continued. It might be possible to interpret the results as an approach to an equilibrium, although the isotopic ratio of the Zn^{65} inside the tissue and in the sea water outside undoubtedly were not the same.

If one assumes that isotopic equilibrium were reached between 42 and 48 hours, the concentration of zinc in the tissue can be calculated from isotopic dilution. A decrease in radioactivity in the 25 ml. from 2,576 to 154 counts per minute per ml. would be equivalent to diluting the 25 ml. by the addition of 393.2 ml. of nonradioactive sea water. At a specific gravity of 1.025 this amount would weigh 403 grams. In the experiment the tissue concentrating the Zn^{65} and reducing the counts actually weighed 0.24 grams, or only 1/1679.2 times the weight of water needed to reduce the radioactivity the same amount. The tissue then concentrated the zinc 1,679 times the concentration of the sea water, or 1,679 $\times$ 0.104 γ per gm., or contained 174.6 γ per gm. However, isotopic equilibrium actually had not been reached, so higher zinc concentrations would be possible.

TABLE 7.—*Uptake of zinc 65 by the separated gills of oysters immersed in sea water containing the isotope and nonradioactive zinc*

Hours of exposure	Radioactivity of water (counts per minute)	Hours of exposure	Radioactivity of water (counts per minute)
0	2,576	24	458
6	1,841	26	342
18	835	42	164
19.5	749	45	165
21.5	572	48	132

The results of another experiment with oyster gills are presented in table 8 to demonstrate that the zinc of the tissue is exchangeable with that of the surrounding sea water. In this test, gills of oysters were placed in sea water to which had been added Zn^{65}. After 21½ hours an equilibrium appeared to be reached. The gills were then removed from the radioactive sea water and placed in sea water to which had been added EDTA. This salt would chelate the greater part

TABLE 8.—*Uptake of zinc 65 by the separated gills of oysters immersed in sea water containing the isotope, and loss of this isotope from these gills when placed in nonradioactive sea water containing EDTA*

Hours of exposure	Radioactivity of sea water (counts per minute)	Hours of exposure	Radioactivity of sea water (counts per minute)
Sea water:		Sea water—Continued	
0	2,671	27	1,106
1	2,631	45.5	1,074
2	2,508	Sea water and EDTA:	
3	2,416	0	0
5	2,208	4	275
9	1,819	20	1,246
21.5	1,154	23	1,174
24	1,165	25	1,215

of the zinc leaving the gills and limit that available for exchange. From the results of the measurements of the radioactivity in the sea water containing the chelating compound, an increase in radioactivity occurred, which demonstrated that zinc passed out of the gills to the water. It seems evident that a great part of the zinc in oyster tissue is exchangeable with that of the surrounding sea water, and the total amount present in the gills is thousands of times that of the sea water.

Distribution of Radioactive Zinc in Oysters and Scallops

Radioactive zinc was injected into oysters, and their tissues or organs were analyzed for radioactivity after 2 hours. The site of the injection varied. In some tests the Zn^{65} was placed in the adductor muscle, and in others in the visceral mass or in the pericardial cavity. There was considerable radioactivity in the shell liquor and blood that was lost on shucking. In some instances this amounted to almost one-third of the injected dose. The gills had almost twice the radioactivity of the other organs and tissues. There was considerable Zn^{65} in the liver and body mass. The heart was relatively high in activity, having about 70 percent of the amount found in the liver. The adductor muscle was much less radioactive than the other organs and tissues.

Bay scallops were immersed in sea water to which had been added Zn^{65} to give a concentration of 0.01 μc per ml. At the end of 2 hours, the scallops were carefully dissected and their organs and tissues analyzed for Zn^{65} content. The scallops rapidly took up the Zn^{65} with all the organs having considerable radioactivity (table 9). A large amount was in the kidney. The liver and associated organs were quite radioactive, as were also the gills.

TABLE 9.—*Tissue distribution of zinc 65 in the bay scallop after exposure for 2 hours to sea water containing 10 mμc (millimicrocuries) zinc 65 per milliliter*

[Average of 10 scallops]

Organ	Weight in grams	Zinc65 content mμc/gm.
Kidney	0.595	1,384.31
Liver	2.085	243.14
Gills	3.924	218.43
Testis and ovary	1.401	138.04
Foot	.191	130.59
Rectum	.070	119.61
Heart	.127	105.10
Adductor muscle	3.769	99.61
Mantle	3.495	91.76

TABLE 10.—*Extraction of zinc 65 from oyster tissues*

Oyster tissue	Weight in grams	Activity in counts per minute	Activity in counts per minute/gm.
Whole homogenate	1.68	1,147	683
Treated with water	1.08		
Extract		400	
Residue		333	
		733	679
Treated with TCA	1.20		
Extract		828	
Residue		0	
		828	690

Extraction of Zinc From Oyster Tissues

Twenty oysters, exposed for 48 hours to sea water to which had been added 0.01 μc of Zn^{65} per ml., were opened and their meats ground in a blender. This material was further ground to a finer paste with a tissue grinder. Weighed portions of the finely ground oyster tissues were then placed in centrifuge tubes. To one was added 5 ml. of water, the material stirred occasionally during a 15-minute extraction period, and the liquid extract separated by centrifugation. A second extraction was made with another 5 ml. of water, and the extracted material was combined and diluted to a known volume. The radioactivity of an aliquot of the water extract was measured. The residue left after centrifugation was dissolved in concentrated HNO_3 and made to a fixed volume. The radioactivity of an aliquot of this was likewise determined. Another portion of weighed tissue homogenate was extracted in a similar manner but with a 10-percent solution of TCA. The radioactivity of the extract and residue were then measured. A third portion of weighed homogenate was dissolved in concentrated HNO_3, made to a fixed volume, and the radioactivity of an aliquot determined.

The Zn^{65} of the oyster tissues was only partially extracted with water. However, all of the isotope was removed from the tissues by treatment with TCA (table 10).

METABOLISM OF RADIOACTIVE ZINC BY FISH

Uptake of Radioactive Zinc From the Digestive Tract

Two series of tests were made to follow the uptake of Zn^{65} from the digestive tract by croakers *Micropogon undulatus*. In one series the nuclide in solution with high specific activity was pipetted directly into the stomach. In the other, the

dose of Zn^{65}, with 50 micrograms of carrier zinc in the form of the sulfate per gram of fish, was solidified in gelatin and placed down their throats. After they were given the radioactive zinc, the fish were returned to a tank of flowing sea water and sacrificed after intervals of time up to 48 hours.

After collection of a blood sample, the organs and tissues of the fish were carefully dissected. The parts of the digestive tract were wet-ashed with nitric acid and the ash taken up in dilute hydrocholoric acid and made to a fixed volume with water. Aliquots of these solutions were placed in small vials for radioactivity measurements. After dissection of the various organs and removal of a portion of integument, of muscle, and of bone, the remainder of the fish was homogenized in water in a blender, and an aliquot of the homogenate was placed in a small vial. The various samples in the vials were placed in the well of a scintillation detector and the contained radioactivity measured. The results were corrected for weight of sample, dilution, and the dosage given to the different-sized fish and compared with an aliquot of the dosing material. The computations of microcurie strengths were based on the efficiency of the counting arrangement for dilutions of the original shipment and the reported Zn^{65} content.

The gelatin containing the zinc was broken down in the stomach rather promptly and passed into the intestines in somewhat liquefied form. Two hours after administration, about 60 percent of the dose was in the digestive tract, most of it in the stomach (table 11). Between 2 and 6 hours, most of the dose had left the stomach and apparently had entered the body of the fish. There was only a small percentage of the dose in the intestines at any time. Very little was found in the pyloric caeca.

The Zn^{65} pipetted directly into the stomach entered the intestines more promptly. However, uptake from the intestines was somewhat less rapid than in the tests in which added carrier was employed (table 12). The percentage of the dose in the intestines remained high for 12 hours after dosing. Nearly 10 percent of the dose was in the fish tissues at 24 hours, much of it entering very early. However, the Zn^{65} not accounted for in the digestive tract and the remainder of the fish body was 50 percent in 4 hours. It increased to 71 percent after 24 hours and to 87 percent after 48 hours. It was likely excreted.

TABLE 11.—*Zinc 65 content of digestive tract of croakers following its administration by mouth in gelatin*

Organ	Percentage of dose remaining after—		
	2 hours	6 hours	12 hours
Stomach	50.2	8.4	7.5
Intestines	8.7	11.3	15.6
Pyloric caeca	.6	.9	.9
Total	59.5	20.6	24.0

The changes in concentration of Zn^{65} in the various organs and tissues of the croakers following administration of the nuclide by pipetting into the digestive tract are listed in table 13. There was rapid entry of the zinc into the blood, accompanied by an uptake by the kidney. There was a very great accumulation by the liver, which also took place soon after entry of the isotope into the blood. The greatest accumulation by the internal organs was observed after 6 hours. Following this the levels rapidly fell off, the decrease being more marked in the blood than in the liver and kidney. The build up of radioactivity by the spleen and the gonads was somewhat slower than that in the other organs. Aside from the rapid uptake and loss by the kidney and liver, there was a small and continued accumulation in bone, integument, and muscle tissues. It seems that the zinc entering the blood from the digestive tract was rapidly removed by the kidney and liver. Removal of part by the gills seems probable, and the concentrations reported may reflect a good supply of blood to the filaments. The slow continued uptake by bone, skin and scales, and muscle indicates an accumulation of zinc in these tissues with a relatively slow turnover time of zinc-containing compounds.

From an extremely careful and painstaking dissection of a croaker and a weighing of the organs and parts, the percentage composition of the fish was ascertained. In other fish of known weight the different internal organs were taken in their entirety for the samples. From this information and the radiological measurements it was possible to compute the distribution of the Zn^{65} in the tissues and organs of the entire croaker after administration of this isotope. These calculations for a 12-hour fish receiving Zn^{65} in gelatin are given in table 14.

TABLE 12.—*Distribution of zinc 65 in croakers following pipetting of the nuclide into the stomach*

Distribution	Percentage of dose remaining after—					
	2 hours	4 hours	6 hours	12 hours	24 hours	48 hours
Digestive tract:						
Stomach	59.7	0.7	0.7	0.4	9.8	1.2
Intestines	20.4	42.2	42.6	48.3	6.3	3.9
Pyloric caeca	6.9	3.9	11.4	2.9	2.9	1.0
Total	87.0	46.8	54.7	51.6	19.0	6.1
Fish body	3.6	2.4	7.9	6.7	9.7	6.8
Unaccounted for	9.4	50.8	37.4	41.7	71.3	87.1

TABLE 13.—*Changes in the zinc 65 content of the various organs and tissues of croakers following its administration*

[Dose: 1.55 microcuries per gram of fish. Values listed in millimicrocuries per gram of fresh tissue]

Tissue or organ	Zinc 65 content (mμc/gm.) after—					
	2 hours	4 hours	6 hours	12 hours	24 hours	48 hours
Blood	0.93	8.16	28.61	7.21	9.70	3.49
Heart	.02	1.60	10.66	3.72	5.11	3.91
Spleen	0	1.60	15.06	6.97	12.83	3.86
Gill filaments	.09	2.54	10.97	4.48	8.09	4.52
Liver	.11	3.14	57.46	20.64	22.00	11.72
Kidney	1.50	3.64	27.03	10.09	18.52	12.26
Gonads	.05	.27	2.44	1.61	2.98	2.57
Muscle	.01	.06	.31	.21	.43	2.21
Bone	.02	.41	1.42	1.27	2.37	1.19
Integument	0	.17	1.10	1.21	2.32	1.06

Although the internal organs rapidly take up Zn^{65} in large amounts, they constitute only about 2 percent of the weight of the entire fish. The uptake and rate of loss in these organs is usually rapid and much of the physiology and metabolism of elements is explained in the changes in concentrations in these organs. While the rate of uptake in muscle and bone may be slow, these tissues account for 91 percent of the weight of the fish. The slow accumulation of elements in these tissues is of considerable importance.

In the croakers tested 12 hours after dosing, the greatest amount of Zn^{65} in the fish was in the muscles. The muscles and bones had 66 percent of the total radioactive zinc present in the fish.

Retention of Radioactive Zinc in the Body

The retention of Zn^{65} was measured in experiments using the pinfish, *Lagodon rhomboides*. Following an exposure of the fish for 4 days to sea water to which had been added Zn^{65}, they were returned to a laboratory tank of flowing sea water. At intervals after exposure up to 25 days, three fish were taken for measurement of their contained radioactivity. After removal of water from the surface of the fish by blotting with paper toweling,

TABLE 14.—*Zinc 65 distribution in entire fish 12 hours after ingestion of the isotope*

[Dose [1] per fish: 6,100 mμc]

Organ or tissue	Percent of total weight	Weight in grams	Zinc 65 in mμc/gm.	Zinc 65 in mμc per tissue or organ	Percent of total zinc 65 of body
Muscle	80	48.80	1.6	78.1	44.7
Bone	11	6.71	5.5	36.9	21.1
Gills	2	1.22	10.9	13.3	7.6
Liver	.8	.49	40.7	19.9	11.4
Gonads	.4	.24	17.6	4.2	2.4
Kidney	.3	.18	41.5	7.5	4.3
Heart	.2	.12	14.0	1.7	1.0
Spleen	.1	.06	25.3	1.5	.9
Remainder [2]	5.2	3.17	[3] 3.7	11.7	6.7
Total		60.99		174.8	

[1] Three percent of dose in tissues (178.8 mμc); 24 percent in digestive tract; 73 percent not accounted for, mostly excreted.
[2] Skin, scales, digestive tract, blood, brain, eyes, and other parts.
[3] Based on skin and scales.

the fish were weighed and homogenized with added distilled water in a blender. An aliquot of the homogenate of the fish was weighed and dried to constant weight at 98° C., and the percentage of moisture determined. Five other aliquots were taken, placed in vials, and weighed, and the contained radioactivity measured in the well of a scintillation crystal detector. Because of differences in the amount of water added in homogenizing, the results of the radioactivity measurements were calculated on a dry-weight basis.

The relative radioactivity of the fish during 25 days following their return to nonradioactive flowing sea water is plotted in the graph of figure 1. There was initially a marked loss of the Zn^{65} from the fish when returned to flowing sea water following the exposure. However, 7 or 8 percent of that initially present was retained throughout the 25 days of observation. It is apparent that some Zn^{65}-containing compounds in the body of the fish have a very slow rate of turnover. A part of any contained Zn^{65} in the fish will be present over very long periods of time since the loss during 25 days was extremely slight, as shown by the lack of any appreciable slope in the curve of the line of figure 1. The loss from the tissues cannot amount to much more than that resulting from radiological decay. Because of the long half-life of Zn^{65} (about 250 days) and the relatively great fluctuations in individual samples, the observations reported were not corrected for decay.

DISCUSSION

The measurements made throughout the year of the zinc content of the sea water at the labora-

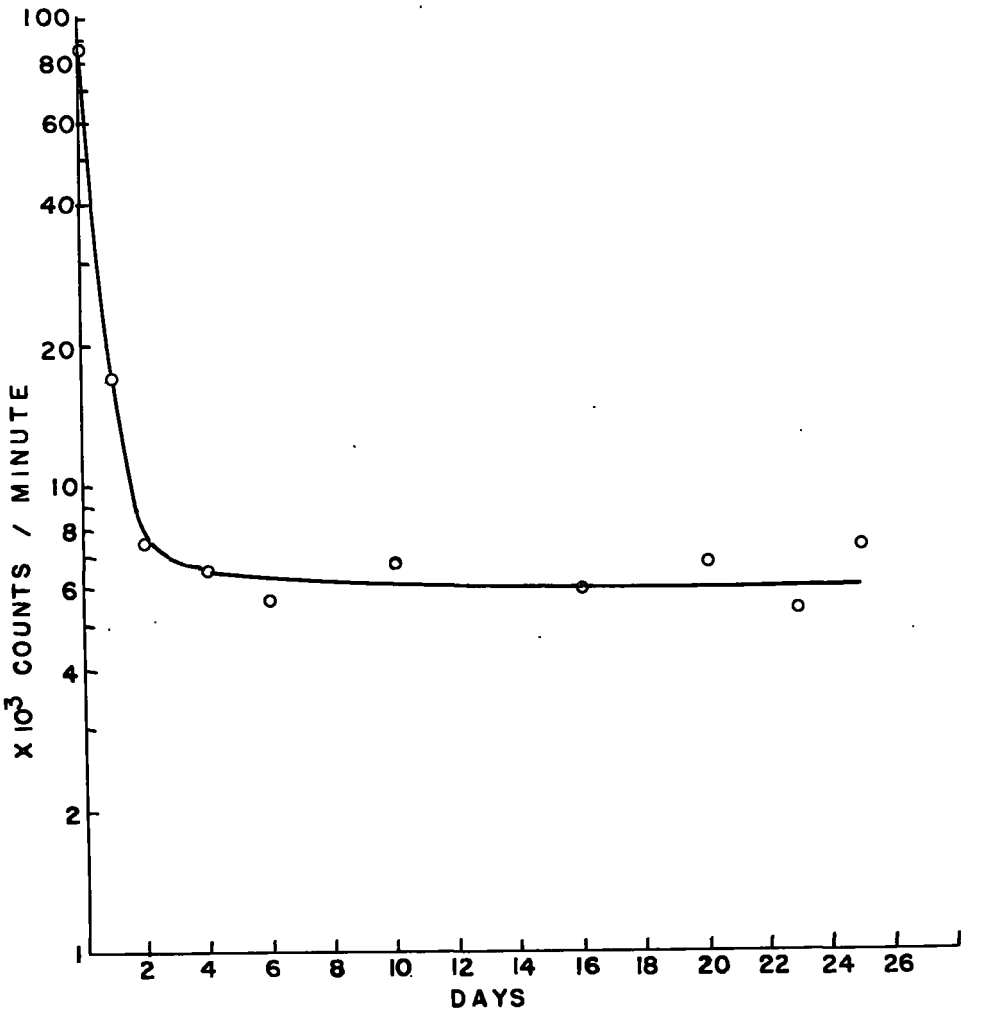

FIGURE 1.—Loss of contained Zn^{65} from the pinfish, *Lagodon rhomboides*, following return to flowing sea water.

tory dock are well within the values that may be expected for such inshore waters. For Tokyo Bay, Ise Bay, and Misaki Channel, Morita (1950) found a range in zinc content from 2.8 γ to 11.7 γ per liter, with an average of 5.6 γ. Buch (1944) reported an average of 10.8 γ per liter, with a range of 4.5 γ to 23 γ for the Gulf of Bothnia along the coast of Finland within harbors and areas of low salinity and where there was evidence of considerable pollution. Wattenberg (1943) gives a range from 5 γ to 30 γ per liter for the western Baltic, not greatly different from Buch for the eastern Baltic. Noddack and Noddack (1940), for a fjord of the Swedish coast, found a content of slightly more than 14 γ of zinc per liter (14 γ per kg.). For samples taken along the coast of Great Britain, some in inside waters, Black and Mitchell (1952) report zinc concentrations from 9 γ to 21 γ per liter. Kuroda (1940) reports zinc concentrations of 7 γ per liter off the Honshu coast of Japan, and Bodansky (1920) gives a value close to 7.5 γ per liter (7.3 γ per kg.) for a sample from the Gulf of Mexico taken close to shore at Galveston.

A seasonal change in the zinc content of the water collected at the laboratory dock appeared in the data with low values occurring in the winter months (table 1). The significance of this is not known. From the data obtained, there was no indication that the amount of zinc present in the water at low tide was greater than at high tide. Salinity changes at this location are usually slight even throughout the year. However, a great lowering of the salinity, normally close to that of

the more open sea, to an extremely low value of about 12 parts per thousand following heavy rains from a hurricane was accompanied by a higher zinc content of the water. Changes in the zinc content at this location may be influenced somewhat by runoff and pollution.

The zinc content in the tissues of oysters in the few samples tested varied considerably (table 2), but the range of from about 300 γ to 1,000 γ per gm. of fresh meats for oysters in which metal contamination is not definitely known is quite similar to that reported by many investigators (Bertrand and Vladesco, 1923; Bodansky, 1920; Hiltner and Wichmann, 1919; Hubbell and Mendel, 1927; McHargue 1924; Orton 1924). The high values found in oysters from Long Island Sound and the upper Chesapeake Bay were likely related to metal pollution of the water. Similarly high values for oysters for these locations and a polluted water off New Jersey were given in the analyses of various investigators listed by Hiltner and Wichmann (1919). Galtsoff (1937) reports similar high values for oysters of Long Island Sound. Mention might be made that the values for zinc concentrations in different mollusks reported by McHargue (1924) were for moisture-free samples rather than for living substance as quoted by Vinogradov (1953, table 218, p. 359) and so are much less than would appear from reference to Vinogradov's table.

Mollusks in general are known to be high in their zinc content, and these along with crustaceans, are richest in zinc when compared with other invertebrate groups (Vinogradov 1953). Lamellibranchs contain large quantities of zinc, but there is considerable variation with higher concentrations in oysters than in others. In our investigations less zinc was found in the clam *Venus mercenaria* than in the oyster *Crassostrea virginica*, and still less in the scallop *Pecten irradians*. Hubbell and Mendel (1927), Bodansky (1920), and McHargue (1924), report less zinc in clams than in oysters. Bertrand and Vladesco (1923) give much lower values for the scallop *Pecten jacobaeus* than for the Portuguese oyster *Crassostrea angulata*.

In oysters the gills were notably high in zinc content, but considerable amounts were present in the mantle and labial palps, and in the remainder of the body, which included the hepatopancreas. Low concentrations were present in the adductor muscle. Based on the distribution of Zn^{65} in the tissues and organs of scallops, the gills were likewise high in zinc, as were also the kidney and hepatopancreas. The adductor muscle was low. Earlier work has pointed out high concentrations of zinc in the gills of oysters and low amounts in the adductor muscle (Bertrand and Vladesco, 1923; Bodansky 1920; Galtsoff 1937; and Koga 1934).

The results reported on the uptake of Zn^{65} by *Nitzschia* clearly indicate that this species of phytoplankton does accumulate considerable amounts of zinc. No information on the zinc content of marine phytoplankton could be found in the literature. Small amounts of zinc, less than those found in terrestrial plants, have been reported in the ash of *Laminaria saccharina* and *Fucus vesiculosus*, and in the dry matter of *Macrocystis pyrifera* (Vinogradov 1953). Based on the zinc concentrations reported for inshore waters, the amounts found in these plants indicate that these species do concentrate zinc. Black and Mitchell (1952) studied the concentration factors for zinc in algae (fresh weight to trace element in the surrounding sea water) and report values for 5 different species ranging from 400 to 1,400.

Small amounts of zinc appear to have a stimulating effect on the growth of many plants, and small amounts appear to be necessary for their growth and well-being. The beneficial action of zinc is less evident in green plants. The lack of available zinc in the soil for growth of certain nut-producing and fruit trees, and the diseases of citrus and other species of plants resulting from this lack are well known (Brenchley 1943, 1947; Chandler 1937; Chesters and Rolinson, 1951; and others). The essentiality of small amounts of zinc for the laboratory culture of many species of phytoplankton has been investigated (Ondratscheck 1941). The amounts required appear to be small. In the experiments reported on the culture of *Nitzschia closterium* in media with very limited zinc concentrations, no effects on the rate of cell division were apparent. Very little zinc was necessary for cell multiplication in this species. With the zinc concentrations available to phytoplankton cells in the sea, and with the less rapid division rate as compared to the laboratory culture of these forms, it seems quite unlikely that a zinc deficiency would limit phytoplankton growth in the sea.

Zinc has been reported (Greenfield 1942) as affecting photosynthesis in *Chlorella vulgaris*, but the amounts required were very great (10^{-2} molar zinc sulphate) since the exposure times were limited to 20 minutes. In our experiments cell multiplication of *Nitzschia* was reduced in cultures grown in zinc concentrations of 250 γ per liter or stronger. The exact toxic strength is not known, but the division rate was not lessened at concentrations of 100 γ per liter. This is at least three times the highest zinc concentrations reported for sea water. It seems likely from this, and from the previous discussion, that neither high nor low zinc concentrations will limit the growth and reproduction of phytoplankton in the sea.

There are appreciable amounts of zinc in the tissues of marine fishes. According to the analyses listed by Vinogradov (1953), there is more zinc than copper and much more than iron. Bertrand and Vladesco (1922) determined the zinc content of muscle tissues of eels and flounders. Bodansky (1920) in his analyses of 14 common marine fishes reports species differences, with rather high values in the spotted trout and flounders and an extremely high concentration in sea catfish. The two analyses of fish by Noddack and Noddack (1940) are about comparable to some of the lower values reported by Bodansky when one considers that their analyses are based on dry weight. The values reported by Vinogradov (1953) for these authors are listed as for living material, which makes them appear high.

No previous work has been reported on the changes in the zinc content of the tissues of marine fish following ingestion. The measurements of the uptake of Zn^{65} following oral administration to croakers show a rapid entry of the isotope into the blood with great accumulation in the internal organs, particularly the liver and spleen. The supporting tissues slowly took up the isotope. Much of the zinc entering the body was quickly taken up by the gills and kidney. The decrease in the zinc content of the gills indicated an early excretion of zinc through these structures. High concentrations of zinc in the liver and spleen of marine fishes were reported by Bodansky (1922). He also reports rather great concentrations in bones and, in marine catfish, in the gills.

Although much of the oral dose of Zn^{65} was not accounted for and considerable amounts of that entering the blood were likely excreted, marine fish can accumulate radioactivity from the uptake of Zn^{65} if present in their food. With accumulation of zinc by phytoplankton, and again by certain species of invertebrates, it seems not unlikely that radioactive zinc, if present in the sea water, will appear in concentrated amounts in the tissues of marine fishes.

The slow uptake of Zn^{65} by the structural tissues with accumulation in the bones and muscles would indicate that the loss would likewise be slow, a slow rate of turnover of the zinc-containing compounds. The observations reported on pinfish show almost no loss after the first day for a period of 25 days. Obviously, if Zn^{65} is taken into the bodies of marine fishes, certain amounts will be present and measurable for very long periods of time. When Zn^{65} was given orally to cows (Bergh 1950), the isotope was present in the body for some time and continued to appear in the milk after it was virtually absent from urine and feces. That Zn^{65} remains in the body for considerable lengths of time is indicated from the finding that intravenously injected Zn^{65} was present in the bodies of dogs up to 6 months (Vallee, Fluharty, and Gibson, 1950).

It seems possible that the nonfission-product isotope Zn^{65}, found in the bodies of marine fish in the Pacific Ocean, as mentioned in the introduction, was, perhaps, present in the water and was accumulated by the fish from marine life farther down the food chain. Because of the long biological half life and long retention of this nuclide by marine fishes, the Zn^{65} could have been accumulated many months prior to the radiological determinations.

SUMMARY

1. The zinc content of sea-water samples collected from inshore waters along the Atlantic and Gulf of Mexico coasts averaged 10.6 γ (micrograms) per liter and ranged from a trace to 24.56 γ per liter; the higher values were for samples from areas known to receive metal contamination.

2. There was a seasonal difference in the zinc content of the sea water at Beaufort, N. C., the lower values occurring during the winter months. The monthly averages ranged from 2.8 γ to 14.6 γ per liter. The average of all the observations was 9.6 γ per liter.

3. That oysters, clams, and scallops contain

large amounts of zinc, thousands of times more than the sea water per unit of weight, was confirmed. In these the greatest accumulation is by oysters, less by hard-shell clams, and least by bay scallops.

4. Radioactive zinc present in the surrounding water is rapidly taken up in great amounts by these shellfish, probably because of the great difference between the zinc content of the water and that in the tissues. Much of the zinc in the mollusks is exchangeable with that of the water.

5. High concentrations of the Zn^{65} injected into or taken up by oysters and scallops occur in the gills. Considerable amounts accumulate in the kidney of scallops. There is also accumulation in the hepatopancreas of the shellfish, but only small amounts in the adductor muscle.

6. The marine diatom, *Nitzschia closterium*, takes up large amounts of Zn^{65} when it is present in the sea water. Although the greater part of the zinc of the cells is exchangeable with that of the water, very little accumulated Zn^{65} leaves the cell when they are resuspended in nonradioactive sea water. This species of marine phytoplankton appears to accumulate considerable amounts of zinc.

7. Marine fish quickly take zinc into the body from the digestive tract. Apparently much of it is excreted rather promptly. High blood concentrations of Zn^{65} from feeding of the nuclide to fish were quickly followed by rapid uptake by the kidney, liver, and other internal organs. The Zn^{65} concentrations of these and the blood very quickly declined after reaching this early peak. The liver had the greatest accumulation. A slow and long-continued accumulation took place in bone, integument, and muscle tissues.

8. Although there is an immediate loss of accumulated Zn^{65} when marine fish exposed to the nuclide in sea water are returned to flowing nonradioactive water, a small percentage remains with only very slight loss over periods of many days.

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RELATIVE VALUE OF TEN GENERA OF MICRO-ORGANISMS AS FOODS FOR OYSTER AND CLAM LARVAE

By HARRY C. DAVIS AND ROBERT R. GUILLARD

(This report presents the findings of a cooperative project of the Fish and Wildlife Service, United States Department of the Interior, and the Oyster Institute of North America.)

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ABSTRACT

Twelve species of micro-organisms, representing ten different genera, were used in feeding experiments to determine their relative value as foods for larvae of oysters (*Crassostrea virginica*) and clams (*Venus mercenaria*). *Isochrysis galbana* and *Monochrysis lutheri* were approximately equal in value as foods for either species of larvae, and were the best single foods for oyster larvae. Together with *Chlorococcum* sp. they were also the best single foods for clam larvae. Somewhat more rapid growth of both oyster and clam larvae was obtained by feeding a mixture of *Isochrysis galbana*, *Monochrysis lutheri*, *Dunaliella euchlora*, and *Platymonas* sp. than was obtained by feeding equal quantities of any of these foods separately.

Growth of larvae of both oysters and clams was comparatively good in each of five concentrations of *Isochrysis* and *Monochrysis* tested. The rate of growth did not fall off rapidly nor was there any mortality at the higher concentrations of these foods, as there was when equally high concentrations of *Chlorella* sp. (Lewin's isolate) were used.

The presence, and perhaps thickness, of cell walls and the degree of toxicity of the metabolites are believed to be important factors in determining the usability of micro-organisms as foods for bivalve larvae.

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The increasing interest in pond and hatchery culture of lamellibranchs as a dependable source of seed stock has focused attention on the need for additional information on the effect of various micro-organisms on the survival and growth of larvae of these mollusks. We need to know not only which organisms the larvae can utilize as foods, but also which forms produce toxic metabolites that could interfere with growth or kill the larvae, should such micro-organisms become too numerous (Loosanoff et al., 1954). If we are to fertilize ponds to increase the number of food organisms, we need to know the optimum concentration of such organisms and the range of concentrations that the larvae can tolerate and still grow at an acceptable rate.

We are reporting the results of some feeding experiments designed to determine the relative food value to larvae of oysters (*Crassostrea virginica*) and clams (*Venus mercenaria*) of representatives from ten genera of micro-organisms, and of one experiment designed to test the effect on larval growth of five different concentrations of the two micro-organisms that proved to be of most value as foods.

We wish to express our gratitude to Dr. V. L. Loosanoff for assistance and constructive criticism throughout these experiments, to Mrs. Barbara Myers for the statistical treatment of our data, to C. A. Nomejko for preparing the figures, and to Miss Norma Pritchard for many of the larval measurements.

FOOD ORGANISMS TESTED

Four of the genera fed to oyster and clam larvae were representatives of the Chrysophyta. *Isochrysis galbana* Parke (1949), *Monochrysis lutheri* Droop (1953) and *Prymnesium parvum* Carter (1937) are motile unicells of the Order Chrysomonadales. For bacteria-free subcultures of these organisms we are indebted to Drs. L. Provasoli and J. McLaughlin of the Haskins Laboratories, New York. (Dr. Provasoli isolated bacteria-free cultures of *Isochrysis* from the original Parke cultures). The fourth organism, *Phaeodactylum tricornutum* Bohlin (1897), has been considered a diatom and has been widely used under the name of *Nitzschia closterium* (Ehrenberg) Wm. Smith forma *minutissima* Allen and Nelson (1910). Following Hendey (1954), we consider it a chrysophyte of undetermined systematic position.

The remaining six genera were representatives of the Class Chlorophyceae. *Dunaliella*, *Chlamydomonas*, and *Platymonas* are motile unicells of the Order Volvocales, while *Chlorococcum* and *Chlorella*, of the Order Chlorococcales, are nonmotile except that *Chlorococcum* has motile zoospores. *Stichococcus* is a nonmotile unicell of the Order Ulotrichales.

Isochrysis, *Monochrysis*, *Prymnesium*, and *Dunaliella* are naked and normally undergo cell division while motile. *Chlamydomonas* and *Platymonas* have cell walls and divide while nonmotile, producing 2, 4, and sometimes 8 small, thin-walled flagellated cells. *Chlorococcum*, although it has cell walls and is nonmotile, produces naked, motile zoospores. *Chlorella* produces autospores that are nonmotile and have cell walls from the time they are liberated from the parent cell. *Stichococcus*, like *Chlorella*, has neither a motile stage nor a naked stage. It belongs to an order that is essentially filamentous but the "filaments" of *Stichococcus* seldom consist of more than two cells. *Phaeodactylum* is nonmotile and has a cell wall that may be weakly siliceous (table 1).

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TABLE 1.—*Micro-organisms used in feeding experiments with larval oysters and clams*

Organism	Source	Approximate size (microns)	Thousands of cells/ml. of larval culture	Cell walls
1. *Isochrysis galbana*	Parke (1949)	5.5×3×2.5	120	No
2. *Monochrysis lutheri*	Droop (1954)	7×2.5	110	No
3. *Prymnesium parvum*	Droop (1954)	9×4.5×3.5	30	No
4. *Phaeodactylum tricornutum*	(1)	To 3.5×27 [2]	55	[2] Yes
5. *Dunaliella euchlora*	(3)	11×6	40	No
6. *Dunaliella* sp.	(3)	11×6	50	No
7. *Chlamydomonas* sp. (Cambridge collection #11/35)	Lewin(?)	8.5×3.5	70	Yes
8. *Platymonas* sp. #1	Guillard at Woods Hole, Mass.	11×8.5×5	27	Yes
9. *Chlorococcum* sp.	Guillard at Milford, Conn.	6 to 14 (zoospores, 3–5)	20	[4] Yes
10. *Chlorella* sp. (Indiana U. collection #580)	Lewin at Milford, Conn.	To 13 (average 4–7)	110	Yes
11. *Chlorella* sp. "A"	Guillard at Milford, Conn.	To 8 (average 4.5)	100	Yes
12. *Stichococcus* sp.	Ryther (1954)	2×2 to 6	550	Yes

[1] Our subculture was obtained from Dr. John Ryther, Woods Hole Oceanographic Institution. It is believed to be derived from the Plymouth Laboratory culture described by Wilson (1946).
[2] Typical cultures had about 5 percent "oval" cells 7.5 microns in length, and less than ½ percent "triradiate" cells. Cell walls weakly siliceous.
[3] *Dunaliella euchlora* and *Dunaliella* sp. are very similar in appearance and in culture requirements. It is possible they are different clones of the same strain, the origin of which is not known. *D. euchlora* (Lerche 1937) was identified by Dr. R. A. Lewin, and is the organism used by Ryther (1956).
[4] Zoospores of *Chlorococcum* sp. are naked.

METHODS

Food Production

The algal cultures were grown under fluorescent white and cool-white lamps providing a light intensity of roughly 500 F. C. Culture temperatures were maintained between 19.0° and 23.0° C. Bacteria-free, 75-ml. liquid stock cultures were maintained in 250-ml. Ehrlenmeyer flasks, while cultures used for feeding were grown in volumes of 500 ml. to 1 liter either in 2-liter Ehrlenmeyer or in 2,800-ml. Fernbach flasks. The latter cultures attained suitable densities in 5 to 15 days, so that the volume required for feeding was only 5 ml. to 33 ml. per liter of sea water in the containers in which the larvae were grown.

All algae were grown in Long Island Sound sea water (salinity 22.0–27.0 p. p. t.) enriched as follows:

MAJOR ELEMENTS

NaH_2PO_4	20	mg./l.
Ferric sequestrine (NaFeEDTA)—13% Fe)	10	mg./l.
and either		
$NaNO_3$	150	mg./l.
or		
$NaNO_3$ plus NH_4Cl	150 + 50	mg./l.

TRACE ELEMENTS

Cu	0.005	mg./l.
Zn	0.01	mg./l.
Co	0.005	mg./l.
Mn	0.1	mg./l.
Mo	0.01	mg./l.

VITAMINS

Thiamine HCl	0.2	mg./l.
Biotin	1	μg./l.
B_{12}	1	μg./l.
Folic acid	2	μg./l.
Paba	10	μg./l.
Nicotinic acid	0.1	mg./l.
Inisotol	1.0	mg./l.
Calcium pantothenate	0.2	mg./l.
Pyradoxine HCl	0.1	mg./l.

Although the requirements of the different micro-organisms for the various ions and vitamins have not been established, the medium either with or without NH_4^+ was suitable for all, and it was desired to standardize the medium as much as possible. Only *Monochrysis* and *Chlamydomonas* were supplied NH_4^+, although a few others may utilize it more readily than NO_3^- as a source of nitrogen. The medium both with and without ammonium has been found nontoxic to clam and oyster larvae in the concentrations used in feeding.

Larval Culture

The technique for obtaining fertilized eggs, permitting them to develop to straight-hinge larvae, and of handling the larvae were the same as previously described by the senior author (Davis 1953), except that 3-liter polyethylene containers were used for the experimental larval cultures rather than the cumbersome 20-liter earthenware jars used previously. We attempted to set up the cultures with 30,000 to 45,000 straight-hinge larvae per culture or 10 to 15 larvae per ml. Actually the average numbers of larvae per ml. were as follows:

	Oyster larvae	*Clam larvae*
Experiment 1	10	13
Experiment 2	16	14
Experiment 3	9	10

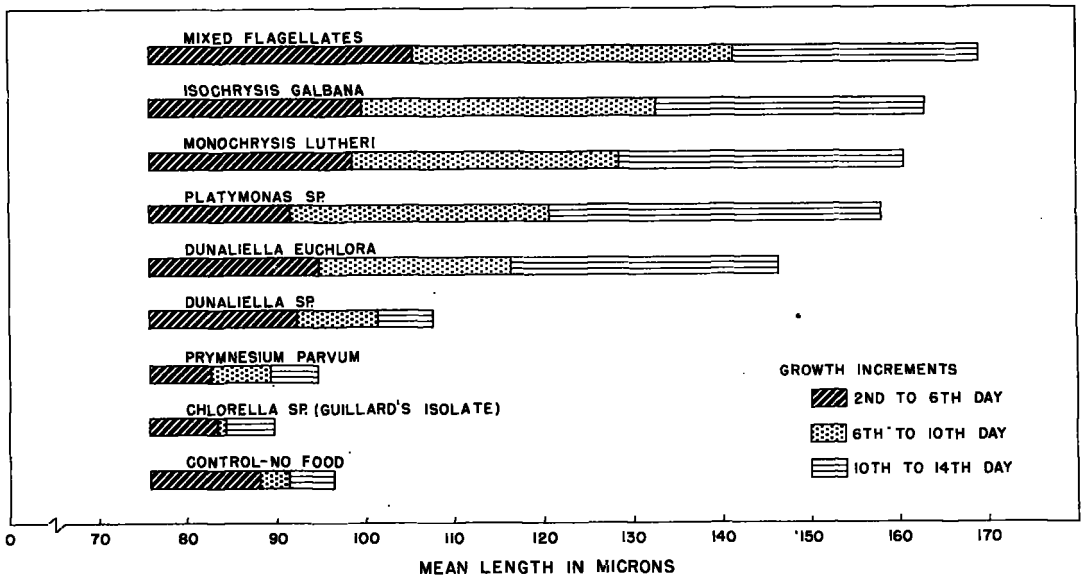

FIGURE 1.—Growth of larvae of oysters (*Crassostrea virginica*) in cultures receiving different micro-organisms at the rate of 10×10^{-3}mm.^{3} of packed cells per milliliter per day (experiment 1). Concentration of oyster larvae averaged 10 per ml. Plots were based on mean length of 100 larvae from each of the duplicate cultures. Mixed flagellates consisted of equal quantities (by packed cell volume) of *Isochrysis*, *Monochrysis*, *Dunaliella euchlora*, and *Platymonas*.

The foods were tested on oyster and clam larvae simultaneously so that the condition of the foods and of the sea water was the same for larvae of both species. Two cultures of oyster larvae and two cultures of clam larvae were used to test each food. To find whether a mixture of food organisms might give better growth of larvae than any species separately, one pair of cultures of each species of larvae in the first and second experiments received a mixture consisting of equal quantities of *Isochrysis galbana*, *Monochrysis lutheri*, *Dunaliella euchlora*, and *Platymonas* sp. In addition, in each experiment, one pair of cultures of each species of larvae served as controls and received no supplemental food.

To equate the quantities of food given, since the average size of individual cells varies with the species of food organisms (table 1), we fed at a rate of 10×10^{-3}mm.^{3} of packed cells per milliliter of larval culture per day. The wet-packed cell volume of a 10-ml. sample of each food culture was measured using Hopkins tubes and a relative centrifugal force of about 1,000 for 25 minutes. The volume of each food culture required to give 10×10^{-3}mm.^{3} of packed cells per ml. of larval culture was then calculated, and this amount was fed daily.

EFFECTS OF MICRO-ORGANISMS ON OYSTER LARVAE

The relative value of the different micro-organisms as foods for oyster larvae was studied in three experiments. Seven species individually and a mixture of four of them were tested in the first experiment (fig. 1). The second experiment was a replica of the first except that three species not previously tested were also included (fig. 2, upper part of graph). In a third experiment, two additional species not available for use in the first and second experiments were tested and *Monochrysis* was repeated for comparison (fig. 2, lower part of graph).

The ranking of the various foods remained remarkably constant throughout, although the growth of oyster larvae in all cultures of the second experiment was somewhat slower than in either of the other experiments. A statistical comparison of the ranking of the eight foods common to the first and second experiment shows a correlation in their order of rank of 0.87, or less than 1 chance in 100 that such good agreement between their order of rank in the two experiments could occur by chance.

In the two experiments in which the mixture of *Isochrysis*, *Monochrysis*, *D. euchlora*, and *Platy-*

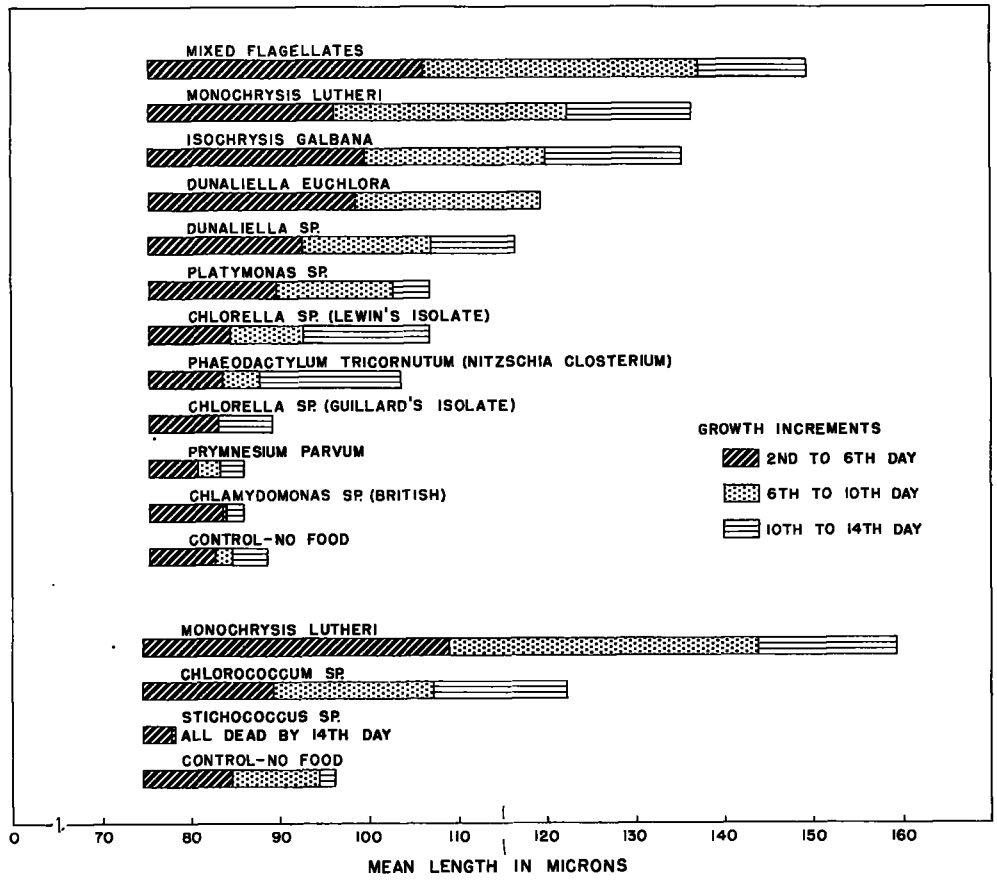

FIGURE 2.—Growth of larvae of oysters (*Crassostrea virginica*) in cultures receiving different micro-organisms at the rate of $10x10^{-3}$mm.^{3} packed cells per milliliter per day (experiment 2, upper part of graph; experiment 3, lower part of graph). Concentration of oyster larvae averaged 16 per ml. in second experiment and 9 per ml. in third experiment. Plots were based on mean length of 100 larvae from each of the duplicate cultures. Mixed flagellates consisted of equal quantities (by packed cell volume) of *Isochrysis*, *Monochrysis*, *Dunaliella euchlora*, and *Platymonas*.

monas was tested, it proved to be the best food (figs. 1 and 2). At each measuring period, oyster larvae receiving this food were significantly larger in both experiments than larvae receiving any of the individual foods separately.

Isochrysis and *Monochrysis* proved to be the best of the individual foods for oyster larvae, and were of almost equal value. Thus, while *Isochrysis* gave slightly better growth of larvae than did *Monochrysis* in the first experiment (fig. 1), *Monochrysis* proved to be slightly the better food in the second experiment (fig. 2, upper part of graph). Larvae receiving either of these two foods were significantly larger at 14 days, in both experiments, than larvae receiving any of the other single foods, except that larvae receiving *Platymonas* were almost as large in the first experiment.

Both species of *Dunaliella* appear identical microscopically, but oyster larvae receiving *D. euchlora* were significantly larger than larvae receiving *Dunaliella* sp. at 6 and 10 days in both experiments, and in the first experiment, were much larger than those receiving *Dunaliella* sp. at 14 days. In the second experiment, although oyster larvae receiving *D. euchlora* grew almost as rapidly as larvae receiving *Isochrysis* for the first 10 days, they did not grow at all between the 10th and 14th days. Such a radical change in the food value of *D. euchlora* appears strange, but we believe we may have been feeding very young cultures of *D. euchlora* for the first 10 days and much older cultures, in which toxic metabolites may have become highly concentrated, during the last 4 days of the experiment.

Oyster larvae receiving *Platymonas* were consistently even smaller at 6 days than larvae receiving *Dunaliella* sp., and they continued throughout the second experiment to grow less rapidly than

larvae receiving the latter food (fig. 2). In the first experiment, however, by the 10th day larvae receiving *Platymonas* were larger than larvae receiving either species of *Dunaliella*, and by the 14th day were almost as large as larvae receiving *Monochrysis* (fig. 1). It was also noted that the digestive gland of larvae receiving *Platymonas* was dark olive green in the first experiment, whereas in the second experiment the digestive gland of larvae receiving this food was more nearly reddish brown. We believe, therefore, that the difference in food value of *Platymonas* in the two experiments reflected a difference in the physiological state of the *Platymonas* cultures that probably included not only a difference in thickness of cell walls but also a difference in chemical composition.

Chlorella sp. (Lewin's isolate) was not tested in the first experiment. In the second experiment it proved to be a very much better food than *Chlorella* sp. (Guillard's isolate) and almost equal in value to *Platymonas*. It should be noted, however, that at 6 days neither *Chlorella*-fed culture was appreciably better than the unfed control culture, while larvae receiving *Platymonas* were significantly larger than those in the control culture (fig. 2). Larvae receiving *Chlorella* sp. (Guillard's isolate) grew less rapidly than larvae in the control culture in the first experiment (fig. 1), but did not significantly differ in size from larvae in the controls in the second experiment. However, larvae receiving this food did not grow at all between the 6th and 10th day in the second experiment (fig. 2), and suffered a significantly higher mortality than the control in both experiments.

Chlorococcum sp. was tested in the third experiment (fig. 2, lower part of graph). Since the unfed control and the *Monochrysis*-fed control cultures both grew faster than similarly treated cultures in the second experiment, direct comparison with foods used in the previous experiment is impossible. *Chlorococcum* would appear to have about the same food value for oyster larvae as Lewin's *Chlorella*, although the fairly good growth of larvae receiving *Chlorococcum* from the 2d to 6th day may indicate that the value of this food is more similar to that of *Platymonas*.

Oyster larvae receiving *Phaeodactylum* had about the same mean length as those receiving Lewin's *Chlorella* (fig. 2), but mean length is somewhat misleading in this instance. The majority of the oyster larvae in cultures receiving *Phaeodactylum* were apparently unable to utilize this food and did not grow at all. The comparatively few larvae that could utilize it did grow quite well, however, and by the 14th day several had reached 200 microns in length or were almost as large as the largest larvae in cultures receiving our best foods. Moreover, survival of larvae receiving this food was excellent and there was no indication that *Phaeodactylum* produced toxic metabolites.

Three organisms, in addition to Guillard's *Chlorella*, proved useless or toxic to oyster larvae. *Chlamydomonas* sp. (British isolate) proved to be of even less food value to oyster larvae than Guillard's *Chlorella* (fig. 2) and, as indicated by larval mortality, was almost as toxic. Larvae in cultures receiving *Prymnesium parvum* did not grow as rapidly as larvae in the unfed controls in either experiment 1 or 2 (figs. 1 and 2). Moreover, mortality of larvae in cultures receiving this "food" was significantly higher than in the control cultures in both experiments. *Stichococcus* sp. was the poorest of any of the foods tested (fig. 2), and was also the most toxic.

Experiments With Older Larvae

In two short experiments we compared the rate of growth of older oyster larvae when fed *Chlorella* with their rate of growth when fed mixed flagellates. In experiment A, in which the initial mean length of the larvae was 165.41 μ, measurements after 4 days of feeding indicated that the mean increase in length of the larvae fed *Chlorella* was less than one-half that of larvae fed mixed flagellates (table 2).

Both cultures were continued until setting, and the spat was collected. We counted only the spat that occurred on the white inner face of the test shells. Although each culture had an equal number of larvae at the beginning of the experiment when the larvae were 14 days old, we collected 2,180 spat (18th to 27th day) from the culture fed mixed flagellates, and only 680 (18th to 35th day) from the culture fed *Chlorella* sp.

In experiment B, in which the initial mean length was 149.75 μ (table 2), the differences in the rate of growth of older oyster larvae fed cultures of *Chlorella* and mixed flagellates were even more striking. However, these cultures were infested with rotifers from the start, and probably the data should only be considered as in general agreement with the first experiment.

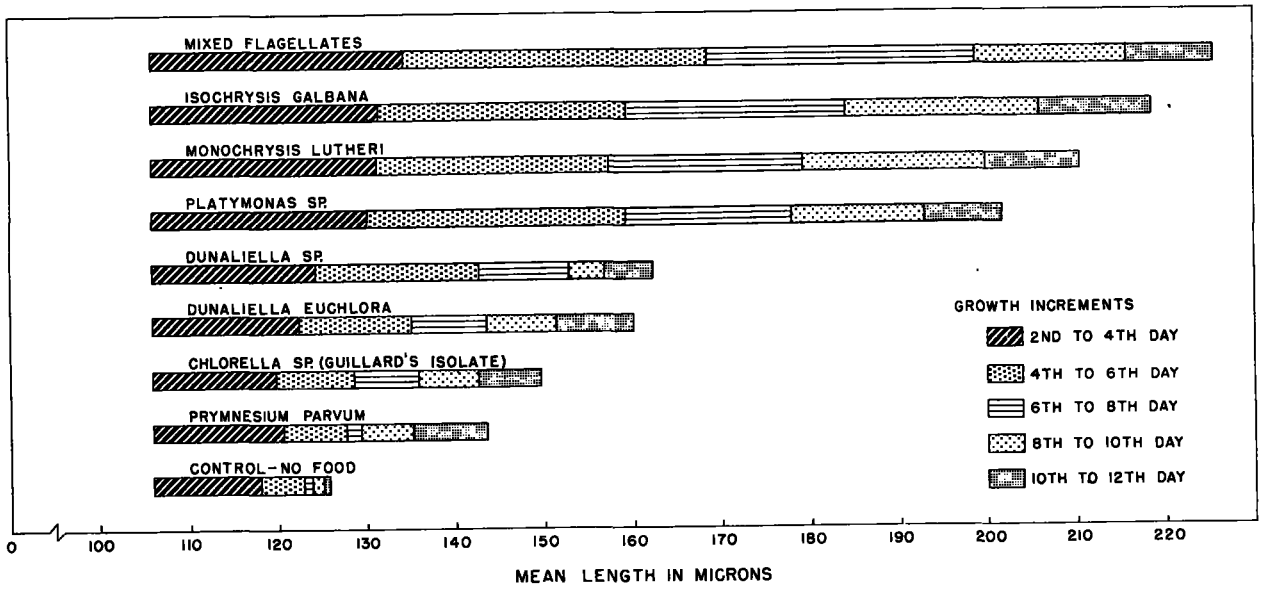

FIGURE 3.—Growth of clam larvae (*Venus mercenaria*) in cultures receiving different micro-organisms at the rate of 10×10^{-3} mm.^{3} of packed cells per milliliter per day (experiment 1). Concentration of clam larvae averaged 13 larvae per ml. Plots were based on the mean length of 100 larvae from each of duplicate cultures. Mixed flagellates consisted of equal quantities (by packed cell volume) of *Isochrysis*, *Monochrysis*, *Dunaliella euchlora*, and *Platymonas*.

TABLE 2.—*Growth of older oyster larvae fed cultures of* Chlorella *and of mixed flagellates*

Culture	Experiment A Mean length of larvae (microns)			Experiment B [1] Mean length of larvae (microns)		
	Initial	After 4 days	Increase	Initial	After 6 days	Increase
Chlorella sp.	165.41	188.65	23.24	149.75	152.90	3.15
Chlorella (Guillard's)				149.75	157.30	7.55
Mixed flagellates	165.41	216.35	50.94	149.75	182.50	32.75

[1] Initial larval culture heavily contaminated with rotifers which reduced rate of growth of all cultures in this experiment.

EFFECTS OF MICRO-ORGANISMS ON CLAM LARVAE

The relative value of the different micro-organisms as foods for clam larvae was tested in experiment 1 (fig. 3), experiment 2 (fig. 4, upper part of graph), and experiment 3 (fig. 4, lower part of graph) simultaneously with the tests on oyster larvae.

Growth of clam larvae, like that of oyster larvae, was considerably slower in the second experiment than it was in the first. As with oyster larvae, however, the ranking as foods for clam larvae, of the eight micro-organisms tested in both experiments, was almost precisely the same. The correlation in the order of ranking of the foods in these two experiments was 0.98, the only difference being that *Monochrysis* and *Isochrysis* had exchanged places.

With clam larvae, as with oyster larvae, the mixture of *Isochrysis*, *Monochrysis*, *Dunaliella euchlora*, and *Platymonas* was the best food. In the first experiment clam larvae receiving this mixture were significantly larger, at each measuring period, than larvae receiving any of the food organisms separately (fig. 3). In the second experiment the mixture ranked below *Monochrysis* on the 6th and 8th days; but was in first place again by the 12th day (fig. 4).

Isochrysis and *Monochrysis* were of approximately equal value to clam larvae, and were the best two of the single foods tested in both the first and second experiments (figs. 3 and 4). However, *Chlorococcum*, by comparison with *Monochrysis* in the third experiment, appears to be at least as good for clam larvae as *Monochrysis* and *Isochrysis* and, perhaps, as good as the mixed flagellates (fig. 4). *Platymonas* also, for the first 8 days of the first experiment, was of approximately the same value for clam larvae as was *Monochrysis*. By the 12th day, even in the first experiment, larvae receiving *Platymonas* were significantly smaller than those receiving *Monochrysis* and throughout the second experiment *Platymonas* was a significantly poorer food than either *Monochrysis* or *Isochrysis*. As was noted in oyster larvae, the coloring of the digestive gland of the clam larvae receiving *Platymonas* was dark olive

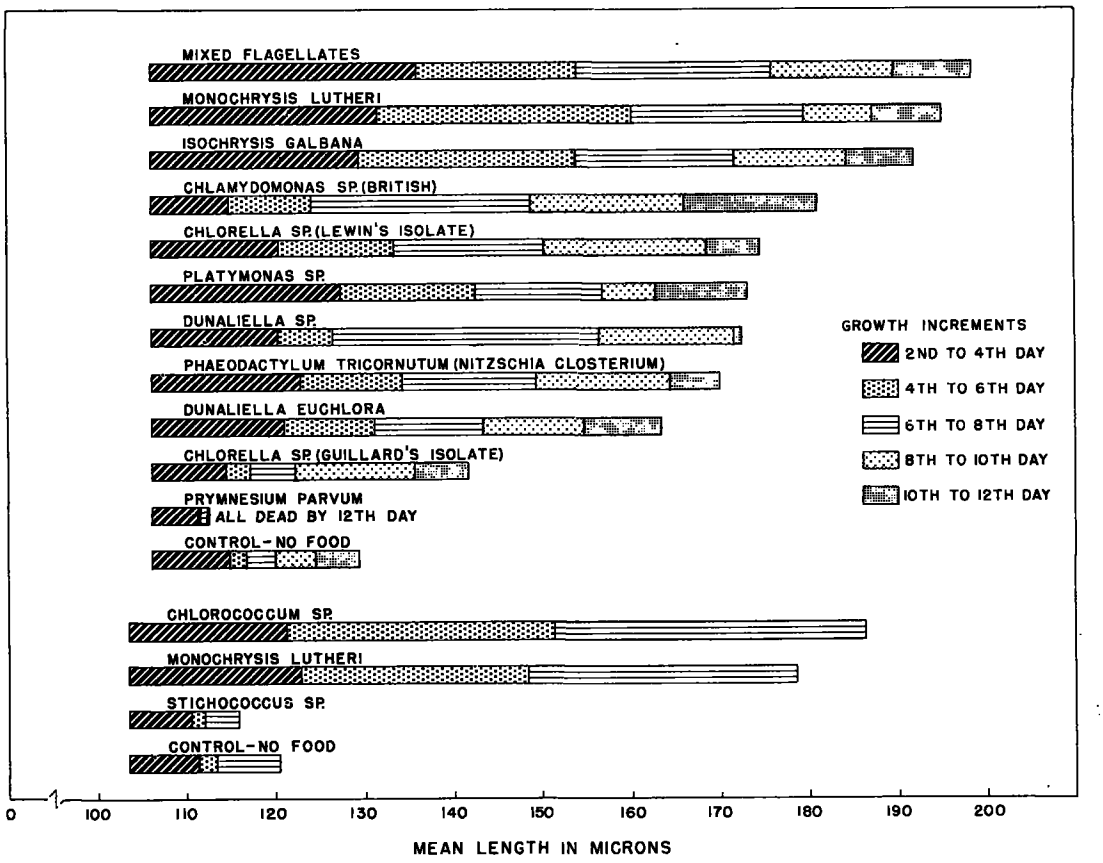

FIGURE 4.—Growth of clam larvae (*Venus mercenaria*) in cultures receiving different micro-organisms at the rate of 10×10^{-3} mm.^{3} of packed cells per milliliter per day (experiment 2, upper part of graph; experiment 3, lower part of graph). Concentration of clam larvae averaged 14 per ml. in the second experiment and approximately 10 larvae per ml. in the third experiment. Plots were based on mean length of 100 larvae from each of duplicate cultures. Mixed flagellates consisted of equal quantities (by packed cell volume) of *Isochrysis*, *Monochrysis*, *Dunaliella euchlora*, and *Platymonas*.

green in the first experiment and more nearly reddish brown in the second.

Two food organisms not tested in the first experiment, *Chlamydomonas* and Lewin's *Chlorella*, ranked above *Platymonas* as foods for clam larvae by the end of the second experiment (fig. 4). After only 2 days of feeding, it was observed that in each of the cultures receiving *Chlamydomonas*, almost precisely 50 percent of the clam larvae had dark green digestive glands and were growing. The remaining 50 percent of the larvae were almost completely colorless, had not grown, and showed no evidence of utilizing *Chlamydomonas*. This colorless group of larvae apparently never did utilize this food and eventually almost all of them died. Those larvae that did utilize *Chlamydomonas* showed a good rate of growth and by the 12th day larvae receiving this food ranked fourth in mean length but, due to the mortality among those larvae that never did utilize it, these cultures now contained only about one-half as many larvae as were present in cultures receiving other foods. Clam larvae receiving Lewin's *Chlorella*, as in previously reported experiments, grew at a fairly uniform rate but, as shown by this experiment, there are several better foods, even for clam larvae.

Phaeodactylum (*Nitzschia closterium* var. *minutissima*) has been used extensively as a food for clam larvae by Turner (personal communication). As shown by our second experiment, this food, like Lewin's *Chlorella*, gave a reasonably good rate of growth of clam larvae and the rate of growth was fairly uniform. On the basis of equal packed-cell volumes, however, as a food for clam larvae *Phaeodactylum* ranked eighth in the group of food organisms tested in these experiments (fig. 4).

Both species of *Dunaliella* were comparatively poor foods for clam larvae in the first experiment (fig. 3). In both experiments (1 and 2), growth

of larvae receiving *Dunaliella* sp. varied considerably from one measuring period to the next, while larvae receiving *Dunaliella euchlora* grew at a fairly uniform rate. *Dunaliella* sp., however, was the better of the two as a food for clam larvae in both experiments, and was almost as good as *Platymonas* in the second. *Dunaliella euchlora*, on the other hand, was the poorest of the really usable foods for clam larvae thus far tested (fig. 4).

Chlorella sp. (Guillard's isolate) was utilized by clam larvae in both experiments and did not appear toxic in the concentration used (table 1). Nevertheless, the rate of growth of clam larvae receiving this food was so slow that it is not considered a practical food to use.

The other two organisms tested, *Prymnesium parvum* and *Stichococcus* sp., both probably produce metabolites that are quite toxic to bivalve larvae. In the first experiment, all the clam larvae in one culture receiving *Prymnesium* were dead by the 12th day and in the second experiment all larvae in both cultures receiving this food were dead by the 12th day. *Prymnesium*, however, can be ingested and digested by clam larvae. This is indicated by the coloration of the digestive glands of some larvae, and by the survival of clam larvae in one culture of the first experiment and their significantly larger size compared with the controls at 12 days. *Stichococcus* did not cause excessive mortality of clam larvae, but larvae receiving this food grew even more slowly than those in the unfed control cultures. Gibor (1956) found that neither the larvae of *Artemia salina* nor those of *Tigriopus* grew at a normal rate when fed his *Stichococcus* sp. Walne (1956) working with larvae of *Ostrea edulis* also found *Prymnesium parvum* to be toxic although, in general, organisms of the Class Chrysophyceae, such as *Isochrysis galbana* and *Chromulina pleiades*, were more readily utilized than representatives of the other classes that he had tested. He found *Chlorella stigmatophora* gave poor growth of larvae and concludes that "those members of the Chlorococcales which have a thick cell wall are poor food for oyster larvae."

EFFECTS OF DIFFERENT CONCENTRATIONS OF *ISOCHRYSIS* AND *MONOCHRYSIS*

Since *Isochrysis* and *Monochrysis* were the two best foods for both oyster and clam larvae, an experiment was designed to determine the optimum concentration of these foods for most rapid growth of these larvae. Concentrations of 2.5×10^{-3} mm.^{3}, 5×10^{-3} mm.^{3}, 10×10^{-3} mm.^{3}, 20×10^{-3} mm.^{3}, and 40×10^{-3} mm.^{3} of packed wet cells per milliliter of larval culture were chosen to make the data as comparable as possible to the data on clam larvae reported by Loosanoff, Davis, and Chanley (1953) using *Chlorella* sp. (Lewin's isolate) as the food.

On Oyster Larvae

As shown by comparison with the controls, growth of oyster larvae was quite good at all the concentrations of *Isochrysis* and *Monochrysis* tested (fig. 5). Although on the 6th day, a concentration of 100,000 cells per ml. of *Isochrysis* was optimum by a slight margin, by the 10th day this concentration was slightly poorer than either of the two higher concentrations tested. At 14 days, the oyster larvae receiving 400,000 cells of *Isochrysis* per ml. had the greatest mean length. At this time, the mean lengths of larvae were in the same order as the concentrations of food, and the differences in mean length of larvae between successive concentrations were highly significant.

Oyster larvae that received 250,000 cells of *Monochrysis* per ml. were significantly larger, at each measuring period, than larvae that received the next higher or the next lower concentration of this food. Oyster larvae grew quite well, however, over a relatively wide range of concentrations of either *Monochrysis* or *Isochrysis*.

The slightly poorer growth of oyster larvae at the two highest concentrations of *Isochrysis*, during the first 6 days, was probably the result of mechanical interference with feeding; there is no indication of toxic metabolites with this food. The slightly slower growth of oyster larvae at the highest concentration of *Monochrysis* may indicate that *Monochrysis* produces slightly toxic external metabolites, since this concentration seems to retard growth somewhat, even during the later larval stages.

On Clam Larvae

With clam larvae we found that, within the range tested, there was no rapid falling off of the rate of growth after passing the optimum concentration of either *Monochrysis* or *Isochrysis*, as there was with *Chlorella* (fig. 6). Although 200,000 cells per milliliter of *Isochrysis* appears to be the optimum concentration, there was little difference in the rate of growth of clam larvae over the

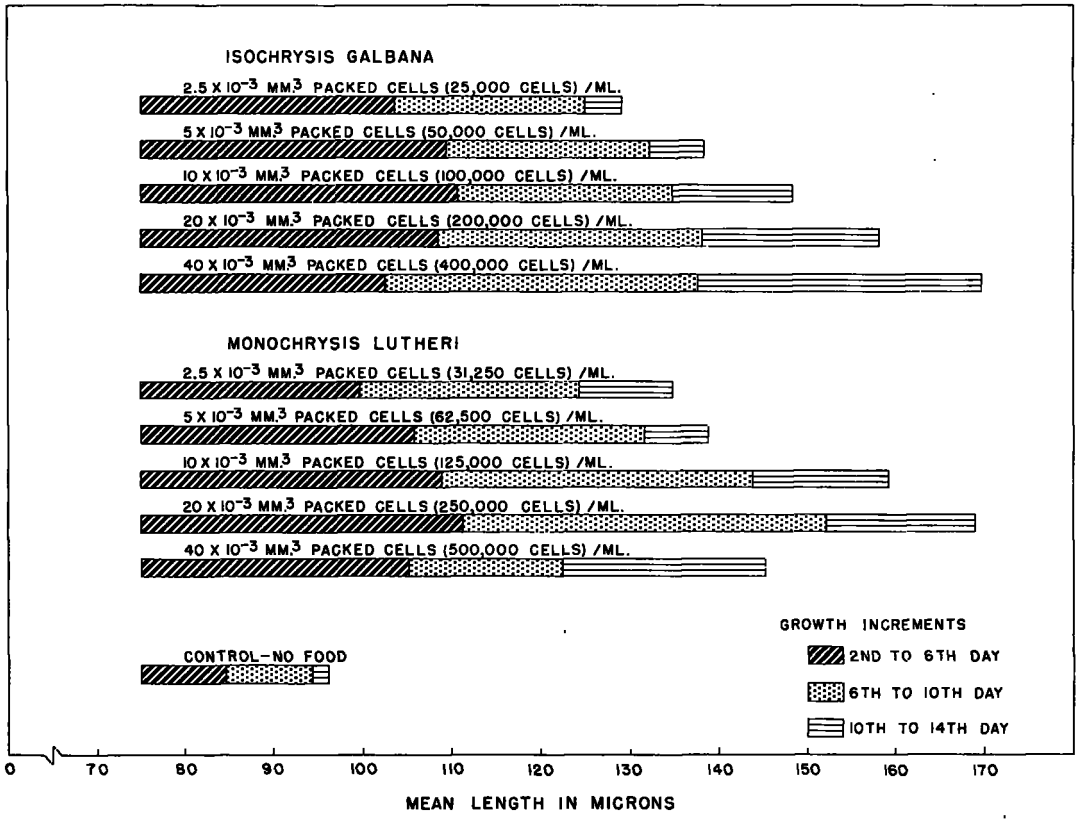

FIGURE 5.—Growth of oyster larvae (*Crassostrea virginica*) in cultures receiving five different concentrations of *Isochrysis* and of *Monochrysis*. The concentration of oyster larvae averaged 9 per ml. Plots were based on the mean length of 100 larvae from each of duplicate cultures.

range of 50,000 to 400,000 cells per ml. of this food. Likewise, although 250,000 cells per ml. appears to be the optimum concentration of *Monochrysis*, there was little difference in the rate of growth of clam larvae in concentrations of this food ranging from 125,000 to 500,000 cells per ml., at least through the 8th day. Clam larvae grew normally in concentrations of either *Isochrysis* or *Monochrysis* equal to the concentration at which Lewin's *Chlorella* was lethal. We believe this may indicate that the external metabolites of *Monochrysis* or *Isochrysis* are much less toxic to clam larvae than are those of *Chlorella*.

DISCUSSION

It is probably significant that in these experiments the four best foods for oyster larvae—*Isochrysis*, *Monochrysis*, and the two species of *Dunaliella*—were all naked flagellates. If we exclude *Prymnesium*, a naked flagellate that was toxic, even the poorest of the naked flagellates, *Dunaliella* sp., was consistently a better food, during the first 6 days, than any of the organisms that had cell walls. Moreover, *Platymonas* and *Chlorococcum* were the only two organisms tested having cell walls that gave appreciably better growth of oyster larvae than no food during the first 6 days. Apparently, oyster larvae cannot readily utilize organisms having cell walls, particularly during the early larval stages. That older oyster larvae can utilize forms having cell walls was demonstrated in the first experiment by the rapid growth after the 6th day of larvae receiving *Platymonas*, and by the reasonably good growth of older oyster larvae receiving *Chlorococcum*, Lewin's *Chlorella*, or *Phaeodactylum*.

Clam larvae, unlike oyster larvae, were able to utilize several forms having cell walls from the earliest larval stages. Thus, even at 4 days clam larvae receiving *Platymonas*, *Phaeodactylum*, *Chlorococcum*, or Lewin's *Chlorella* were significantly larger than the unfed controls, and as large or larger than larvae receiving the two species of *Dunaliella*, which are naked flagellates. Moreover, *Chlorococcum*, a form having cell walls, was possibly the best food yet tested for clam larvae.

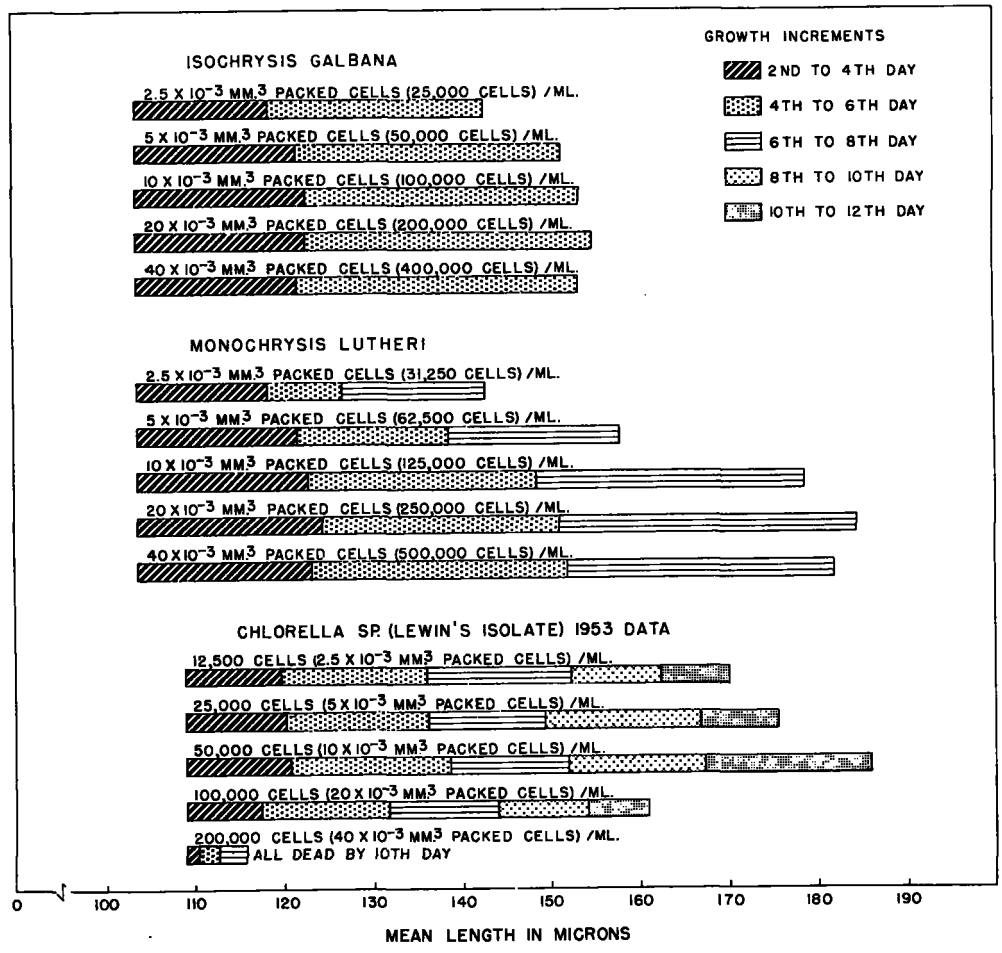

FIGURE 6.—Growth of clam larvae (*Venus mercenaria*) in cultures receiving five different concentrations of *Isochrysis*, of *Monochrysis*, and of *Chlorella* sp. (Lewin's isolate). The concentration of clam larvae averaged 10 per ml. Plots were based on the mean length of 100 larvae from each of duplicate cultures.

Nevertheless, at 4 days larvae receiving *Monochrysis* and *Isochrysis*, the two best naked flagellates, were significantly larger than larvae receiving any of the organisms with cell walls, except *Platymonas*. This may indicate that the presence, or perhaps the thickness of the cell wall, affects the utilization of a food even by clam larvae during the very early larval stages.

Gibor (1956), similarly, found that growth of larvae of *Artemia salina* was faster when fed any one of three Polyblepharidaceae (*Stephanophora gracilis*, *Dunaliella viridis*, and *Dunaliella salina*) than when these larvae were fed either his *Platymonas* sp. or his *Stichococcus* sp. He also postulates that this may have been due to the presence of a rigid cellulose cell wall in the latter two species.

Another factor that appears to be important in determining the value of micro-organisms as foods for bivalve larvae is the toxicity of their metabolites and the quantity of such metabolites they produce. As was shown by Loosanoff, Davis, and Chanley (1954), *Chlorella* sp. (Lewin's isolate) produced toxic metabolites that killed clam larvae when a sufficient volume of the filtrate from a *Chlorella* culture was added to the larval culture. Moreover, Davis and Chanley (1955) showed that the first evidence of the toxic effect of several substances on clam larvae was a reduction in the rate of growth of these larvae. Lucas (1955) has pointed out that metabolites of a given micro-organism may affect other aquatic organisms in quite different ways, promoting growth of some while hindering growth of others.

Gibor (1956) considered the possibility that his *Stichococcus* sp. was producing an "inhibitor to the growth" of *Artemia* larvae, but in the experiment in which he attempted to test this hypothesis he

apparently had no control for comparison and, perhaps erroneously, concluded that "Good development of the larvae showed that no inhibitor was produced."

Obviously, to be of food value to bivalve larvae, a micro-organism must be small enough, or break up into fragments small enough, to be ingested by the larvae, and must contain the necessary food elements in its body or in its storage products. Nevertheless, we believe that much of the difference in food value of closely related micro-organisms is directly attributable to differences in the quantity or toxicity of their metabolites. Thus, *Prymnesium*, which is fairly closely related to *Monochrysis* and *Isochrysis*, is small enough to be ingested and is, apparently, readily digested, but it is of little or no value as a food because of its toxicity. We have some evidence, moreover, that the toxic metabolites of *Prymnesium* are not primarily external, but are retained in the organism itself. It would seem highly probable also, from observations on the rate of growth of the larvae and on their mortality, that one of the primary differences between *Chlorella* sp. (Lewin's isolate) and *Chlorella* sp. (Guillard's isolate) as a larval food is the greater toxicity of the metabolites of the latter.

The differences between the rates of growth of clam and oyster larvae receiving the two species of *Dunaliella* were also possibly only reflections of differences in the toxicity of the metabolites of these two foods. In this case, however, it would be necessary to assume that the metabolites of *Dunaliella* sp. were more toxic to oyster larvae than were those of *D. euchlora*, and that the reverse was true for clam larvae. *D. euchlora* also reversed the usual trend in that it was the only food thus far tested that appeared to be a comparatively good food for oyster larvae but a comparatively poor one for clam larvae. Gibor (1956) also found that the food value of *Dunaliella viridis* differed from that of *D. salina* and that the food value of *D. salina* varied from one experiment to another.

Chlamydomonas, likewise, appeared to produce metabolites toxic to oyster larvae, but the pattern of growth shown by clam larvae receiving this food suggests that both the toxicity of metabolites and an inability of many of the clam larvae to digest the cell walls of *Chlamydomonas* were involved. *Phaeodactylum*, unlike *Chlamydomonas*, did not appear to produce toxic metabolites and the failure of the majority of oyster larvae to utilize these organisms probably reflects an inability of the majority of the larvae to digest the cell walls of *Phaeodactylum*.

In pond or hatchery practice, it is the numbers of such organisms as *Monochrysis* and *Isochrysis* that we would want to increase by fertilization. Since both clam and oyster larvae grow quite well throughout a wide range of concentrations of these micro-organisms, and since the metabolites of *Monochrysis* and *Isochrysis* appear to be very low in toxicity, it would not be necessary to control their numbers as rigidly as would be necessary with organisms such as *Chlorella*.

SUMMARY

1. Representatives of 10 genera of micro-organisms were tested in feeding experiments to determine their relative value as foods for larvae of oysters and clams.

2. *Isochrysis galbana* and *Monochrysis lutheri* were of approximately equal value and were the best single foods for oyster larvae.

3. A mixture of *Isochrysis* and *Monochrysis* of the Class Chrysophyceae, with *Platymonas* sp. and *Dunaliella euchlora* of the Class Chlorophyceae provided better growth of oyster larvae than did any of these foods singly.

4. With the exception of *Prymnesium parvum*, which is toxic, even the least valuable of the naked flagellates was a better food for young oyster larvae than were any of the micro-organisms with cell walls, but older oyster larvae can utilize some forms having cell walls.

5. *Stichococcus* sp., *Prymnesium parvum*, and *Chlamydomonas* sp. (British isolate) reduced the rate of growth of oyster larvae below that of the unfed controls, and *Chlorella* sp. (Guillard's isolate) was slightly poorer than no food in one experiment and slightly better in the other.

6. The mixture of flagellates provided better growth of clam larvae than did equal quantities of any of the single foods tested.

7. *Chlorococcum*, *Isochrysis*, and *Monochrysis* were the three best single foods for clam larvae.

8. Clam larvae can utilize several forms having cell walls even from the earliest larval stages.

9. *Stichococcus* sp. and *Prymnesium parvum*, both highly toxic, were the only two micro-organisms tested that were of no food value to clam larvae.

10. *Isochrysis* gave no evidence of toxicity even

in the highest concentration tested and the optimum concentration of *Isochrysis* for either oyster or clam larvae was at least double the optimum concentration of *Chlorella* sp. (Lewin's isolate).

11. Both oyster and clam larvae grew normally even in the highest concentration of *Monochrysis* tested and the optimum concentration of this food for either species of larvae was also at least double that for *Chlorella* sp. (Lewin's isolate).

12. We believe from these observations that *Isochrysis* and *Monochrysis* produce very little, if any, toxic metabolites.

13. The presence, or perhaps thickness, of cell walls and the degree of toxicity of the external metabolites are probably important factors in determining the usability of micro-organisms as foods by bivalve larvae.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

LIVING AND ANCIENT POPULATIONS OF THE CLAM *Gemma gemma* IN A MAINE COAST TIDAL FLAT

By W. H. BRADLEY and PETER COOKE

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ABSTRACT

Sagadahoc Bay is about 2 miles long and half a mile wide; its southern end is open to the Gulf of Maine. At low tide, about a mile of flat is exposed; the seaward two-thirds of this is made up of fine sand and the other third is muddy. *Gemma gemma* lives in great abundance in the sandy sediment but is scarce in the muddy sediment.

Gemma is ovoviviparous, produces young through much of the summer, has a life expectancy of about 2.2 years, and a maximum life span of about 4 years. Shells range in length from about 0.02 to 0.2 inch (0.6 mm. to nearly 5 mm.). In subdued light, *Gemma* feeds with only the siphons exposed above the sediment surface. It feeds most actively in the dark, when it raises the colored posterior half of the shell above the sediment surface and moves about somewhat as the much larger clam *Spisula* does. An average population of 25 gemmas per square inch draws food from about 16 percent of the bottom layer of water.

Gemmas are most numerous in the sandy midsection of the flat where the tidal currents close to the bottom are maximum (0.3 to 0.4 foot per second). Gemmas are distributed in a bunched pattern. In a statistical sense, they have a log normal distribution. *Gemma* and *Mya* have occupied the flat jointly for more than 1,000 years; *Mya* being numerically dominant in the muddy areas, *Gemma* in the sandy areas. The two clams tend to be incompatible either because they compete for food or for some other reason.

The total *Gemma* population of the bay in 1954 was about 11.5×10^9. In 1950, it was about twice as great, and in 1956 it was about 54 percent less than that of 1954.

Ancient *Gemma* shells are distributed irregularly from the surface down to as much as 4 feet below the surface. The average population over the past 400 years was about half, or less than half, of what it was in the interval 1950–55.

Research is needed to determine the food temperature tolerances and the toxicity of metabolic wastes of both *Gemma gemma* and *Mya arenaria*. The hypothesis is advanced, without supporting data, that *Gemma* is favored by the recent warming of the climate and that *Mya* is adversely affected. The *Gemma* population, by 1956, decreased to less than 25 percent of what it was in 1950. If *Gemma* is a competitor of *Mya* and the *Gemma* population continues small or declines further, this should permit *Mya* to reestablish itself in the sandy part of the flat.

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LIVING AND ANCIENT POPULATIONS OF THE CLAM *GEMMA GEMMA* IN A MAINE COAST TIDAL FLAT

BY W. H. BRADLEY and PETER COOKE, *United States Geological Survey*

During a study of the late geologic history and present-day processes of sedimentation and erosion in Sagadahoc Bay (Maine) the senior author noted the great abundance of living gemmas in the sandy parts of the extensive intertidal flat and the lesser, but still comparable, abundance of their dead shells to depths of 3 or 4 feet below the present surface. Large areas of the sandy part of the flat contain 25 or more living gemmas per square inch, and as many as 190 per square inch have been counted. Although these tiny clams rarely, if ever, reach 0.2 inch (5 mm.) in length, their present abundance suggests that they may play a more significant role in the economy of the tidal flat today than in the past. Some of the observations we made suggest that *Gemma* is a competitor of minute *Mya* larvae and that the recent marked decline of the population of *Mya*, the well-known soft-shell clam of commerce, in the sandy part of the Sagadahoc Bay tidal flat may have been caused partly by this competition.

Two facts make it possible to consider the *Gemma* population in this bay as an isolated community. One is that the physical environment of the tidal flat and its recent geologic history have limited the *Gemma* population to essentially the same area for at least the past thousand years; the other is that gemmas, unlike other clams in these waters, reproduce ovoviviparously, and therefore their young are not transported, except in very small numbers by rare events, to other *Gemma* communities in neighboring bays, or vice versa. We have attempted to identify and evaluate some of the factors operating within the community, particularly within the past 400 years, that may have affected the changing size and other characteristics of the population.

NOTE.—Approved for publication July 12, 1957. Fishery Bulletin 137.

Our study of the present and past *Gemma* populations is a byproduct of the geologic study of the Sagadahoc Bay tidal flat undertaken in 1949 in response to a suggestion made jointly by Joseph M. Trefethen, then State Geologist of Maine, and Robert L. Dow and Dana Wallace of the Maine Department of Sea and Shore Fisheries. The purpose of the study was to see whether changes could be found in the regimen of sedimentation and erosion that might help to account for the observed progressive decline in the population of the soft-shelled clam *Mya arenaria*. Many of the results of these investigations have been published in another paper (Bradley 1957). Nothing was found in the regimen of sedimentation and erosion that could account for the decline of the *Mya* population.

Biologists of the U. S. Fish and Wildlife Service and of the Maine Department of Sea and Shore Fisheries have for some years been engaged in comprehensive studies of *Mya arenaria*, its changing populations, growth rates, food supplies, and larval abundance and distribution in Sagadahoc and other bays along the Atlantic coast. They have also been carrying on comparable studies of the life history and habits of *Mya* predators. It is a pleasure to acknowledge the generous help of scientists of the U. S. Fish and Wildlife Service, especially John Glude and Walter Welch, and the Maine Department of Sea and Shore Fisheries, and from the former State Geologist of Maine. We wish also to thank Joel Hedgpeth of the Scripps Institution of Oceanography for his helpful criticisms of the manuscript. The manuscript was also read critically by my colleagues John T. Hack, Harry S. Ladd, and Wendell P. Woodring of the U. S. Geological Survey and we are grateful for their suggestions. Other Survey colleagues participated in the investigation and are mentioned at appropriate places in the text.

Most of the field work on which this paper is based was done in the summers of 1954 and 1955, but during the summers of 1950, 1956, and 1957 the senior author sampled the living *Gemma* population over parts of the flat and in 1950 had an opportunity to observe the distribution of *Gemma* shells in the sidewalls of many pits that were dug in the flat in order to determine the stratigraphy of the sediments. The senior author also visited the flat briefly in February 1956.

ECOLOGY

Physical environment

Sagadahoc Bay is at the southern end of Georgetown Island, roughly 10 miles south by east from the city of Bath (fig. 1). The bay is about 2¼ miles long, north to south, and approximately half a mile wide, though it widens into the fair-sized Bedroom Cove on its western side. At its southern end, Sagadahoc Bay is open to the ocean. Low bedrock hills that have a thin gravelly soil surround the bay except at the north end where there is a long salt marsh. Another much smaller salt marsh fills a small cove in the bedrock terrain on the eastern side of the bay. At the northern end of the bay and around much of Bedroom Cove, are sandy beaches. The rest of Sagadahoc Bay is bordered either by steep rocky shores or gently sloping shores of sandy mud overgrown with cordgrass (*Spartina alterniflora* and *Spartina patens*). In the northern part of the bay two elongate masses of bedrock rise above the surface of the flat. These are known locally as the Black Rocks Islands.

No fresh-water streams of consequence enter Sagadahoc Bay. Small springs bring to the bay its only fresh water except in times of heavy rains and melting snow when the salt marsh at the head of the bay collects a considerable quantity of fresh water, which drains off into the bay. Lesser amounts of fresh water drain into the bay during heavy rains from small gulches and hill wash. During the winter and spring, when the ground is frozen, appreciably larger volumes of fresh water enter from these gulches and hill wash. Intense rains flood the tidal flat temporarily with a sheet of water one-half to 2 or 3 inches deep, making the flat look almost as though the tide had not gone out.

At average low tides, the upper mile of the bay is exposed as a muddy and sandy tidal flat. Extreme low tides expose about one-fifth of a mile more.

Virtually all the tidal flat proper lies below mean sea level. From the average low-tide line, the surface of the flat rises only about 4½ feet in its length of nearly a mile. Water drains off this flat continuously while it is exposed between tides. The sandy mud, which makes up most of the flat, is sufficiently porous that it slowly yields its contained water at a nearly uniform rate from all parts of the flat that slope. Parts of abandoned channels and extremely shallow depressions remain ponded between tides though they continue to drain very slowly. A few small, slightly higher areas that consist of relatively clean, fine sand drain out nearly dry between tides.

Two kinds of sediment make up the great bulk of the flat; one, medium- to fine-grained, well-sorted sand that contains little very fine sand and silt and a few tenths of one percent of organic matter; the other, similar fine sand, which is made soft and muddy by a somewhat greater content of very fine sand, silt, and clay and about 2 percent of organic matter. Figure 2 shows the size distribution and the degree of sorting of representative samples of these two kinds of sediment. Figure 3 shows the distribution on the flat of these two dominant kinds of sediment. Almost everywhere the boundaries between these two kinds of sediment are characterized by a subtle gradation from one into the other. Gemmas live in both kinds of sediment but are far more abundant in the sandy sediment.

The soft muddy sediment represents a relatively quiet environment where the finest particles settle to the bottom and accumulate. The sandy sediment represents an environment where the bottom is frequently (nearly every tide) stirred up by waves and tidal currents so that most of the silt and clay-sized particles and much of the organic matter are winnowed out and transported elsewhere.

In the muddy sediment it is obvious that most of the organic matter is fecal, for the form of the feces is quite evident. Presumably most of the fecal matter that retains its form comes from small worms, which are abundant in the mud. Although the sandy sediment contains only about one-tenth as much organic matter, it is still adequate to darken the sand and give it a drab or olive cast, especially just below the surface. Probably most

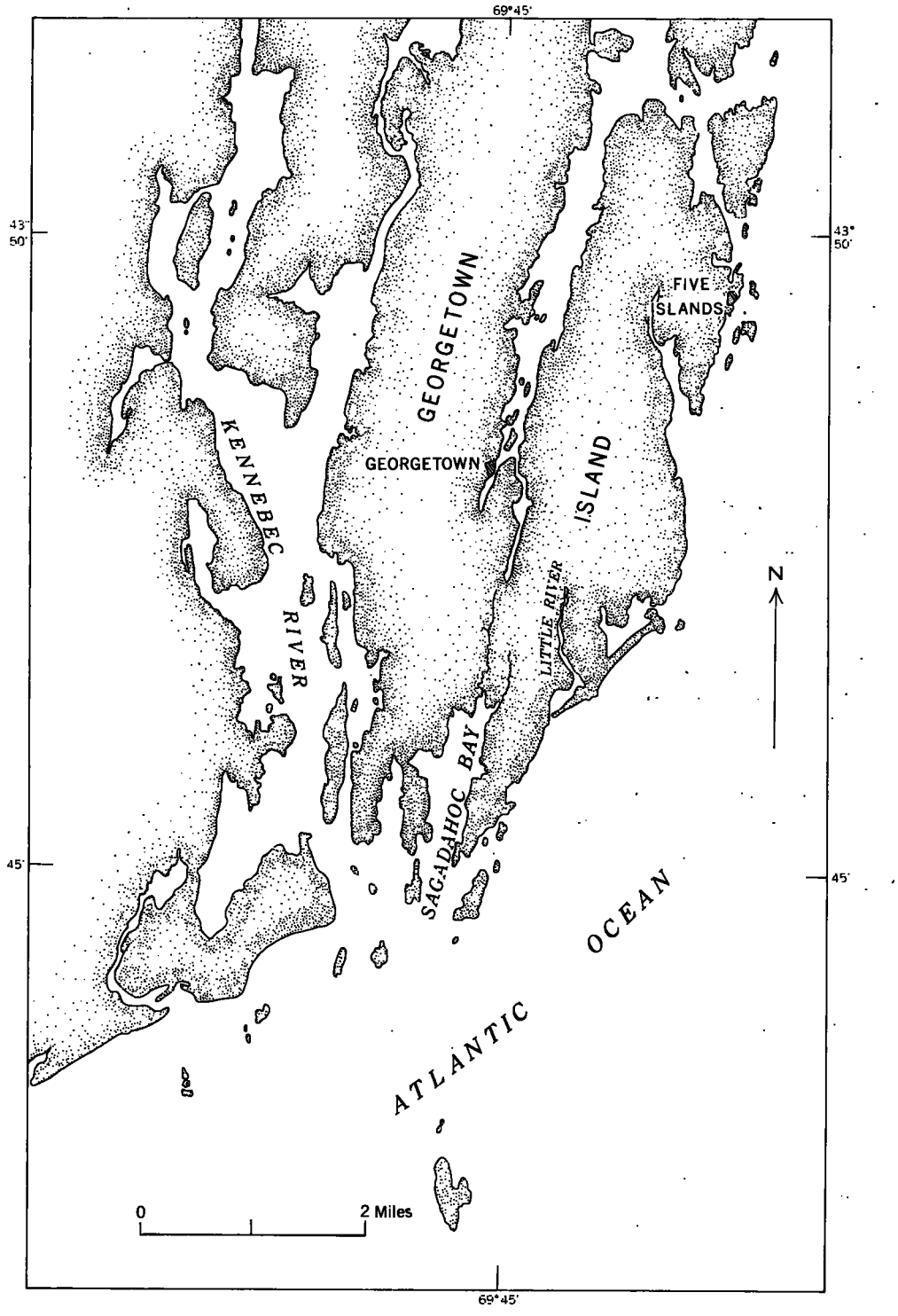


Figure 1.—Location of Sagadahoc Bay, Maine, the mouth of the Kennebec River, and Little River.

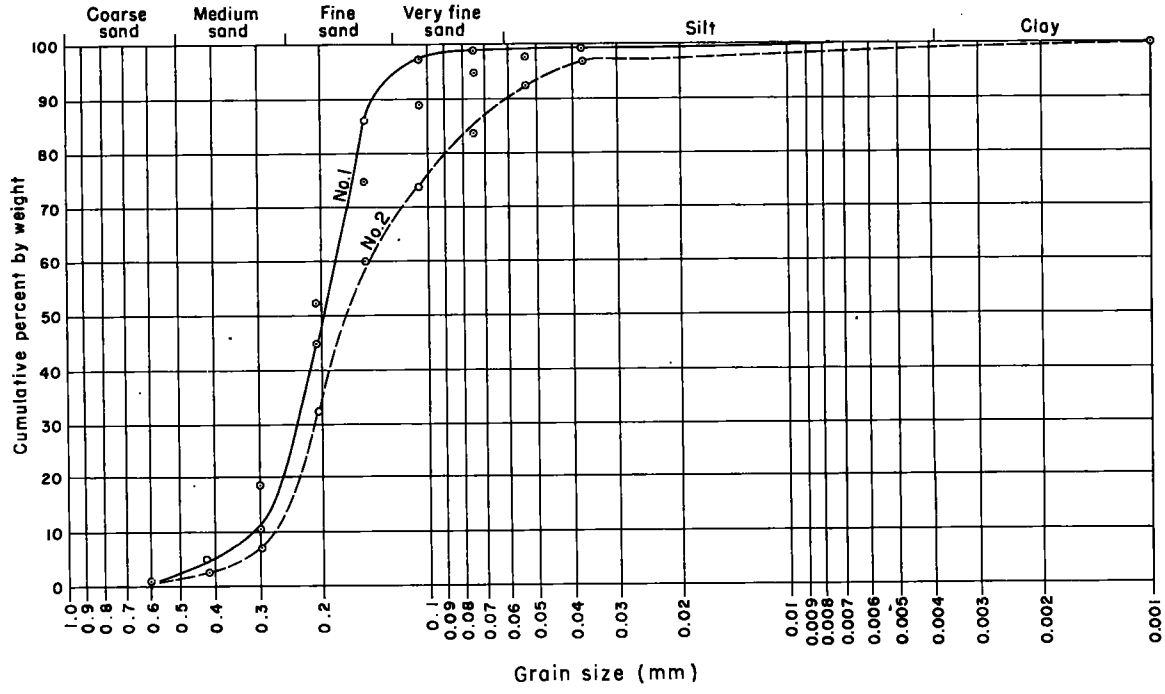


Figure 2.—Cumulative curves show size distribution and degree of sorting of grains that form the two dominant kinds of sediment in Sagadahoc Bay: (1) Sandy sediment that characterizes midsection and outer parts of the flat; (2) Muddy sediment that characterizes the quieter coves and the area at the head of the Bay.

of the organic matter in the sand is also fecal though recognizable feces are rare. Particulate organic detritus is locally common, though mostly near the low-tide zone. In winter this particulate organic detritus, presumably derived mostly from *Spartina*, is more abundant and is distributed more generally over the flat.

Both the muddy and sandy sediment have rather well-defined surficial zones in which the decomposing organic matter is being oxidized. This layer is thin in the muddy sediment, a small fraction of an inch, and is hardly perceptible in the very soft deep muds, which contain the most organic matter. In the sandy sediment the oxidizing zone ranges in depth from a small fraction of an inch to two or more inches and averages about an inch. The depth of the oxidizing zone is a function of permeability of the sediment and the depth to which the sediment is stirred by the waves during each tide.

Below the oxidizing zone the sediments, both muddy and sandy, are gray to almost black and are reducing environments containing hydrogen sulphide. Little difference was found in either the pH or redox potential (Eh) of the two kinds of sediment near the surface. The pH at or slightly below the surface of the sediments ranged from 7.02 to 7.45 and the Eh from +304 to +394. At a depth of 2.4 inches the pH ranged from 7.13 to 7.43 and the Eh from −124 to −194. The water close to the bottom had a pH range of 8.11 to 8.48 and was oxidizing (Eh +275 to +320) but no more so than the surface layers of the mud and sand. At depths of 2 to 3 feet below the surface of the sediment the pH and Eh values are only slightly lower than at a depth of 2.4 inches below the surface.

The uppermost half inch of sediment, both mud and sand when exposed at low tide, ranges in temperature from below the freezing point of salt water in the winter to at least 84° F. in the summer. In sunny weather, heat is absorbed by the dark sediment so that its temperature sometimes rises 20° F. higher than the air temperature. Few winter-temperature measurements were made, but in February 1956, on a clear sunny but windy day, the air temperature near noon was 27.5° F., whereas the temperature of the fine sand one-fourth inch below the surface was 41° F.

Most gemmas dig in about one-fourth inch

SAGADAHOC BAY TIDAL FLAT
GEORGETOWN, MAINE

MAPPED JULY–AUGUST 1949

BY

W. H. BRADLEY AND W. H. CONDON
U.S. GEOLOGICAL SURVEY

200 0 1000 Feet

Contour interval 0.5 feet
Datum is mean sea level

18°
MAGNETIC NORTH
TRUE NORTH
APPROXIMATE MEAN DECLINATION, 1945

EXPLANATION

Soft sandy mud containing a relatively large proportion of silt and clay

Medium and fine-grained sand containing relatively little silt and clay

Metamorphic rock and pegmatite

Salt marsh grass, *Spartina*

C-9
Current-measurement station, dominant flow directions

16
Hole number

Water area

(14)
Core stations

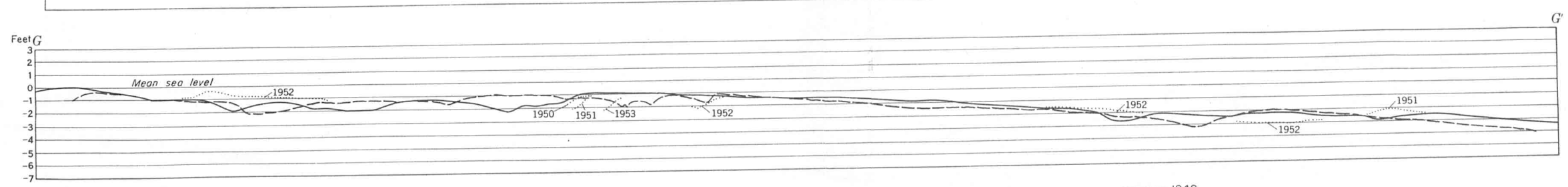
Upper and lower limits of beaches

Triangulation station

*
Isolated boulders

A-A' — E-E'
Current velocity profiles

H-H', J-J', K-K'
Refraction seismic profiles



Profiles of the intertidal area measured along lines G-G' and F-F' each year, 1949–54 inclusive. 1949 and 1954 profiles complete, others partial to show significent departures.

1949
1954
1950–53 as noted

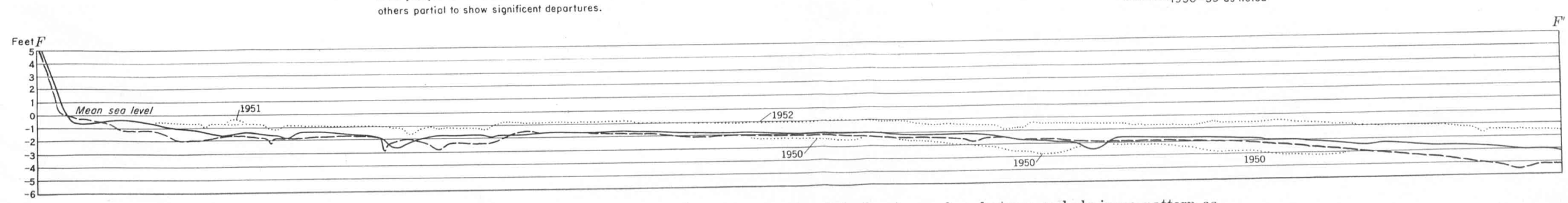


Figure 3.—Map of the Sagadahoc Bay tidal flat at average low tide showing surface features and drainage pattern as of 1949: Location of test holes dug in 1950, core stations where short cores were taken in 1954, the location of current-measurement stations, and the location of refraction seismic profiles.

below the surface but a few go deeper, even to three-fourths inch. At one place near the midsection of the flat, we measured the depths shown in table 1 to which they had dug and from many casual observations, we believe this is fairly typical, though just after a heavy downpour of rain that literally flooded the flat we found that they had dug in at least one-half inch below the surface.

In the summer of 1956, J. R. Balsley of the U. S. Geological Survey and the senior author measured the thermal conductivity of the sandy sediment in the midsection of the flat and the muddy sediment near the head of the bay. The sandy sediment has a thermal conductivity of about 4.4×10^{-3} cal per cm sec °C and the muddy sediment slightly more, 4.6×10^{-3} cal per cm sec °C. The moisture content of the sandy sediment is 20.1 percent of wet sample and the muddy sediment 21.2 percent. The specific heat of these sediments is about 0.24 ± 5 percent cal per gm °C and the thermal diffusivity is about 0.009 ± 10 percent cm^2 per sec. The thermal conductivities were measured with a probe designed by Arthur H. Lachenbruch of the U. S. Geological Survey and he made all the computations given above.

During the winter (observations made on 1 day only Feb. 21, 1956) the gemmas were found to be distributed rather unevenly through a much greater range of depths than in the summer (table 1). As they were inactive it was not surprising to find them oriented predominantly on their sides, as are most dead shells found either at the surface or at any depths below the surface where we have observed them. It seems possible that the hibernating gemmas reach these depths by settling through the fine sand when storm waves stir it up. Some doubt is cast on this inference, however, by the fact that the heavy mineral sand grains, garnet, magnetite, hornblende, and others, have not similarly concentrated to depths of several inches. On the contrary, they are randomly distributed as though there had never been any opportunity for them to settle selectively.

We were surprised to see, during the summer, that gemmas, when they dig in, do not remain oriented with their posterior ends up, but are rather erratically positioned: four of the 40 had their anterior ends up.

TABLE 1.—*Summer and winter depth distribution of living gemmas*

Depths (inches)	Numbers of gemmas		Depths (inches)	Numbers of gemmas	
	Summer	Winter		Summer	Winter
⅛	3		1		27
¼	28	19	2		39
⅜	7		3		22
½	1		5		1
¾	1				

During large storms, gemmas get buried to considerable but unknown depths. Because gemmas are strong, active animals, we were curious to know how deeply they could be buried and still rise to the surface and survive. Accordingly, we made the following simple tests in a small aquarium. Live gemmas of about equal size were sieved from the flat and transferred to a large, deep receptacle filled with sand from the flat. This sand was wet-sieved to remove all other gemmas. The aquarium was divided by a vertical septum; on one side 10 living gemmas (the controls) were set on the surface; on the other side of the septum 10 living gemmas were buried beneath 2 inches of sand. For the next two days or so the aquarium was filled with fresh sea water and then drained at roughly tidal intervals to simulate the tides. This same experiment was repeated twice more, but the depths of burial were 4 and 8 inches, respectively. Each experiment was started with freshly collected gemmas. The results (table 2) suggest that gemmas can extricate themselves from remarkably deep burial.

TABLE 2.—*Survival of* Gemma gemma *at selected depths*

At depth of—	Date planted	Date recovered	Number planted	Number recovered [1]
2 inches:				
test clams	Aug. 30	Sept. 1	10	10
control clams	Aug. 30	Sept. 1	10	[2] 10
4 inches:				
test clams	Sept. 1	Sept. 3	10	7
control clams	Sept. 1	Sept. 3	10	10
8 inches:				
test clams	Sept. 3	Sept. 5	10	5
control clams	Sept. 3	Sept. 5	10	10

[1] Feeding.
[2] At the surface, half emerged.

These tests were made on uncrowded animals in prime condition. Older or much younger animals might have been less successful, particularly if they had been much crowded.

The tide in Sagadahoc Bay averages about 9.6 feet, and ranges from a little more than 5 to

nearly 13 feet. The velocities of the tidal currents in the bay play a significant role in the economy of the shellfish living there because their food is brought to them in suspension in the water that passes over them. Of particular value is a knowledge of the velocities close to the bottom where they are not usually measured. Accordingly, special equipment was designed and made for us by Arthur H. Frazier, Chief of the U. S. Geological Survey's Water Resources Development Laboratory at Columbus, Ohio (fig. 4).

During the summer of 1953, Charles E. Knox, hydraulic engineer from the Boston office of the Geological Survey, measured the current velocities at 17 stations in the intertidal part of Sagadahoc Bay. The stations, selected in consultation with John Glude of the U. S. Fish and Wildlife Service, were located where the velocities are most nearly representative of flow over the flat and are least affected by the faster-flowing water in the major drainage channels. The velocities observed at these stations were related by time to the corresponding water-surface elevations shown by an automatic stage recorder, which was installed near the low-tide line. Current velocities were measured continuously at 0.1 foot, and 1.0 foot, and 3.0 feet above the bottom, but only the velocities at 0.1 foot above the bottom were fully worked out.

On the basis of data obtained during July and August 1953, bottom velocities measured at the 17 stations gave similar patterns. The velocities at the start of incoming tide were the highest recorded during the tidal cycle and ranged from 0.35 fps. to 0.82 fps. The velocities decreased rapidly and then leveled off, reaching a minimum around the change of tide. Minimum velocities ranged from zero to 0.15 fps. Measurable velocities were recorded at all but one station in Bedroom Cove. The velocities increased after the turn of the tide and reached another peak as the water drained off the flat. These peak velocities as the water drained off ranged from 0.20 fps. to 0.58 fps. The velocities at the start of a tidal cycle averaged about 25 percent higher than those near the end.

The velocities varied rather uniformly throughout the bay. In Bedroom Cove they were about half those in other parts of the bay. The velocities in the upper end of the main part of the bay were about 35 percent lower than those farther out in the bay.

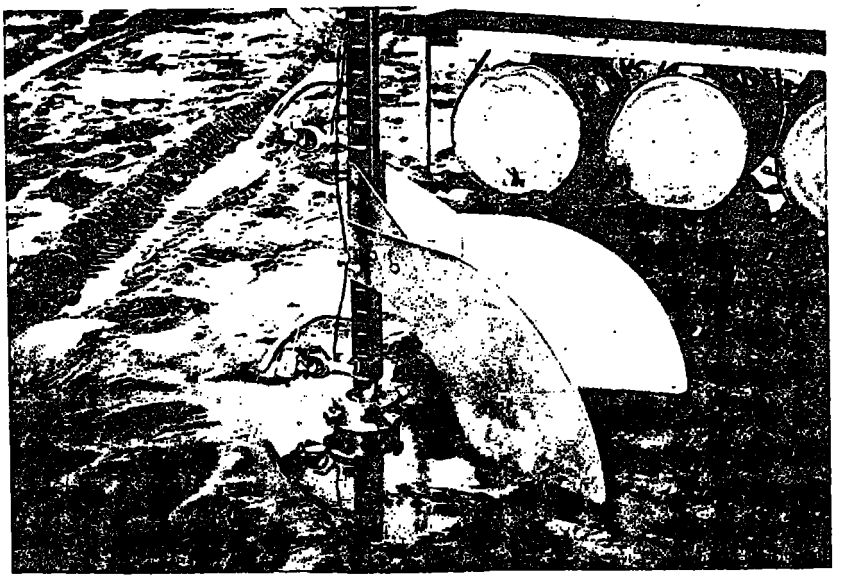


FIGURE 4.—Pygmy Price current meters mounted near the bottom of a tube which surrounds a stainless steel rod. The tube hangs from a pivot at the top of the rod so it is free to rotate as the rudders dictate. The steel rod is set in the cone-shaped bottom of an iron pipe driven 3 feet into the mud. Centering collar at top of the pipe provides for plumbing the rod. The corks resting against the current-meter rotors prevent rotation in the wind but rise when the tide comes in to let the rotors turn only when fully submerged. Impulses from the three current meters were recorded on paper tape moving through a battery-driven, clock-controlled recording device, which was supported on a float.

The average velocities varied directly with the range of the tide and for the tide of August 18, 1953 (7.7 ft.), were 30 percent lower than those for the tide of August 25–26, 1953 (11.2 ft.). Flow into and from the bay varied at a fairly uniform rate. However, there were times, especially when a pronounced swell was running, when the water moved in surges, that is, seiches were established. These surges, which have a period of something less than 10 minutes, may be edge waves described by Munk, Snodgrass, and Carrier (1956, pp. 127–129). At these times, the current moved alternately in and out for intervals of several minutes, especially near the turn of the tide. The same seiches have been observed at the low-tide line. The recorded velocity was the resultant of the two velocities.

The detailed observations and graphs may be consulted in an open-file report (Knox and Bradley, 1954) on deposit at the library of the U. S. Geological Survey.

Surface water velocities (ca. 30 inches below the surface) were measured from stick-buoy surveys on August 8, 1952 and averaged nearly 0.3 fps. on the flood tide and 0.59 fps. on the ebb tide. These are averages over nearly the full length of the intertidal zone on a tide whose range was greater than average.

The waters of Sagadahoc Bay have somewhat less than ocean salinity owing to the freshening of a large area off the entrance to the bay by the Kennebec River, whose mouth is adjacent to Sagadahoc Bay on the west. For several miles out to sea beyond the mouth of the Kennebec River, the surface water has salinities of 25.1 to 25.4 parts per thousand. In Sagadahoc Bay, during the summer, the salinities range from about 26 parts per thousand at the entrance to 29.8 near the landward end. More saline water comes into Sagadahoc Bay from the east through the narrow passage between Indian Point and Salters Island and accounts for the greater salinities within the bay. Summer evaporation from the much warmer water near the head of the bay tends to increase the salinities at the head of the bay. Generally, these shallow waters are turbulent enough so that all the water in any vertical column is effectively mixed.

The long rocky ribs that form the east and west sides of Sagadahoc Bay refract the ocean waves, regardless of their orientation at sea, and direct them up the bay with their crests essentially normal to the long axis of the bay. During storms, two zones of breakers form, one seaward from the average low-tide line and the other farther up the bay. The positions of these zones of breakers, of course, shift with the stage of the tide and the size of the waves.

During quieter times, the waves that come in over the intertidal area of the bay generally have steep flanks and wide flat troughs. These are only the crests of ocean waves whose bottoms have been sheared off by the shoaling bottom in the outer half of the bay. As each of these waves passes over the bottom, it creates beneath it, and in back of it, a family of horizontal parallel vortices (fig. 5). The hydrodynamics of these vortices (Russell 1952, pp. 114–116) is such that they have at first small orbits and high orbital velocity, but immediately the axis of the vortex begins to rise, the orbit grows larger, and the orbital velocity decreases. Such wave-generated vortices are effective erosive agents, which not only move detritus and fine sand grains but doubtless also small gemmas and myas. This is the process that throws the surface of the sandy part of the flat into its characteristic, ever-present ripples.

Gemma life cycle

Gemma gemma is ovoviviparous and according to Sullivan (1948, p. 2) "the larvae pass their entire veliger stage in the adult and on liberation settle in a cluster around the parent." Sullivan notes further (p. 31) that "*Gemma* eggs are large, and so are the earliest shelled larvae. The smallest larva measured was 272x295 microns. When liberated, they are generally around 340x410 microns." Apparently they are liberated through the summer nearly up to freezing weather for we have found minute forms all through July and August and some in February. These must have been born very late in summer as they showed very little growth beyond the larval shell. On the Sagadahoc flat, gemmas grow to a maximum length of almost 0.2 inch (5 mm.) but the bulk of the mature population averages nearer 0.16 inch (4 mm.) in length.

According to our observations, the gemmas living in Sagadahoc Bay today live at most 4 years but the great bulk of them live only 2 years. These age determinations are based on growth increments

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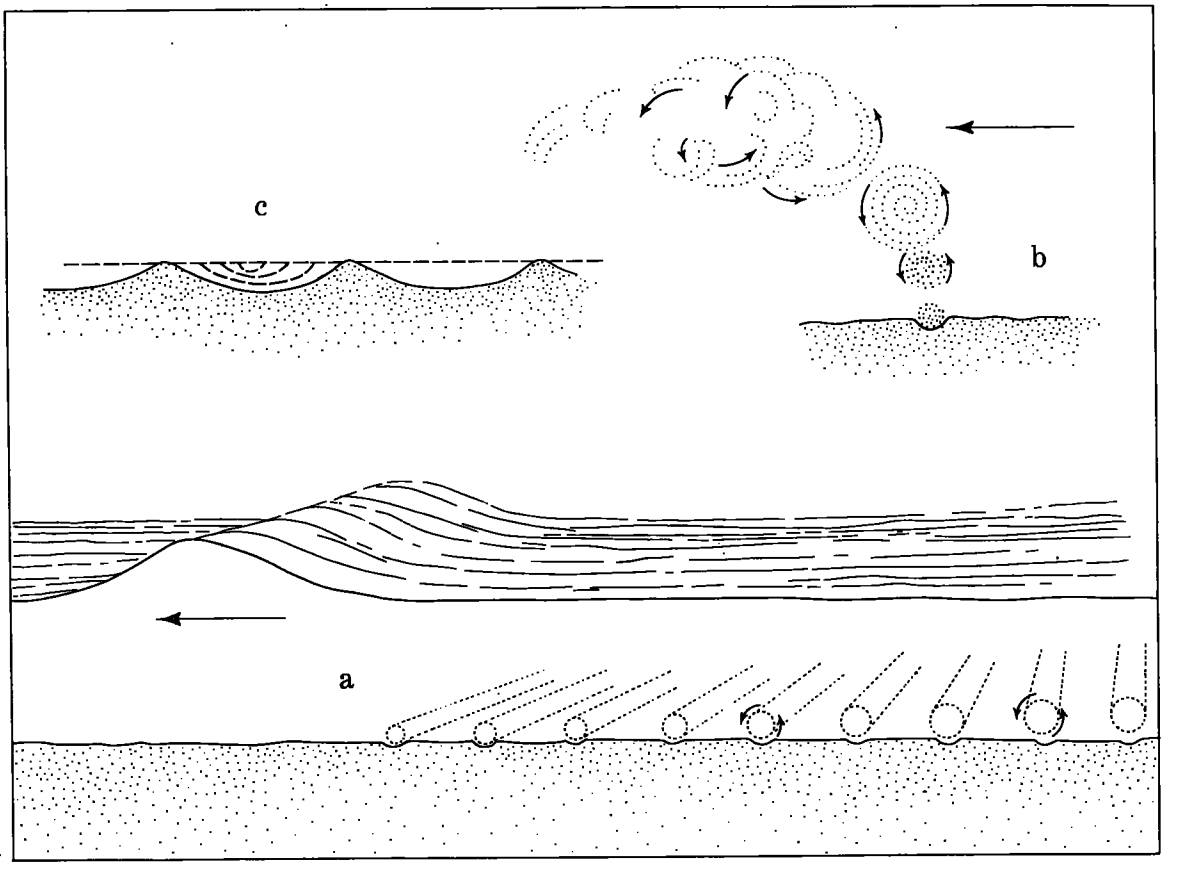

FIGURE 5.—Family of horizontal vortices (a) that form below waves traveling up the tidal flat have at first small orbits and high orbital velocity; each vortex (b) erodes a trough, rises, enlarges its orbit, decreases its orbital velocity, becomes turbulent and dissipates; ripple marks (c) formed by scour of successive families of wave-generated horizontal vortices.

of the shells of living gemmas. On most shells the larval stage is sharply defined and, except on those less than 1 year old, is deeply corroded, white, and chalky (fig. 6). On shells less than a year old the larval shell is recognizable by its rugose surface and by a fine bounding groove. Shell grown after expulsion from the parent is glassy smooth (fig. 6). The first year's growth is plainly set off from the second year's growth by a groove. In the 2-, 3-, and 4-year olds the first year's growth has many chalky blotches and the second year's growth of shell is sparsely marked with white chalky blotches. Chalky spots more than a year old are pitted. Also, the second year's shell, especially on the posterior end, is a deeper violet. Both this color difference and the groove representing the winter cessation of growth are more conspicuous from the posterior end (fig. 6).

In all the following age determinations (both living and dead shells) the animal was considered to be 2 years old if it lived into the second year, even though it may have died early in that year. In the same way, those that lived into the third and fourth years were counted as 3- and 4-year olds.

Gemmas that lived in Sagadahoc Bay many years ago lived longer and apparently grew somewhat more slowly than those that live there today. Some grew for 6 years, and possibly longer, but after the fifth year the growth zones are too narrow and obscure to be very reliable indicators. The ages of 202 gemma shells were determined from an extensive shell-pavement layer that underlies much of the sandy part of the flat at depths ranging from 20 to 24 inches below the present surface. The age distributions of the living, modern dead, and ancient gemmas are shown in table 3. The modern dead gemmas were collected in February 1956 from the surface of the flat near the southern end of Black Rocks Islands.

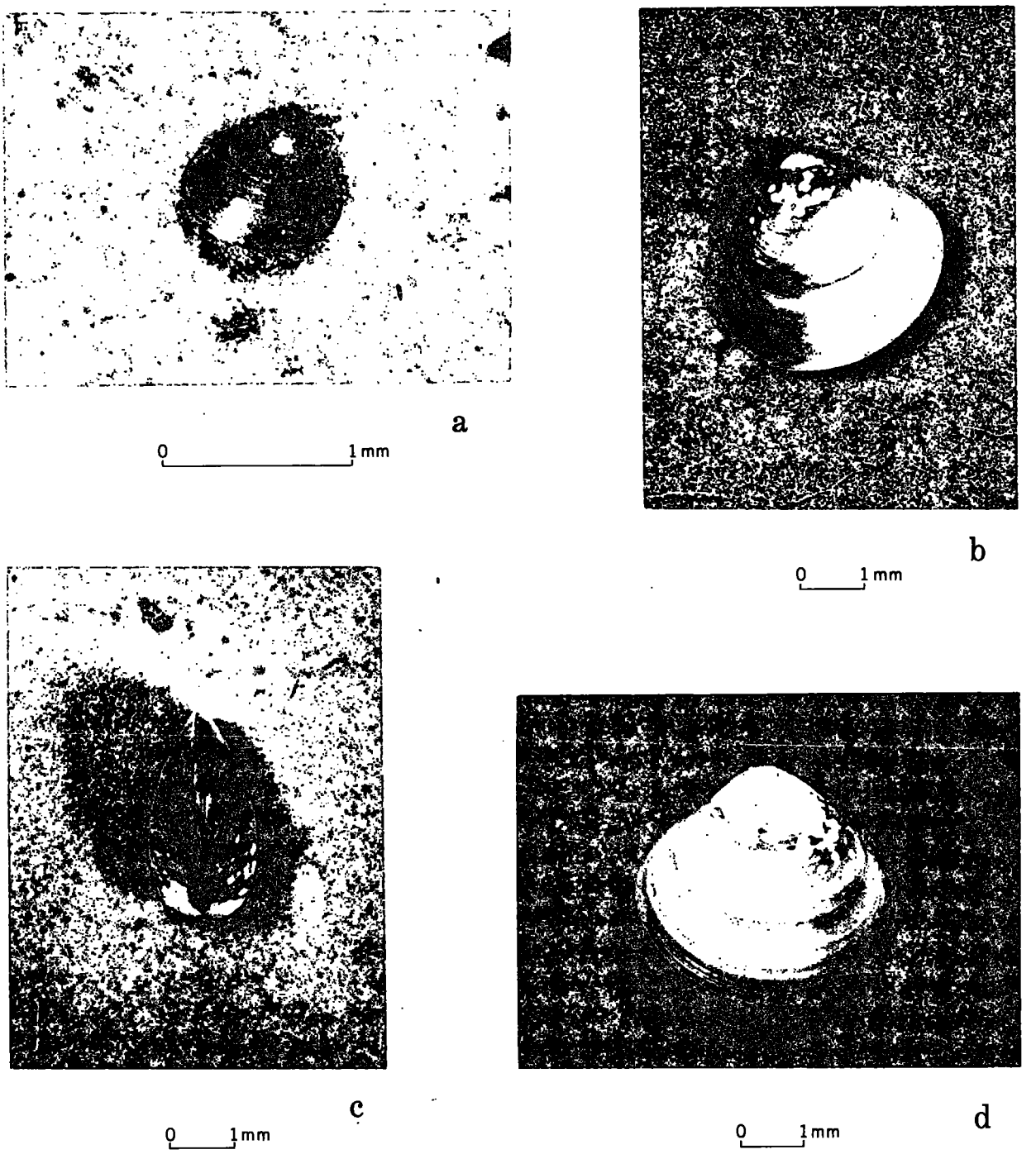

FIGURE 6.—*Gemma gemma* showing first-year form (*a*) with rugose larval cap and clear glassy, deep violet post-larval growth; two-year old individual (*b*) having white, chalky larval cap, chalky blotches on the first year growth, and clear glassy second year growth; posterior view (*c*) of same 2-year old showing the darker violet band close to the margin of the first year's growth; a 3-year old (*d*) showing corroded larval cap, chalky first year growth, sparsely blotched second year growth, and a narrow band of clear third year growth.

A small number of the shells in the living population have obscure growth bands and so their ages are indeterminate. In the ancient *Gemma* population the ages of more shells were indeterminate, principally because the surface layers of shell had flaked off. Only sound shells whose growth zones were clearly marked were used in making the counts listed in table 3.

TABLE 3.—*Age distribution of living, modern dead, and ancient gemmas in the Sagadahoc Bay tidal flat*

Age classes	Living (1949)	Living (1955)	Modern[1] dead (1955)	Ancient
1-year-olds	5	345	30	44
2-year-olds	12	1,208	155	71
3-year-olds	32	32	83	79
4-year-olds	1		8	[2] 8
Totals counted	50	1,585	276	202
Average age (years)	2.6	1.8	2.2	2.25

[1] Those that died in 1955 plus a small but unknown number that died in preceding years.
[2] Includes some 5- and 6-year olds and possibly some still older.

The age distribution of the living gemmas apparently differs somewhat from year to year, although the average age seems to be decreasing progressively. In 1949 it was 2.6 years; in 1955 it was only 1.8 years. Some allowance must be made in this comparison for the fact that in the 1949 age class we determined the ages of only 50 gemmas whereas for the 1955 class we determined the ages of 1,585 (table 3). This table shows that the 1955 population was abnormally deficient in individuals over 2 years old.

Because the climate has been warming progressively for the past 30 years or more, it is pertinent to raise the question whether the life span of *Gemma gemma* along the Maine coast may not be decreasing. Much farther south (Chesapeake Bay), *Gemma gemma* has a life span of only 1 year (J. P. E. Morrison; oral communication, 1955). But many more vital statistics on the Maine *Gemma gemma* than we have collected will be required to determine if such a secular change is taking place.

A less extreme explanation, and perhaps therefore more probable, is that the decrease in life span resulted from the crowding of the gemmas while the population was so dense during 1950 (and possibly 1951–53). Pearl, Miner, and Parker (1927, pp. 293–296) found in their experiments with fruit flies, that density of population markedly decreases life duration, particularly when the density increases greatly over the optimum.

The average at death of both the modern *Gemma* population and the ancient *Gemma* population is essentially the same (2.2 years), despite the fact that the ancient animals grew somewhat more slowly and, at least, a few of them lived longer.

As discussed later (p. 325–27), Comparison of 1950, 1954, 1955, 1956, and 1957 population, the *Gemma* population in Sagadahoc Bay decreased progressively for the years 1954, 1955, and 1956. Moreover, it decreased a proportionate amount between 1950 and 1954, but as we took no census in the years 1951–53 we do not know whether the decline was at a uniform rate (fig. 13).

We wonder whether the apparent decrease in life span shown in table 3, especially the very small number more than 2 years old in the 1955 living population, may not account in part for some of the observed decline in the population. A stable population of animals whose average life span, for example, is 4 years, can be sustained by a 25-percent annual replacement, but if the life span is reduced to 2 years it would require 50-percent annual replacement to maintain that same population. Of course, if the replacement rate remains constant the population must be reduced by half. Clearly, the *Gemma* population in Sagadahoc Bay has declined much more in the interval 1950–56 than the apparent decrease in the life span of the gemmas could account for; hence, other factors must be sought to account for the decrease in the *Gemma* population.

Surely something abnormal is happening in the population, because in each census the number of 1-year olds is markedly less than the number of 2-year olds (table 3), whereas in a stable population it should be the other way around. Even allowing for 25-percent loss of the minute individuals, which is generous in our method of sampling (p. 319–20) the numbers of 1-year olds are discrepantly small. Considering the small size of the youngest gemmas and the fact that most small particles are winnowed out of the sandy part of the flat by waves and currents, it seems probable to us that a sizable percentage of the minute gemmas are similarly winnowed out and either moved up the flat into a muddy and much less favorable environment or moved seaward beyond the low-tide line where they cannot live. This

would account for the observed abnormal deficiency of 1-year olds in the population. If this is so, an abnormally high frequency of summer storms would have a depleting effect on the population of *Gemma* and vice versa.

We have very little information on seasonal changes in the abundances of *Gemma* in this bay, but that little suggests no change.

TABLE 4.—*Winter and summer Gemma counts per 8-inch diameter sample*

Stations	February 1956	July 1956
H	60	67
I	98	74
J	132	123
K	50	74
Means	85.0	84.5

Feeding habits

Gemmas that live in the sandy areas have relatively thick, strong shells that are strongly colored, deep violet or purple in the small ones and lighter violet in the mature shells. The mature ones, however, have only about one-half or less of the posterior ends colored. When the clam is feeding in the dark, this colored posterior end rises above the surface of the sand. In the dark, they move around somewhat as *Spisula* does. In subdued light, they feed with only their siphons exposed. It is doubtful whether they feed at all when strong sunlight penetrates to the bottom, that is, in shallow, clear water. But in Sagadahoc Bay the water is generally somewhat turbid so that a few feet of water over the part of the flat where the gemmas are most abundant probably dims even midday summer sun enough so that they feed, at least with only their siphons exposed.

An attempt was made to determine the area over which individual mature gemmas feed. To do this a small aquarium was set up with sandy mud from the flat with its contained gemmas. No running sea water was available, but at appropriate intervals the water was poured off and some hours later fresh sea water was added, thereby roughly simulating the tides.

We found that the gemmas fed much more actively at night, or indeed at any time when kept in the dark. They are so shy of light that observations had to be made within a minute or less after the aquarium was uncovered. In those brief intervals we could make no measurements; only estimate dimensions by visual comparison with the known average dimensions of the shells. In general the siphons protrude about the equivalent of a shell width and most of the time they are kept in, or nearly in, the plane of the valve openings. Occasionally the siphons are moved slowly about in a semicircle. The effective area from which they draw food was estimated to be roughly equal to the area of the side of the shell, about 0.0065 square inch (4.2 square mm.), but this is probably a minimum because gemmas move about, at least in the dark. The longest furrow observed in the aquarium was a little more than 1.2 inches. Where several mature gemmas by chance came into contact they pushed and shoved one another with considerable vigor.

If we assume that the probable minimum area from which each gemma draws food is 0.0065 in.^{2} (4.2 mm.^{2}) and that there are 25 mature gemmas per square inch in the central sandy part of the tidal flat—roughly the average density in 1954—then these gemmas are drawing food from about 16 percent of the bottom layer of water passing over them. The present living *Gemma* population (1950) ranges from 1 or 2 per square inch near the margins of the flat to as many as 190 per square inch in the sandy central part of the flat (fig. 7).

LIVING POPULATION

Distribution

Gemmas live in virtually all parts of the Sagadahoc Bay except a narrow irregular zone around the margins (fig. 8). They are much more numerous in the large areas of the flat where the sediment is relatively clean, fine-grained sand, and they evidently find a nearly optimum environment in the midsection of the flat.

Gemmas that live in the sandy areas, have thick strong shells and are white with violet posterior ends. Those that live in the muddy areas have thin, delicate shells, which are easy to crush between the thumb and finger. The mud-dwellers have paler colors and in some areas are light brown.

Apparently gemmas, like many intertidal species, must be wet virtually all the time, for they are extremely rare or absent from places, either sandy or muddy, that drain out nearly dry between tides. They prosper only in intertidal areas where the slopes are gentle and where the

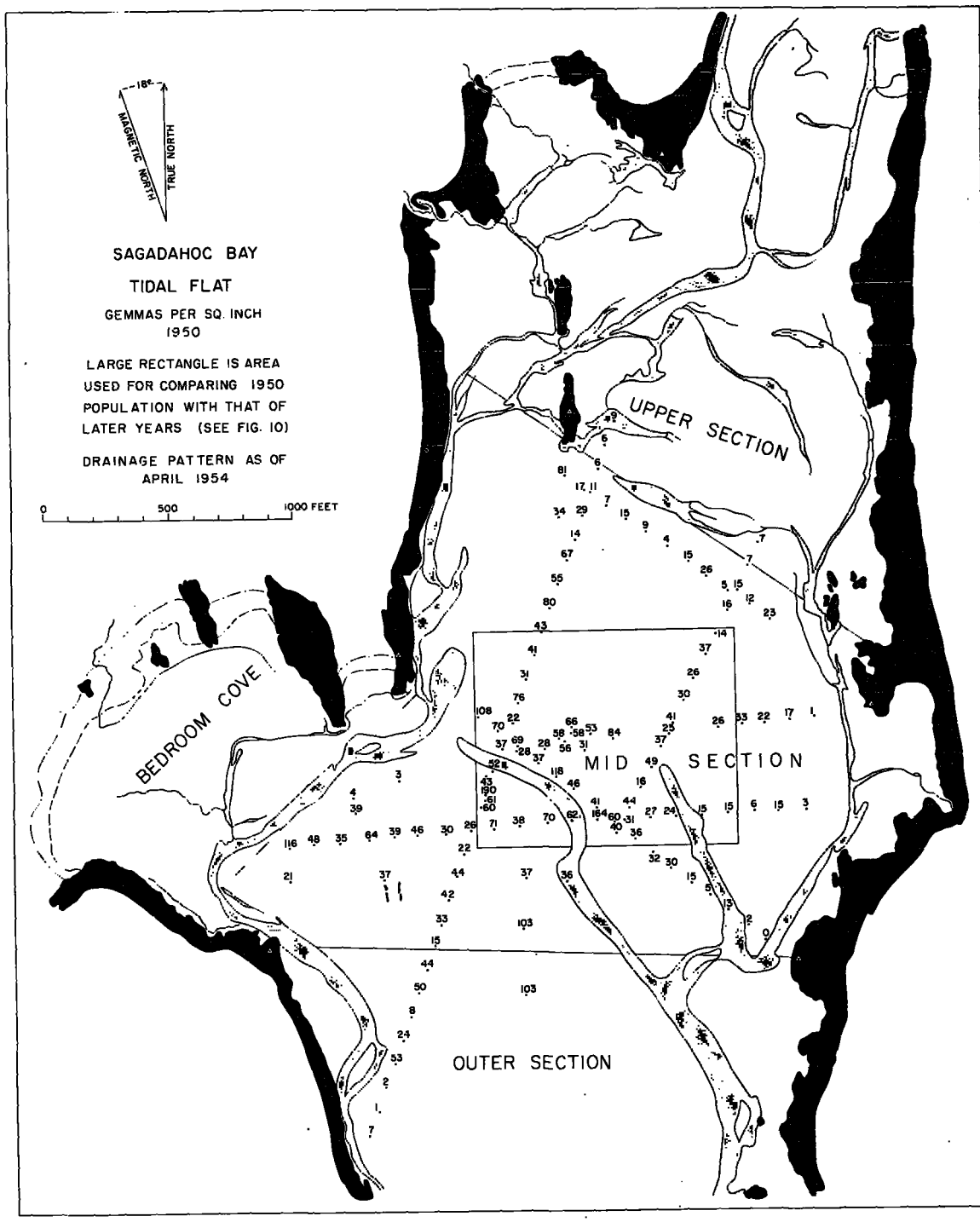

FIGURE 7.—Distribution of sampling stations used in the 1950 *Gemma* census. Numbers are gemmas per square inch. Large rectangle is area sampled in 1955, 1956, and 1957 for comparison with 1950 and 1954 populations.

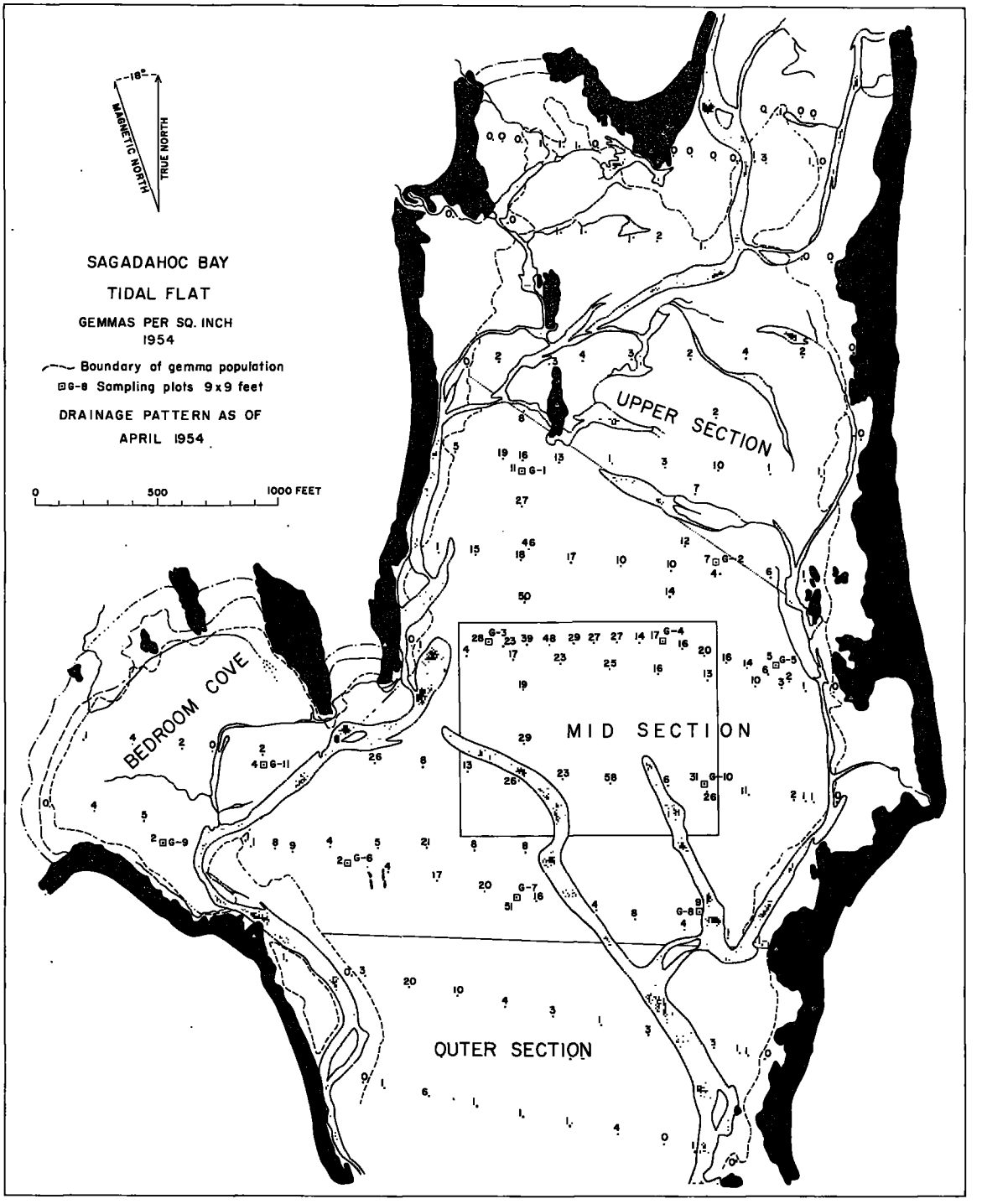

FIGURE 8.—Distribution of sampling stations used in the 1954 *Gemma* census. Numbers are gemmas per square inch. Dashed line around margins of the flat is the outer boundary of the *Gemma* population. The distribution of special sampling plots 9 by 9 feet square (G–1 to G–11) are also shown together with the large rectangle used for comparing the *Gemma* population from year to year.

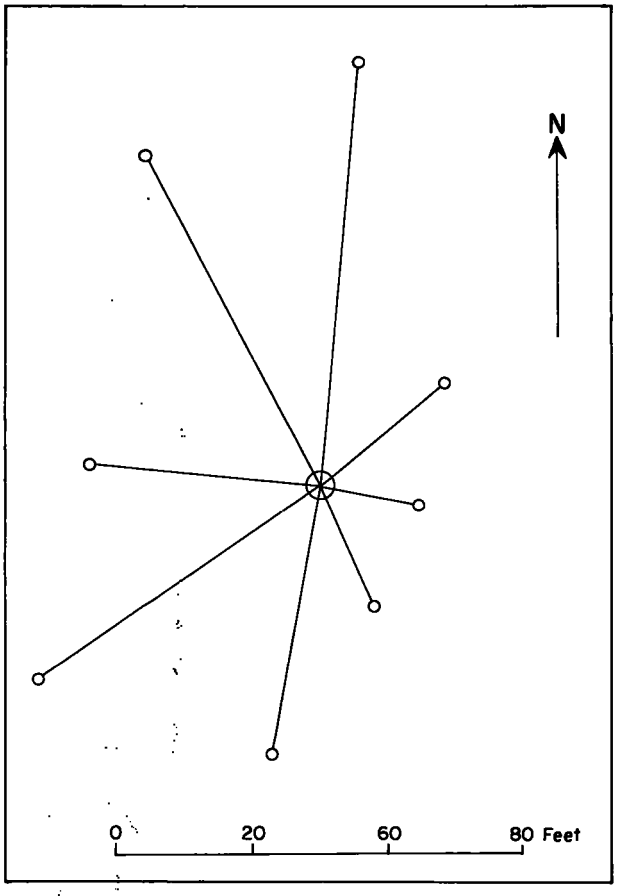

FIGURE 9.—Directions and distances that colored sand grains were moved radially from a point source by waves and tidal currents in 15 days of average summer weather during the summer of 1950. The colored grains were of about the same size and density of the average sand grains in the sandy part of the flat.

sediments are fine grained enough to keep the pore spaces filled with water while the tide is out.

As noted above, gemmas move about while feeding or while searching for better feeding grounds. Perhaps this movement alone could account for their present ubiquity in the sandy parts of the Sagadahoc Bay tidal flat. But waves, especially those generated by big storms, move gemmas in large numbers and probably for considerable distances. Patently, small gemmas are moved about more than the mature ones. Judging by the measured migration of sand grains on this flat (fig. 9), the dominant tendency of the waves is to move gemmas northward up the long axis of the flat. Nevertheless, the sand grains, which average about 0.005 inch (0.12 mm.) in diameter, are also moved in all other directions and doubtless also are gemmas. These and other related observations are discussed in another report (Bradley, pp. 666–669).

A small percentage of mature gemmas acquire tufts of the green alga, *Enteromorpha compressa*, which ensures their transport by waves of even moderate size. Whenever mature gemmas containing young in their mantles are transported to a favorable environment, new centers of relatively greater population density come into being.

Both these saltatory means of distribution help to account for the observed uneven distribution of the *Gemma* population in an extensive, monotonously uniform sandy flat where uniformity of distribution might be expected.

The sandy part of the flat, with the exception of a few small marginal areas, is always rippled, and the ripple crests are nearly normal to the long axis of the bay. The size and shape of the ripples, of course, is determined by the size of the waves and the depth of the water during the preceding high tide. Most common are ripples that are asymmetric and whose wave lengths are 5 or 6 inches from crest to crest. Amplitudes of the ripples differ from tide to tide but rarely exceed one inch.

During one low tide we sampled the number of living gemmas at 18 stations in the midsection of the flat and found that on the average there were 20 per square inch in the troughs, 16 per square inch on the crests, and 24 on the midpart of the long back slope.

The surface of the whole flat is interrupted at intervals of a quarter of a mile or less by low transverse ridges and adjacent broad shallow swales. These features have roughly the same form as gigantic asymmetric ripples whose steep faces are landward. On one of these ridges we found from rather extensive sampling that there are about 22 gemmas per square inch on the ridge and about 15 per square inch in the adjacent swale.

Further observations are needed to determine whether this distribution of gemmas with respect to the sand ripples and larger topographic features, is determined by the waves or whether the gemmas move to those positions because they are in some way more favorable.

The 1950 and 1954 counts (figs. 7 and 8) show that gemmas are much more abundant in the midsection of the tidal flat than they are else-

where. This environment is evidently more favorable than elsewhere. The favorable factor may be a greater food supply made available to that area by the tidal currents, which flow over it 30 to 36 percent faster than they do farther up the flat. At a depth of 0.1 foot above the bottom the average tidal currents run over this midsection of the flat about 0.3 foot per second during the tides with small ranges and about 0.4 fps. during the large tidal ranges. A little farther up the flat the corresponding average velocities are 0.23 and 0.29 foot per second (Knox and Bradley, 1954, p. 7, table 11). The greater velocities over the midsection of the flat are doubtless due to the fact that the bay narrows here. Tidal velocities were not measured farther seaward, but we infer that they are less until one comes to the low-tide zone where the bay narrows again. Neither gemmas nor myas, however, live in significant numbers near the low-tide line.

In the midsection of the flat polychaete worms are common and locally abundant. Two species, *Spio setosa* and *Pygospio elegans*, which were kindly identified for us by Dr. Marian H. Pettibone of the University of New Hampshire, outnumber all others by an overwhelming margin. Roughly, the larger worm *Spio setosa* is most numerous in the western and northern parts of the midsection of the flat and *Pygospio elegans* is most numerous in the eastern part of the midsection of the flat. In the central part of the midsection of the flat where gemmas are most numerous, neither worm is common.

Methods of sampling

All the counts of the living gemmas were made on the flat after wet-sieving the sample through a 20-mesh screen (diameter of opening 0.033 in. or 0.84 mm.). This quickly removes virtually all the sand but has the disadvantage of losing an unknown number of the smallest gemmas, those between about 0.016 in. and 0.039 in. (0.4 and 1.0 mm.). Nevertheless, a considerable number of these minute forms are found after wet-sieving because they have a strong tendency to be trapped by the capillary film on the wires of the screen. To determine the probable maximum number of minute gemmas that could pass the 20-mesh screen, two 3-inch diameter samples were taken side by side, air dried, and sieved dry. The counts of gemmas caught on the several screens were as follows:

Screen	Gemmas caught	Size ranges
No. 9 mesh	344	0.14 in. (3.5 mm.).
No. 20 mesh	147	0.047–0.12 in. (1.2–3.1 mm.).
No. 32 and 65 mesh	72	0.024–0.39 in. (0.6–1.0 mm.).

Nearly 13 percent passed the 20-mesh screen dry. This undoubtedly represents a maximum for samples with this size range. During the summer of 1950, all the samples were taken with a cylindrical cutter 1¾ inches in diameter (2.4 square inches), which took the top 1 inch of sediment. In 1954, 1955, 1956, and 1957 we used a cutter 3 inches in diameter (7.06 square inches), which took a sample 1⅜ inches deep. The deeper sample is better because we have occasionally found mature gemmas that deep, presumably buried by shifting sand.

The pattern of sampling of the living *Gemma* population was unfortunately not consistent. In 1950 the sampling was incidental to other studies made on the tidal flat, and the pattern of sampling, therefore, was determined in part by the plan of those studies (fig. 7). In 1954 the pattern of sampling was designed to obtain as good a representation of the total living population as possible (fig. 8). In 1955, 1956, and 1957 only a part of the midsection of the flat was sampled (fig. 10), primarily to compare the population of 1955, 1956, and 1957 with that in the same area in 1954 and 1950.

During the summer of 1954 we sampled systematically along rather regularly spaced traverses and at close intervals along the margins of the flat but also sampled 11 square areas 9 feet on a side in some detail. The locations of these squares are shown on the map (fig. 8) as G–1, G–7, etc. Each square was divided into 81 squares 1 foot on a side. Three-inch diameter samples were taken from the centers of 23 of these smaller squares according to the pattern shown in fig. 11. But for one of the 9-foot squares we took samples from alternate 1-foot squares, which yielded a total of 41 samples. This pattern of sampling was adopted to see whether we could evaluate the reliability of our single widely spaced samples taken in traverses roughly normal to the long axis of the flat (fig. 8). We also wished

to appraise the spottiness or uniformity of gemmas in relatively small areas, which were selected as typical of various parts of the flat. The distributions are shown in table 5 (see also fig. 12).

After discussions with W. C. Krumbein of Northwestern University about the statistical significance of our 1954 and 1950 sampling, we decided to sample in the summer of 1955 enough of the flat to permit a reliable comparison of the 1950, 1954, and 1955 populations. The pattern of sampling in 1956 and 1957 was like that of 1955. A rectangle, 875 by 1,050 feet, was laid out in the midsection of the flat (fig. 10). Following Krumbein's counsel, we subdivided this into 30 squares 175 feet on a side and took a 3-inch diameter sample from the center of each square. These samples were used as a basis for estimating the 1955 *Gemma* population. Using a table of random numbers, 10 of these 175-foot squares were selected and each was subdivided into 49 squares 25 feet on a side. Then two of these 25-foot squares were selected at random from each of the ten 175-foot squares. Each 25-foot square so selected was subdivided into squares 1 foot on a side. Again using a table of random numbers, two 1-foot squares were selected and from the center of each

TABLE 5.—*Numbers of gemmas in 3-in. diameter samples in 9 by 9 foot square plots, G–1 to G–11 of fig. 8*

Sample plot	Number of samples	Minimum	Median	Maximum	Mean	Standard deviation	Average no. per sq. in.
G–1	23	22	74	244	76	52	11
G–2	23	28	49	85	51	13	7
G–3	23	82	200	382	195	66	28
G–4	23	48	104	208	118	43	17
G–5	23	5	28	77	33	21	5
G–6	23	7	33	75	33	16	5
G–7	23	208	324	644	357	118	51
G–8	23	19	62	138	64	27	9
G–9	23	2	14	41	16	10	2
G–10	41	105	212	456	221	78	31
G–11	23	9	27	41	24	8	3

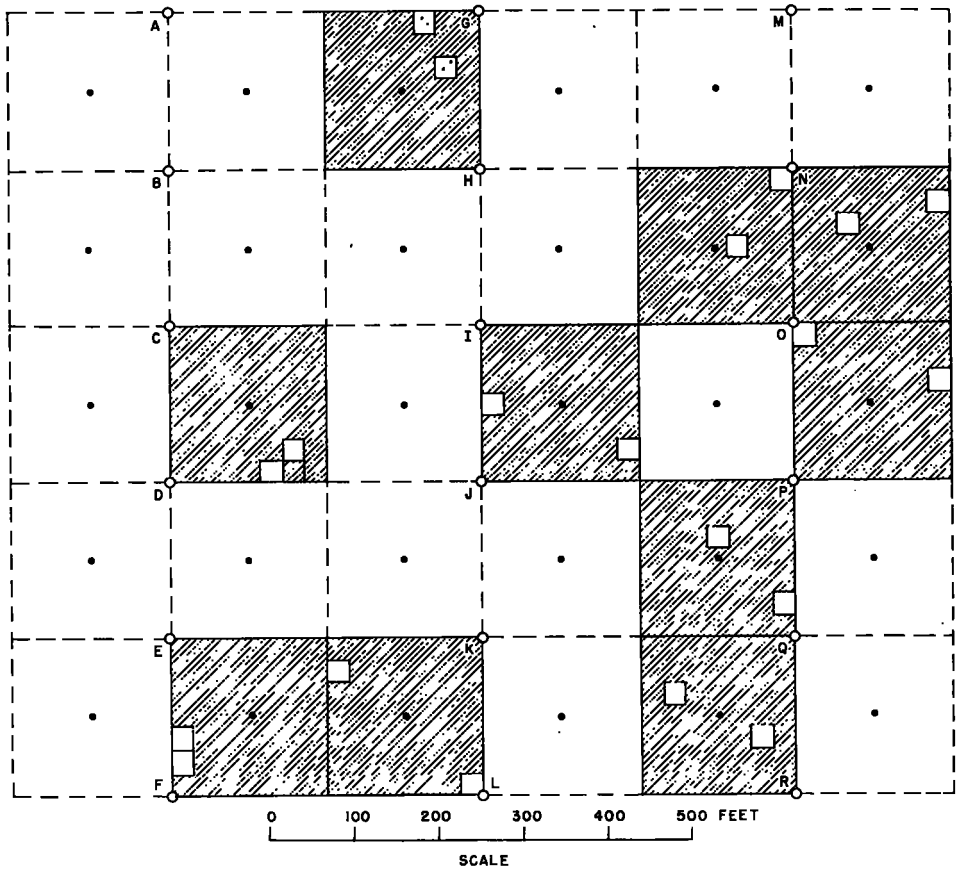

FIGURE 10.—Plan of detailed sampling for 1955 designed by W. C. Krumbein. The rectangle is 1,050 feet by 875 feet, the larger squares are 175 feet on a side, and the smaller squares are 25 feet on a side. Three lines of stakes, lettered A through R, were fixed on the tidal flat by plane table survey. All other positions in the rectangle were measured from those stakes. Sampling procedure is described in the text.

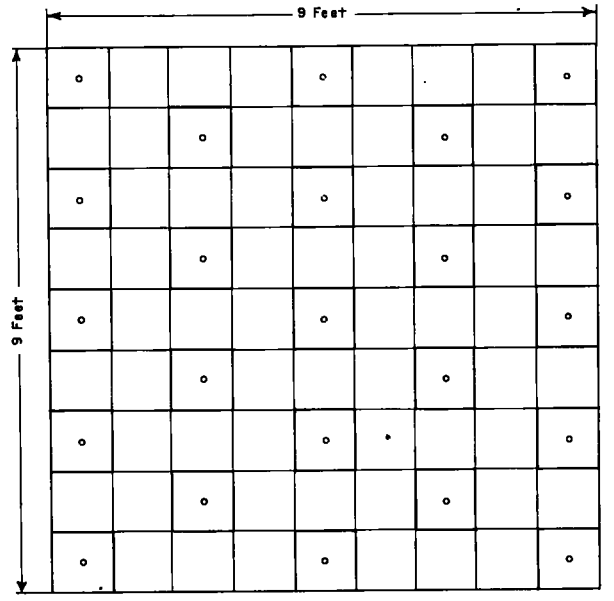

FIGURE 11.—Plan of 1954 sampling plots designated G–1 to G–11 located on map figure 8. The smaller squares are 1 foot on a side and samples were taken from the center of 23 such squares as indicated. In plot G–10 samples were taken from alternate 1-foot squares making a total of 41 instead of 23.

of these 1-foot squares we took a sample 3 inches in diameter.

Analysis of nested samples

Table 6 shows the distribution of gemmas in the 40 nested samples. We wanted to get a measure of the variability with different sample spacing. From the raw data we found the following average differences in numbers of gemmas counted: Between 175-foot squares 229.2; between 25-foot squares 95.3; and between 1-foot squares 30.9. To test the significance of the differences, W. C. Krumbein kindly made an analysis of variance and reported as follows:

The nested samples give some information about the variability with different sample spacings. I used logs directly and obtained the following mean squares in log terms.

TABLE 6.—*Numbers of gemmas per 3-inch diameter sample taken from the randomized and nested plots (fig. 10)*

25-foot squares	1-foot squares	175-foot squares									
		I	II	III	IV	V	VI	VII	VIII	IX	X
A	1	175	129	118	181	227	147	104	115	159	75
	2	98	123	105	213	222	88	44	102	161	61
B	1	199	72	128	325	126	116	76	63	80	24
	2	109	47	111	259	82	114	30	99	84	32

TABLE 7.—*Analysis of variance*

	Sum of squares	Degrees of freedom	Mean squares
Between 175 foot squares	1.6062	9	0.1785
Between 25 foot squares	0.5458	10	0.0546
Between 1 foot squares	0.3249	20	0.0162

Two F tests can be made. The first is 0.1785/0.0546= 3.27, which is significant at the 5-percent level. It suggests that there is greater variability between large squares than there is between small squares in a large square. Similarly, the test 0.0546/0.0162=3.37, which is significant at the 1-percent level, and it states that there is more variability between small squares in a large square than there is between samples in a small square.

The differences between the 175-foot squares probably reflect an already recognized decrease in the numbers of gemmas in all directions away from an area of peak abundance (fig. 8). This area of peak abundance is northwest of the center of the sandy part of the flat and presumably represents optimum conditions for *Gemma*. The differences between 25-foot squares may also reflect in part this same "regional" distribution but in larger measure they, like the differences between the 1-foot squares, reflect the general spottiness of the *Gemma* distribution.

A crude measure of the scale of the spottiness is shown by the average range in the numbers of gemmas. Within the 175-foot squares the mean range is 81.2; within the 25-foot squares it is 95.3; but between samples within the 1-foot squares, it is only 31. The bunched groups of gemmas occupy areas between the area of the 25-foot squares and the 1-foot squares. (See fig. 12.)

Pattern of distribution

The 9-foot-square plots sampled in 1954 provide data that reveal something of the pattern of *Gemma* distribution in the Sagadahoc Bay tidal flat. In analyzing these data we follow G. E. Hutchinson's illuminating paper, Concept of Pattern in Ecology, (1953, pp. 1–12). He defines pattern (p. 3) as "the structure which results from the distributions of organisms in, or from, their interactions with, their environments", and visualizes five kinds: Vectorial patterns, which are distributions of organisms determined by external forces, such as light, temperature, humidity, or density gradients, changes of state in certain directions, currents, and winds; reproductive

patterns, which are determined by genetic continuity, offspring remaining near the parent; social patterns, which are determined by signaling of various kinds, leading either to spacing or aggregation; coactive patterns, which are determined by interaction between species in competition; and stochastic patterns, which are determined by random forces.

From the fact that *Gemma* is ovoviviparous it is reasonable to expect that the organism continually tends to establish a reproductive or superdispersed pattern. The reproductive pattern, however, continually tends to be destroyed by the action of waves and currents and this disturbing vector is enhanced to some extent by the plumes of *Entero-*

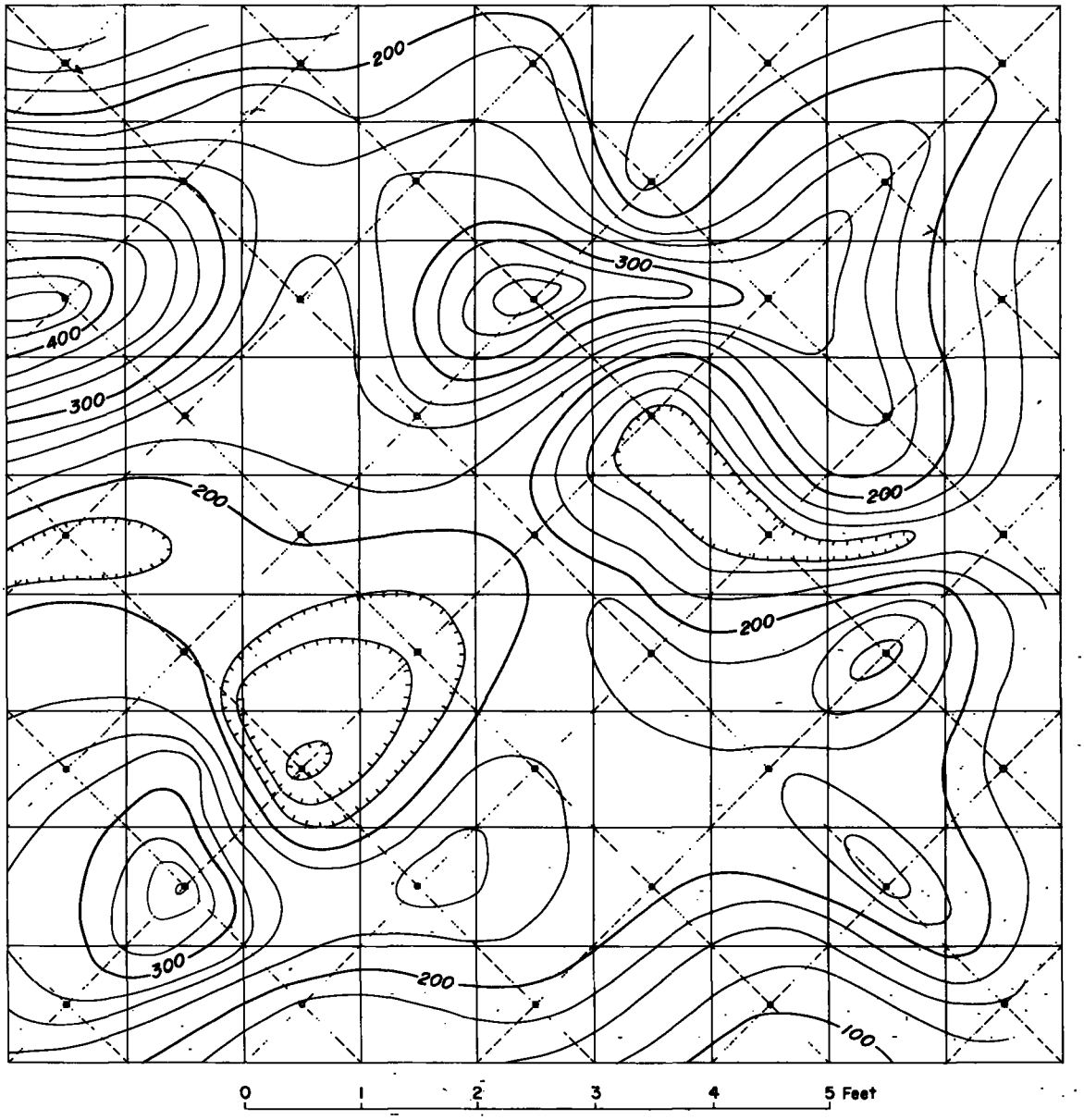

FIGURE 12.—Bunched distribution of gemmas in a 9 by 9 foot square, G–10. Contours represent lines of equal numbers of gemmas and are based on counts of the clams in 3-inch diameter samples indicated by the black dots in the centers of 41 alternate 1-foot squares. In drawing the contours, it was assumed that the numbers of gemmas decreased, or increased, at a uniform rate across the spaces between samples. Hachured contours indicate closed "depressions".

morpha compressa, which the gemmas acquire during the summer.

The resultant of these several factors is a population that has a bunched, or modified reproductive pattern of distribution (fig. 12). The bunches range in size from a little more than 1 square foot to several square feet. Because the contours were spaced uniformly between control points (samples) the bunchiness is to some extent minimized, but it is doubtful whether there is a bunched pattern of still smaller scale superposed on the pattern shown by the contours in figure 12.

A more significant aspect of the *Gemma* population is that it has a log normal distribution. This was suggested by W. C. Krumbein and demonstrated by my colleague John T. Hack who plotted the data on log probability paper and ran a chi-square test of fit. Standard statistical tests can therefore be applied to the data provided they are first converted to logs.

If *Gemma* and *Mya* are in any sense competitors one might expect that gemmas would find the areas close to large myas less favorable than farther away. Moreover, as both clams get their food from water that flows over them, the least desirable places for gemmas should lie along lines representing the dominant direction of flow of the tidal currents. In Sagadahoc Bay, this direction is roughly north-south, hence the least favorable spots for gemmas should be just north and just south of each mature mya. The same reasoning would apply if the inimical factor were metabolic wastes from the mya. Of these two critical spots, the one in the lee of the mya siphon during incoming tides should be the less desirable, on the assumption that the mya would always be robbing the gemma of the best nutrients brought in from the sea by the rising tide. To test this idea the senior author, in July 1956, sampled 5 areas around individual myas living within the large sampling rectangle shown in figures 10 and 7. The samples (3 inches in diameter) were taken at fixed intervals along 8 rays of a star whose center was the siphon hole of a living mya. The innermost ring of samples was 5 inches from the center, the next ring 1 foot, and the third ring 2 feet. At some of the stations, rings of samples at radial distances of 3, 4, and 5 feet were also added, but the larger number of samples required more than one tide to count the contained gemmas, and it seemed highly desirable to restrict the sampling of each plot to one low tide to avoid movements of the gemmas. Areas of this size are not likely to contain other undetected myas because in this part of the flat myas occur almost always as individuals spaced several to many feet apart.

We have assumed, perhaps unwarrantedly, that if the proximal positions along the north-south line through a mya siphon are the least favorable spots for gemmas there will be, on the average, fewer gemmas in those spots. To determine if this is so, the number of gemmas in each pair of north-south proximal samples were averaged (col. 3, table 8) and then the rest of the samples at each station were averaged to give the average number of gemmas per sample (7.06 square inches) at that station. This is referred to hereafter as the station population (col. 2, table 8). The table shows that the number of gemmas in each pair of north-south proximal samples is consistently smaller than the respective station populations. The last column of table 8 gives the differences as percentages of station populations. Each percentage figure is preceded by a negative sign to show that the average number of gemmas in each pair of north-south proximal samples is smaller than the corresponding station population.

TABLE 8.—*Distribution of gemmas around individual myas*

Station	Number of samples	Station population	Average number gemmas per pair in north-south proximal samples	Differences	Differences as percent of station population
1	36	115.6	86.5	28.9	−25.0
2	32	62.6	46.0	16.6	−26.5
3	25	99.0	63.0	36.0	−36.4
4	24	114.2	101.0	13.2	−11.6
5	22	82.0	62.5	19.5	−23.8
Means		94.6	71.8	22.8	−24.6

Because the station populations differ considerably in density and because at each station the ranges in numbers of gemmas are rather large (table 9), it may be that the consistently low counts found in the 5 pairs of north-south proximal samples are the result of chance. To test this we made a T test of the significance of the differences between the means of the north-south proximal pairs at the 5 stations and the means of the respective station populations. By pairing the observations and analyzing only the differences we get rid of the station-to-station differences that are

presumably due to small differences in favorability of environment and, also, we need not assume that the variance of each north-south proximal pair equals the variance of its respective station population (Dixon and Massey, 1951, p. 106). As the *Gemma* population has a log normal distribution, logs are used throughout.

TABLE 9.—*Ranges and medians of the total numbers of gemmas counted at each of 5 stations*

Station	Minimum	Median	Maximum
1	45	108	177
2	15	61	144
3	33	106	176
4	54	103	202
5	17	77	166

Table 10 shows that the observed differences between the north-south proximal pairs and the mean population at each station are significant at the 98-percent level and we can rule out chance.

The deleterious influence of the myas extends north and south beyond the north-south proximal pairs of samples. This is shown by the fact that the counts in all four proximal samples (2 north and 2 south) are consistently lower than the respective station population means. Indeed, the average difference for all 5 stations is 23.7 percent less. By contrast the percentage differences of the east-west proximal pairs from their respective station populations are decidedly erratic (+10.4, −10.4, −50.0, +1.3, +2.0). So also are the percentage differences for a pair of samples selected at random from each station population (−19.6, +23.2, +36.5, −30.2, +18.8).

TABLE 10.—*"T" test of differences between the means of the north-south proximal pairs at the 5 sampling stations.*

Stations	log N.-S. proximal pairs	log Station populations	Differences
1	1.935	2.04	0.105
2	1.66	1.75	.090
3	1.80	1.96	.160
4	2.00	2.03	.030
5	1.63	1.86	.230
Means	1.805	1.928	0.123

Mean 0.123.
Total squares 0.0985.
$t=3.64$.
$t_{4d.\,f.\,(0.9875)}=3.50$.

Inspection of the five pairs of north-south proximal samples shows that the numbers of gemmas in four of the five samples lying north, or landward, from a mya siphon are smaller than those lying seaward, or south. As mentioned above, this is what would be expected if the mya were indeed robbing the gemmas just north of it of the best (or greatest amount of) food being brought in from the sea by the incoming tides. Whether so few samples can give reliable testimony on this point is certainly debatable. For what they are worth, the actual counts are given in table 11, along with the sizes and approximate ages and conditions of the five myas at the stations sampled.

TABLE 11.—*Numbers of gemmas north and south of individual myas and lengths and ages of the myas*

Stations	Gemmas north of a mya	Gemmas south of a mya	Differences	Length of myas (inches)	Approximate ages (years)	Condition of mya siphon
1	87	86	+1	2.0	?	Limp.
2	41	51	−10	3.25	6	Active.
3	61	65	−4	3.5	7	Active.
4	92	110	−18	3.75	9+	Very limp.
5	17	106	−89	3.0	6	Very active.
Means	60	84				

The smaller numbers of gemmas living within a foot north and south of mature mya individuals seems to support the inference that *Mya* and *Gemma* compete for food. To be sure, diminished food supply might not be the only factor that adversely affects the neighboring gemmas. Conceivably metabolic wastes expelled by *Mya* have an undesirable effect. But whatever may be the inimical factors, it seems to us reasonable, since both *Mya* and *Gemma* are filter feeders, to turn the argument around and postulate that a dense population of gemmas might have a similarly bad effect on newly set minute larval myas. The difference in size (length) between mature gemmas and minute larval myas is very nearly the same as that between mature mya and mature gemma. But the difference in body weight (soft parts), and hence the energy requirements, between the mature mya and the mature gemma is probably many times greater than the difference in body weight between the mature gemma and the minute, newly set larval mya. (Average weight fresh meat of 5 myas=38.9 gms.; average weight fresh meat 6 gemmas=0.0065 gms.; ratio 1:6000; weight of newly set larval myas is unknown but is probably much more than 0.0065 gms.÷6000). But this body weight difference may be more than offset by the close spacing of the gemmas (fig. 18) and

the fact that the gemmas raise their siphons appreciably above the sediment surface while feeding. We believe it probable that the dense population of *Gemma* in the large sandy part of the flat during the past decade, or more, has been largely the cause of the vanishingly small set of *Mya* in that part of the flat. See page 332.

It may be that the sandy part of the Sagadahoc Bay flat, during the past thousand years, has been subjected to an alternation of variable external factors that favored first, *Mya* and then *Gemma*, and vice versa. Conceivably, abnormally dry summers may have favored *Gemma* and abnormally wet summers caused high mortality among its juveniles. Conceivably also, extended intervals of unusually calm weather at times of *Mya* set may have favored *Mya* whereas storminess at times of set or when the juvenile myas are quite mobile in the spring [1] would have a correspondingly adverse effect on *Mya* populations. In general, factors such as these would favor or inhibit one species without much affecting the other and vice versa.

Though we have no knowledge about *Mya's* heat tolerance it may be that abnormally warm, dry summers, or the progressive rise in mean annual temperature observed over the past few decades raises the mud temperature during the daytime low-tide intervals above the point where *Mya* can prosper. In Chesapeake Bay *Mya arenaria* lives below the low tide. Does it do so because the high summer temperatures in the intertidal zone are too unfavorable? *Gemma gemma* also lives below the low-tide zone in Chesapeake Bay. The heat tolerance of *Mya* seems to us worth investigating for if it is increased summer heat in the tidal flats of New England that is the cause of declining *Mya* populations, then no remedial measures will be effective. In the summer of 1955 we measured temperatures between 63° and 64° F. for depths of 6 to 8 inches, the depths at which large myas live. For depths of 2½ inches we measured temperatures between 66° and 67° F.

During the past few decades two additional external factors have been operating against the *Mya* population, first, man and then the green crab, *Carcinides maenas*. Young green crabs may prey also on *Gemma*. We have seen a little evidence of this in the form of chipped and broken gemma shells. Such chipped shells were found only close to the Black Rocks Islands, never out in the midsection of the flat. Today *Gemma* is in almost sole possession of the sandy part of the flat, the *Mya* population having become very small.

Comparison of 1950, 1954, 1955, 1956 and 1957 populations

Because the bulk of the *Gemma* population is concentrated in the central part of the flat, we selected a large rectangle (see figs. 7 and 10) to use as a basis for comparing the population from year to year. This procedure is open to criticism because it takes no account of the fact that the gemmas living in the muddy sediments at the head of the bay and in Bedroom Cove, for example, are not represented. Conceivably the factors that cause fluctuations in the numbers of gemmas living in the sandy part of the flat may not operate in the muddy areas or may operate in a less decisive manner. But it is the sandy parts of the flat we are primarily concerned with rather than changes in the total population of the Sagadahoc Bay tidal flat.

In the 1950 *Gemma* census, 51 samples fell in the large rectangle; in 1954 only 29 samples fell in the same area but they were more regularly spaced. A simple comparison of the means of the numbers of gemmas counted in these two years showed that the population in 1954 was only about half what it had been in 1950. A more rigorous analysis of these data was made for us by W. C. Krumbein who found that the population in 1950 was 2.07 times that in 1954 and that the 95-percent confidence limits on the ratio of the population in 1950 to the population in 1954 were 1.81 and 2.37.

To compare the 1954 population with that found in 1955 we used the 29 samples within the large rectangle counted in 1954 and the 30 regularly spaced samples counted within the rectangle in 1955 (fig. 10). The nested and randomized samples counted in 1955 were not used for this comparison. The ratio of the means of the 1954 and 1955 counts shows that the population within the rectangle had decreased by a factor of 1.24 between the summers of 1954 and 1955,

[1] I am indebted to John Glude of the U. S. Fish and Wildlife Service for calling my attention to the spring mass migrations of juvenile myas. Indeed, Glude and his colleagues at Boothbay Harbor, Maine, now believe that such sandy flats as make up a large part of the one in Sagadahoc Bay are more likely to acquire and sustain a *Mya* population by such mass migrations of juveniles than by direct set of spat.

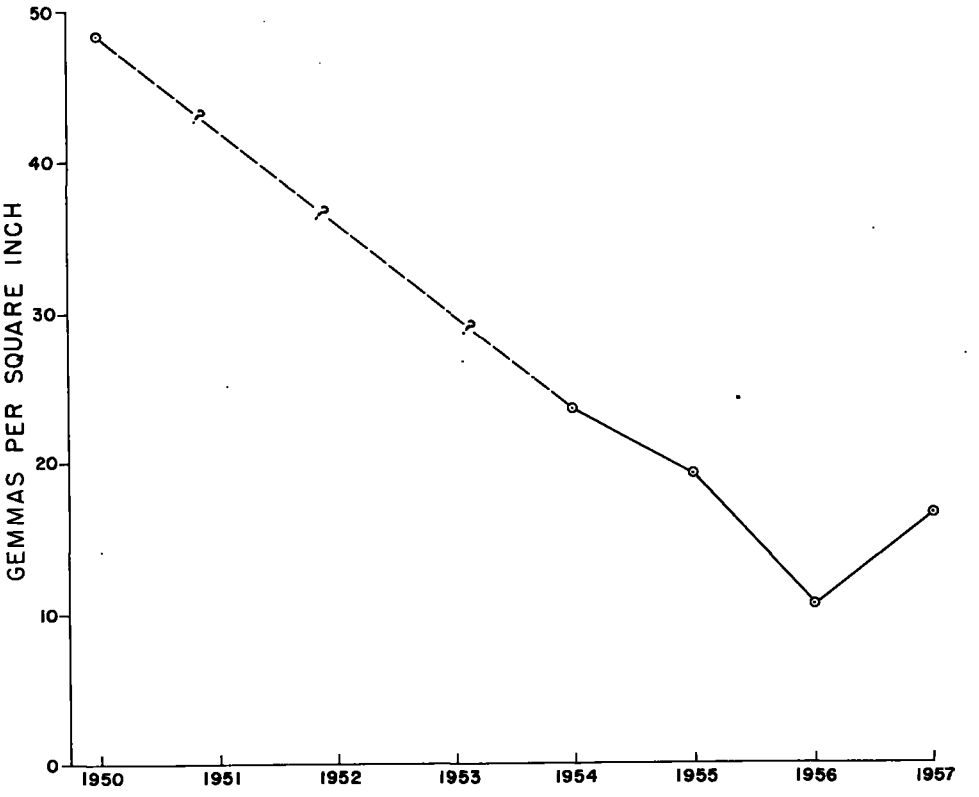

FIGURE 13.—Changes in the *Gemma* population in the interval July 1950 to July 1957.

that is, by about 20 percent. We also analyzed these data by the same procedure Krumbein used in comparing the 1950 and 1954 populations and found that the 1954 population was 1.27 times that in 1955 and that the 95-percent confidence limits on the ratio of the population in 1954 to the population in 1955 were 1.20 and 1.34.

The close correspondence found between the ratio of the means and the values found by the statistical analysis (2.0 vs. 2.07 and 1.24 vs. 1.27) suggests that for comparison of annual changes in such a population the additional effort of making a statistical analysis is not warranted.

In July 1956, the senior author again took a census of the *Gemma* population in the large rectangle laid out in 1955 (fig. 10), but this time the samples were taken at all the corners of the 175-foot squares. This gave 42 regularly spaced samples instead of the 30 taken in 1955 from the center of each of the 175-foot squares. The 1956 pattern also extends the sampling area to the full area of the large rectangle. This change in sampling pattern did not impair the comparability of the two sets of data, because it was found that the largest difference between the 1955 and 1956 counts comes in the internal part of the large rectangle rather than in the peripheral parts. One might have expected that the peripheral samples would be generally low, because the *Gemma* population is known to decrease toward the margins of the tidal flat.

The mean number of gemmas per sample (3 in. diameter, 7.06 square inches) found in these 42 samples in 1956 was only 77, which contrasts markedly with the mean number 135 found in 1955 and 346 in 1950.

From the sampling done in 1950, 1954, 1955, and 1956 it is evident that the *Gemma* population was decreasing rapidly. The *Gemma* population was 4.5 times larger in 1950 than in 1956 (fig. 13). But in July 1957 the senior author took another census of the *Gemma* population, following the 1956 pattern, and found that this downward trend had reversed. The mean number of gemmas

per sample (3 in. diameter, 7.06 square inches) was 119. Only additional counts can reveal the future trend of the *Gemma* population.

The progressive and marked decline in the *Gemma* population between 1950 and 1956 may have resulted from successively larger losses of minute gemmas by winnowing-out of newly born gemmas by wave action. See page 318.

Whether this marked decline in the *Gemma* population is casually involved we do not know, but in July 1956 for the first time since the senior author started to study this flat in 1949 he found juvenile myas in the sandy part of the flat where gemmas have been most numerous in the past 8 years. These juvenile myas ranged in length from about 0.25 to about 0.75 inch (6 to 20 mm.). In 1957 he found no juvenile myas.

Total population

The total *Gemma* population in Sagadahoc Bay (summer 1954) was about 11.5×10^9 and was distributed as shown in the following table.

TABLE 12.—*Percentage distribution of the* Gemma *population by subdivisions of the tidal flat* (fig. 8)

Subdivision	Percent of total area (191 acres)	Percent of *Gemma* population
Upper section	23	4.9
Mid-section	51	89.5
Outer section	17	5.4
Bedroom Cove	9	0.2

The population was estimated from 146 sampling stations distributed more or less evenly over the flat as shown on the map (fig. 8), but included also the averages obtained from counts in the 9- by 9-foot squares (G–1 to G–11). In all, more than 42,000 gemmas were counted during the summer of 1954. In making this estimate it was assumed that the mean of all the observed numbers of gemmas per square inch in each of the subdivisions of the flat represented the actual average number per unit area for each subdivision. This assumption is probably more nearly valid for the midsection of the flat because of the greater number of counts made there.

ANCIENT GEMMA POPULATION

Late geologic history of the flat

One of the primary objectives of studying the Sagadahoc Bay tidal flat was to determine, if possible, its late geologic history. By this we meant the last few hundred, or few thousand years, depending upon our luck in finding evidence of successive events that we could date. During the summer of 1950, the senior author, assisted by William Fairley and Herbert Schneider, then graduate students at the University of Maine, dug more than 50 test pits in the flat to depths of 3 feet or more. The pits were distributed approximately along the long axis of the flat and along a line transverse to this axis.

In these pits we found two highly distinctive layers, which we called shell-pavement layers (fig. 15). These have been described in detail in another paper (Bradley, 1957, pp. 670–678). All that need be repeated here is the senior author's belief that these two layers, which are remarkably uniform over most of the sandy part of the flat, each probably formed as a result of an

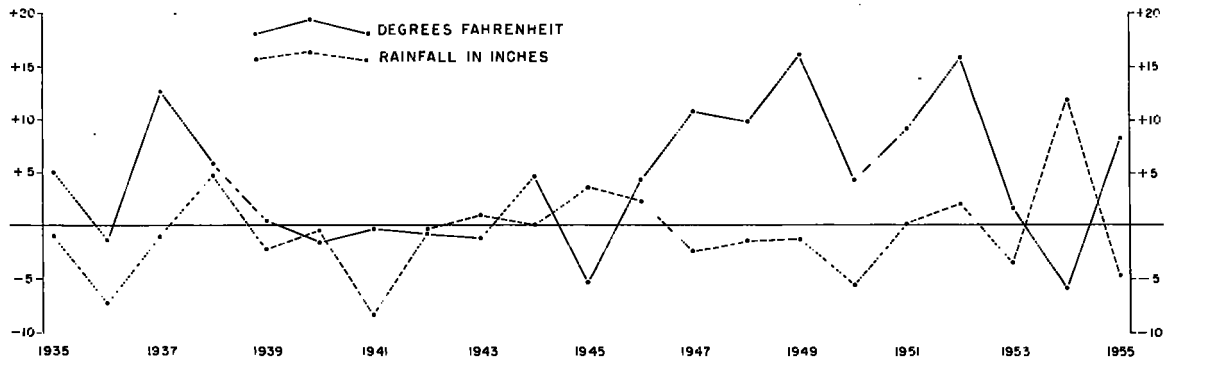

FIGURE 14.—Departures from normal mean temperatures and rainfall at Portland, Maine, for the months of May through September of each year. The values shown are the algebraic sums above or below the normal mean. Only the summer months, May through September, are shown because most of the life activities of *Gemma* occur during those months.

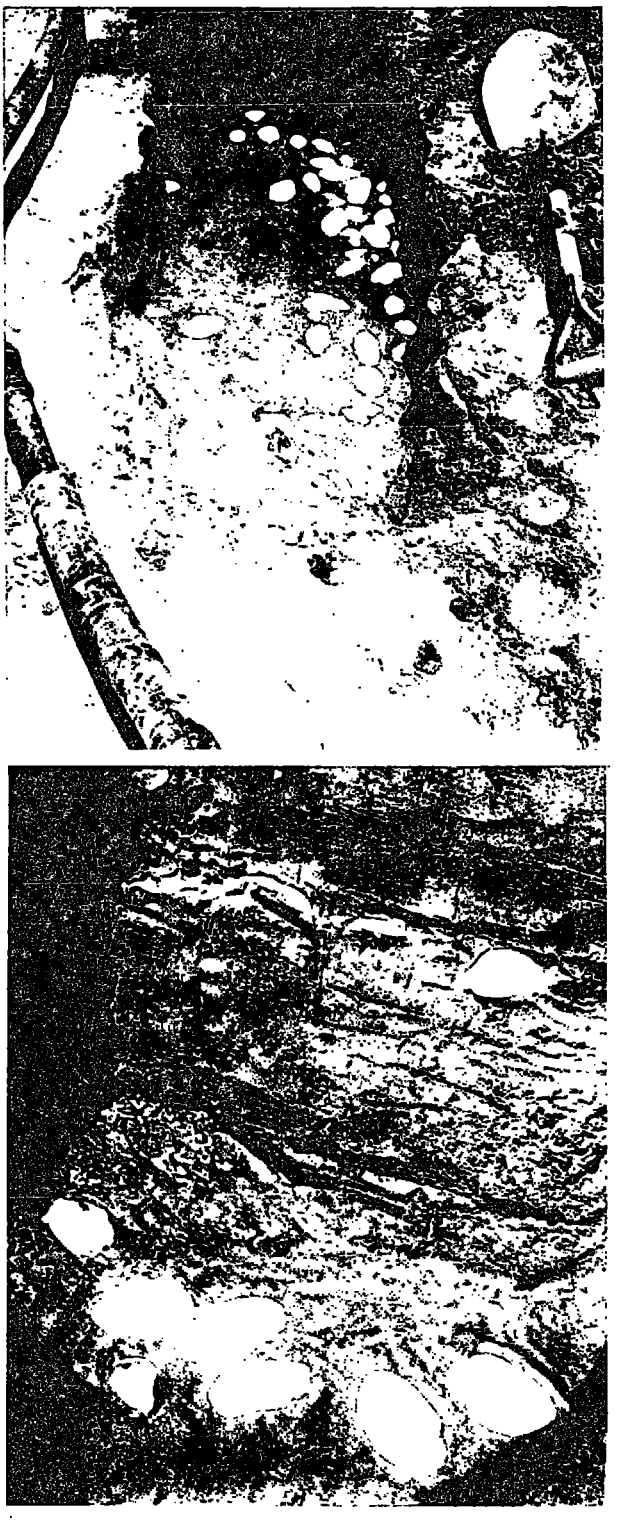

FIGURE 15.—Distribution and attitude of large *Mya* and other shells in a portion of the upper shell pavement layer (*above*); and (*below*) a section through the same shell pavement. Below that is a portion of the lower shell-pavement layer. For discussion of these shell pavement layers see text and an earlier paper by the senior author (Bradley 1956, pp. 670–678).

earthquake that happened at high tide and that jolted a layer of sand 1 or 2 feet thick into loose packing so that most of the loose stuff ran down the gentle slope into the sea. Presumably this flow followed the slumping into deep water of a large prism of submerged sand that partly filled the outer part of the bay, as it does today. Evidently the shells in this fluid sand layer and and many of the more dense mineral grains settled to the bottom where they came to rest to make the shell pavements.

Mya shells from the lower of the two layers (roughly 3 feet below the present surface) have been determined by the C^{14} method (by Meyer Rubin, U. S. Geological Survey) to be 1,050 $\pm$ 160 years old (sample W–40). After this catastrophic event the flat built up its sand surface again and new populations of *Mya*, *Gemma*, and other organisms reestablished themselves. Then, about 600 years later, a similar catastrophe occurred and the upper shell pavement was formed in the same way. This now lies 20 to 24 inches below the present surface of the flat and has a radiocarbon age of 390 $\pm$ 160 years (sample W–328) or about 400 years. After this last catastrophe the sand built up to its present level and was again repopulated. We infer, from geologic evidence, that the lower part and perhaps much of it filled in rather rapidly. Mya shells are scarce in the lower two thirds of the sandy sediment that covers the younger shell pavement layer. Nevertheless, the *Mya* population that occupied the uppermost 6- to 9-inch portion was really large and produced a rewarding commercial yield for several decades until it began to fail soon after the end of World War II. Gemma shells, on the contrary, are scattered through this layer from top to bottom. In the summer of 1955 we collected, from a depth of about one foot, a small group of mya, gemma, and gastropod shells for C^{14} age determination (sample W–329), but our laboratory report indicates that they are less than 200 years old. In other words, these shells are so young that the uncertainties of the radiocarbon dating procedure are about as large as the absolute age.

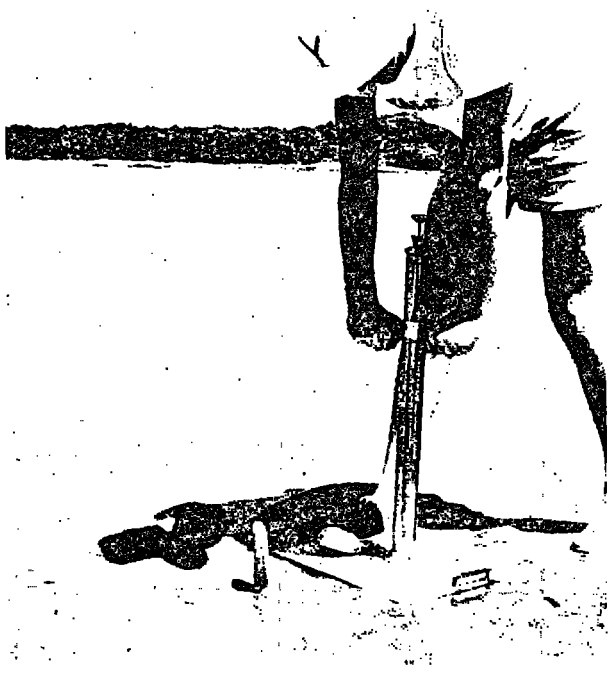

FIGURE. 16.—Piston-type core sampler in operation.

Sampling the ancient population

In the hope that the numbers and distribution of the gemma shells in the sandy sediment overlying the 400-year-old shell-pavement layer might reveal something about both the size of successive ancient *Gemma* populations and the rate at which the sediments accumulated, we took 33 core samples (summer of 1954) distributed over the sandy part of the flat and counted their contained gemma shells.

The coring device (fig. 16) was designed and built for this project and used the piston principle of Kullenberg (1947, pp. 1–46). The apparatus was designed to take cores 22 inches long and 1½ inches in diameter. Because of one difficulty or another the first several cores taken were short, but 20 of the 33 cores had lengths ranging between 17 and 22 inches. The locations of these are shown on the map (fig. 3), and the discussion in following paragraphs is based wholly on data obtained from these 20 cores.

During the coring operation, portions of the core were extruded an inch at a time. Each such portion was wet-sieved through a 20-mesh screen to remove the sand, and then gemma shells were counted. Gemma shells are so constructed that the valves tend to hold together after death and many were found thus in the cores. Paired valves were, of course, counted as one individual but we also counted all the complete or nearly complete single valves. In reckoning the total number of once-living individuals, we divided the total number of single valves in each sample by 2, thereby arbitrarily pairing them. To this number we added the number of naturally paired valves. No attempt was made to evaluate shell fragments but this introduced no significant error because, with the exception of one sample, shell fragments were uncommon. This procedure in reckoning the total number of once-living gemmas seems to be warranted by the remarkably close proportionality of naturally paired ancient shells to the numbers of accompanying single valves, which we paired arbitrarily (fig. 17). This proportionality held through all the cores.

The numbers of living gemmas were counted separately in the top inch of each core.

The abrupt and locally large changes in numbers of ancient gemma shells with depth in the cores (fig. 17) suggest that it would be relatively easy to correlate the layers of abundance from one core to another. This proved to be wholly illusory, and we were forced to conclude that the peaks of abundance represent small lenticular accumulations of shells and that these lentils have a random distribution. The only systematic relation we could find was that in those parts of the flat where gemmas are abundant today they were also abundant during the past 400 years.

Being unable to correlate layers of ancient gemma shells from core to core we cannot say, for example, that there were recurrent episodes during which the *Gemma* population flourished and was of such and such a magnitude with respect to the current population. We may infer, by analogy with the living populations, that the past populations, fluctuated, but we can furnish no proof.

Comparison of ancient and living populations

We do have a means, nevertheless, of determining with some assurance that the *Gemma* population of 1954 was greater than the mean ancient *Gemma* population that inhabited the flat during the past 400 years. We know, surely, that the *Gemma* shells we found in the cores are the

actual accumulation of the past 400 years or so, the resultant of a long *Gemma* succession and of whatever factors operated during that long interval to destroy, or remove, gemma shells. We know from many repeated observations and counts that, on the average, living gemmas are 3.9 times as abundant as contemporary dead shells (reckoned as above). This means that about two-thirds of the shells are removed from the area of the flat wherein they grew. Waves and wave-generated currents move most of them landward up the flat but during large storms large numbers move seaward beyond the low-tide zone. As we have no reason to believe that this same winnowing did not go on in the past and at essentially the same rate, we feel reasonably safe in concluding that the ancient shells we find in the cores represent, on the average, roughly one-third of the ancient population.

To compare this ancient population, whose shells accumulated over about 400 years, with the living population, we can assume that the living *Gemma* population (1954) persisted unchanged in time for 400 years and calculate how many shells that hypothetical, and constant, population would be expected to have left. In making this calculation we let the 22-inch cores equal the full 400 years. But not all the cores were 22 inches long; they ranged from 22 to 17 inches. So for each inch less than 22 we reduced the time equivalence of each shorter core by 1/22 x 400. This is open to question because it assumes a uniform rate of accumulation of the sand, which we do not know to be true. Nevertheless, it seemed better to make some adjustment for the shorter cores, and it results in minimum estimates of the numbers of shells to be expected. We then took the number of living gemmas per cross sectional area of the core found at and close by the top of each core, divided by 2.2, the life expectancy of the gemmas, multiplied this by the number of years the core represents, and divided the result by 3.9, which is the average number of times greater the living population is than the associated dead shells (table 13). These values should be, within the limits of our knowledge, directly comparable with the total number of dead shells (ancient and modern) found in each core.

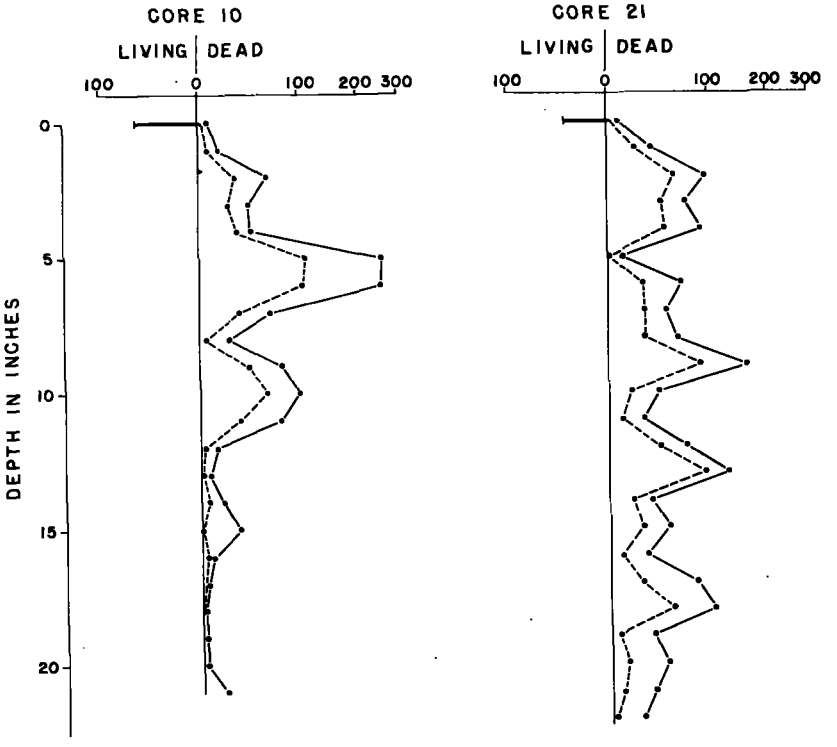

FIGURE 17.—Number and distribution of dead gemmas in two cores and the number of living gemmas at the top of each core. Dotted lines indicate complete gemma shells with both valves in place; solid lines indicate total number of dead gemmas; i. e., naturally paired valves plus all single valves arbitrarily paired.

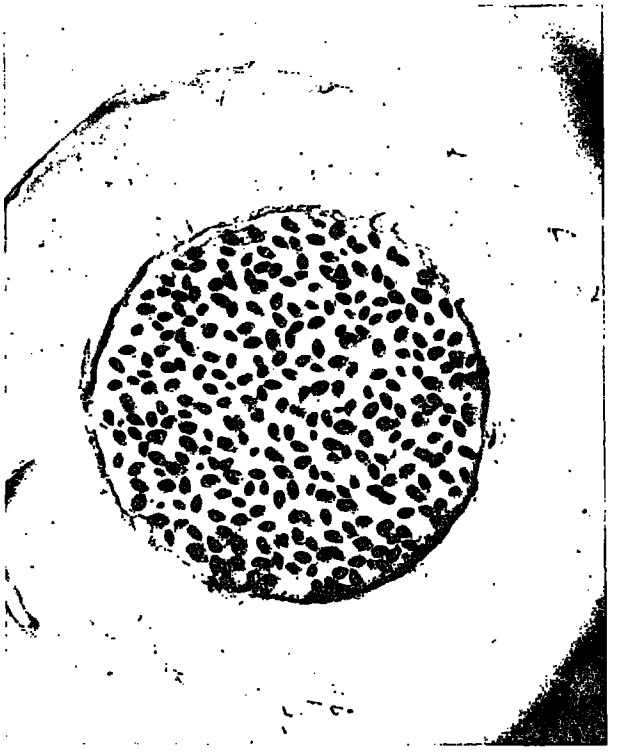

FIGURE 18.—About 200 gemmas, mostly mature, screened from one sample 3 inches in diameter (7.06 square inches) and mounted in putty within a ring 3 inches in diameter. They are mounted in feeding position and, though arbitrarily distributed rather uniformly, give a good idea of what the sandy bottom of Sagadahoc Bay looks like where the *Gemma* population averages 28 to the square inch.

The ratios of expected shells to the numbers actually found differ through a wide range. This was expected from the spotty pattern (modified reproductive) of the living gemmas, the spotty vertical distribution of the dead gemma shells, and the small cross section (1.76 square inches) of the cores that sampled both. The numbers used for the living gemmas, however, are somewhat better representations of the living population because they are the means of the number found in the top of each core and the number found in a sample 3 inches in diameter taken close by and at the time the core was taken. Because of the variables in these factors, and the relatively small number of cores, we are inclined to believe that only the mean of all 20 ratios (2.0) is likely to be significant. It indicates that the 1954 population was about twice as large as the average population over the past 400 years. Actually this factor 2 is probably

TABLE 13.—*Comparison of ancient Gemma shells, D, with the number, E, to be expected from projecting the 1954 living population (held constant) back over 400 years*

[The projection is made in accordance with the formula $E = T\left(\frac{n}{2.2}\right)/3.9$ where n is the number of live gemmas per area of the core barrel found at, and close by, the top of each core; 2.2 is the life expectancy of the gemmas; T is thespan of years represented by each core; and 3.9 the ratio of living to dead gemmas found on the flat today.]

Core Number	n	D	E	$\frac{E}{D}$
10	52	1,087	2,300	2.30
11	35	1,257	1,480	1.18
12	96	884	4,065	4.60
16	72	722	3,360	4.66
17	79	907	3,180	3.50
18	56	1,247	2,470	1.98
19	49	836	2,285	2.74
20	15	1,206	665	.55
21	21	1,290	980	.76
22	40	1,156	1,865	1.61
23	28	449	1,130	2.52
24	21	802	760	.95
25	16	227	645	2.84
26	23	840	970	1.15
27	18	406	725	1.79
28	14	339	565	1.64
29	3	120	115	.96
30	31	813	1,185	1.46
31	29	913	1,225	1.34
32	25	519	1,008	1.94
Mean Ratio				2.02

a minimum figure because the number of dead shells found in the whole 400-year column of sediment was used in the calculations and certainly this includes a definite, but unknown, number of dead shells from the *Gemma* population of the past decade. The intensive work of the clam diggers alone would have ensured this, but, in addition, there have been several hurricanes in the past decade and at least one very large winter storm (Feb. 1952) that blanketed the flat with a layer of new sand, which ranged from a fraction of an inch thick at the extreme northern (landward) end of the flat to more than a foot thick in the low-tide zone.

If the 1950 *Gemma* population had been used for the comparison, the mean ratio would have been approximately 4, because the 1950 *Gemma* population was twice as large as that of 1954. If the 1956 population were used, the ratio would be only about 0.9.

CONCLUSIONS AND RECOMMENDATIONS

Our study of the past and present *Gemma* populations in the Sagadahoc Bay tidal flat show that *Gemma gemma* and *Mya arenaria* have occupied the flat jointly for at least 1,000 years. Our interpretation of the subsurface evidence indicates that twice during this 1,000-year interval the *Mya* and

Gemma populations were removed catastrophically from most of the sandy part of the flat and that the two populations each time reestablished themselves. We infer, but cannot prove, that during this long interval various external factors such as storminess or protracted calms and summer drought or summer rains, or overcrowding, and the increase or decrease in numbers of predators, may have alternately favored or inhibited one species or the other. We assume that both species of clams are nourished by the same kinds of organic substances, living or not, that are brought to them suspended (or perhaps even dissolved like sugars and amino acids, Lucas 1955, pp. 142–145) in the water that flows over them. Research is needed to determine whether this assumption is valid.

We have shown by analyzing the population densities of gemmas in the immediate vicinity of mature mya individuals (pp. 323–25) that the myas exert some sort of unfavorable effect on the gemmas; either depriving them of food or in some other way creating an unfavorable environment. Other field evidence seems to support our findings of incompatibility between the 2 species.

On the Little River flat, which is just east of Sagadahoc Bay (fig. 1), casual examination showed that there is a marked inverse relation between the abundance of *Gemma* and the abundance of *Mya*.

Observations made during the summer of 1950 suggest that *Gemma*, when present in great abundance, may create an environment that is unfavorable to even mature myas. During that summer we dug more than 50 pits and, as these pits were 2 feet or more in diameter and a few were trenches several feet long, we had an opportunity to see a fair sample of the *Mya* population, particularly in the sandy part of the flat. Before the summer was over, we became impressed with the number of myas that had recently died or were in such a weakened condition that they could not retract their siphons, which hung down limply. These dead, dying, and abnormally weak clams were in the sandy part of the flat where they had once been numerous but where, at that time, gemmas were extraordinarily abundant, up to 190 per square inch in one place.

The *Gemma* population that summer was, on the average, twice as dense as it was in the summer of 1954 and 4.5 times as dense as in 1956. It may have been only coincidence, but this was near the middle of a series of abnormally warm and dry summers (fig. 14). We have inferred that warm dry summers favor *Gemma* because Sullivan (1948, p. 3) has shown that juvenile gemmas are killed rather quickly by fresh water. Heavy rains at low tide flood the flat with fresh or nearly fresh water, which stands for several hours in the troughs between sand ripples. We must not, of course, ignore the possibility that the same series of abnormally warm, dry summers may have had an adverse effect on the myas, either through elevated temperature directly or perhaps indirectly through increased metabolic rates and essentially fixed food supply. Research is needed on the tolerance of *Mya* for moderately elevated temperatures applied intermittently (i. e. tidal cycles). If *Mya* is adversely affected by such elevated temperatures, their moribund condition may have been independent of the presence of an extraordinary abundance of gemmas. An undetected disease of the myas might also have accounted for their lack of vitality.

After witnessing this unusual *Mya* mortality and knowing that the *Mya* population has gone through a marked decline, one wonders whether the decrease in density of the population has gone below a critical value, which alone might have raised the death rate, as it did in the *Drosophila* population that Pearl and his associates (1927, pp. 293, 316) studied.

Other observations on the Sagadahoc Bay flat reinforce our belief that *Gemma* and *Mya* tend to be incompatible. During the seven summers, 1949–55, we found no new set of *Mya* juveniles on the sandy part of the flat except (and we believe this is significant) in a few well-drained areas where *Gemma* is absent or extremely rare. But in July 1956 a small number of juvenile myas (6 to 20 mm. long) were found in the sandy part of the flat where gemmas have been most numerous. This may be significant in view of the fact that the *Gemma* population in 1956 was less than a quarter of what it was in 1950 (fig. 13). Plankton studies carried on by the biologists of the U. S. Fish and Wildlife Service during these years showed that the waters of Sagadahoc Bay contained about the expected abundance of *Mya* larvae throughout the summer. Moreover, new sets of *Mya* have continued during these years in the muddy parts of Sagadahoc Bay where the *Gemma* population is sparse, although, according

to the U. S. Fish and Wildlife biologists the total *Mya* population, even in the muddy areas, has continued to decline with the years.

We believe that the balance between these two species has been seriously upset by the greatly intensified digging for *Mya* during, and for several years after, World War II and, to a much lesser extent, by increased depredations on the *Mya* population by the mounting numbers of the green crab *Carcinides*. Both factors have tended to deplete the *Mya* population and permit rapid growth of the *Gemma* population.

Our inquiry has led to several inferences and suggestions but few conclusive results. This must be so until more research is undertaken—mostly in the laboratory. The principal deficiency in our knowledge is the food of both *Gemma gemma* and *Mya arenaria*, not only the specific kinds but the amounts that each require. It is desirable also to know whether the kinds of food differ with the ages of these two clams. A promising line of inquiry would be to explore the reactions of each species to the metabolic wastes of the other. These wastes may contain substances that are inimical to the welfare of potentially competitive species. Only when we understand these things can we say in what ways *Gemma* and *Mya* tend to be incompatible with one another. The marked decline in the *Gemma* population from 1950 to 1956 suggests the possibility that the gemmas may cyclically increase in numbers, become overcrowded, and then decrease in numbers, thereby providing first unfavorable summers for the set and growth of *Mya* spat and then a series of summers that are more favorable. Progressive loss of minute gemmas by wave action may, as noted earlier in this paper, have caused the present decline of the *Gemma* population. Significant decrease in the numbers of gemmas, regardless of cause, will according to our view increase the capacity of the sandy part of the flat to support a larger clam population, either *Gemma* or *Mya*. If the *Gemma* population becomes very small, say less than half of the 1956 density, it will be interesting indeed to see whether *Mya* or *Gemma* first succeeds in taking advantage of the newly enlarged capacity.

Another subject that perhaps warrants investigation is the heat tolerances of both *Gemma* and *Mya* in both early juvenile and mature stages of growth. Our reasons for suggesting that heat may be a critical factor is that the climate has been growing progressively warmer and the fact that for a time, while the *Mya* population was falling off most conspicuously, we had in New England a succession of abnormally warm, dry summers. Then there is the fact that farther south, in Chesapeake Bay, both these clams live below the low-tide zone, but whether or not high summer heat determines this is unknown to us.

If heat is a critical factor one might expect its effect to be most telling during summer daylight low tides. We found that the flat absorbs considerable heat from the sun and sky and that appreciable amounts of heat are conducted in a few hours to depths of 6 to 8 inches where mature myas live.

The heat tolerances of such mollusks, at various stages of growth, should be readily determinable in any well-equipped marine laboratory. If the secular warming of the climate accounts in any significant degree for the decreasing *Mya* population of New England then remedial measures are, of course, futile.

We recommend that research on the food, temperature tolerances, and metabolic wastes of both *Gemma* and *Mya* be undertaken to gain a better understanding of the fundamentals involved. Once the dominant foods are determined, some effort should be made to appraise the amounts contained in the waters that flow over the surface of the flat. The current velocities of these bottom waters are already known in Sagadahoc Bay. If we knew the kinds and amounts of foods used, a good estimate of the carrying capacity of the bay could be made. We also recommend that a census of both *Gemma* and *Mya* be continued for a few more summers to test the suggestion that the present decline in the *Gemma* population may provide optimum opportunity for a natural set and growth of *Mya* spat in the sandy part of this flat.

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DISTRIBUTION, ABUNDANCE, AND HABITS OF PELAGIC SHARKS IN THE CENTRAL PACIFIC OCEAN

BY DONALD W. STRASBURG

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ABSTRACT

The distribution and abundance of the central Pacific pelagic sharks was investigated by longline fishing methods during 1952–55. In this period more than 6,000 sharks were caught; these belonged to 12 species. Great blue, whitetip, and silky sharks predominated. Bonito, thresher, mackerel, and other species were uncommon or rare.

Several significant facets of the biology of the common sharks were evident. The wide-ranging great blue shark made pronounced seasonal migrations during which sexual segregation occurred and reproduction probably took place. Vertical distribution of the great blue shark was limited in the north by the 45°–69° F. isotherms, and it was truly an oceanic species. The whitetip and silky sharks were denizens of the Tropics, and showed no particular migratory tendencies; the former was oceanic but the latter tended to be neritic.

In equatorial waters, great blues and whitetips were more abundant in warm years, and the silky more abundant in cold years. The species considered here fed principally on small fish and squid. The great blue shark was virtually harmless to the tuna catch. Only 1 percent of the catch was damaged where it abounded, as compared with 20 percent damaged in regions where the whitetip and silky sharks were dominant. In the great blue shark both the behavioral and geographical types of sexual segregation were found, and sexual segregation itself was related to latitude, shark length, and season.

DISTRIBUTION, ABUNDANCE, AND HABITS OF PELAGIC SHARKS IN THE CENTRAL PACIFIC OCEAN

By Donald W. Strasburg, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

The Pacific Oceanic Fishery Investigations (POFI) of the United States Fish and Wildlife Service is authorized to investigate the high seas fishery resources of the tropical and subtropical Pacific Ocean. A large part of POFI's research program has dealt with the biology of tunas, the stocks of which have been sampled extensively by longline fishing. In addition to tuna, spearfish, and other species of commercial importance, an incidental product of longlining has been the capture of numerous pelagic sharks. Information on the occurrence of these sharks is of importance to both the biologist and the commercial fisherman because of the sharks' competitive and predatory relation to tuna and also because of the damage sharks inflict on hooked tuna. Apart from discussions in systematic and general works (Bigelow and Schroeder, 1948, Englehardt 1913, Norman 1949, and Norman and Fraser, 1949) and the usually fragmentary data in faunal reports, little is known of the biology of high seas sharks, and any information on their abundance, distribution, and habits is of practical and academic interest.

This report is primarily based on the shark catches recorded during the years 1952 through 1955. During this period the POFI ships *John R. Manning*, *Charles H. Gilbert*, and *Hugh M. Smith* conducted 26 longline cruises, which obtained sharks in the central Pacific between 50° N. and 20° S. latitude, and 110° W., and 175° E. longitude (fig. 1). During the same period of years, four privately owned, commercial vessels, the *Cavalieri*, *Commonwealth*, *North American*, and *Oceanic*, operating in conjunction with POFI, made a total of eight cruises to the Line Islands area. Data from all the above cruises were utilized only when the shark catches were recorded by species. Although a considerable portion of these data have routinely been listed in reports by workers concerned primarily with tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955; Shomura and Otsu, 1956; Iversen and Yoshida, 1956), it seems advisable to provide a summary of the catch and effort for the various cruises (table 1).

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METHODS

The longline gear used by POFI as a tool for sampling the abundance of tunas (and sharks) has been described by Niska (1953) and Mann (1955). A unit or basket of longline gear consists of 210 fathoms of mainline supporting a number of hook droppers, usually 3 fathoms in length, and buoyed at its end by floats attached to 5-, 10-, or 15-fathom floatlines. Numerous baskets are joined together to form a set, each basket being placed in the water in a slack condition so that the 210-fathom mainline sags and subtends a distance of only about 150 fathoms between floats. The number of droppers per basket was typically 6, 11, or 13, although experimental gear employing 14, 15, and 21 droppers was occasionally used during the period under consideration. Bait consisted of frozen herring, sardines, or squid. Setting of longlines usually started at dawn and required about an hour. Recovery commenced at noon and was usually completed in 4½ hours. The last basket set was the first one retrieved.

In their classic treatise on North Atlantic sharks Bigelow and Schroeder (1948) frequently refer to nomenclatorial confusion resulting in nonacceptability of shark records. This confusion has several causative factors, chief of which is the lack of large preserved specimens available for systematic study. Further complicating the situation is the existence of several sets of names for sharks, e. g., one set for Atlantic species, another

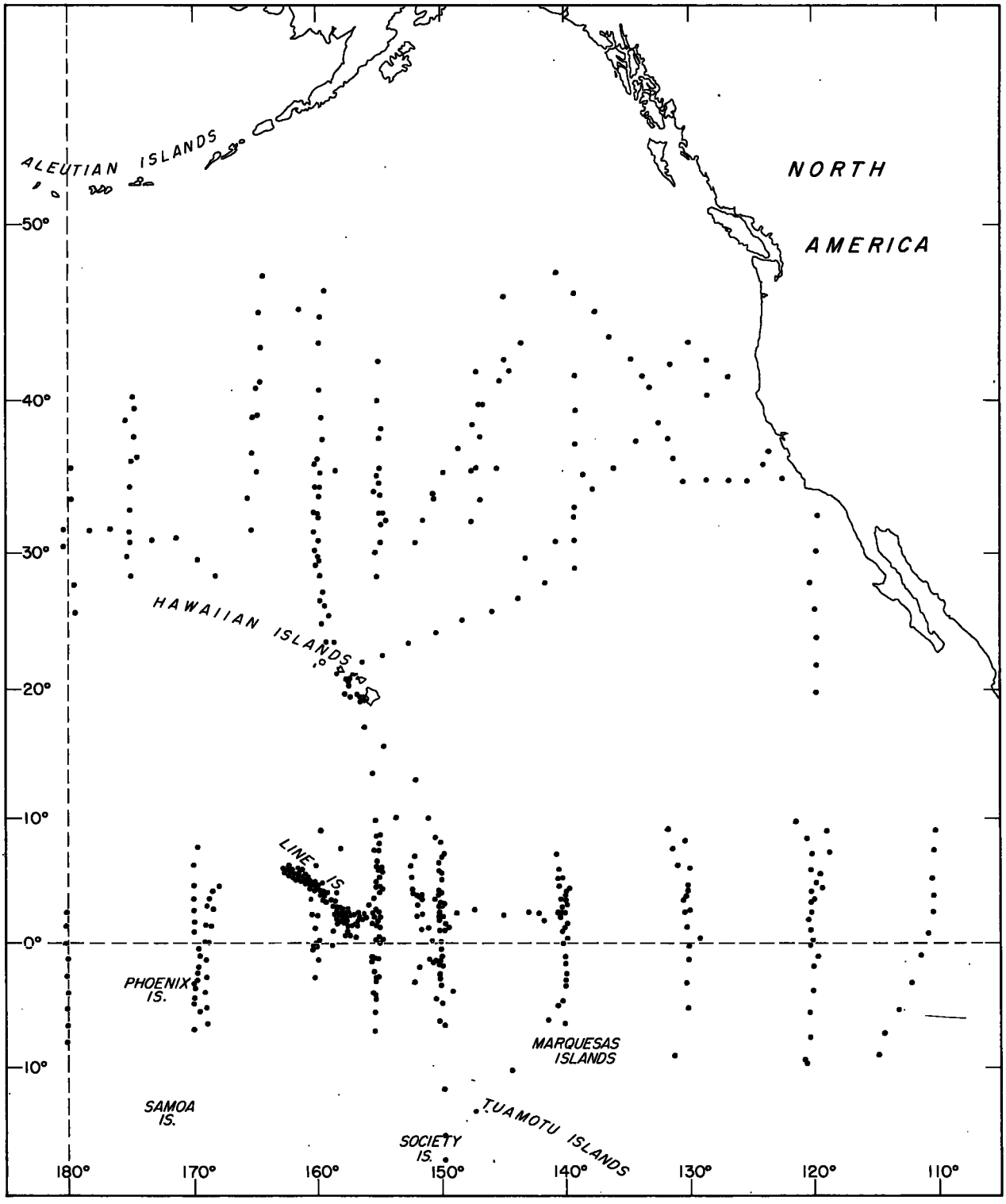

FIGURE 1.—Location of longline stations from which the sharks reported on were obtained.

TABLE 1.—*POFI and commercial longline cruises yielding identified sharks during the period 1952–55*

Vessel	Cruise	General operational area [1]	Date	Number of stations	Total hooks	Shark catch			
						Great blue	Whitetip	Silky	Other
John R. Manning	11	Equator at 159° W., 169° W., 180°.	January–March 1952	27	6,960	51	71	31	1
	12	Equator at 140° W., 150° W	August–September 1952	18	4,560	13	59	5	8
	13	Equator at 150° W., 169° W	October–November 1952	27	7,620	20	131	19	0
	14	Equator at 140° W., 150° W	January–March 1953	33	8,850	25	140	25	3
	15	Equator at 150° W., 170° W	April–June 1953	28	9,521	47	109	42	9
	16	Equator at 155° W., 160° W	July–August 1953	26	8,811	47	47	139	5
	17	Line Islands	October–November 1953	6	2,418	2	2	48	1
	18	Equator at 155° W., Line Islands.	December 1953	14	7,140	15	76	92	5
	19	22° N.–36° N., 145°.–160° W	January–March 1954	18	14,014	91	3	0	11
	20	Line Islands	May–June 1954	27	15,764	32	108	268	3
	21	Hawaiian Islands	July 1954	5	2,052	7	4	0	0
	22	22° N.–47° N., 159° W.–177° W	September–October 1954	16	11,869	170	1	0	6
	23	22° N.–37° N., 157° W.–180°	December 1954–February 1955.	18	13,415	131	0	0	4
	24	Line Islands	March–April 1955	10	6,422	15	32	79	7
	25	28° N.–41° N., 158° W.–175° W	May–June 1955	18	8,318	229	0	0	23
	26	30° N.–47° N., 122° W.–152° W	July–September 1955	38	19,609	719	0	0	16
	27	Line Islands	October 1955	11	6,928	11	9	121	9
	28	do	November–December 1955	5	3,955	7	25	35	0
Charles H. Gilbert	1	Equator at 120° W., 130° W	May–June 1952	14	3,360	16	32	16	0
	10	Hawaiian Islands	March 1953	3	623	4	2	0	0
	15	South of Baja California, and Equator at 110° W., 155° W.	February–April 1954	32	15,271	323	31	51	8
	20	Line Islands	March–April 1955	14	9,054	43	14	130	9
	23	36° N.–47° N., 145° W.–165° W	September–October 1955	8	4,147	54	0	0	1
Hugh M. Smith	18	Equator at 120° W., 130° W	October–November 1952	23	5,520	59	83	28	2
	19	Line Islands	January–February 1953	8	2,160	6	3	68	1
	29	22° N.–42° N., 139° W.–156° W	May–June 1955	30	15,600	318	0	0	14
Commonwealth	1	Line Islands	July–August 1954	11	5,500	2	28	54	3
	3	do	May 1955	11	3,537	6	1	28	18
	4	do	July–August 1955	12	4,095	7	1	102	5
	5	do	September–October 1955	10	4,210	10	5	55	3
North American	1	do	January–February 1954	27	21,283	30	19	258	31
	2	do	March–April 1954	40	35,965	58	86	347	23
Cavalieri	1	Equator at 140° W., 150° W	August–September 1952	26	11,454	42	65	3	8
Oceanic	1	Line Islands	June 1954	9	3,762	2	0	132	6
Total					303,767	2,512	1,187	2,176	243

[1] The term "Equator" denotes fishing in the equatorial area, and not necessarily along 0°. The position of the Line Islands is bounded roughly by 0°–10° N. latitude and 155° W.–165° W. longitude.

for northwest Pacific species, a third for Hawaiian forms, etc., a situation comparable to that found for other pelagic fish such as the tunas, marlins, and flying fishes. For comparative purposes it is thus necessary to note the identification sources and procedures and the disposition of the material upon which this report is based.

The principal references used in making the identifications were Bigelow and Schroeder's treatise (1948), supplemented by the reports of Roedel and Ripley (1950), Roedel (1953), and Schultz et al. (1953). On early cruises sharks were brought aboard, identified, measured, and frequently photographed. Occasionally jaws, patches of skin, embryos, and entire adult specimens were preserved, and laboratory examination of this material has since confirmed the recorded field identifications with the reservations that the names "thresher" and "hammerhead" are based on 3 and 2 species, respectively. As biologists and fishermen became better acquainted with the various species fewer sharks were landed, and identification was often based on the gross aspects of the animals as they lay in the water alongside the vessel. There is thus a possibility of an occasional error in identification, particularly with *Isurus glaucus* and *Lamna ditropis*, which are rather similar in appearance. Specimens of each species considered are to be shipped to the United States National Museum to serve as a permanent record.

The vernacular names of sharks are used throughout the remainder of this study. These names and their currently accepted scientific equivalents are as follows:

Whitetip shark—— *Pterolamiops longimanus* (Poey).

Blacktip shark—— *Carcharhinus melanopterus* (Quoy and Gaimard).

Silky shark—— *Eulamia floridanus* (Bigelow, Schroeder, and Springer).

Great blue shark—— *Prionace glauca* (Linnaeus).

Soupfin shark—— *Galeorhinus zyopterus* Jordan and Gilbert.

Bonito shark—— *Isurus glaucus* Müller and Henle.

Mackerel shark—— *Lamna ditropis* Hubbs and Follett.

Thresher shark	*Alopias pelagicus* Nakamura.
	Alopias superciliosus (Lowe).
	Alopias vulpinus (Bonnaterre).
Hammerhead shark	*Sphyrna lewini* (Griffith).
	Sphyrna zygaena (Linnaeus).

Representative length-frequency distributions of the three most common pelagic sharks are shown in figure 2; these will acquaint the reader with the size of the sharks encountered. Insofar as possible common names have been taken from the list proposed by the American Fisheries Society (1948). For those species not covered by this list, vernacular names were derived from Bigelow and Schroeder's treatise (1948). Latin names follow the latter authors except for the carcharhinid genera lacking spiracles. Here Springer's revision (1950, 1951) has been employed with the result that the former *Carcharhinus longimanus* and *C. floridanus* are now referred to *Pterolamiops* and *Eulamia* respectively. Identification of *Sphyrna lewini* was made in accordance with Fraser-Brunner's synopsis of the hammerhead sharks (1950).

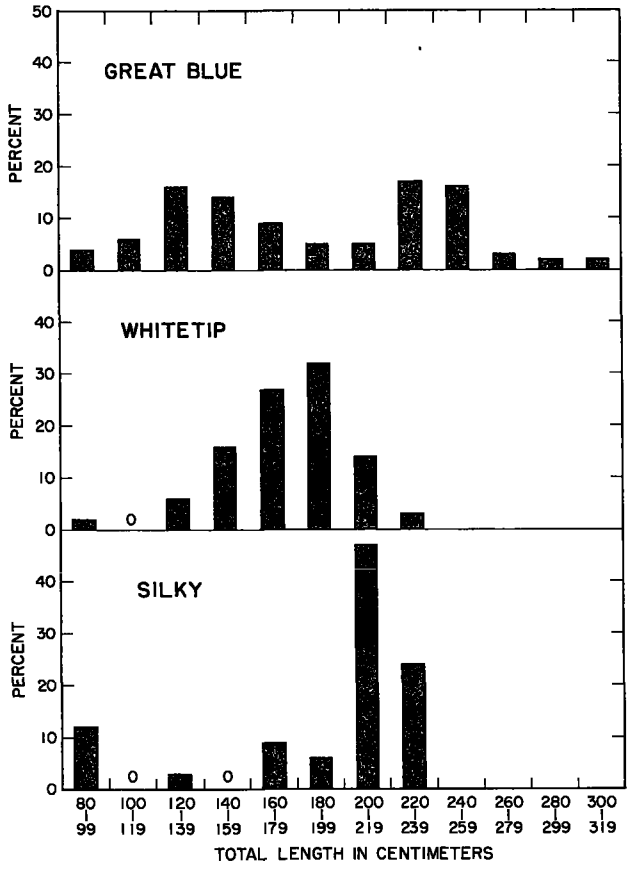

FIGURE 2.—Typical length-frequency distributions of pelagic sharks commonly occurring in longline catches in the central Pacific. Based on 106 great blue, 63 whitetip, and 34 silky sharks.

It was thought desirable to express shark abundance in terms of fishing effort, as average catch per hundred hooks per day for a certain unit of area. The operational region was accordingly divided into quadrates measuring 5 degrees on a side, and catch and effort were calculated for each areal unit. Iversen and Yoshida (1956) and Murphy and Shomura (1955) found differences in efficiency between two types of gear in catching yellowfin tuna, but all gear types were here considered equally efficient in catching sharks. It frequently happened that longline fishing stations were conducted along specified meridians or parallels, and these were also the boundaries of quadrates. Usually, the line drifted with the current so that fishing was restricted to one or the other of the quadrates, but when operations actually extended over two quadrates, the entire catch was assigned to the quadrate in which most fishing appeared to take place. This assignment took into account set and drift of the current, time spent in each quadrate, and vessel course and speed. Similarly, stations occupying parts of more than 1 day were assigned the date on which most fishing was conducted. For ease in presentation the data summarized by 5-degree quadrates have been regrouped on a 10-degree basis and are used in this form throughout most of the analyses.

The author wishes to thank all POFI scientific and vessel personnel for their efforts in landing and handling the sharks on which this report is based. Collection of shark data was begun at POFI by Dr. William F. Royce.

GENERAL RANGE AND ABUNDANCE

The distribution and abundance of the central Pacific pelagic sharks considered here are summarized in figures 3 and 4. It is apparent that high seas sharks are widely distributed as a group and that their abundance, expressed as average catch per hundred hooks per day, is usually less than that of tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955; Shomura and Otsu, 1956; Iversen and Yoshida, 1956). On the other hand the present data indicate a greater abundance of sharks than do those of Nomura et al. (Shomura and Murphy, 1955).

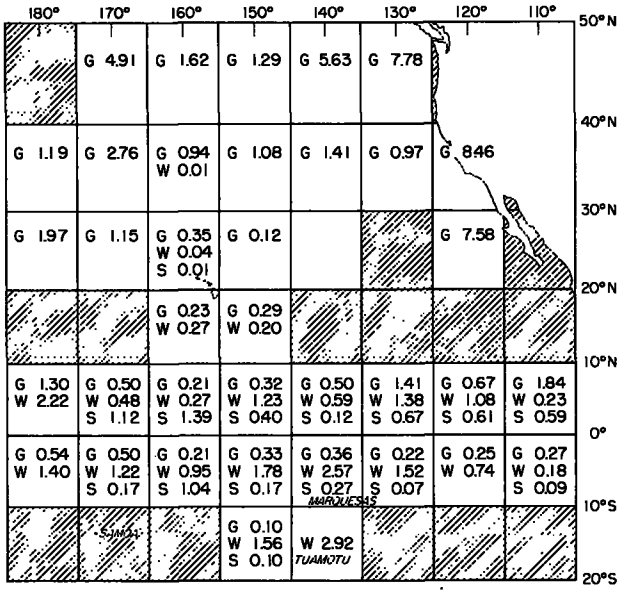

FIGURE 3.—Distribution and abundance of three common pelagic sharks. Abundance expressed as average catch per hundred hooks per day; hatched areas not sampled. *G*=great blue, *W*=whitetip, *S*=silky shark.

Inspection of figures 3 and 4 shows that the great blue shark is wide ranging throughout the area considered whereas certain of the other species occur within rather narrowly circumscribed

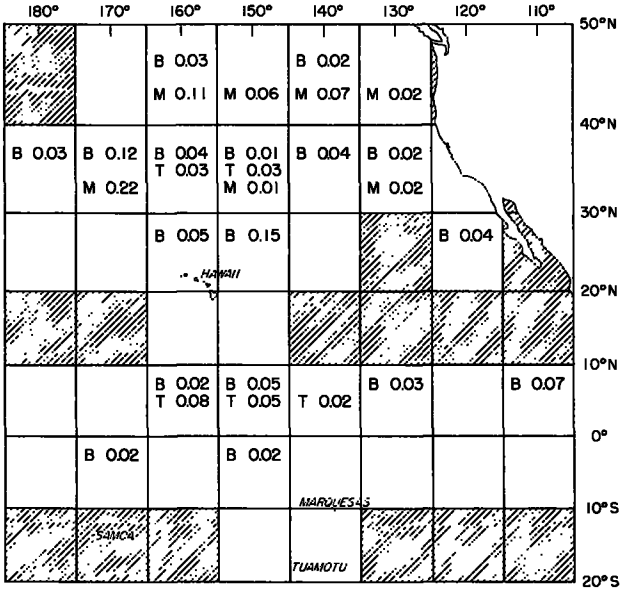

FIGURE 4.—Distribution and abundance of three uncommon pelagic sharks. Abundance expressed as average catch per hundred hooks per day; hatched areas not sampled. *B*=bonito, *T*=thresher (3 species), *M*=mackerel shark.

limits. In addition, the great blue is easily the most abundant shark in terms of POFI's longline catch, for its 2,512 records constitute about 41 percent of the entire shark catch. Its area of greatest abundance lies north of 20° N. latitude in the eastern part of the Pacific.

The bonito shark has almost the same range as the great blue shark (fig. 4), but as only 74 of the former were taken the catch was almost negligible when reduced to an effort basis. The present data indicate no centers of abundance for the bonito shark although Bigelow and Schroeder (1948: 129–130) list its Atlantic counterpart as a tropical and warm-temperate species which is particularly common in the Canary and Bahamas Islands (between 20° N. and 30° N. latitude).

The silky and whitetip sharks are equatorial species, the range of the former being practically restricted to a band about 10 degrees (600 miles) on either side of the Equator, whereas that of the latter is bounded roughly by 20° N. and 20° S. latitude (fig. 3). The total catch south of 10° N. latitude consisted of 4,157 sharks of which 2,175 (52 percent) were silkies and 1,173 (28 percent) were whitetips. Despite the fact that the catch contained nearly twice as many silkies as whitetips, in terms of catch-per-hundred-hooks in the open ocean areas the whitetip is actually the more abundant of the two species (fig. 3), thus confirming Hubbs' (1951) observation that it is common in the equatorial Pacific. As implied by Bullis (1955) and pointed out by Mather and Day (1954) and Backus et al. (1956), the whitetip rather than the great blue is probably the most abundant warm-water pelagic shark.

It is of interest that the silky shark was not reported from the Pacific until the tentative identification in 1953 (Murphy and Shomura, 1953b), and its presence there was confirmed in 1956 (Iversen and Yoshida).

The region of maximum abundance for the silky shark is centered around the Line Islands area (between 0° and 10° N. and 155° W. to 165° W.), which is also the center of abundance of equatorial yellowfin tuna (Sette 1955). Whitetip concentration is more diffuse, the species being more strictly oceanic (Bigelow and Schroeder, 1948), and not congregating near land (most longlining in the Line Islands was conducted quite close to land). It has been postulated that the whitetip's oceanic existence represents a gen-

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eral avoidance of reduced salinities (Bigelow and Schroeder, 1948), but Backus et al. (1956) found the whitetip occurring over a wide salinity range and alternatively suggested that land avoidance may simply be the result of unfavorable food competition with faster-moving neritic species.

The catch data for the mackerel shark consist of 28 records, 26 of which are from north of 35° N. latitude indicating that this shark is a temperate- or cold-water form (fig. 4). Not shown in figure 4 is a single record from the Line Islands which is most likely based on a misidentified bonito shark.

Little can be said of the distribution and abundance of central Pacific thresher sharks except that they are uncommon (only 127 were taken) and have a tendency to congregate near land in the equatorial region as is shown later. All three species (*Alopias pelagicus*, *A. superciliosus*, and *A. vulpinus*) were taken within about 300 miles of Christmas Island in the Line Islands group, but the identity of the boreal records shown in figure 4 could not be determined.

No distributional charts were prepared for soupfin, hammerhead, or blacktip sharks as only 8, 4, and 2 specimens, respectively, were taken. The soupfins were obtained off the coast of southern California, 1 hammerhead (*Sphyrna lewini*) came from the area bordered by 0°–5° N., 120°–125° W., another (*S. zygaena*) was from 0°–5° N., and 110°–115° W., and 2 others, identified only as "hammerheads," were obtained just east of the Line Islands. The 2 blacktips were taken near shore in the Marquesas Islands, and this species should not be regarded as oceanic (Schultz et al. 1953: 15).

VARIATIONS IN SHARK ABUNDANCE WITH LATITUDE AND SEASON

Geographical variations in abundance were examined by plotting average catch per unit of effort for 10-degree bands of latitude, and temporal variations were studied by recording the data by season. The northern seasons (spring, Mar. 21 to June 20; summer, June 21 to Sept. 20; autumn, Sept. 21 to Dec. 20; winter, Dec. 21 to Mar. 20) were used with the assumption that antipodal season-reversal would not be significant in the latitudinal distribution considered. For the uncommon species (bonito, mackerel, thresher hammerhead, soupfin, and blacktip sharks), seasonal subdivision resulted in so few records per season that very little was indicated. As a consequence this section deals with the three abundant species, the great blue, the whitetip, and the silky.

In the Pacific, heavy concentrations of great blues occur only north of about 20° N. latitude

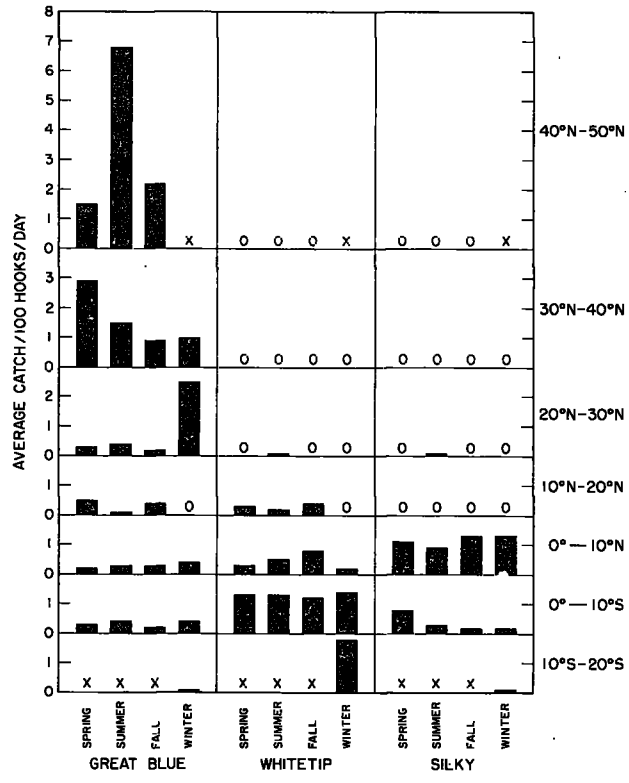

FIGURE 5.—Abundance of pelagic sharks by latitude and season. Based on 2,512 great blues, 1,187 whitetips, and 2,176 silkies. X=no fishing effort, O=no catch.

(figs. 3, 5). Since the southern limits of our sampling lay between 15° S. and 20° S. it is not possible to say whether similar concentrations also exist in the Southern Hemisphere. In the Atlantic large numbers of great blues have been reported from both high and low latitudes (Bigelow and Schroeder, 1948), and the species is particularly numerous off the west coast of South Africa at about 30° S. latitude (Smith 1950).

When the seasonal aspects of great blue distribution are considered (fig. 5), it appears that fluctuations are small or absent in the warm waters between 20° N. and 20° S. Between 20° N. and 30°

N. the species is most common in the winter, from 30° N. to 40° N. in the spring, and from 40° N. to 50° N. in the summer. These varying spatial and temporal concentrations indicate a north-south migration of this species, and judging from the relative constancy of its numbers in the Tropics, we deduce that temperature changes are their basis.

As pointed out by Shomura and Otsu (1956) there exists in the North Pacific a latitudinally shifting transition zone between the relatively cold Aleutian Current and the relatively warm North Pacific Current. This zone lies between latitudes 31° N. and 36° N. in the winter, and between latitudes 41° N. and 46° N. in the fall (fig. 6). Shomura and Otsu (ibid.) indicate that albacore move north and south with the advance and retreat of this zone, and the present data show that great blue sharks do also. Most of the larger catches of the great blue were made in or just south of the transition zone in water with surface temperatures ranging from 56° to 74° F., depending on the season (fig. 6). This range of surface temperatures cannot be considered as limiting their geographical occurrence because many great blues were taken from deeper, cool water in the Tropics (see p. 344).

Returning to figure 5, seasonal migrations of the great blues apparently extend only as far south as 20° N., although the absence of these sharks from the winter catch between 10° N. and 20° N. may indicate that migration also occurs there. With the onset of autumn a return southern migration presumably takes place, but this may occur outside the fishery since it is not evident from the catch data. It would seem that the number of northern migrants is augmented from populations extralimital to this study, otherwise it is difficult to explain the disparity between summer abundance at 40° N.–50° N. and spring abundance at 30° N.–40° N.

There is also the likelihood that the increase in numerical abundance in the areas to the north is the result of females giving birth to young. Large numbers of very small great blues were captured by longline in the areas during the spring, summer, and autumn. The smallest of these were about a foot and a half in total length, exactly the same size as large embryos (p. 354), and there can be little doubt that they were born shortly before capture. Unfortunately, length measurements were not routinely recorded for sharks and it is impossible to state what percentage of the popu-

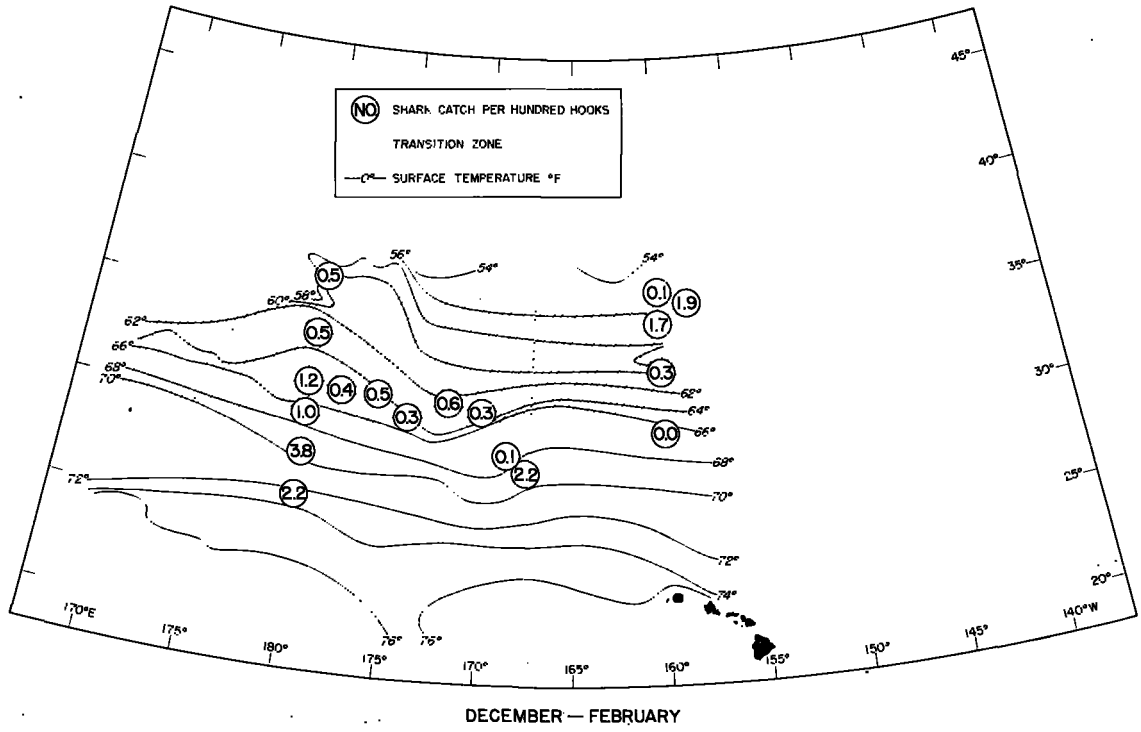

FIGURE 6a.—Relation between the great blue shark catch rate and position of transition zone, December–February. (After Shomura and Otsu, 1956.)

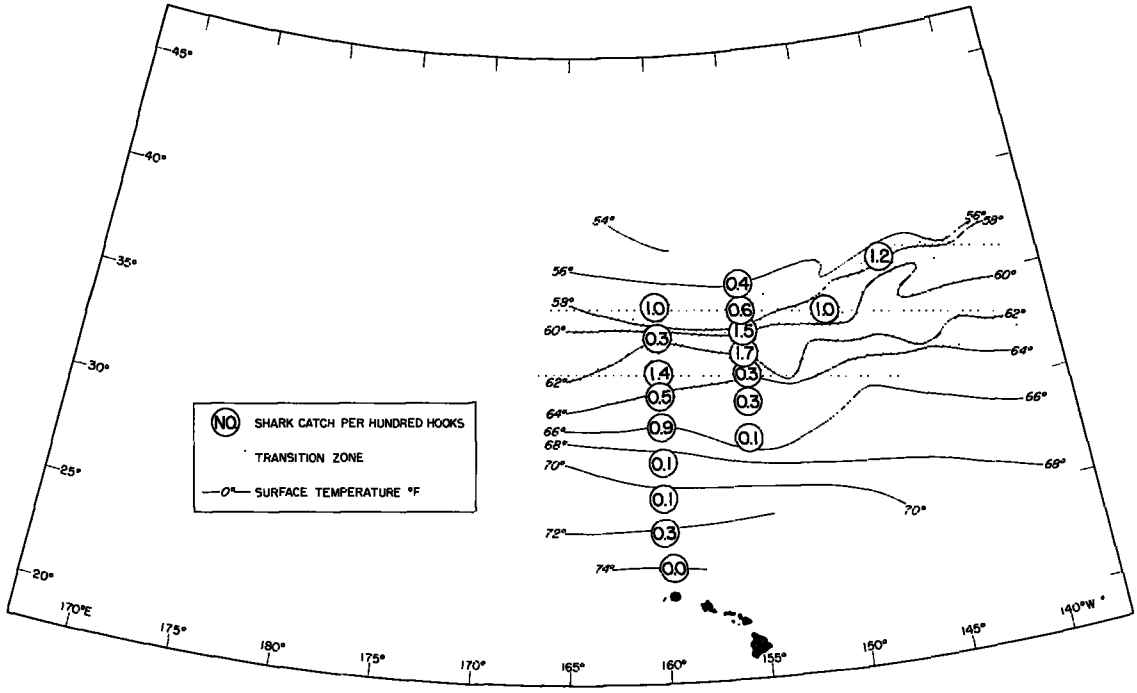

FIGURE 6b.—Relation between the great blue shark catch rate and position of transition zone, January–March. (After Shomura and Otsu, 1956.)

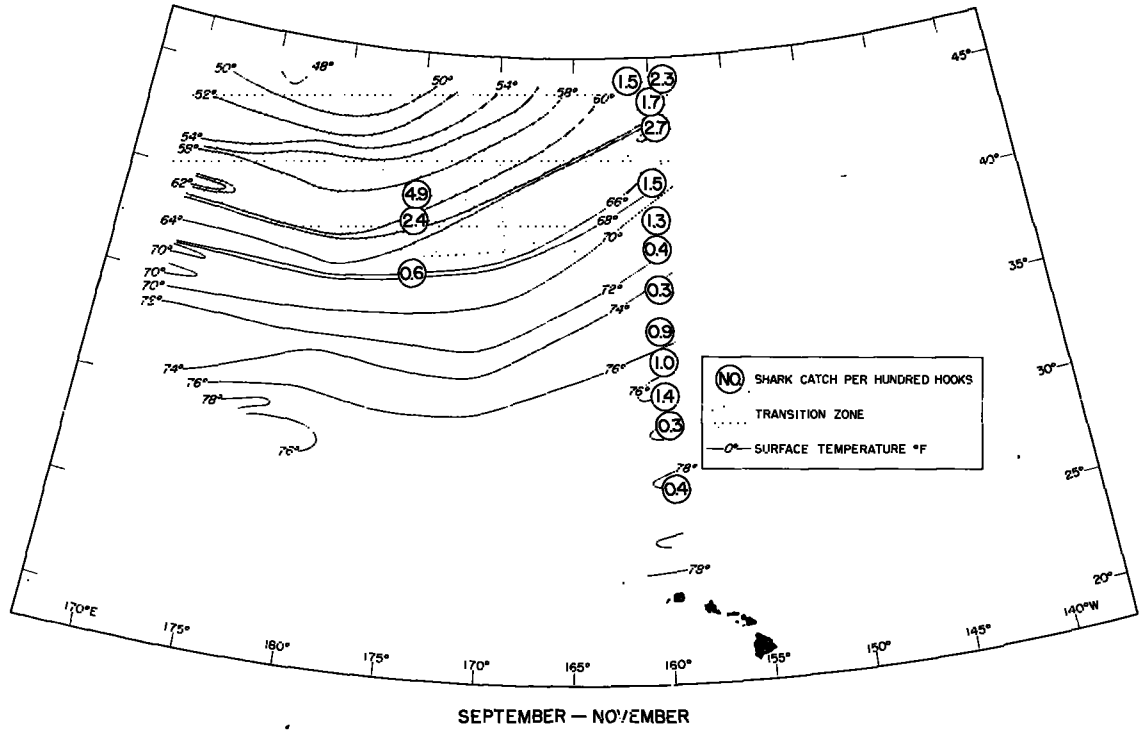

FIGURE 6c.—Relation between the great blue shark catch rate and position of transition zone, September–November. (After Shomura and Otsu, 1956.)

lation was newly born. The fact that small great blues were rarely encountered in warmer waters suggests that migrations may be a reproductive phenomenon having a close relation to the position of the transition zone.

The present data are inadequate for a discussion of the longitudinal aspects of migration.

The whitetip and silky sharks, occurring as they do solely within the Tropics, do not exhibit marked fluctuations in abundance. Figure 5 indicates that, within the limits of our sampling, whitetip numbers are greatest between 0° and 10° S., whereas the area of maximum silky concentration lies between 0° and 10° N. In neither region is there much change in numbers during the year. The significance of the large winter catch of whitetips between 10° S. and 20° S. cannot be determined until more seasons are represented in the catch data. Peripheral to these areas of concentration there is some evidence of seasonal fluctuations, the whitetip being more numerous in the summer to the north, and the silky more numerous in the spring to the south. Finally, the most northerly records of each species were obtained in the summer.

DISTRIBUTION BY DEPTH

Although the use of chemical sounding tubes to ascertain the fishing depth of the longline (Graham and Stewart [1]) is now standard procedure on POFI cruises, such information was not available for the majority of the cruises on which this report is based. The vertical distribution of sharks has accordingly been evaluated from the relative depth of the hook of capture. The use and applicability of this method have been discussed by Murphy and Shomura (1953a, 1953b, 1955) and Shomura and Murphy (1955), and the treatment employed here is similar to that used by these authors. Hooks were classified as shallow, intermediate, and deep, but because the number of hooks per basket varied between cruises it was necessary to weight each category in inverse proportion to the number of hooks involved. The arrangement of hooks within a basket for the three types of longline used and the relative hook depths are illustrated in figure 7. Table 2 summarizes

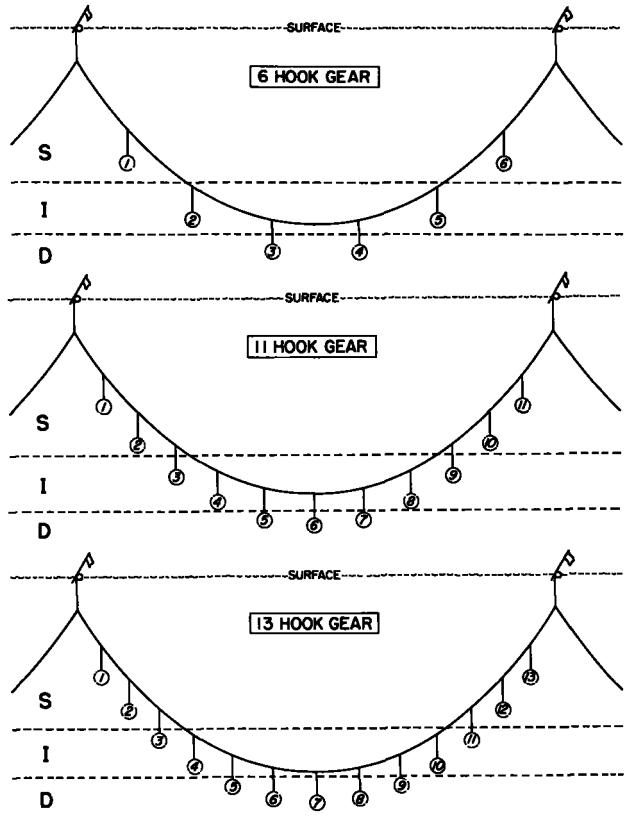

FIGURE 7.—Arrangement of a unit (basket) of each of the three types of longline employed in this study, showing floatlines, mainline, hook-bearing dropper lines, and the general lay of the gear with respect to the surface. Relative hook depths are indicated as shallow (*S*), intermediate (*I*), and deep (*D*).

TABLE 2.—*Depth assignment of hooks*

Type of gear	Relative depth and hook number			Relative weight applied to depth categories
	Shallow	Intermediate	Deep	
6-hook	1, 6	2, 5	3, 4	1:1:1
11-hook	1, 2, 10, 11	3, 4, 8, 9	5, 6, 7	¾:¾:1
13-hook	1, 2, 12, 13	3, 4, 10, 11	5, 6, 7, 8, 9	1:1:⅘

hook number, relative depth, and relative weight for the three types of gear considered.

The actual depths implied by shallow, intermediate, and deep have been estimated from the data of Murphy and Shomura (1953a), Iversen and Yoshida (1957) and Stewart and Graham,[2] for 6-, 11-, and 13-hook gear, respectively. Although the depth categories are not strictly comparable between the three gear types, the following ranges are illustrative of the depths sampled:

[1] Estimating the maximum fishing depth of longline gear with chemical sounding tubes, by Joseph J. Graham and Dorothy D. Stewart. U. S. Fish and Wildlife Service. (Manuscript.)

[2] Unpublished data in files of Pacific Oceanic Fishery Investigations.

shallow, 160 to 280 feet; intermediate, 280 to 430 feet; and deep, 370 to 500 feet. Pooling of results from different kinds of longline gear was minimized by selecting data by latitude and gear type. All catch records from north of 30° N. latitude were derived from 13-hook gear, whereas the majority of records south of 20° N. latitude were based on 6-hook gear, with a few catches from 11- or 13-hook baskets. Between 20° N. and 30° N. latitude the catches from only 11- and 13-hook gear were analyzed. Shark catch expressed as percentage occurrence on shallow, intermediate, and deep hooks is presented graphically in figure 8.

The great blue is wide-ranging and as such would be expected to be broadly eurythermal (fig. 3). The depth distribution data shown in figure 8 are at variance with this in that they show the species as being taken mainly on shallow hooks in the northernmost parts of its range, and mostly on deep hooks south of the Equator. Numerous observations of free-swimming great blues confirm this depth distribution picture, for the species was frequently seen swimming at the surface in the north but never so in the Tropics (not even in pursuit of a hooked and bleeding tuna). This shift in vertical distribution is possibly an example of "tropical submergence," and implies a narrower degree of eurythermality for the species. Lines of evidence supporting this idea are as follows.

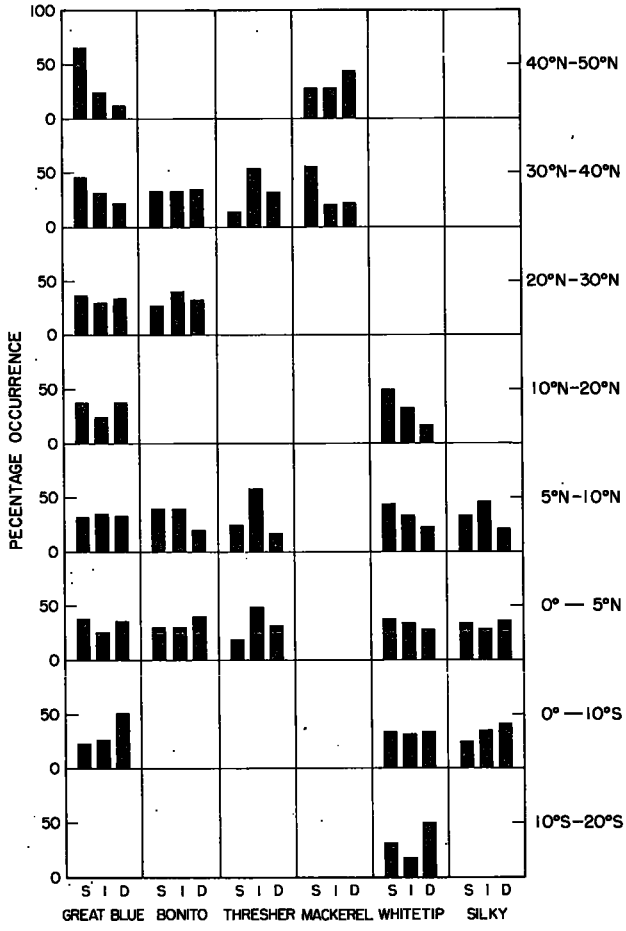

FIGURE 8.—Vertical distribution of pelagic sharks by latitude. Histograms depict percentage occurrence on shallow (S), intermediate (I), and deep hooks (D). Data are based on following catches: 1,318 great blues, 33 bonitos, 486 whitetips, 311 silkies, 27 mackerels, and 62 threshers.

Stewart and Graham [3] have calculated temperatures for the depth of capture of 1,200 great blue sharks taken north of 25° N. From their data the frequency of occurrence of great blues in 5-degree temperature categories was as follows:

Temperature:	*Frequency of occurrence great blue shark*
40° to 44° F.	5
45° to 49° F.	311
50° to 54° F.	524
55° to 59° F.	285
60° to 64° F.	44
65° to 69° F.	24
70° to 74° F.	7

Ninety-nine percent of the above sharks were from temperatures between 45° and 69° F., and 86 percent were captured in or below the thermocline. These temperature data are biased to an unknown degree on the cold side (they were derived from estimated maximum hook depths), but they nevertheless indicate that temperatures between about 45° and 69° F. are preferred by the great blue shark. When the depths of the 45°–69° F. isotherms are examined by latitude (c. f. McGary et al., 1956; Cromwell 1954) it is seen that isotherms in the range 50°–69° F. follow the vertical distribution of the great blue (fig. 8). These isotherms either reach the surface or are very shallow between 40° N. and 50° N. latitude but gradually deepen to the south, ultimately lying as deep or deeper than the deepest hooks (this occurs between 20° N. and 30° N. where the isotherm depth range is roughly 500–800 feet). The 50°–69° F. isotherms continue at this depth as far south as the scope of this study except for a marked shallowing at about 10° N. latitude where they ap-

[3] Unpublished data in files of Pacific Oceanic Fishery Investigations.

proach to within 200–600 feet of the surface. Their broad depth range here renders their shoaling insignificant, and the great blue's depth distribution does not show an accompanying shallowing.

Another factor which could account for the increased surface abundance of the great blue to the north is a pronounced seasonal increase in the food supply. Although no direct measures of the standing crop of shark forage (principally small fish and squid) are presently available, an idea of its potential magnitude can be obtained from variations in zooplankton abundance (McGary et al., 1956: 24–26). Between Midway Island and 40° N. latitude zooplankton volumes were about equal for oblique hauls from 0 to 40 meters, which sampled entirely above the thermocline, also for hauls made from the surface to 140 meters and hence, reaching or penetrating the thermocline; in addition, the average volume per haul was uniformly small (16–27 cubic centimeters per 1,000 cubic meters strained) at these latitudes. Between 40° N. and 45° N. latitude the shallow hauls yielded about 1.5 times as much zooplankton as the deeper hauls, and the volume of the catches increased to an average of 64 and 44 cc., respectively. From 45° N. to 50° N. latitude, the shallow hauls caught 1.75 times as much zooplankton as the deeper hauls, and average volumes increased to 168 and 98 cc., respectively. This marked increase in surface zooplankton toward the north is similar in general respects to the distributional picture seen in the sharks themselves.

The vertical distribution of bonito, mackerel, and thresher sharks, shown in figure 8, is based on few records and is probably not very reliable. Bonito and thresher sharks appear to be eurythermal, but three species are involved in the latter and the status of each is dubious. The only explanations offered for the apparent latitudinal shift in vertical distribution of the mackerel shark are (1) that the data may be misleading because of the small sample size (12 and 15 specimens), or (2) that both the shallow- and deep-hook catches were from about the same temperature. With reference to the data of McGary et al. (1956), it is seen that between 40° N. and 50° N. latitude at certain depths the isotherms are very steep so that both the deep and shallow hooks could fish in water of the same temperature.

In common with the other species occurring in the equatorial area, neither the whitetip nor the silky shark shows much latitudinal change in vertical distribution. The whitetip appears to be principally a surface dweller north of the Equator and more bathypelagic to the south, whereas the silky is almost uniformly distributed in depth to the north and is more deep-swimming to the south. The shoaling of the 60°–70° F. isotherms to 200–400 feet at about 10° N. latitude (Cromwell 1954) may explain the whitetip's shallow distribution in that general area, and similarly the deepening of isotherms south of 5° S. latitude could account for both sharks' deeper occurrence there.

VARIATIONS IN ABUNDANCE WITH LONG-TERM TEMPERATURE CYCLES

In the foregoing paragraphs frequent mention has been made of temperature as a factor regulating the spatial distribution of certain sharks. It is of interest, therefore, to examine abundance fluctuations in an area where temperatures are well known and relatively constant, and where shark numbers might be expected to vary directly or indirectly (through food chains, competition, etc.) with slight thermal changes. The region selected for this was the band of equatorial water extending from about 175° E. longitude to 110° W. longitude and bordered by 10° N. and 10° S. latitude. Shark catches from this region were segregated by species, year, and month, reduced to an effort basis, and plotted as anomalies between monthly means and the 4-year mean for each of the three common species. Similar data for surface temperature have been compiled by T. S. Austin, who has kindly made them available to this study. It should be noted, however, that the temperature anomalies are derived from a 6-year mean. Figure 9 shows the relation between shark abundance and temperature fluctuations.

As can be seen from figure 9, the years 1952 and 1953 were characterized by relatively warm surface temperatures (although quite variable in 1952), and 1954–55 by relatively cold conditions. The abundance of both whitetip and great blue sharks was greater during the warm years and lesser during the cold years, the same situation as found for yellowfin tuna.[4] Silky shark abund-

[4] Murphy and Shomura, unpublished data.

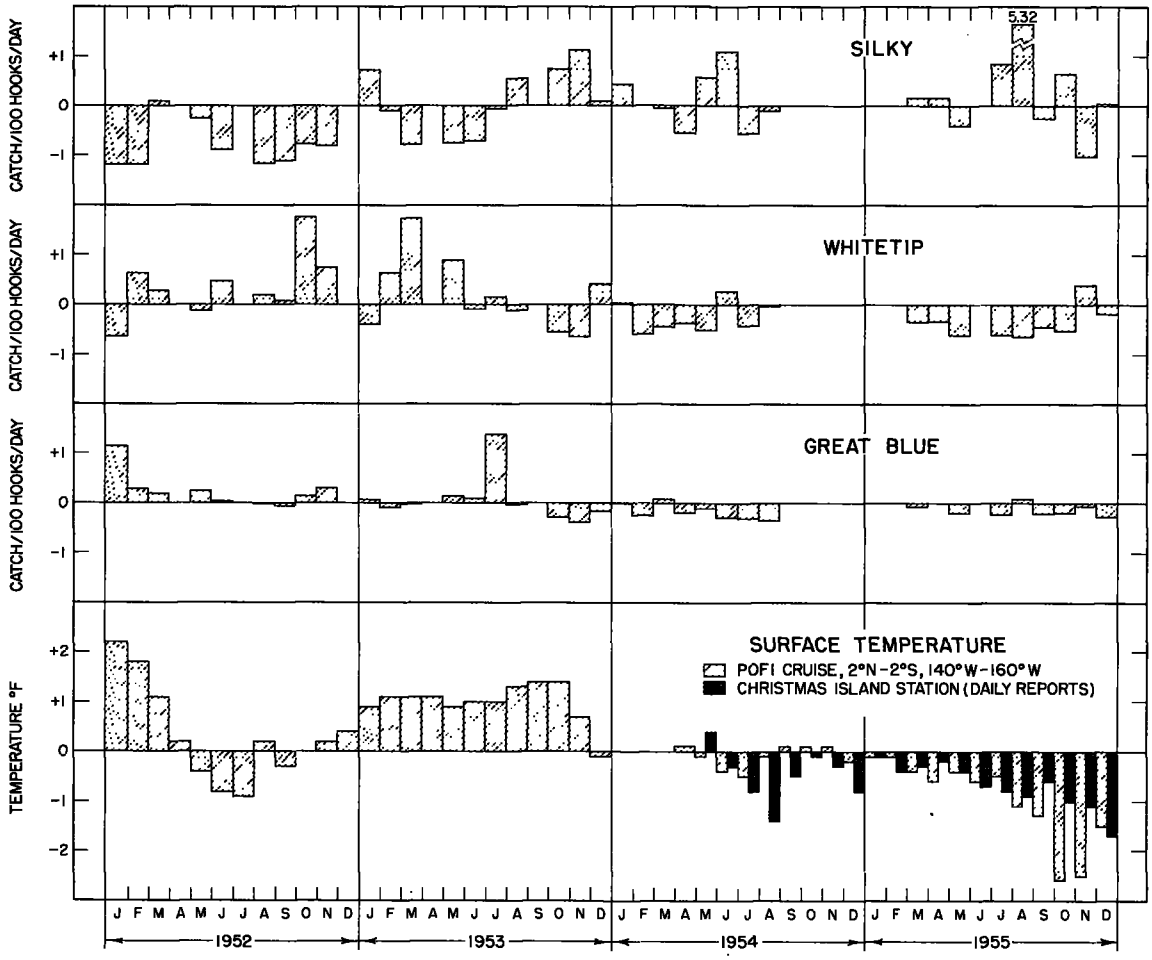

FIGURE 9.—Relation between shark catch and surface water temperature in the equatorial area. Shark histograms depict monthly deviations from 1952–55 means, based on entire catch between 10° N. and 10° S. latitude. Temperature histograms show monthly deviations from 1950–55 means.

ance, on the other hand, appears to be complementary to the other two, but why this should be so is difficult to understand. From the standpoints of latitudinal and depth distribution (figs. 3 and 8), the silky and the whitetip are similar although the silky shark has a narrower latitudinal range. One would assume, on an a priori basis, that the silky was more dependent on warm temperature than the whitetip, and would further deduce that a reduction in its numbers would be brought about by colder rather than warmer water.

Perhaps a portion of the irregularity in the catch data stems from sampling artifacts, for several types of longline gear were in use and fishing was both insular and oceanic. In several instances where whitetip and great blue abundance was anomalous with respect to temperature (notably the last 6 months of 1953) silky shark abundance retained its complementary relation to the other two species, and did not follow the temperature fluctuation. This may represent a behavioral interaction between the silky shark and one or more of the others. A similar situation involving these same sharks is discussed in a later section dealing with abundance versus distance from land.

VARIATIONS IN ABUNDANCE WITH LONGITUDE IN THE EQUATORIAL PACIFIC

A large portion of POFI's research program has been devoted to an evaluation of the fishery resources of the equatorial region of the central Pacific. Intensive sampling of fish stocks, plank-

ton, and the physical and chemical environment has been undertaken, and a considerable body of knowledge of the interrelationships of these properties has been assembled. Physically the region is characterized by the easterly flowing Equatorial Countercurrent between 5° N. and 10° N. latitude, and by the westerly flowing South Equatorial Current to the south of this. Between 5° N. and the Equator there exists a zone of enrichment which reaches optimum conditions, biologically speaking, between 140° W. and 160° W. longitude. Here the sequence of trade winds, divergence, and upwelling brings nutrient-rich water into the euphotic zone, with a resultant increase in biological productivity. An increase in abundance in this area has been shown for zooplankton (King and Demond, 1953), tuna (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955), and sea birds (King and Pyle, 1957) so it would not be surprising to find a similar increase in the number of pelagic sharks.

To examine further the geographic variation in shark abundance the catch records for all species were reduced to terms of average catch per hundred hooks per day for 5-degree intervals of latitude and 10-degree intervals of longitude between 10° N. and 10° S. latitude, and 175° E. and 110° W. longitude (fig. 10). The 4,133 records considered include 2,174 silky, 1,151 whitetip, 641 great blue, and small numbers of bonito, thresher, hammerhead, and blacktip sharks. Because of the effects of land on species composition the species data were pooled.

In the region of the Equatorial Countercurrent (5° N. to 10° N. in the central Pacific) shark numbers generally decreased from east to west, the configuration of this decline being nearly identical to that found for zooplankton volumes (King and Hida, 1957). A difference between the zooplankton and shark abundance patterns is that the former peaks at 140° W. and declines east of that point, whereas shark abundance appears to be minimal at 140° W. and to rise to the eastward. Because of the generally close correlation between shark numbers and zooplankton volumes it would seem that basic food abundance, and not temperature or proximity to land (see p. 348) is the factor influencing shark distribution in the Countercurrent area. King and Hida (loc. cit.) state that the east-to-west decline in zooplankton parallels

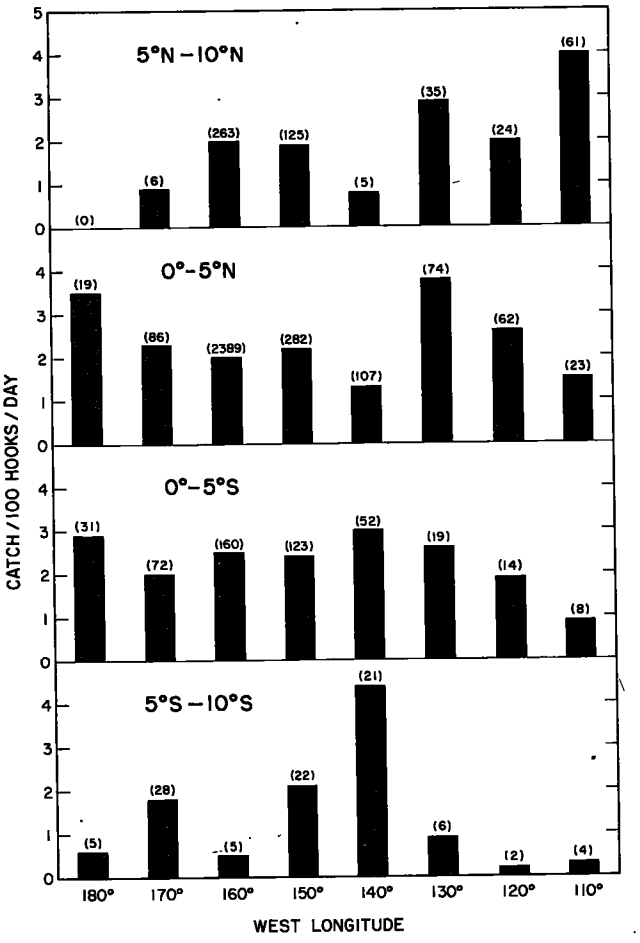

FIGURE 10.—Abundance of pelagic sharks in equatorial waters, all species combined. Each histogram depicts abundance for the area 5 degrees on each side of the numbered coordinate of longitude and within each 5-degree band of latitude. Numbers in parentheses represent actual catch.

a decrease in surface enrichment caused by a slackening of wind and deepening of the thermocline.

Between 5° N. and 5° S. (South Equatorial Current) there are two types of distributions in the biotic indices. One involves a gradual doming of abundance with maximal values occurring between 140° W. and 160° W., the other the reverse situation with minimal values occurring at these central longitudes, and increases to the east and west. King and Hida (1957) found the first type for yellowfin tuna and zooplankton, and it also occurs for sharks between the Equator and 10° S. (fig. 10). The second situation obtains for inorganic phosphate (King and Hida, loc. cit.) and for sharks between 5° N. and the Equator. It is

difficult to reconcile these seemingly antithetical patterns, for one would presume the distribution of organisms high in the food chain to correspond closely to that of the nutrients below them. Perhaps the decline in shark numbers at 140° W. longitude is brought about by food competition between sharks and yellowfin tuna. As shown by Murphy and Shomura (1955), yellowfin are particularly abundant at this longitude between the Equator and about 7° N. latitude. South of the Equator there is close agreement between the longitudinal distributions of sharks, yellowfin tuna, and plankton.

SHARK DISTRIBUTION WITH RESPECT TO LAND

The effect of land or proximity of land on the distribution of a pelagic marine animal provides an interesting problem. For certain oceanic species the presence of land acts only as a barrier to movements, whereas others congregate about islands and other land masses to feed or to reproduce. It occasionally happens that oceanic fish abound in insular environments, either because of the islands' intrinsic nutritive richness or because they lie in the path of rich oceanic currents. The latter situation is apparently true for Christmas Island, a member of the Line Islands group. Here an atoll is located in the path of flow of enriched equatorial water, and maximum abundance of yellowfin tuna occurs in a narrow band extending from Christmas eastward for several hundred miles (Sette 1955).

The POFI longline surveys have provided information on the distribution of sharks in relation to nearness of land. Proximity to land was determined by measuring the distance between the noon position of a fishing station (recovery of longline gear usually started at noon) and the nearest portion of Christmas Island. Shark abundance in neritic situations is contrasted with that of the open ocean in figure 11.

Three distributional patterns are apparent for the sharks shown in figure 11. The thresher sharks (3 species) are definitely neritic, their abundance falling close to zero 40 miles from shore. The silky shark (noted as semipelagic, Springer 1950) occurs in moderate numbers on the high seas but is about twice as plentiful in the neritic region. Two sharks, the whitetip and the great blue, are truly oceanic species, and their numbers steadily increase as land is left behind.

The zone delimited by the categories 10–19 and 50–59 miles from land is essentially a region where the physical and ecological characteristics of the neritic and oceanic provinces intergrade. It is of interest that in this transitional area none of the sharks considered exists in the same degree of abundance as it does in more landward or seaward

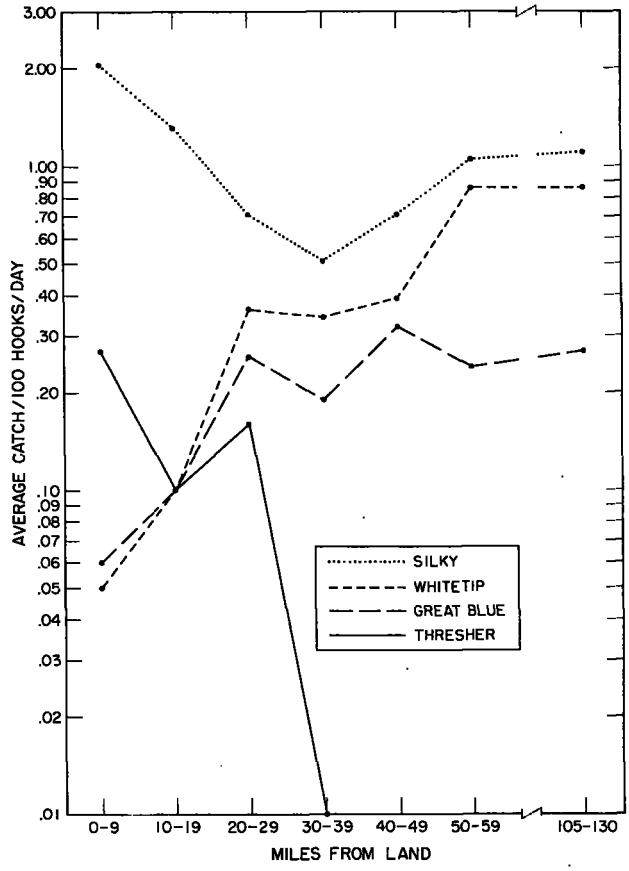

FIGURE 11.—Abundance of pelagic sharks with regard to distance from land. Data derived from Christmas Island area and region to eastward between 1° N. and 3° N. latitude. Based on 997 silky, 210 whitetip, 133 great blue, and 86 thresher sharks.

locales. Perhaps the intermediate nature of the physical environment favors neither the neritic nor the oceanic species, or perhaps abundance fluctuations represent biotic interaction between one or more sharks and other organisms. If the latter, then interaction is most likely in the realm of food competition, for predation and other immediately deleterious relationships are probably inconsequential for large sharks.

The species of sharks discussed here subsist principally on small fish and squid and have this diet in common with yellowfin tuna (Reintjes and King, 1953) and bigeye tuna (King and Ikehara, 1956). As to swimming speeds, it would appear almost certain that the tunas are much faster than the sharks, and that among the sharks themselves there may be considerable differences in speed. It has been suggested that whitetips are relatively slow swimmers compared to silky sharks (Backus et al., 1956), with the whitetip's cruising speed being estimated at about a mile an hour by Strasburg (1957). Also confirming this slowness is the fact that, although several silky sharks have been taken while trolling at 6 to 8 knots, only 1 whitetip was so captured during several thousand hours of trolling by POFI vessels. This lack of speed would place the whitetip in an unfavorable competitive position with both the yellowfin tuna and the silky shark, the abundance of each of which increases as Christmas Island is approached (see Shomura and Murphy, 1956 for yellowfin data). It appears, therefore, that the generally inverse relation between whitetip and silky abundance shown in figure 11 may represent a competitive interaction between the two.

FOOD HABITS OF PELAGIC SHARKS

The fact that sharks are broadly carnivorous is common knowledge, but the food of many of the pelagic species is not particularly well known. Unfortunately, the stomach contents of longline-caught sharks were not routinely examined by POFI, and as a consequence the ensuing discussion is not based on a large body of data. Another factor reducing the number of records is that more than half of the 265 stomachs examined were empty. A summary of the results of our food study is presented in table 3.

As evidenced by the information in table 3, pelagic sharks subsist mainly on small fish and squid. Bigelow and Schroeder (1948) and Backus et al. (1956) have shown that the whitetip and bonito sharks also consume large fish such as tuna, and this is also indicated by the present data. In the present case, however, it could not be determined whether tuna were only preyed on after they had been hooked. The more neritic silky shark included littoral forms such as *Diodon* and crabs in its diet, and other sharks did the same in suitable locales. One tendency not shown in table 3 is that a number of thresher sharks were foul-hooked by the tail. Their capture probably resulted from attempts to herd the dangling bait with their tails (Breder 1929).

Pelagic sharks as a group are opportunistic feeders, commonly taking almost any available food, and often ingesting articles of little or no nutritive value. Several species tend to congregate around ships, and have been seen to swallow such items as paper cartons, tin cans, and scraps of cloth, along with considerable amounts of

TABLE 3.—*Food of longline-caught sharks*

Shark species	Number of stomachs in which occurred—																										Number of empty stomachs	Number of stomachs examined
	Fish													Longline bait			Flying fish eggs		Cephalopods			Miscellaneous					
	Alepisaurus (Lancet fish)	*Neothunnus* (Yellowfin tuna)	*Katsuwonus* (Skipjack)	Unidentified tuna	Tuna-like fish	*Diodon* (Spiny puffer)	*Mola* (Ocean sunfish)	Bramids (Pomfrets)	Echeneids (Sucker fish)	Myctophids (Lantern fish)	Ostraciids (Trunkfish)	Stingray	Unidentified fish	Herring	Sardines	Unidentified bait	Attached to feathers	Unattached	Squid	Octopus	Unid. cephalopods	Crabs	Shrimp	Sea bird (booby)	Blubber (?)		
Great blue	5			2				1	1	1	1		25	4	10		4	2	19	1	20	2	2	1	1	76	140
Whitetip	2	1						1				1	6	2	24				10	1	2					35	73
Silky						2							1		2				3			1				22	29
Bonito	1	1			1		1						1			1			2							6	13
Thresher	1		1										3	2					1							2	7
Blacktip													1													0	1
Hammerhead:																											
S. zygaena				1																						0	1
S. lewini													1						1							0	1
Total	9	2	1	3	1	2	1	1	1	1	1	1	38	8	36	1	4	2	36	2	22	3	2	1	1	141	265

garbage and fish scraps. The indiscriminate nature of this type of feeding suggests a low degree of visual (and olfactory?) acuity coupled with voracious feeding behavior, both of which are well known for sharks, and which would seem to belie their ability to capture squid, tuna, and sea birds unless these were moribund or dead. On the other hand, the author has seen a team of 2 or 3 whitetips slowly herd and capture squid around a surface light at night, and has also removed large pieces of tuna flesh from whitetip stomachs in areas where no fishing was taking place. Finally, a bigeye tuna (*Parathunnus sibi*) captured on a POFI longline cruise bore a pair of large U-shaped scars suspiciously resembling shark jaws in shape. The indications are that some pelagic sharks can be both fast moving and selective feeders, and perhaps the unpredictable rapacity of their feeding enables them to capture what would seem to be elusive, highly motile prey.

Some mention must also be made of a rather artificial food habit of sharks, namely the damage they inflict on longline-caught tuna. Other workers have noted that damage is virtually absent from the more northerly portions of POFI's investigative area (Shomura and Otsu, 1956) but averages about 20 percent of the longline catch in equatorial waters (Murphy and Shomura, 1955; Iversen and Yoshida, 1956). It is obvious that shark damage to hooked tuna is ultimately limited by both shark abundance and the availability of tuna, and that the interaction of these two factors coupled with the behavioral characteristics of sharks is what determines the extent of the damage. For the purposes of the present study all species of longline-caught tuna (*Neo-*

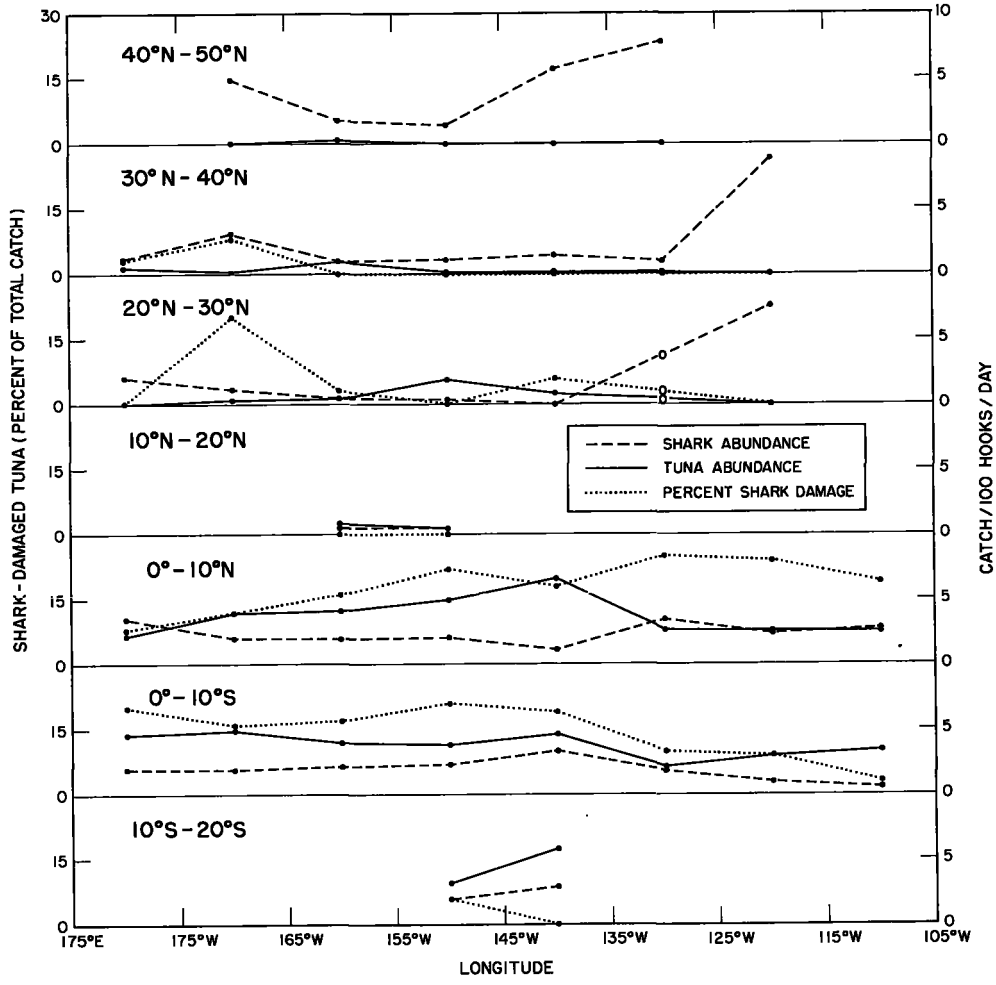

FIGURE 12.—Shark damage to tuna contrasted with shark and tuna abundance. 0=no sample.

thunnus macropterus, *Parathunnus sibi*, *Germo alalunga*, and *Katsuwonus pelamis*) are lumped as "tuna," and all shark species are combined.

North of about 30° N. latitude POFI's longline tuna catch has been minimal, and shark damage affected only about 1 percent of it (fig. 12, and Shomura and Otsu, 1956). Between 20° N. and 30° N. latitude tuna abundance increased whereas shark damage was only slight or moderate (fig. 12). The prominent peaking of shark damage between 20°–30° N. latitude and 165°–175° W. longitude is an artifact caused by a very small sample (1 damaged tuna out of 5 caught). In these northern areas the abundant shark is the great blue (fig. 3), and it would seem that this species is not particularly deleterious to the fishery, other accounts to the contrary (c. f. Bigelow and Schroeder 1948: 286).

In equatorial waters tuna abundance is equal to or greater than shark abundance (fig. 12), and shark damage is at its greatest here, frequently involving as much as 20 percent of the tuna catch. The principal culprits in this region are the whitetip and silky sharks, with the bonito being of much less importance (figs. 3 and 4, and numerous observations by POFI biologists). From the equatorial situation one might suppose a good

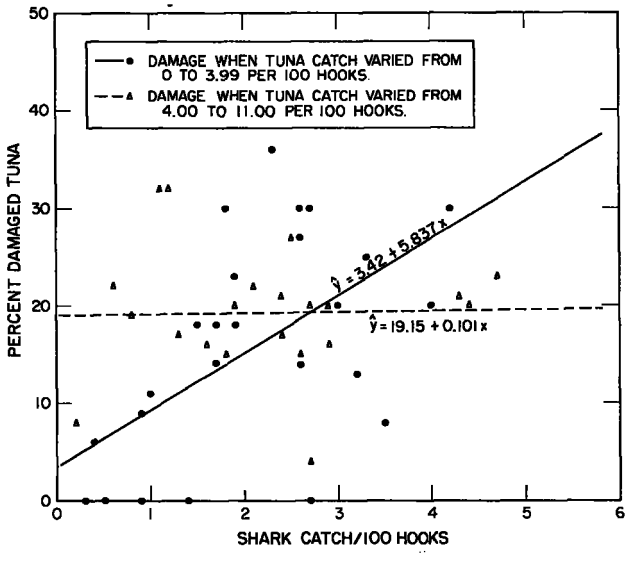

FIGURE 13.—Relation between shark damage of longline-caught tuna and shark abundance. Based on catch records of 8,797 tuna (of which 1,511 were damaged) and 4,133 sharks. All catches made between 10° N. and 10° S. latitude. When tuna catch low, b=5.837, p <0.01; when tuna catch high, b=0.101, p >0.5.

positive correlation to exist between shark and tuna abundance, but this was not found by Iversen and Yoshida (1956). These authors found a strong relation between shark catch rate and shark damage on a monthly basis, but this breaks down, in part, when studied on a nonsecular basis. When tuna abundance is low there is a correlation (r=0.573) between shark abundance and shark damage (fig. 13), but when tuna abundance is high there is almost no relation between the two (r= 0.019). A possible explanation of these phenomena is that an abundance of tuna probably indicates an abundance of forage organisms so that a large natural food supply (either tuna or forage) is available to the sharks. The sharks are well-fed and not interested in longline-caught fish. Conversely, a dearth of tuna and other forage animals would enhance the attractiveness of hooked tuna, and proportionally more of the catch would be eaten by sharks.

SEXUAL SEGREGATION

Among sharks there appear to be two basic types of sexual segregation or tendency to school by sex. In behavioral segregation individuals school with others of similar size, thus sorting the sexes in the case of a dimorphic species such as *Squalus acanthias* (Ford 1921). In what has been called geographical segregation (Backus et al., 1956) the sexes school separately because of differences in habits. Geographical segregation has been found for *Scyliorhinus canicula* by Ford (op. cit.), for the soupfin (Ripley 1946), for *Galeorhinus australis* by Olsen (1954), the great blue (Bigelow and Schroeder, 1948), and the whitetip (Krefft 1954; Backus et al., 1956). These authors have related geographical segregation to season, region, depth, distance from land, and degree of sexual maturity, with the underlying causative factor generally being regarded as reproductive in nature. In two cases (Olsen 1954; Backus et al., 1956) the existence of definite breeding grounds has been mentioned.

The present data are scanty as to sex of the sharks caught, but nevertheless they indicate that both behavioral and geographical segregation may occur in the same species. This study is primarily restricted to the great blue because sex was not recorded for adequate numbers of the other species. An inherent fault in the data is that be-

cause of the length of the longline gear (7 to 10 miles in each set) a single day's catch may actually contain samples from several schools.

Table 4 illustrates the degree of unisexual predominance in the catches from 36 longline stations where sharks were sexed and at least 4 specimens of a species were taken. In the great blue shark the sex ratio varied from about 1:1 to a tremendous preponderance of one sex. The data on the whitetip and the silky were not so extensive and did not show this degree of variability.

TABLE 4.—*Instances of unisexual predominance in shark catches* [1]

Species and number of specimens examined	Frequency of occurrence of predominant sex (in percent)					
	50–59	60–69	70–79	80–89	90–99	100
Great blue (283)	6	3	5	3	2	10
Whitetip (29)		1	2	1		1
Silky (11)				1		1

[1] Units are number of stations showing predominance. The smallest station considered yielded 4 sharks of any one species.

In determining whether preponderance of either sex was of the behavioral or geographical type of segregation the great blue shark data were analyzed in several ways. When the percentage of males was plotted by latitude (fig. 14), males comprised a smaller proportion of the northern catch than they did of the southern. This difference is most striking when the unisexual catches are considered, but it is also apparent in mixed catches and the entire catch (unisexual and mixed data pooled). There can be no doubt that latitudinal variation in sex ratio represents geographical segregation but the biological aspects of this phenomenon are not so easily classified.

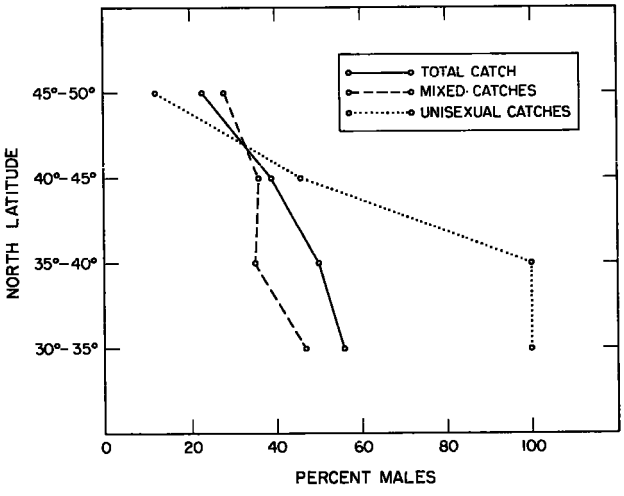

FIGURE 14.—Sex composition of great blue shark catch by latitude. Based on 255 records of which 184 were from mixed and 71 from unisexual catches.

If the mean total length of great blues is plotted by sex and latitude (fig. 15), it appears that in mixed catches (pooled from several stations) both sexes are about the same size at any latitude, and the mean length decreases to the north. The lengths of sharks from unisexual catches are slightly to considerably greater than those of mixed catches, but there is little relation between the lengths of males and females. If our catches actually represent schools then it is not illogical to presume that unisexual schools are derived from mixed schools by a behavioral size-sorting mechanism. Judging from the overlap between the standard deviations of mixed and unisexual school lengths, this mechanism becomes operative at lengths between about 110 and 160 centimeters. It is unlikely that segregation of such small sharks has a direct reproductive significance, for the smallest gravid females known were from 208 to 214 cm. in length (Bigelow and Schroeder, 1948, and in this paper p. 354).

Because the causative agent for behavioral segregation is thought to be size dimorphism between the sexes (Backus et al., 1956), it was reasoned that the difference between male and female lengths in individual mixed catches should be related to the sex ratio of the catch. This relation is shown in figure 16 which indicates that the greater the size difference between the sexes the greater the disparity in sex ratio. Where females are larger than the males most of the catch is male, and where males are larger than the females most of the catch is female. A similar situation obtains for the soupfin shark (Ripley 1946). Such a situation not only poses the question of why large sharks should be of opposite sex from the rest of the school, but it is also rather contrary to the principal tenet of behavioral schooling, that members of a school be of like size. The regression in figure 16 is significant ($p=0.02$) only when the two points to the extreme left are included.

The available data are too few to form more than an outline of the secular aspects of sexual segregation. They are derived from a sample of 255 great blues taken between 30° N. and 50° N. latitude over a period of several years. Both mixed and unisexual catches were made in the

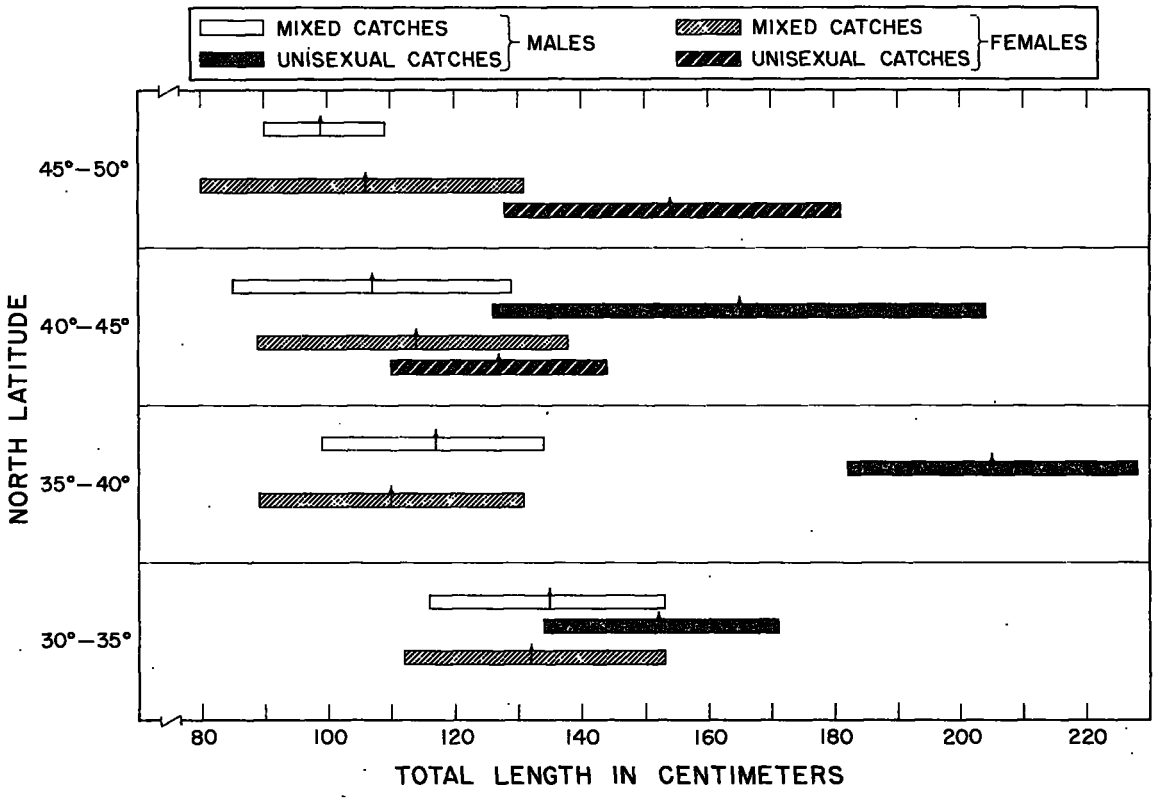

FIGURE 15.—Length composition of unisexual and mixed catches of great blue sharks at various latitudes. Vertical lines are means; blocks are one standard deviation on each side of mean.

summer and autumn but only mixed catches were taken in the winter and spring. On a percentage basis mixed catches contained the following proportions of males: spring 36 percent, summer 33 percent, autumn 22 percent, and winter 47 percent. The autumnal disparity in sex ratio is also of interest in that the two unisexual catches made in that season were composed of males. The low male ratio in summer mixed catches is similarly reflected in the unisexual data, for here only 2 all-male (versus 4 all-female) catches were made. From these sketchy data it appears that the great blue catch is composed of about equal numbers of both sexes in the winter, and that females gain predominance in the spring. Unisexual schools form during the summer and autumn and probably reassemble as mixed schools in the winter. The data are too few to present a latitudinal picture of these changes.

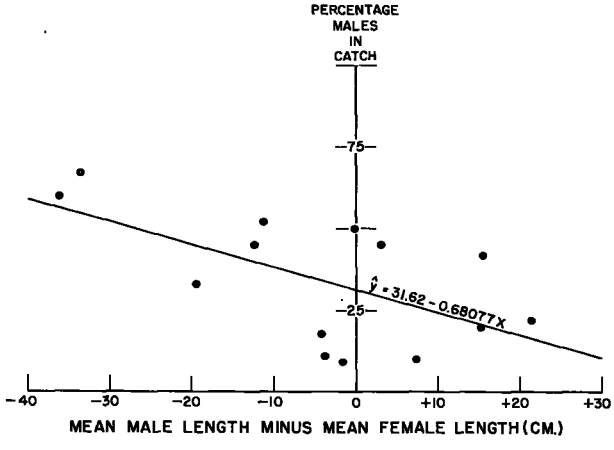

FIGURE 16.—Relation between sex and size composition of individual mixed great blue shark catches. Based on 172 sharks taken in catches containing from 5 to 24 individuals. Regression line fitted by method of least squares.

When the mean lengths of great blues are plotted by sex and season (fig. 17), it is evident that autumn is not only the period of greatest disparity in sex ratio but is also the time of greatest length difference between the sexes. Unfortunately, the data were necessarily derived from pooled mixed and unisexual catch records and are thus rather unreliable (in the case of unisexual records there is no particular reason for

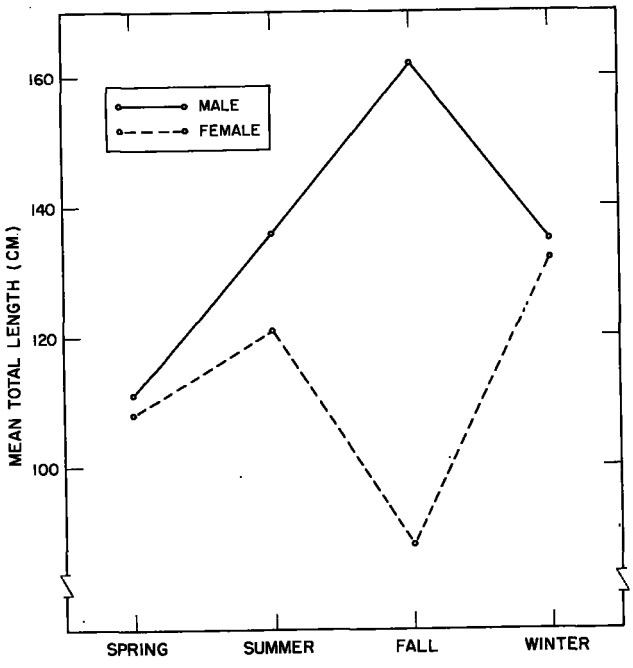

FIGURE 17.—Mean total length of great blue sharks by sex and season. Based upon 112 males and 143 females from mixed and unisexual catches taken between 30° N. and 50° N. latitude.

one school to resemble another in its length composition). The increase in mean length over the spring-to-fall interval probably reflects an availability fluctuation more strongly than growth.

REPRODUCTION

The available data on reproduction in the female are based on observations on the following: 18 great blues, 19 silkies, 32 whitetips, and 4 threshers (2 *A. pelagicus*, 1 *A. vulpinus*, 1 *A. superciliosus*). All of these except 6 great blues and 1 whitetip were taken in equatorial waters, with most specimens coming from the Line Islands area. Although the data are meager they are presented because of the general lack of knowledge of the reproductive habits of pelagic sharks.

Of the 12 great blue sharks from the equatorial Pacific the smallest gravid female measured 214 cm. and the largest 244 cm. Nongravid females from this region ranged from 188 to 243 cm. in total length. Embryos were found during February, March, May, August, October, and December, with the largest fetuses (22–28 cm.) occurring in March and May. Nongravid females as large or larger than the pregnant ones were encountered from January through August. The number of embryos per female ranged from 4 to 38, and in 1 litter of 18 their distribution was 8 on the left side and 10 on the right. There was no apparent correlation between embryo size and time of year.

The 6 nonequatorial great blue females were taken between 24° N. and 35° N. latitude. The 4 gravid specimens ranged from 208 to 247 cm. in total length and contained from 23 to about 40 embryos, the distribution of which was bilateral (16 on the left side and 17 on the right in 1 specimen). All 6 females were taken in January and February and here again there was no relation between embryo size and time of year. One female obtained in February gave birth to between 30 and 40 pups on deck (fig. 18), and these were the largest great blue embryos taken, suggesting that they were very near term. Further confirming this conclusion is the fact that their length range (34–48 cm.) approximates the foot-and-a-half length of the smallest longline-caught great blues. Also, the pups were very active at birth and appeared ready to fend for themselves. All emerged tail first.

All 19 female silky sharks were taken from the equatorial region, and of these 12 were gravid and 7 not. Both gravid and nongravid females were taken throughout the year, the range in total length of the former being 213 to 236 cm., and of the latter, 186 to 218 cm. The number of young observed varied from 2 to 11, with a mean value of 6.5 per female. The total length was recorded for 32 embryos and ranged from 37 to 66 cm., the upper extreme suggesting that the pups are quite sizeable when born. There again appeared to be no relation between embryo size and time of year. Uterine distribution of embryos was recorded for 2 females, one of which had 4 embryos on each side, the other having 2 on the left and 5 on the right. The single litter sexed contained 2 male and 7 female embryos.

Only 3 of the 32 female whitetips examined contained embryos, these 3 being equatorial specimens. A 210-cm. specimen was taken in April and contained 6 fetuses from 36 to 40 cm. in total length, a 196-cm. female obtained in May had five 20- to 28-cm. embryos, and a 195-cm. female taken in December contained 7 averaging 18 cm. in total length. These fragmentary data suggest a rather different developmental picture from that noted by

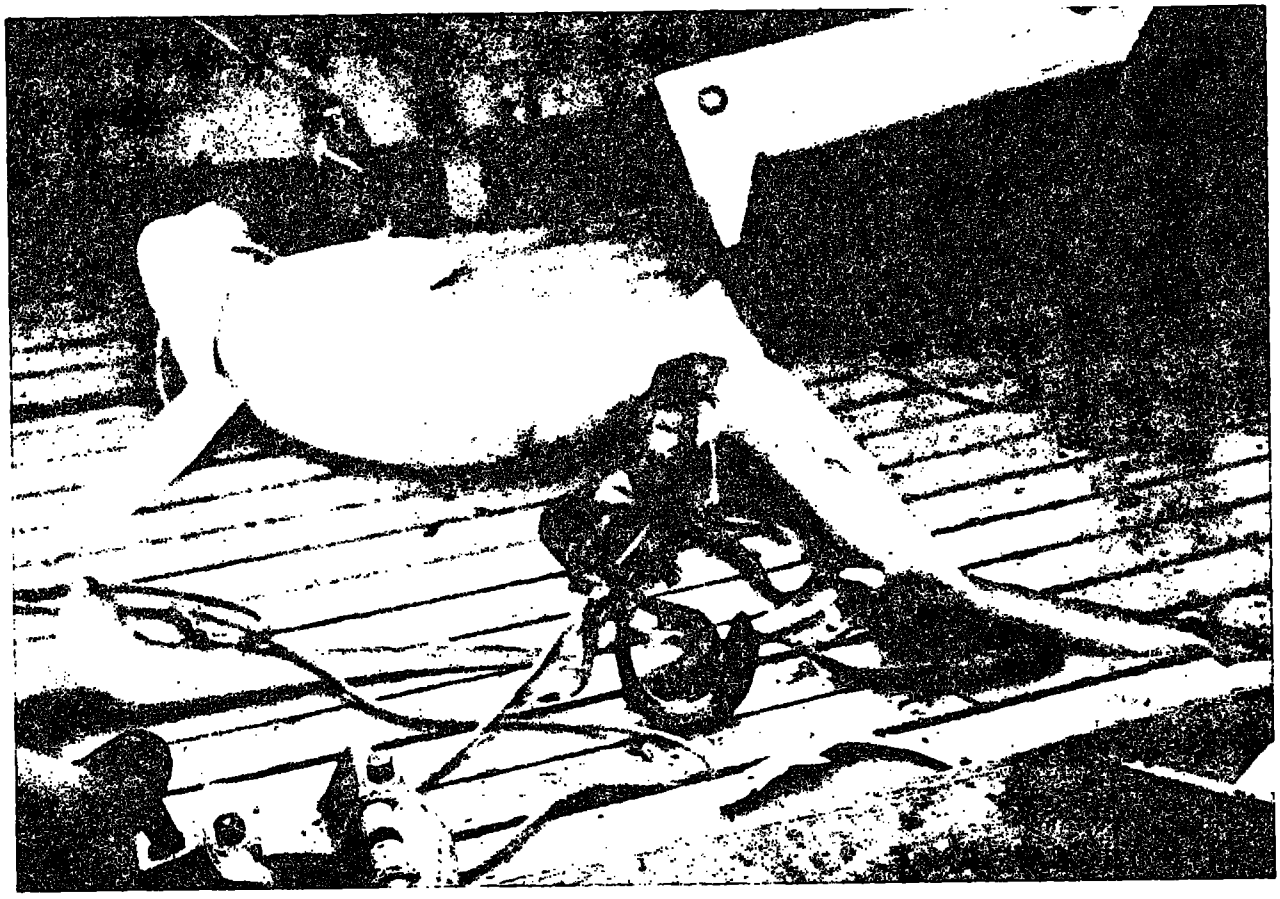

FIGURE 18.—Female great blue shark giving birth to young on deck of the *John R. Manning*. Nine young can be seen on deck while a tenth, still enveloped in its embryonic membranes, is just emerging.

Backus et al. (1956) for the whitetip of the Gulf of Mexico and the West Indies, as the central Pacific embryos were rather small at all times of the year. One Hawaiian and 28 equatorial whitetip females contained no young. These infertile females were taken throughout the year and ranged in length from 99 to 246 cm.; about one-fourth of this group were as large or larger than the gravid females.

With regard to thresher sharks, the single female *Alopias vulpinus* examined was captured on June 4, 1954, just to the west of Christmas Island (Line group). This thresher measured 315 cm. in total length and contained 2 fetuses, one of which was 114 cm. in total length. Also present were a number of eggs about 0.7 cm. in diameter. Two females of the rather uncommon *A. pelagicus* were examined, the larger (893 cm. total length) being taken on April 7, 1955, off Fanning Island (Line group), and the smaller (167 cm.) on May 4, 1953, at about 9° N. latitude and 150° W. longitude. The larger female contained the apparently typical number of 2 embryos (see Nakamura 1935), and the smaller one was not gravid. On June 7, 1954, a nongravid female of *A. superciliosus* was taken near Christmas Island. Its total length was 328 cm.

MORPHOMETRY AND TAXONOMY

In the early part of the shark investigation morphometric data were recorded for a number of specimens of each species. In order to make these data comparable to those of other investigators, measurements were standardized with those given by Bigelow and Schroeder (1948). Figure 19 depicts the methods used for measuring certain characters; other measurements follow. Eye diameter — greatest horizontal diameter; labial furrow length—length of outer labial furrow; gill slit height—height of gill opening when

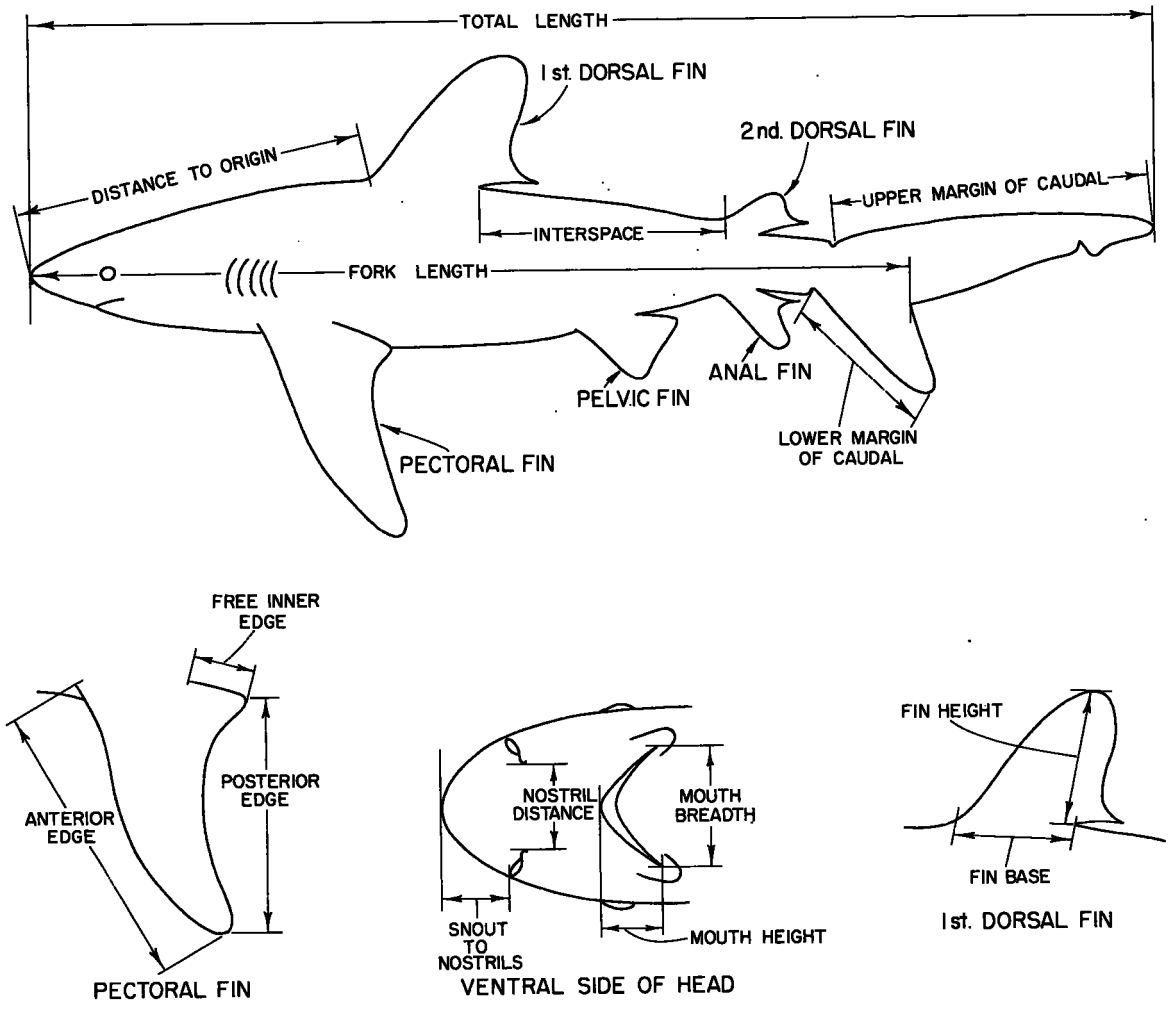

FIGURE 19.—Method of measuring sharks. All distances are straight lines between perpendiculars, with fish lying on belly when possible.

stretched just enough to prevent buckling of anterior edge; trunk breadth and height—maximum breadth and height at pectoral origin; lower margin of caudal—distance from rear edge of ventral precaudal pit to tip of lower caudal lobe; free clasper-distance from point where clasper leaves anal fin (lateral side) to tip of clasper.

Table 5 summarizes the morphometric data obtained in this study. For the common species the mean and the range are given for each character considered, although the range was not necessarily derived from individuals of maximal and minimal length. The original data were tabulated by sex, but with a very few exceptions overlapping was complete or nearly so, and it did not appear necessary to segregate the final data in this manner.

The volume of morphometric data available for whitetip, silky, and great blue sharks makes possible a comparison between the central Pacific and other forms. Morphometric data for Atlantic specimens were obtained from Bigelow and Schroeder's descriptions (1948) even though these were derived from only a few specimens. For all three species it appears that in the Pacific specimens the distance between the snout and all fins except the anal is greater than in Atlantic material, and also that the second dorsal, the anal, and the upper caudal lobe are smaller in the Pacific. In Pacific whitetips the lower caudal lobe and the various pectoral fin measurements are relatively greater than in the Atlantic, whereas in Pacific silkies and great blues these structures

TABLE 5.—*Shark morphometrics*

[Values expressed as hundredths of total length. Columns indicating range express the range for each character, and not the measurements of the largest and the smallest shark. See pp. 355–56 for measurement methods]

Item	Whitetip (8 males, 8 females)			*P. insularum*[1]	Silky (7 males, 5 females)			Great blue (17 males, 5 females)			Bonito (11 males, 2 females)			Mackerel (1 male, 1 female)	Thresher (*A. pelagicus*) (1 male, 2 female)	Thresher (*A. superciliosus*) (1 female)	Thresher (*A. vulpinus*) (1 female)	Hammerhead (*S. zygaena*) (1 male)	Hammerhead (*S. lewini*) (1 male)	Blacktip (1 male, 1?)
	Smallest	Largest	Mean	Type	Smallest	Largest	Mean	Smallest	Largest	Mean	Smallest	Largest	Mean	Mean	Mean					Mean
Total length (cm.)	72.0	243.1	116.0	213.0	87.7	227.0	192.7	121.7	304.5	234.3	125.1	257.9	205.9	96.0	290.2	327.7	317.0	266.3	301.8	143.2
Fork length	77.3	83.5	80.0		78.5	83.6	80.7	80.1	83.2	81.9	86.8	92.2	88.0	86.2	53.6	57.4	52.5	77.8	80.4	78.6
Snout—1 D	31.3	34.2	32.6	33.3	32.4	35.0	34.1	36.2	39.8	37.9	35.6	38.6	37.3	34.4	25.6	30.4	24.6	27.3	28.2	33.4
Snout—2 D	61.9	65.3	63.2	65.3	63.9	66.7	64.9	62.4	67.2	64.7	69.5	73.2	70.5	67.8	43.0	46.1	41.3	63.5	64.1	63.8
Snout—upper C	71.3	76.6	72.5	74.2	73.0	77.8	74.0	74.0	76.4	75.5	77.9	80.1	79.3	76.6	48.1	51.1	45.9	73.1	74.2	75.0
Snout—pectoral	20.9	24.2	22.5	22.5	20.7	23.7	22.0	19.8	25.0	22.1	23.5	28.0	26.3	29.8	14.4	15.8	14.6	19.8	19.6	20.5
Snout—pelvic	49.5	54.5	51.8		47.6	52.1	49.5	48.0	54.3	50.8	53.9	57.6	55.8	54.8	36.7	38.0	34.8	45.4	46.4	48.7
Snout—anal	61.8	66.2	63.8		61.8	65.8	64.0	61.4	67.5	64.0	70.2	74.1	71.7	67.6	44.6	48.9	43.7	59.8	61.4	63.6
Interspace 1 & 2 D	19.4	22.7	21.1	22.1	22.5	25.3	23.9	19.0	26.4	20.9	24.6	27.0	25.7	25.9	16.7	9.5	12.8		28.1	23.8
Interspace 2 D & C	5.4	7.9	6.4	6.0	6.6	7.9	7.1	7.1	10.0	7.7	7.7	9.0	8.4	7.8	4.1	4.6	4.5	8.5	8.2	7.2
Interspace A & C	3.9	5.1	4.5	3.8	5.3	7.3	6.5	6.9	10.0	7.4	7.2	9.3	7.8	7.8	3.0	2.7	3.1	7.8	7.8	6.5
Origin Pect.—pelvic	28.1	35.2	30.6		26.2	29.9	28.1	26.1	32.9	29.0	22.8	32.0	29.6	26.6	22.7	23.3	20.8	25.7	27.2	27.8
Origin Pelvic—anal	12.1	14.3	13.0		13.6	17.2	15.3	12.1	15.3	13.5	15.6	17.8	16.9	15.1	8.8	11.0	9.5	14.6	14.3	15.9
Snout—nostrils	2.5	3.4	3.0		3.4	4.7	3.9	3.4	4.9	4.2	4.3	5.4	4.8	5.2	2.8	3.1	2.8		4.1	3.2
Snout—mouth	6.1	7.3	6.8		6.5	8.4	7.1	7.9	10.4	8.6	6.2	7.2	6.6	6.7	4.2	4.5	4.1	4.5	4.1	6.4
Mouth breadth	8.8	10.1	9.3		7.4	8.9	8.4	3.0	7.7	6.4	6.4	7.9	7.1	9.5	3.4	4.2	3.6	7.4	7.2	8.8
Mouth height	4.1	6.1	4.9		4.1	6.0	4.9	3.0	4.9	3.8	5.4	6.9	6.1	5.6	2.3	2.4	2.0	3.4	4.7	5.4
Eye diameter	.9	1.8	1.3		.9	1.9	1.3	1.0	2.0	1.5	1.5	2.1	1.7	2.2	1.4	2.0	1.4	1.2	1.1	1.4
Nostril distance	5.6	6.0	5.8		5.1	5.8	5.3	3.3	3.8	3.5	3.3	4.6	3.7	3.8	1.2	1.5	1.2	20.5	20.7	5.4
Labial furrow length	0	2.2	.8		.4	1.1	.6	0	1.4	.6	0	3.7	2.1	1.6	1.9	.9	.6		.3	.6
Height gill slit 1	2.9	4.8	3.3	3.5	2.6	3.5	3.1	2.0	3.3	2.5	6.5	8.2	7.4	8.0	2.4	2.5	1.9	3.0	3.0	2.8
Height gill slit 2	3.4	4.7	3.8	3.8	2.9	4.0	3.3	2.1	3.7	2.9	6.5	8.2	7.3	7.5	2.6	2.7	2.1	3.2	3.2	3.1
Height gill slit 3	3.3	4.9	4.1	4.1	2.9	4.4	3.5	2.3	3.7	2.9	6.3	8.0	7.2	7.5	2.7	2.9	2.2	3.2	3.4	3.2
Height gill slit 4	2.8	4.6	3.7	3.8	2.6	3.7	3.1	2.0	3.4	2.7	6.4	7.9	7.1	7.4	2.4	2.7	2.1	2.9	3.4	2.8
Height gill slit 5	1.9	3.8	2.7	2.7	1.9	3.0	2.4	1.3	2.7	1.9	6.7	8.1	7.4	6.8	1.7	2.4	1.8	2.0	2.4	2.2
Trunk breadth	12.0	14.6	13.1		11.2	13.1	12.1	9.0	12.1	10.4	10.9	14.4	12.4	16.2	7.1	7.1	7.9	9.0	10.3	12.0
Trunk height	7.8	14.8	12.4	12.1	10.5	12.2	11.4	8.5	12.6	10.6	11.8	15.3	13.7	18.3	10.3	9.2	9.3	11.6	11.4	11.6
Vertical height 1 D	10.0	14.4	12.9		7.5	9.4	8.5	6.2	9.3	7.6	8.6	10.1	9.6	9.8	6.2	7.5	6.6	12.4	12.6	9.0
Base 1 D	10.0	11.3	10.7	9.8	7.6	9.0	8.4	6.5	7.8	7.0	8.2	9.4	8.9	9.4	5.3	6.7	5.2	10.2	9.1	8.6
Vertical height 2 D	2.9	4.2	3.4		1.8	2.5	2.1	2.1	3.1	2.7	.9	2.0	1.4	1.7	.7	.6	.6	2.1	2.3	3.1
Base 2 D	3.0	3.9	3.4	3.0	2.1	2.8	2.4	2.6	3.8	3.5	.8	1.1	1.0	1.4	.6	.8	.6	2.5	2.3	3.6
Vertical height anal	3.3	6.0	4.3		2.3	4.0	3.2	2.5	4.3	3.4	1.0	2.2	1.6	2.0	1.1	1.3	.9	2.9	2.5	3.7
Base anal	3.5	4.7	3.9	4.2	2.8	3.3	3.0	3.1	4.3	3.7	.8	1.4	1.1	1.7	1.0	1.5	.8	3.8	4.0	3.9
Upper margin C	23.4	28.7	27.5	27.9	22.2	27.0	26.0	23.6	26.0	24.5	19.9	22.1	20.7	23.4	51.9	48.9	54.1	26.9	25.8	25.0
Lower margin C	13.5	14.7	14.0	14.1	11.4	13.5	12.6	11.1	14.0	12.2	15.2	17.4	16.2	16.6	7.0		6.6	12.7	12.8	11.6
Pect. ant. edge	21.5	26.1	23.8	18.3?	16.2	20.9	19.3	19.1	23.3	21.3	17.0	25.1	19.6	17.0	17.7	20.1	18.6	14.0	14.1	17.4
Pect. free inner edge	5.1	6.7	5.8	6.6	3.3	4.9	4.4	3.1	4.9	3.9	3.9	5.7	4.5	4.9	1.5	3.0	1.5	2.9	3.1	4.9
Pect. post. edge	19.1	23.4	22.4	17.4?	12.7	18.2	16.7	15.6	20.3	18.6	13.9	22.7	16.8	13.8	17.0	19.7	19.0	11.6	11.7	14.6
Free clasper	2.1	11.2	6.9		2.3	14.2	7.0	2.1	9.6	5.6	2.0	11.2	8.1	4.0				4.6	4.5	

[1] Data from Snyder (1904).

are generally smaller than in their Atlantic counterparts. The gill slit heights of Pacific specimens compare with the Atlantic forms as follows: Pacific great blues, larger; whitetips, smaller; silkies, about the same size.

The other species listed in table 5 either lacked Atlantic counterparts or were represented by an inadequate size range for comparative purposes. The present data for *Alopias pelagicus* are derived from a 354.3-cm. male and 2 females of 166.8 and 349.5 cm., total length. The mean values presented in table 5 agree fairly well with the measurements given by Nakamura (1935) for adult specimens from Taiwan, and where the means do not agree the range in our values (not given here) overlaps Nakamura's figures. Finally, our data for mackerel sharks (*Lamna ditropis*) are based on small specimens (95.8 and 96.1 cm., total length) and do not appear to be comparable to those of the Atlantic mackerel shark (*L. nasus*). For identification purposes it is of interest that our small *ditropis* have a basal lateral denticle on the teeth (as shown by Roedel and Ripley, 1950) but have relatively long snouts. The distance from the snout tip to the anterior edge of the eye is only slightly less than half the distance between the posterior edge of the eye and the first gill slit.

Another identification problem concerns the name to be used for the Pacific whitetip. Our data and those of other authors (Hubbs 1951, Krefft 1954) agree very well with descriptions of the Atlantic whitetip (*Pterolamiops longimanus*) given by Bigelow and Schroeder (1948) and Springer (1950), but there is a possibility that *P. insularum*, which was described from Oahu by Snyder (1904), actually represents the species under discussion. Snyder's measurements of the holotype have been converted to percentage values and listed in table 5 for comparative purposes, but these figures do not solve the problem. The principal differences between *insularum* and other Pacific specimens are in the morphology of the pectoral fin, with this structure being relatively small in *insularum*. This could be caused by either the type being an aberrant specimen, *insularum* being a distinct species, or doubtfully, by much different methods of measurement. It would seem that *longimanus* is the name to be applied to the whitetip reported on here unless future work reveals it to differ from the Atlantic form in some manner not considered at this time.

The length-weight relationships obtaining for the whitetip, silky, bonito, and great blue sharks are shown in figure 20. The data indicate that the whitetip, silky, and bonito sharks have nearly identical weights for any given length, but that the great blue is a lighter fish. In the original plots the data were segregated by sex, and in the

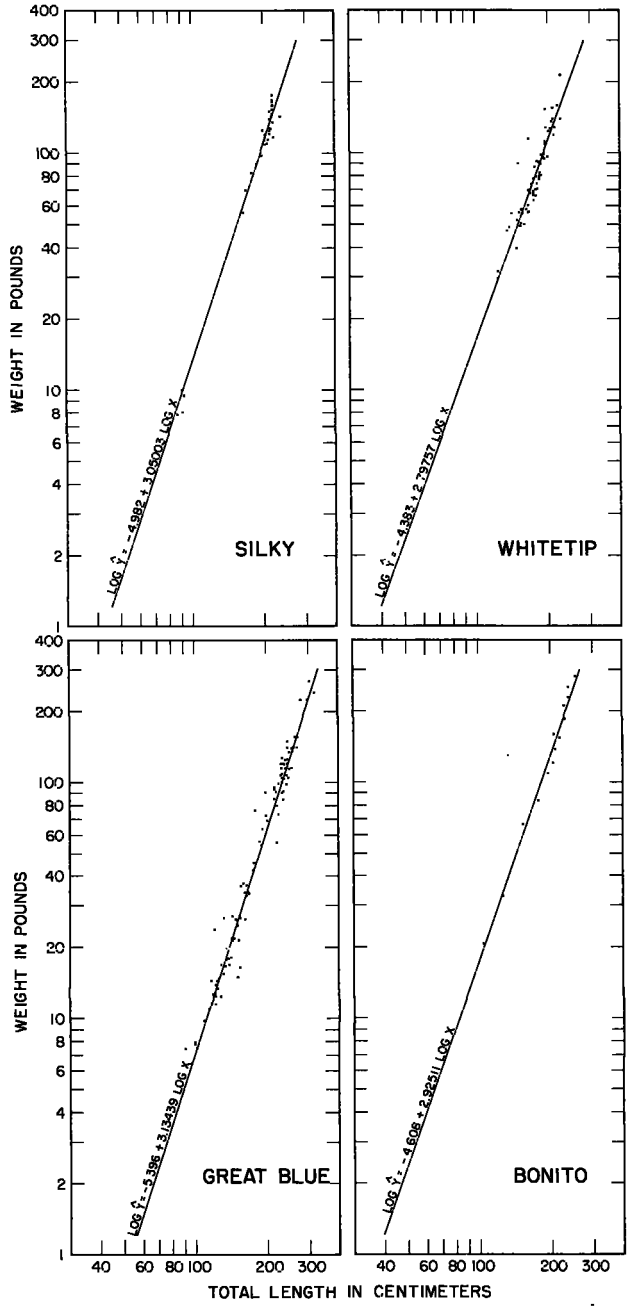

FIGURE 20.—Length-weight relationships for whitetip, silky, bonito, and great blue sharks.

great blue and whitetip sharks females were slightly heavier than males. This is to be expected, for some of the specimens were known to be gravid. The original data were also broken down by locale, but no differences in length-weight of the sharks were noticeable between those from the Line Islands, the Phoenix Islands, various isolated oceanic positions, and the west coast of Central America.

SUMMARY

1. This report is based on the catch records of 34 cruises made in the area between 50° N. and 20° S. latitude and 110° W. and 175° E. longitude during 1952–55. Of 6,118 sharks captured on longline gear, there were 2,512 great blues, 2,176 silkies, 1,187 whitetips, and 243 belonging to 9 relatively uncommon species.

2. The 12 shark species taken show considerable differences in range and abundance. The great blue and the bonito were wide ranging, the former being abundant, the latter uncommon; the whitetip and silky were abundant warm-water forms with the whitetip's range lying roughly between 20° N. and 20° S. latitude and the silky's more narrowly equatorial; the mackerel shark was uncommon and subarctic; the 3 species of thresher sharks were uncommon and equatorial, but may have broader ranges; and the soupfin, hammerhead (2 species), and blacktip were all rare in POFI's catches.

3. The great blue shark appeared to make pronounced northern migrations, probably reproductive in nature, during the warmer parts of the year. Migrations followed the advance and retreat of a transition zone between two major ocean currents. Whitetip and silky sharks were nearly uniformly abundant throughout the year. Their most northerly records were obtained in summer.

4. When the vertical distribution of sharks is analyzed by relative depth of hook-of-capture, the northern great blues are found to be taken principally by shallow hooks and the southern ones by deep hooks. The species apparently favors temperatures between 45° and 69° F. Perhaps also influencing the great blue's vertical distribution in boreal latitudes is the larger amount of food present on the surface. Bonito and thresher sharks were broadly eurythermal, whereas the mackerel appeared to be more nearly stenothermal. The whitetip was surface-dwelling north of the Equator and bathypelagic to the south; the silky shark was uniformly distributed at all hook depths.

5. In the equatorial region the great blue and whitetip sharks were more abundant during warm years than cold, but the silky shark appeared to be the opposite. This difference in abundance may represent a behavioral interaction rather than a temperature-induced phenomenon.

6. In the Equatorial Countercurrent (5° N. to 10° N.) overall shark abundance decreased from east to west between 110° W. and 175° E. longitude, paralleling the situation found for zooplankton volumes. Between 5° N. latitude and the Equator, total shark abundance was minimal at about 140°–150° W. longitude and higher on either side, whereas between the Equator and 10° S. latitude just the reverse occurred. The former situation is similar to that found for inorganic phosphate, the latter similar to that for tuna and zooplankton. The trophic relations obtaining in these situations remain to be demonstrated.

7. The silky and thresher sharks were more abundant near land, whereas the whitetip and great blue were more strictly oceanic, and declined in abundance near islands. There is some evidence for biotic interaction (food competition) between the silky and whitetip sharks in areas intermediate between the neritic and oceanic provinces.

8. All sharks examined were found to subsist principally on small fish and squid, and occasionally to ingest inedible objects. Some species probably capture live tuna on occasion.

9. In northern waters shark damage to hooked tuna averaged only about one percent of the catch, and the abundant shark there, the great blue, is regarded as rather harmless in this respect. In the equatorial area, damage amounted to about 20 percent, and was largely attributed to the silky and whitetip sharks. In this region damage was related to shark abundance only when tuna abundance was low. Shark and tuna abundance themselves were not correlated.

10. Several species of sharks tend to school by sex, and segregation of this type is known as behavioral when caused by size dimorphism between the sexes, or geographical when caused by other factors. The great blue, whitetip, and silky sharks

exhibit sexual segregation to the extent that catches may show a 1 : 1 sex ratio or may consist of solely one sex. For the great blue shark, males comprised an increasingly smaller proportion of the catch to the north, and the mean size of both sexes in mixed catches steadily decreased to the north, with both being about the same length at any latitude. In unisexual catches both sexes were larger than in mixed catches. In individual catches containing both sexes there was a tendency for a few large females to occur with numerous small males or vice versa. On a secular basis it appears that in the winter both sexes occur together in about the same ratio, females begin predominating in the spring, unisexual schools form in the summer and autumn, and reassembly of mixed schools takes place in the winter.

11. Gravid females of the great blue shark measuring from 208 to 247 cm. (total length) were taken throughout the year along with nongravid specimens of the same size range. The largest embryos were found in March and May but no pupping season could be demonstrated. The number of embryos ranged from 4 to about 40, with large pups (34 to 48 cm.) being of the same size as numerous longline-caught specimens. Gravid females of the silky shark, ranging from 213 to 236 cm., were taken throughout the year and were similar in size to nongravid specimens. The number of fetuses per female ranged from 4 to 11.

12. Detailed morphometrics were obtained from 16 whitetip, 12 silky, 22 great blue, 13 bonito, 2 mackerel, 5 thresher, 2 hammerhead, and 2 blacktip sharks. Pacific whitetip, silky, and great blue sharks differed from their Atlantic counterparts in having a greater distance between the snout and all fins except the anal, and also in having smaller anal, second dorsal, and upper caudal fins. Minor differences are shown for other characters, but none of these indicates a lack of conspecificity between the two oceans. The whitetip reported on is termed *Pterolamiops longimanus* on the basis of marked differences between it and the Hawaiian *P. insularum*.

13. Whitetip, silky, and bonito sharks have nearly identical length-weight relationships but the great blue is a lighter, more slender fish. No geographical differences were noted in length-weight.

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DEVELOPMENT AND DISTRIBUTION OF *VINCIGUERRIA LUCETIA* AND RELATED SPECIES IN THE EASTERN PACIFIC

By ELBERT H. AHLSTROM AND ROBERT C. COUNTS

FISHERY BULLETIN 139

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ABSTRACT

Vinciguerria lucetia, family Gonostomatidae, is one of the most abundant pelagic fishes in the eastern North Pacific between the Equator and about 35° N. latitude. It is an important forage fish.

Development is described from the embryonic to the adult stage. The spherical pelagic eggs are moderately small (0.59–0.74 mm.), lack an oil globule, have a segmented yolk and a double shell membrane. The larvae resemble those of the Pacific sardine. The marked metamorphosis has been divided into three stages: prometamorphic, midmetamorphic, and postmetamorphic. Ossification of the vertebral column occurs immediately before metamorphosis. The caudal, dorsal, and anal fins form during the larval period, but procurrent caudal-ray formation is not completed until metamorphosis. Rays do not form in either the pectoral or ventral fins until metamorphosis.

Photophores develop during metamorphosis, at first as white photophores (prometamorphic stage), then as pigmented functional organs. Six or seven pairs of photophores form late, during the midmetamorphic and postmetamorphic stages. Photophore formation is completed and all photophores are pigmented by the end of metamorphosis.

Development is traced from larva to adult for changes in body form, in pigmentation, in sequence of formation of teeth, gill rakers, and other structures.

Distribution of the larvae of *Vinciguerria lucetia* within the area surveyed by cruises of the California Cooperative Oceanic Fisheries Investigations is shown for 2 years, 1951 and 1952. Larvae increase in abundance from southern California to southern Baja California; they are taken throughout the year. The wider distribution in the eastern Pacific, between 14° S. latitude and 35° N. latitude is illustrated, and variation in photophore number with latitude is pointed up. The range in mean number of photophores per side in different localities was from 78.50 to 83.40.

Two other species of *Vinciguerria* occur in the eastern Pacific: *V. nimbaria* and *V. poweriae*. Both occur on the fringes of the area routinely surveyed on CCOFI cruises. Characters used to separate the three species at different stages of development are given.

DEVELOPNENT AND DISTRIBUTION OF *VINCIGUERRIA LUCETIA* AND RELATED SPECIES IN THE EASTERN PACIFIC

By ELBERT H. AHLSTROM and ROBERT C. COUNTS, *Fishery Research Biologists*
BUREAU OF COMMERCIAL FISHERIES

In the extensive area being surveyed routinely in the eastern North Pacific Ocean by the California Cooperative Oceanic Fisheries Investigations (CCOFI), the larvae of three species of fishes commonly occur that might be confused with larvae of *Sardinops caerulea*, the Pacific sardine; these are the larvae of *Vinciguerria lucetia*, *Engraulis mordax*, and *Leuroglossus stilbius*. All three are at least as abundant as sardine larvae, and they often occur together in collections. The larvae of the four species undoubtedly compete for food. In order to be able to recognize the larvae of these four species at all stages of development, even in samples where larvae are poorly preserved, we have made a detailed study of the development of each species. This paper is concerned largely with the development and distribution of *Vinciguerria lucetia*.

Vinciguerria lucetia, family Gonostomatidae, is one of the most abundant pelagic fishes in the eastern North Pacific Ocean; however, it is unlikely that it will ever become a commercially important species. It attains too small a size (2 to 2½ inches) to be esteemed for human food in America. Because of its great abundance, however, it is an important forage fish. This is not entirely speculation; we have examined several stomachs of albacore and skipjack off Baja California and Mexico that were filled with this species alone. Several records of *Vinciguerria*, including the material used by Hildebrand (1946) in describing *V. pacifici* (which we consider to be a synonym of *V. lucetia*), and our record from off the Columbia-Ecuador border, were obtained from stomach contents of tuna.

V. lucetia has a very extensive distribution. We have examined material from the eastern Pacific from 35° N. latitude to about 14° S. latitude. It has been reported from many other regions.

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Although *V. lucetia* is the only species of this genus occurring commonly in the area routinely surveyed on cruises of CCOFI, two other species occur on the fringes of the area: *V. nimbaria* and *V. poweriae*. The latter species has not been reported previously for the eastern Pacific. Characters used to separate the species and records of their occurrence are given in a later section.

We are not attempting a critical review of the species of *Vinciguerria*, as we have seen no material from regions other than the eastern Pacific. This paper will deal principally with *V. lucetia*, but for completeness some attention will be given to the two other species, *V. nimbaria* and *V. poweriae*.

The larvae of *V. lucetia* may not have been described previously. Regan (1916: pl. 5, figs. 6, 7) figured a larva and a metamorphosing individual that he called *Vinciguerria lucetia*. Since these figures show no distinguishing characters, it is impossible to identify the species represented. The larvae of *V. attenuata* and *V. poweriae* were described by Sanzo (1913, 1931). Jespersen and Tåning (1919, 1926) described larvae of *V. nimbaria* (*sanzoi*) and gave excellent descriptions of *V. attenuata* and *V. poweriae* as well. The differences between the larvae of the four species are discussed later in this paper (p. 399).

Most of the material used in this study was collected on cruises of the California Cooperative Oceanic Fisheries Investigations, a program sponsored by the Marine Research Committee of the State of California 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 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.

Dr. Carl L. Hubbs generously placed at our disposal the extensive collections made on expeditions by vessels of the Scripps Institution of Oceanography, and offered useful suggestions throughout the progress of the work. The illustrations of eggs, larvae, and other stages of *Vinciguerria* were prepared by George Mattson, and the charts and graphs by Andrew M. Vrooman and James R. Thrailkill. Several hundred persons have aided in the collection of material at sea.

Vinciguerria lucetia (Garman)

Maurolicus lucetius Garman, 1899. Mem. Mus. Compar. Zool. (Harvard), vol. 24, p. 242, pl. J, fig. 2 (original description).

Vinciguerria lucetia Brauer, 1906. Deutsche Tiefsee-Exped., vol. 15 (1), pp. 97–98, fig. 40 (material with symphyseal photophores referred to *V. lucetia;* probably mixture of *lucetia* and *nimbaria*). Jespersen and Tåning, 1926. Rept. Danish Ocean. Exped. 1908–1910, vol. 2 (Biology), A 12, pp. 26–29 (comparisons of adult characters of *V. lucetia* with 3 other species). Parr, 1931. Bull. Bingham Ocean. Coll., vol. II, No. 4, p. 11 (a number of records from eastern Pacific between 24°30′ N. and 11°05′ N.). Horsburgh, 1935. Proceed. California Acad. Sci. (4th series), vol. 21, pp. 227–229 (fairly detailed description of *lucetia* based on study of 30 specimens).

All of these references, with the exception of Jespersen and Tåning and Parr contain errors, but all pertain wholly or partly to *Vinciguerria lucetia*. Several errors or omissions occur in the original description of *lucetia*. Branchiostegals are invariably 12, not 9 as reported by Garman (1899); the upper opercular photophore is not mentioned. The symphyseal pair of photophores is not referred to by Garman in the text, but is shown in the figure. The isthmian group is given as 8 per side, hence we assume that the symphyseal pair is included in this count. Brauer (1906) referred 37 specimens from the Atlantic and Indian Oceans to *V. lucetia*. He was dealing with metamorphosing material (12 mm.-17.6 mm. long) in which the lateral series of photophores between ventral and anal fins was incomplete. His material probably was a mixture of *lucetia* and *nimbaria*. The record of Zugmayer (1911: 56, pl. II, fig. 4) is inaccurate; his description and figure apparently refer to *V. attenuata*. Unfortunately, this figure was copied as an illustration of *V. lucetia* by Weber and de Beaufort (1913: 119–120, fig. 44). The record of Gilbert (1908: 237) for the Marquesas Islands (Albatross station 3798) was checked by Horsburgh (1935: 229). A comparison of numerable characters of *V. lucetia* as given by various workers is summarized in table 1. Horsburgh (1935) gave modal and range values of morphometric characters for 22 adults and 8 juveniles. He did not include measurements of individual specimens, so we have not been able to compare his morphometric data with ours. We do not substantiate his observation that no great importance can be attached to the presence or absence of symphyseal photophores. We have never found this pair absent in adults, and consider its presence or absence to be diagnostic in separating *lucetia* and *nimbaria* from *attenuata* and *poweriae*.

TABLE 1.—*Numerable characters of* Vinciguerria lucetia *as reported by various workers*

Character	Garman (1899)	Brauer (1906)	Jespersen and Tåning (1926)	Horsburgh (1935)	Our material
Fins:					
Dorsal	14	13–14	13–14	14–15	13–16
Anal	15	14–15	14–16	14–16	13–17
Pectoral	9	8–9	9–10	10	10
Ventral	7	7	7	7	7
Caudal:					
Principal	-------	-------	19	-------	19
Secondary	-------	-------	7–9+4–5	-------	7–10+4–5
Gill rakers	-------	-------	9–10+19–20	27–35	8–10+18–23
Branchiostegals	9	11	----------	-------	12
Photophores:[1]					
Head:					
Orbital	2	2	2	2	2
Opercular	2	3	3	3	3
Symphyseal	1	1	1	1	1
Branchiostegal	8	8	8	8	8
Isthmian	7	7	7	7	7
Ventral:					
IV	14	14–16	14–15	14–16	13–16
VA	10	8–10	9–10	9–10	8–12
Lateral:					
OV	11	11–13	11–12	11–12	10–13
VA	11	5–9	10–11	10–11	9–12
Anal-caudal	14	12–13	13–14	12–16	12–16

[1] Photophore groups are discussed later in this paper (see p. 386). Different workers have used different methods of grouping photophores; we have put the counts of the several workers on a comparable basis.

DEVELOPMENT OF *VINCIGUERRIA LUCETIA*

EGGS

The egg of *Vinciguerria lucetia* is moderately small, spherical, lacks an oil globule, and has a segmented yolk. It is colorless in life and light straw colored in formalin. The shell membrane is double. The thin, inner membrane lies close to the thicker, outer membrane and is irregular in outline; neither membrane is sculptured.

Segmentation of the yolk is quite variable, and this is especially noticeable in early-stage eggs. The yolk in some eggs is nearly homogeneous; in

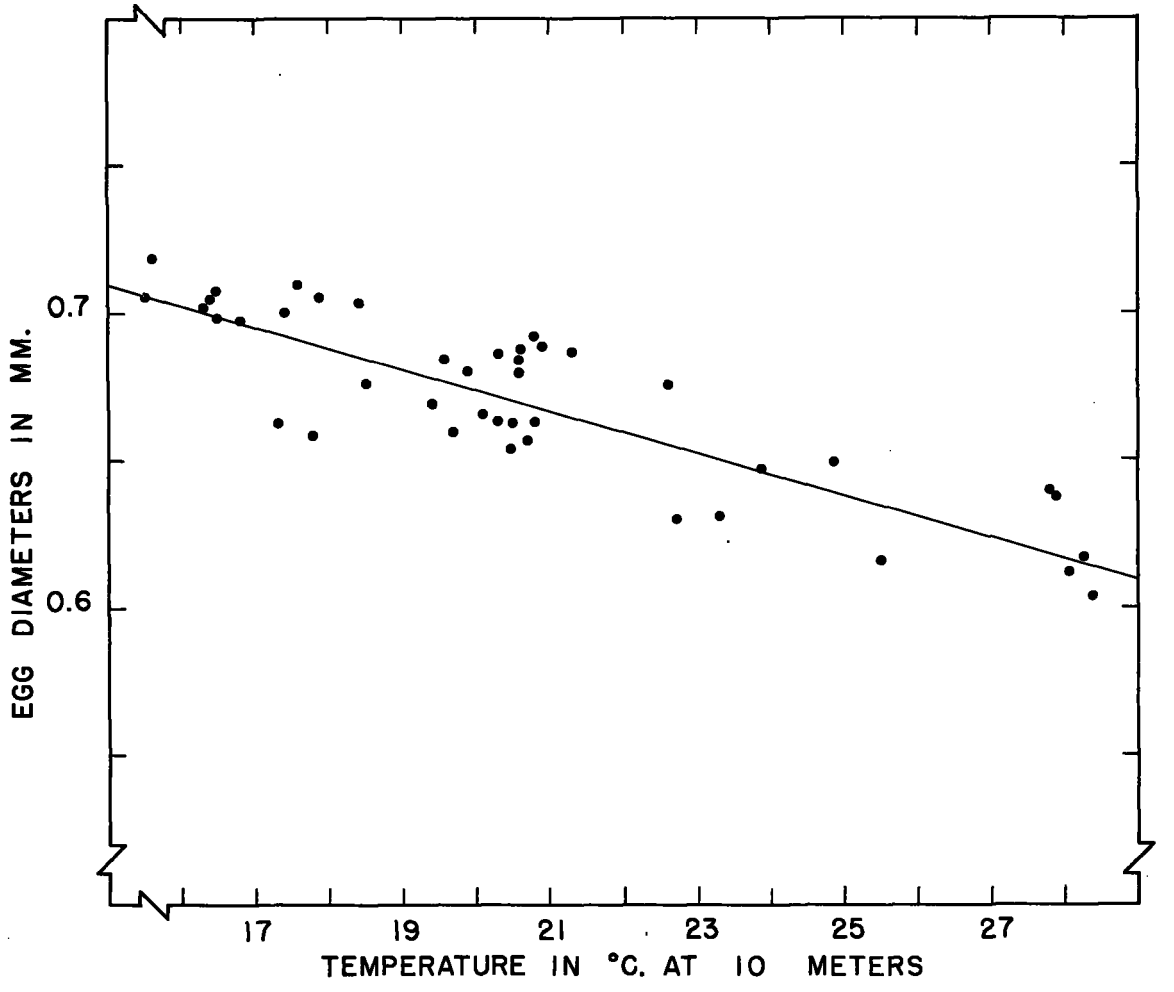

FIGURE 1.—Regression of egg size on temperature in degrees Centigrade, at 10 meters. The line is fitted by the method of least squares. The statistics for the line are as follows: $\bar{x}=20.68$; $\bar{y}=0.67$; $b=-0.0071$; $a=0.816$; $s_{y\cdot x}=0.0155$.

others, partly segmented; in still others, completely segmented. The individual segments are globular, usually variable in size, and relatively few. Occasionally, eggs contain numerous small globules of yolk. The perivitelline space is rather narrow.

Eggs were measured from 42 localities between 32° N. latitude and 10° S. latitude (table 2). The range in diameters of eggs, measured at the outer shell membrane, was from 0.58 to 0.74 millimeters. The range in mean diameters of eggs in different localities was from 0.603 to 0.718 millimeters. There is a cline in egg size with latitude. The relation is probably one of temperature. A plot of egg size against temperature (° C.) is shown in figure 1. The 10-meter temperature is considered representative of the temperature in the upper mixed layer. The larger eggs are taken at the lower temperatures.

The egg of this species has not been described previously, but the eggs of two Mediterranean species, *V. attenuata* and *V. poweriae*, were described by Sanzo (1931). The eggs of these species differ from those of *V. lucetia* in at least two important respects: they have an oil globule and are larger.

The development of *Vinciguerria lucetia* eggs may be divided into the following stages:

1. Early, from fertilization to closure of the blastopore (fig. 2, *a* and *b*);

2. Middle, from closure of the blastopore to the time that the tail begins to curve laterally away from the embryonic axis (fig. 2, *c*); and

3. Late, from the time that the tail curves out of

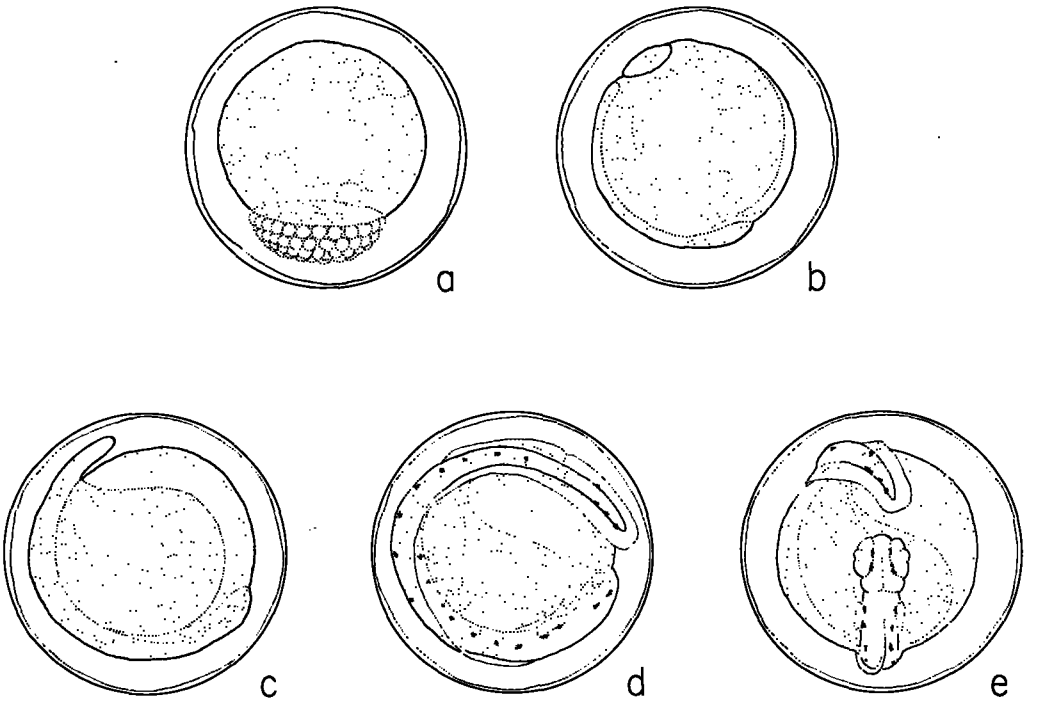

FIGURE 2.—Development of the egg of *Vinciguerria lucetia*: *a*, early stage, at development of blastodermal cap; *b*, early stage, immediately preceding blastopore closure; *c*, middle stage, with separating tail in same plane as embryo; *d*, late stage, just before hatching, lateral view; *e*, late stage, dorsal view.

plane of the embryonic axis to the time of hatching (fig. 2, *d* and *e*).

Early-stage eggs

The vitelline membrane must be quite delicate, for it had been broken in most early-stage eggs studied. The yolk granules remain intact and, as a consequence, the eggs do not become cloudy or opaque as happens when this membrane is ruptured in eggs of hake (Ahlstrom and Counts, 1955: 296) and jack mackerel (Ahlstrom and Ball, 1954: 210). The characters that aid in distinguishing early-stage eggs are (1) size, 0.58–0.74 millimeters, smaller than most pelagic fish eggs; (2) double-shell membrane, although the inner membrane may easily be overlooked; (3) lack of an oil globule; and (4) irregularly segmented yolk.

The embryo at blastopore closure is faintly outlined, but the eye has not yet developed, pigment is not present, and myomeres have not formed.

Middle-stage eggs

The conspicuous changes in development that occur during this stage include (1) eye formation; (2) division of body into myomeres; and (3) appearance of body pigmentation at about the midpoint of the stage. The pigment on middle-stage eggs is relatively simple—a row of dorsal spots on either side of the body; there is no ventral pigment and no pigment on the yolk membrane. The most striking feature about the rows of pigment spots is their dorsolateral placement. The embryos of many fishes, including the sardine, jack mackerel, and Pacific mackerel, have a row of dorsal pigment spots on either side of the notochord, but it is rather unusual for the row to be placed as far laterally as in *Vinciguerria lucetia* embryos. This character is a definite aid in identifying eggs of this species.

Late-stage eggs

It is always easier to identify eggs in the late stage than in the two earlier stages. The embryo is now more fully developed, and such features as total number of myomeres and length of intestine can be used in identification. At least 40 myomeres can be distinguished on late-stage eggs. The intestine extends approximately 0.7 of the body length. The yolk is pulled back into a wedge along the intestine—a feature observed commonly in late-stage eggs of stomiatid fishes, as well.

TABLE 2.—*Diameters of eggs of* Vinciguerria lucetia *from 42 localities in the eastern Pacific*

Station	Latitude	Longitude	Date	Number of eggs measured	Egg diameter (mm.)		Temperature (° C.) at 10 meters
					Mean	Range	
5205-93.70	31°27.9′ N	120°17.8′ W	V-15-52	6	0.706	0.70-0.72	15.5
5205-90.90	31°25′ N	121°59′ W	V-10-52	19	.718	.68-.74	15.6
5408-100.60	30°40.5′ N	118°47′ W	VIII-31-54	50	.703	.66-.74	18.4
5205-97.80	30°36.9′ N	120°29′ W	V-15-52	50	.702	.68-.74	16.3
5308-100.80	30°01′ N	120°07′ W	VIII-17-53	50	.700	.66-.74	17.4
Norpac 96	29°41′ N	120°43.5′ W	IX-16-55	17	.675	.65-.71	18.5
5205-103.80	29°26′ N	119°42′ W	V-22-52	50	.707	.68-.74	16.5
5206-107.65	29°23.5′ N	118°25′ W	VI-20-52	50	.698	.66-.74	16.5
5206-110.55	29°05.2′ N	117°18′ W	VI-19-52	50	.705	.66-.74	16.4
5408-113.40	29°02′ N	115°58.5′ W	VIII-28-54	7	.685	.66-.70	20.3
Norpac 110	28°56′ N	117°38′ W	IX-20-55	29	.679	.65-.70	20.6
5205-107.80	28°52.5′ N	119°20.5′ W	V-25-52	18	.697	.65-.74	16.8
5206-110.80	28°15′ N	118°58′ W	VI-19-52	50	.709	.66-.74	17.6
5206-113.70	28°02′ N	117°55′ W	VI-17-52	50	.705	.66-.74	17.9
Norpac 111	27°56′ N	119°35′ W	IX-18-55	25	.683	.66-.71	19.6
5308-120.50	27°32.5′ N	115°52.5′ W	VIII-12-53	50	.659	.61-.68	19.7
5206-117.70	27°24′ N	117°38′ W	VI-17-52	50	.662	.61-.70	17.3
Norpac 118	27°13.5′ N	116°30.5′ W	VIII-11-55	9	.668	.64-.69	19.4
5401-127.40	26°44.5′ N	114°25′ W	I-16-54	50	.657	.63-.68	17.8
5308-120.80	26°31′ N	117°45′ W	VIII-13-53	50	.665	.63-.70	20.1
5308-130.45	25°59′ N	114°27′ W	VIII-10-53	50	.663	.63-.70	20.8
Norpac 120	25°52.5′ N	119°06′ W	VIII-12-55	17	.691	.66-.73	20.8
5308-130.50	25°49′ N	114°44.5′ W	VIII-10-53	50	.662	.63-.68	20.5
5308-130.60	25°29.5′ N	115°21′ W	VIII-10-53	50	.656	.61-.68	20.7
Norpac 134	25°09′ N	116°02′ W	VIII-11-55	50	.686	.65-.72	21.3
Norpac 121	25°02′ N	120°45′ W	VIII-12-55	50	.683	.64-.73	20.6
5401-140.40	24°27′ N	112°59′ W	I-3-54	50	.663	.63-.68	20.3
5401-150.40	22°43′ N	111°58′ W	I-11-54	50	.653	.63-.68	20.5
Shellback 8	22°37′ N	123°25′ W	V-21-52	50	.679	.65-.70	19.9
Norpac 139	21°53′ N	127°38′ W	VIII-16-55	14	.687	.67-.70	20.6
Shellback 9	21°43′ N	123°58′ W	V-22-52	50	.688	.65-.71	20.9
Norpac 162	20°22′ N	116°19.5′ W	IX-13-55	150	.648	.61-.68	24.9
Norpac 148	19°59.5′ N	124°06′ W	IX-10-55	25	.675	.61-.70	22.6
Shellback 67	15°46′ N	100°35′ W	VI-14-52	12	.611	.59-.62	28.1
Shellback 65	14°00′ N	101°34′ W	VI-13-52	6	.616	.60-.65	28.3
Shellback 64	13°11′ N	102°07′ W	VI-13-52	7	.603	.58-.63	28.4
Shellback 77	6°50′ N	98°07′ W	VI-21-52	4	.638	.60-.68	27.9
Shellback 53	3°57′ N	108°08′ W	VI-9-52	50	.639	.60-.66	27.8
Shellback 47	1°00′ S	111°24′ W	VI-6-52	6	.629	.60-.65	22.7
Shellback 35	2°19′ S	116°50′ W	VI-2-52	3	.615	.60-.64	25.5
Shellback 87	3°03.5′ S	96°18.5′ W	VI-25-52	11	.623	.60-.66	23.3
Shellback 95	9°30′ S	94°08.5′ W	VI-29-52	28	.646	.61-.67	23.9

Dashes of pigment in two lines extend from the forward part of the head between the eyes to the back of the head, and continue behind the head as two rows of dorsolateral pigment spots. Pigment extends to the tip of the notochord, and there are some discrete spots on the ventral margin posterior to the anus. In the caudal area, some pigment may extend into the fin-fold in 2 or 3 streaks.

By the time the embryo is ready to hatch, the tail encircles the head. The fin-fold is wide in the free part of the tail, but narrows anteriorly and ends at the back of the head.

POSTEMBRYONIC STAGES

Postembryonic development has been divided into six stages, which can be characterized as (1) larval, from hatching to photophore formation; (2) prometamorphic, the white photophore stage; (3) midmetamorphic, the stage of rapid change in body proportions, including a marked increase in depth and a change in eye shape from oval to round; (4) postmetamorphic, from the time that the eye becomes round until photophore formation and pigmentation are completed; (5) juvenile, between metamorphosis and sexual maturity; and (6) adult, sexually mature individuals.

The terminology for the stages of metamorphosis is not intended to be general, but clearly separates the stages in the metamorphosis of *Vinciguerria*.

The various stages of development of *Vinciguerria lucetia* were available from newly hatched larvae through mature adults. We have studied a series of specimens of each of the six stages. Development is discussed in the following sequence:

1. Changes in body form from larva to adult;
2. Changes in pigmentation during development;
3. Sequence of calcification, including vertebrae, gill rakers, teeth, branchiostegals, fin formation, supporting structures of fins; scales; and
4. Photophore development.

Changes in body form from larva to adult

In addition to standard length, measurements were made of six body parts: length of head,

depth at pectoral, width of eye, distance from snout to anus, distance from snout to origin of dorsal fin, and distance from snout to insertion of ventral fins.

The number and size range of specimens used in studying body proportion in the various stages of development were as follows:

Stage	Number of specimens measured	Size range (mm.)	Illustrations
Larval	100	2.2–18.2	Figure 3, *a* to *d*.
Prometamorphic	22	13.2–19.2	Figure 8.
Midmetamorphic	49	13.5–19.2	
Postmetamorphic	46	13.2–20.2	Figure 9.
Juvenile and adult	51	19.2–56.0	Figures 12 and 13.

We had the opportunity to study changes in body form during all stages of development, and we found it desirable to treat each stage separately. At least as regards this species, we cannot agree to the statement of Parr (1956: 392) that "One of the primary purposes and needs of taxonomy is to develop expressions that describe a species or other systematic unit as a whole." This is neither possible nor desirable in a species such as *V. lucetia*, that has a marked metamorphosis for, as will be shown, marked changes occur in body proportions during metamorphosis at a time when there is little or no change in standard length; when, in fact, an actual shrinkage has been postulated (Sanzo 1913, 1931). Any function that could express in one equation growth during the larval period, metamorphosis, and later development of *V. lucetia* would be so complex that it would have little meaning.

We have plotted the actual measurements of a body part on standard length for each stage of development. Nearly all of the plots of measurements can be adequately fitted by a straight line using the method of least squares ($y=a+bx$), without further transforming the values. Such regressions have the advantages of simplicity in determining the statistics describing the regressions, and in having an easily comprehended biological interpretation. The slope of the regression (b) gives the rate of growth of the body part with respect to length during the stage of development that is being considered. A number of these regressions are presented in figures, and the statistics describing the series of regressions are given in table 3. All measurements are of preserved material. One of the sources of variation in our measurements results from differences in "relaxation" of specimens at time of preservation. Another source is the preservative used, as specimens in alcohol preserve somewhat differently from those in formaldehyde.

TABLE 3.—*Statistics describing regressions of body measurements on standard length for* Vinciguerria lucetia

Body proportion	Standard length	$\bar{x}$	$\bar{y}$	n	b	a	$sy{\cdot}x$
	Mm.						
Head length:							
Larval	2.2–18.2	8.15	1.73	100	0.214	0.012	0.1219
Prometamorphic	13.2–19.2	16.82	3.52	22	.173	.605	.1604
Midmetamorphic	13.5–19.2	16.58	3.69	50	.159	1.043	.1425
Postmetamorphic	13.2–20.2	16.47	4.33	45	.261	.029	.1395
Juvenile and adult	19.2–56.0	31.91	8.53	51	.263	.140	.3193
Body at depth pectoral:							
Larval	2.2–18.2	8.22	.67	97	.098	−.137	.0727
Prometamorphic	13.2–19.2	16.82	1.67	22	.082	.292	.1736
Midmetamorphic	13.5–19.2	16.58	2.00	50	.097	.397	.1768
Postmetamorphic	13.2–20.2	16.50	2.61	46	.180	−.360	.1724
Juvenile and adult	19.2–56.0	31.91	5.81	51	.174	.240	.3189
Eye width:							
Larval	2.2–18.2	8.50	.34	91	.039	.007	.0340
Prometamorphic	13.2–19.2	16.82	.70	22	.041	.001	.0566
Midmetamorphic	13.5–19.2	16.58	.76	50	.042	.068	.0871
Postmetamorphic	13.2–20.2	16.95	1.27	51	.116	−.687	.1317
Juvenile and adult	19.2–56.0						
Snout to ventral:							
Larval	2.2–18.2	13.78	6.97	11	.469	.506	.1352
Prometamorphic	13.2–19.2	16.82	8.37	22	.469	.475	.2718
Midmetamorphic	13.5–19.2	16.58	7.91	50	.495	−.297	.1726
Postmetamorphic	13.2–20.2	16.50	7.75	46	.445	.396	.1279
Juvenile and adult	19.2–56.0	31.91	15.50	51	.521	−1.132	.3725
Snout to dorsal:							
Larval	2.2–18.2	11.08	7.01	57	.565	.739	.1887
Prometamorphic	13.2–19.2	16.82	10.30	22	.586	.436	.2095
Midmetamorphic	13.5–19.2	16.58	9.76	50	.588	.007	.2240
Postmetamorphic	13.2–20.2	16.50	9.25	46	.504	.938	.1149
Juvenile and adult	19.2–56.0	31.91	17.98	51	.592	.912	.4307
Snout to anus:							
Larval	2.2–18.2	8.15	6.00	100	.734	.020	.2044
Prometamorphic	13.2–19.2	16.82	11.98	22	.665	.804	.2307
Midmetamorphic	13.5–19.2	16.56	11.12	48	.697	−.424	.2071
Postmetamorphic	13.2–20.2	16.50	10.58	46	.607	.564	.1255
Juvenile and adult	19.2–56.0	31.91	20.97	51	.710	−1.668	.5464

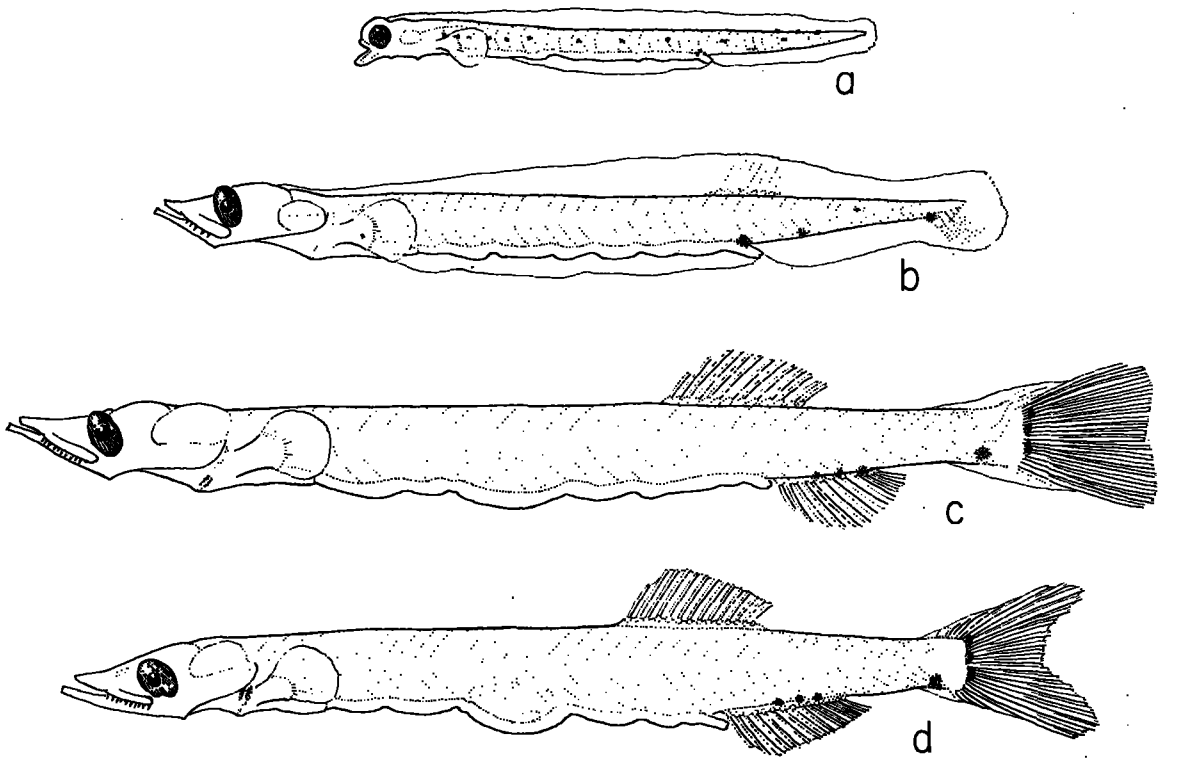

FIGURE 3.—Development of the larva of *Vinciguerria lucetia:* *a*, larva, 2.2 mm. long; *b*, larva, 6.0 mm. long; *c*, larva, 9.0 mm. long; *d*, larva, 13.1 mm. long.

From our study of larval growth in a number of species, we found that a simple size-on-size regression is preferable to a ratio-on-size regression. The regression line will seldom pass through the origin, and for a very simple reason. A body part must have some size at its differentiation. When the head differentiates on an embryo, for example, the embryo is already a millimeter or so in length. It often happens that the head at formation will constitute a different proportion of the standard length than it does subsequently. Whenever this happens, a rectilinear regression of size-on-size will have a y-intercept different from 0. But this line has more validity than one that would pass through the origin, for it will pass through the point representing the size of the part at its initial formation. For this reason, we believe that Parr (op. cit.: 378) is mistaken when he states that a regression curve must pass through the origin.

Larvae.—The larvae (table 4, fig. 3) are thin and threadlike at hatching. The head is moderate in length and width; head length about 20 percent of the standard length; head width slightly greater than body width. The regression of head length on standard length is somewhat curvilinear (fig. 4). For simplicity we have fitted a straight line to the regression by the method of least squares. The regression of head length on standard length for *V. nimbaria* and *V. poweriae* does not appear to be curvilinear. Original measurements of larvae and other stages of development of *V. lucetia* are given in an appendix. The rate of increase in head length during the larval period as thus determined is 0.215 millimeters per 1.0-millimeter increase in standard length.

In very young larvae, the depth (at pectorals) is only about 7 percent of the standard length. The increase in depth during the larval period is at a faster rate than this, being slightly less than 0.1-millimeter for each 1.0-millimeter increase in length (fig. 5).

The eyes are approximately spherical in newly hatched larvae and pigment forms almost immediately. In larvae about 3 millimeters long the eye has become oblong and slightly stalked. In measuring the oblong eye, the width was taken directly across the narrower dimension. The eyes increase

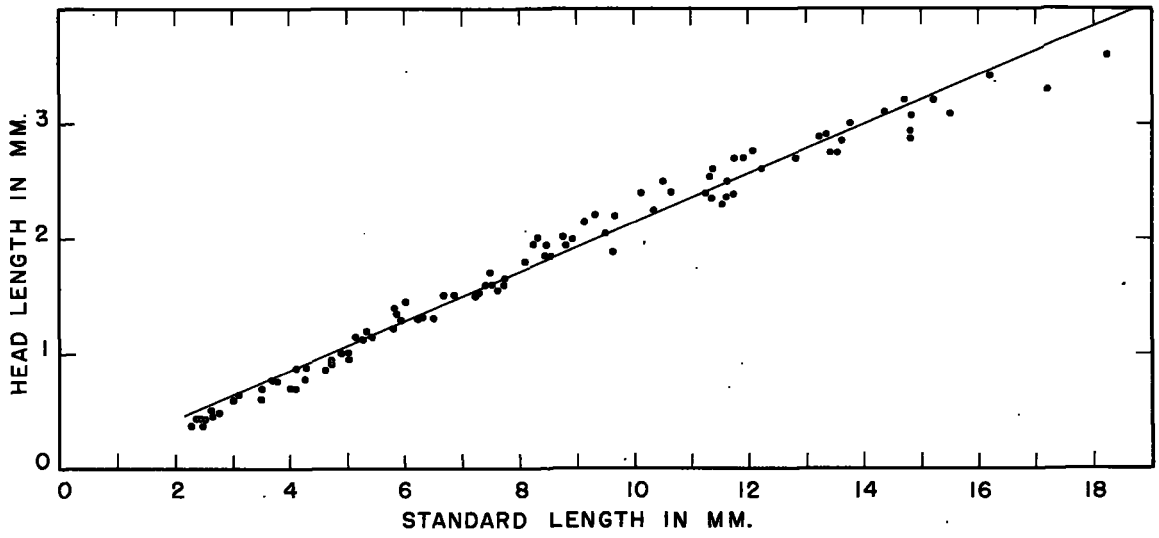

FIGURE 4.—Regression of head length on standard length for *Vinciguerria lucetia* larvae. The measurements were made on 100 specimens, shown in the figure as individual dots. The regression line is fitted to the data by the method of least squares. (Refer to table 3 for statistics describing the line).

in width approximately 0.04 millimeter for each 1.0-millimeter increase in standard length (fig. 6).

The digestive tract underlies much of the body (the distance from snout to anus is over 70 percent of the standard length). The regression of the distance of snout to anus on standard length appears to be slightly curvilinear; however, it is so nearly straight that for practical purposes it can be considered to be a straight line. The regression of the distance from snout to anus on standard

TABLE 4.—*Average counts and measurements of larvae of* Vinciguerria lucetia

[D—dorsal; V—ventral; LP—larval pectoral]

Standard length	Number of specimens	Average body measurements (mm.)							Meristic counts							
		Standard length	Head length	Eye width	Depth at pectoral	Snout to anus	Snout to dorsal	Snout to ventral	Vertebrae	Dorsal fin	Anal fin	Pectoral fins	Ventral fins	Caudal fin		
														Principal	Secondary	
															D	V
2.0–2.4 mm	6	2.4	0.4	0.12	0.17	1.6						LP				
2.5–2.9 mm	4	2.6	.5	.12	.17	1.7						LP				
3.0–3.4 mm	3	3.0	.6	.14	.19	2.1						LP				
3.5–3.9 mm	5	3.6	.7	.15	.22	2.6						LP				
4.0–4.4 mm	5	4.1	.8	.16	.26	3.0						LP				
4.5–4.9 mm	5	4.8	.9	.18	.36	3.5						LP				
5.0–5.4 mm	6	5.2	1.1	.21	.35	3.9						LP				
5.5–5.9 mm	4	5.8	1.3	.22	.40	4.4						LP		5		
6.0–6.4 mm	3	6.2	1.4	.25	.47	4.8						LP		14		
6.5–6.9 mm	3	6.7	1.4	.27	.47	5.0	4.5			4		LP		19		
7.0–7.4 mm	4	7.4	1.6	.28	.52	5.6	5.0		(*)	5		LP		19		
7.5–7.9 mm	4	7.6	1.6	.30	.55	5.7	5.0		(*)	6		LP		19		
8.0–8.4 mm	5	8.3	1.9	.33	.67	6.4	5.5		(*)	11	5	LP		19	1	1
8.5–8.9 mm	4	8.7	2.0	.33	.69	6.4	5.6		(*)	11	7	LP		19	1	1
9.0–9.4 mm	2	9.2	2.2	.38	.78	6.9	6.0		(*)	10	9	LP		19	1	1
9.5–9.9 mm	3	9.6	2.0	.37	.79	7.2	6.2		(*)	12	11	LP		19	1	1
10.0–10.9 mm	4	10.4	2.4	.40	.99	7.8	6.6	5.5	(*)	13	12	LP	Bud	19	2	2
11.0–11.9 mm	11	11.5	2.5	.48	.94	8.9	7.2		(*)	13	12	LP	Bud	19	2	2
12.0–12.9 mm	3	12.4	2.7	.49	1.02	9.1	7.7	6.2	(*)	14	12	LP	Bud	19	2	2
13.0–13.9 mm	6	13.5	2.9	.55	1.21	9.8	8.3	6.9	32	15	15	LP	Bud	19	4	3
14.0–14.9 mm	5	14.7	3.0	.61	1.38	10.7	9.1	7.4	36	15	16	LP	Bud	19	5	4
15.0–15.9 mm	2	15.4	3.2	.58	1.40	11.2	9.2	7.7	38	15	15	LP	Bud	19	6	4
16.0–16.9 mm	1	16.2	3.4	.66	1.60	11.6	10.2		41	14	15	LP	Bud	19	4	4
17.0–17.9 mm	1	17.2	3.3	.60	1.60	12.5	10.4		41	15	15	LP	Bud	19	5	4
18.0–18.2 mm	1	18.2	3.6	.65	1.60	13.1	11.2	9.0	42	16	16	LP	Bud	19	6	4

*Uroneurals associated with urostyle and hypurals are present.

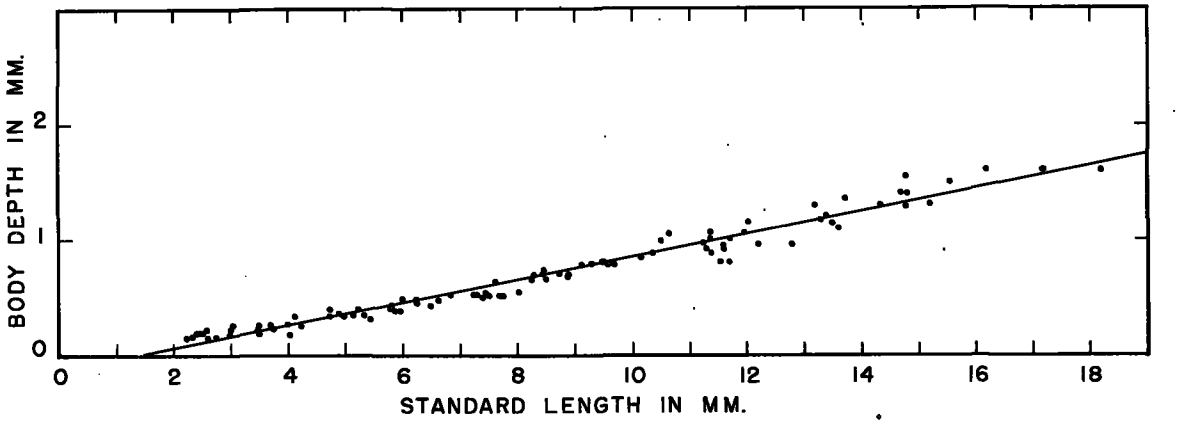

FIGURE 5.—Regression of body depth on standard length for *Vinciguerria lucetia* larvae, fitted by method of least squares (refer to table 3 for statistics describing the line).

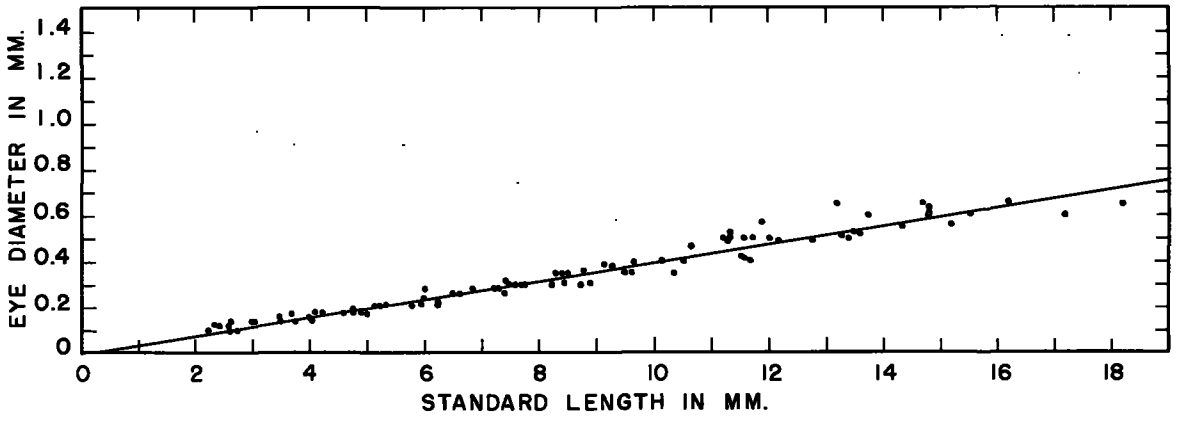

FIGURE 6.—Regression of eye diameter on standard length for *Vinciguerria lucetia* larvae, fitted by method of least squares (refer to table 3 for statistics describing the line).

length when fitted by the method of least squares gives a rate of increase of 0.73 millimeter for each 1.0-millimeter increase in length (fig. 7).

The measurements involving fins, such as the distance from snout to origin of dorsal or snout to insertion of ventrals, are available only for larger larvae. The dorsal fin forms soon after the caudal, and measurements of distance from snout to dorsal are available for most larvae longer than 6.5 millimeters. The ventral fins form at the very end of the larval period; the preventral measurement was available for only 11 larvae out of 100 studied. The snout-dorsal distance increases approximately 0.58 millimeter for each 1.0-millimeter increase in length during the larval period. The snout-ventral distance increases approximately 0.47 millimeter for each 1.0-millimeter increase in length.

Metamorphosing individuals.—Metamorphosis may be characterized as the period during which marked changes occur in body proportions and body structures without any marked increase in standard length. The length may not increase at all, or it may even diminish.

The degree of ossification that takes place during the larval period will have a marked bearing on changes in standard length that can occur during metamorphosis. If the vertebral column, for example, is completely formed before metamorphosis, the standard length cannot decrease to any appreciable extent. In *Vinciguerria*, the vertebral column ossifies immediately prior to metamorphosis. The individual centra are separated from each other by a narrow unossified space. Some compression does occur at these points, but it does not seem reasonable to us that as much shrink-

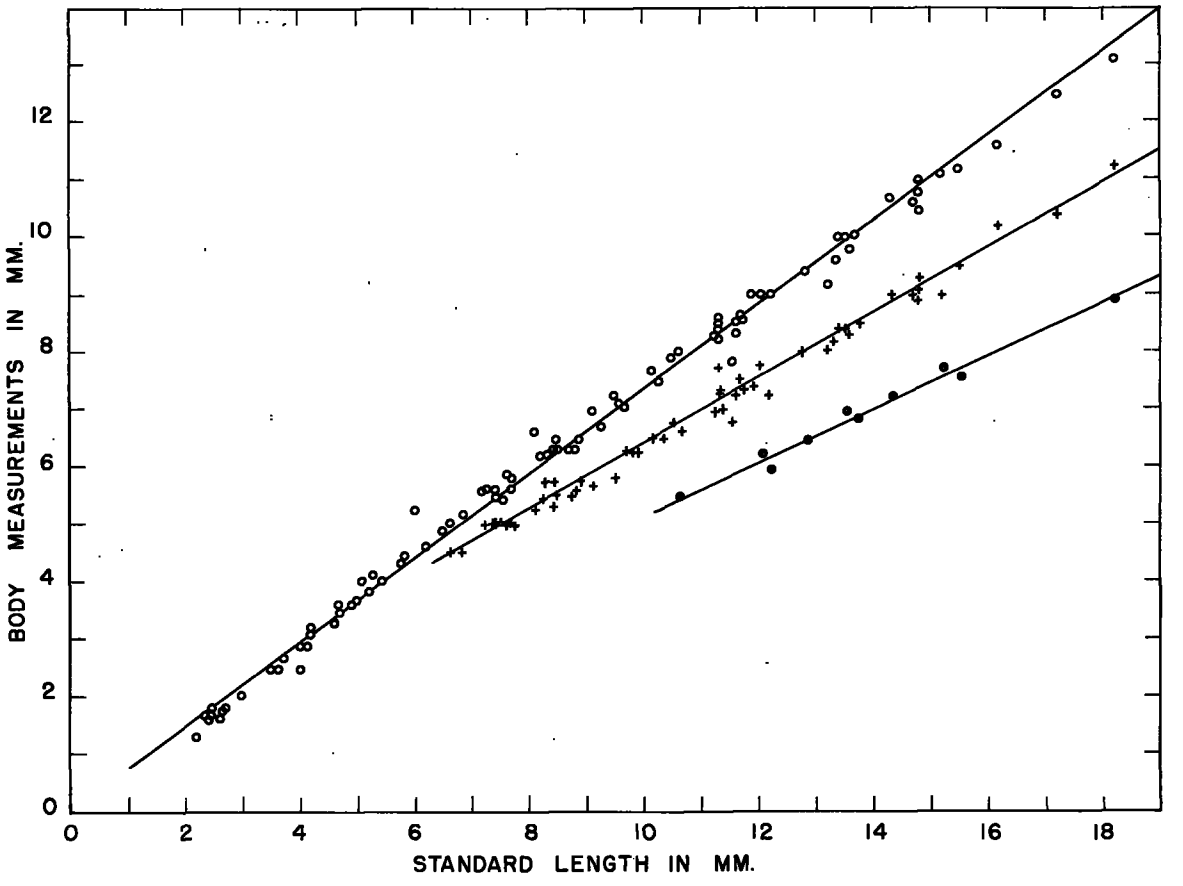

FIGURE 7.—Regression on standard length of distance from snout to anus (open circles), of distance from snout to origin of dorsal (+), and of distance from snout to insertion of ventrals (closed circles) for *Vinciguerria lucetia* larvae. The lines are fitted by the method of least squares. (Refer to table 3 for statistics describing the three lines.)

age could occur as has been postulated by Sanzo. Any species, such as the fresh-water eel, that shrinks markedly during metamorphosis does so before the vertebral column ossifies.

As mentioned previously, metamorphosis of *Vinciguerria* naturally falls into three stages (a prometamorphosing individual in the white photophore stage is shown in figure 8; midmetamorphosis is not illustrated; a postmetamorphosing specimen is shown in figure 9). Regressions of three body measurements on standard length are illustrated in figure 10 for the prometamorphic stage, and in figure 11 for the postmetamorphic.

Specimens of *V. lucetia* metamorphose at a smaller size in the area south of 25° N. latitude than in the northern part of its range. The smallest specimens examined of each of the three stages of metamorphosis in the two regions were as follows:

Stage	Southern Baja California (20°–25° N. latitude)	Southern California and northern Baja California (30°–35° N. latitude)
Prometamorphic	13.2 mm	17.2 mm.
Midmetamorphic	13.5 mm	17.4 mm.
Postmetamorphic	13.2 mm	16.5 mm.

The extent of the changes in body proportion that occur in each of the three stages of metamorphosis can be seen by comparing the average proportions of individuals of the same standard length (table 5). Two sizes have been chosen: 13.5 millimeters, which is at the lower end of the size range of all three stages, and 19.0 millimeters, which is at the upper end.

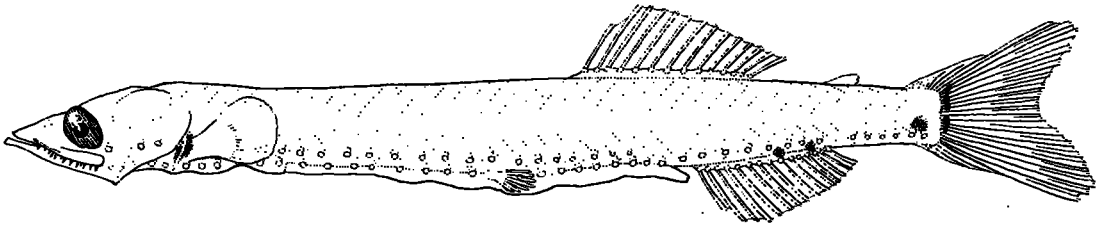

FIGURE 8.—Prometamorphosing specimen of *Vinciguerria lucetia* 15.0 mm. long, collected near Cape San Lucas, Baja California (station 157.10).

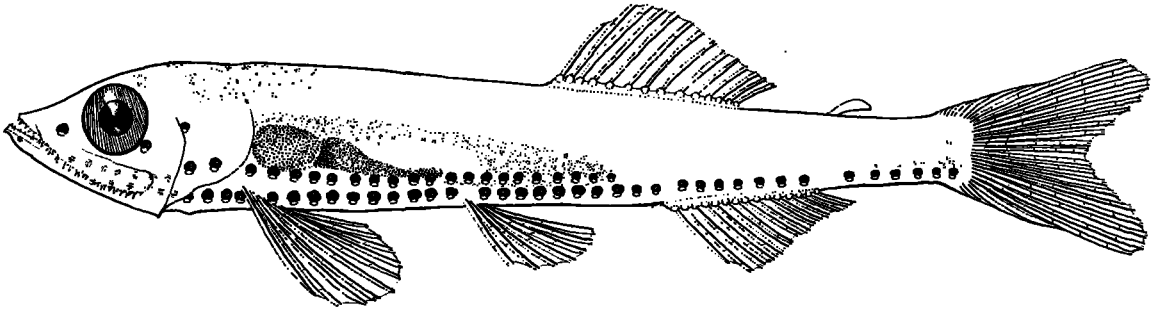

FIGURE 9.—Postmetamorphosing specimen of *Vinciguerria lucetia* 16.0 mm. long, from off southern Baja California (station 153.20).

The following changes occur in the body proportions studied:

Head length: Relative length of the head increases about 20 percent between the larval stage and the postmetamorphic. Prometamorphosing individuals are quite similar to larvae.

Eye diameter: A marked increase in eye diameter occurs between the larval and postmetamorphic stages, amounting to about 80 percent. The eye changes in shape from oval to approximately round, and loses its semistalked condition.

Body depth: A striking increase in body depth results during metamorphosis, amounting to about 80 percent in postmetamorphosing individuals. There is a simultaneous increase in the depth of the abdominal cavity, accompanied by a marked augmentation of pigment in the peritoneal tissues.

Distance from snout to insertion of ventral fins: A slight decrease in this dimension occurs during metamorphosis, amounting to somewhat less than 10 percent.

Distance from snout to origin of dorsal fin: The proportionate distance from snout to origin of dorsal fin is about 10 percent longer in larvae than in postmetamorphosing specimens of the same size.

Distance from snout to anus: There is a greater difference in this dimension between larval and postmetamorphic stages than in the preceding dimension; the decrease during metamorphosis

TABLE 5.—*Average body dimensions and proportions of developmental stages of* Vinciguerria lucetia *at two selected lengths*

[All values based on regression lines]

Stage	Average body measurements (in mm.)						Body proportions as percentage of standard length					
	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
13.5 mm.:												
Larval	2.88	0.54	1.19	6.84	8.37	9.91	21.33	4.00	8.81	50.67	62.00	73.41
Prometamorphic	2.94	.56	1.40	6.81	8.35	9.78	21.78	4.15	10.37	50.44	61.85	72.44
Midmetamorphic	3.19	.63	1.70	6.38	7.95	8.98	23.63	4.67	12.59	47.26	58.89	66.52
Postmetamorphic	3.55	.97	2.07	6.41	7.74	8.80	26.30	7.19	15.33	47.48	57.33	65.19
19.0 mm.:												
Larval	4.05	.75	1.73	9.42	11.48	13.95	21.32	3.95	9.11	49.58	60.42	73.42
Prometamorphic	3.90	.79	1.85	9.39	11.57	13.43	20.53	4.16	9.74	49.42	60.89	70.68
Midmetamorphic	4.07	.86	2.24	9.10	11.18	12.82	21.42	4.53	11.79	47.89	58.84	67.47
Postmetamorphic	4.99	1.41	3.06	8.86	10.51	12.09	26.26	7.42	16.11	46.63	55.32	63.63
Juvenile	5.14	1.65	3.56	8.77	10.34	11.81	27.05	8.68	18.74	46.16	54.42	62.16

amounts to between 13 and 18 percent, depending on size. Some of the decrease in this dimension is due to an actual shortening of the intestine. The intestine, including the anal papilla, extends beyond the origin of the anal fin in late-larval and prometamorphosing individuals, but contracts into a more anterior position, usually between the last two pairs of ventral VA photophores during metamorphosis.

Very little change occurs in total length during metamorphosis. We found the size range of individuals in the three metamorphic stages to be

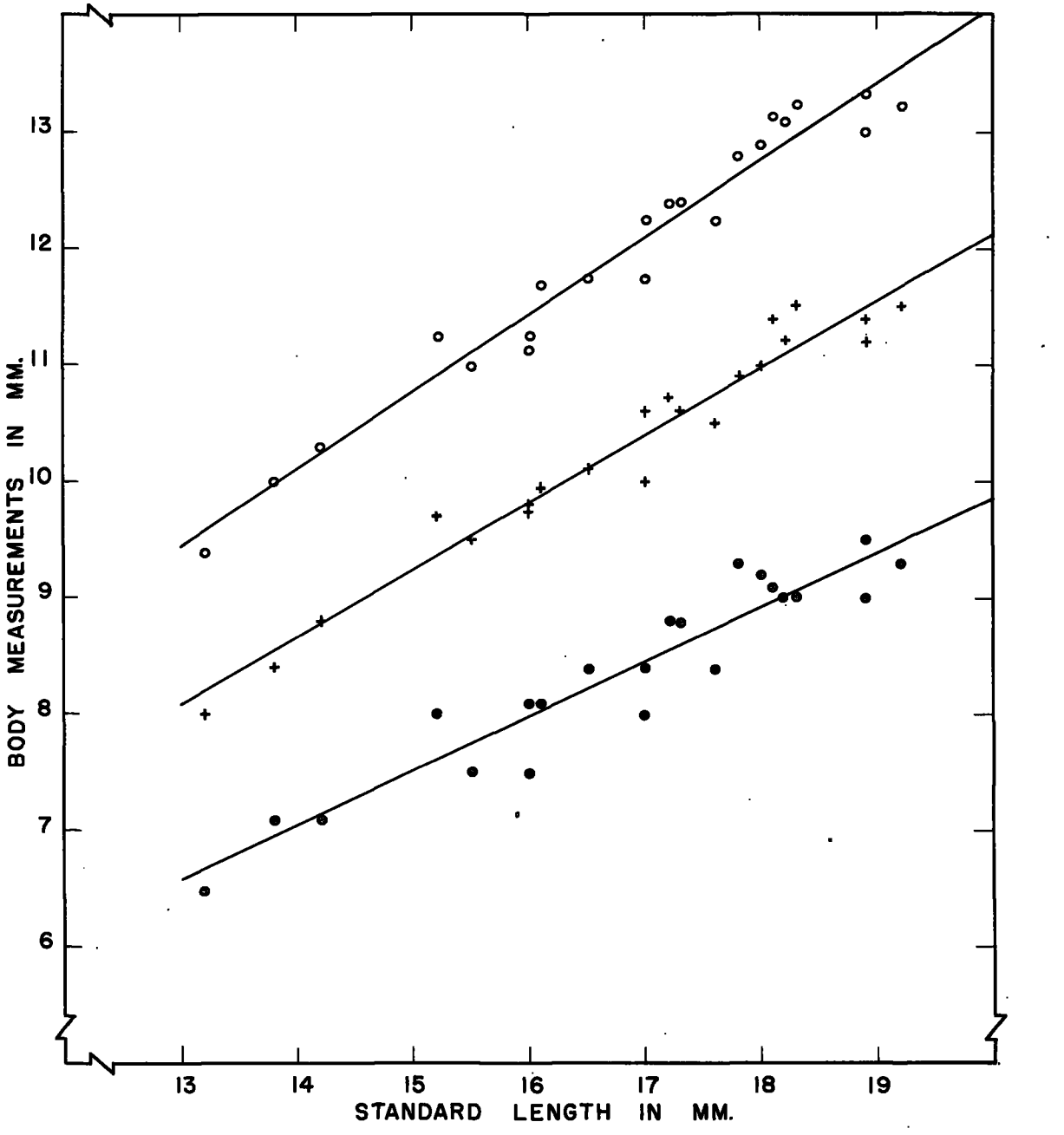

FIGURE 10.—Regressions on standard length of the distances from snout to anus (open circles), from snout to the origin of dorsal fin (+), and from snout to insertion of ventral fins (closed circles) of the prometamorphic stage of *Vinciguerria lucetia*. The lines are fitted by the method of least squares (see table 3).

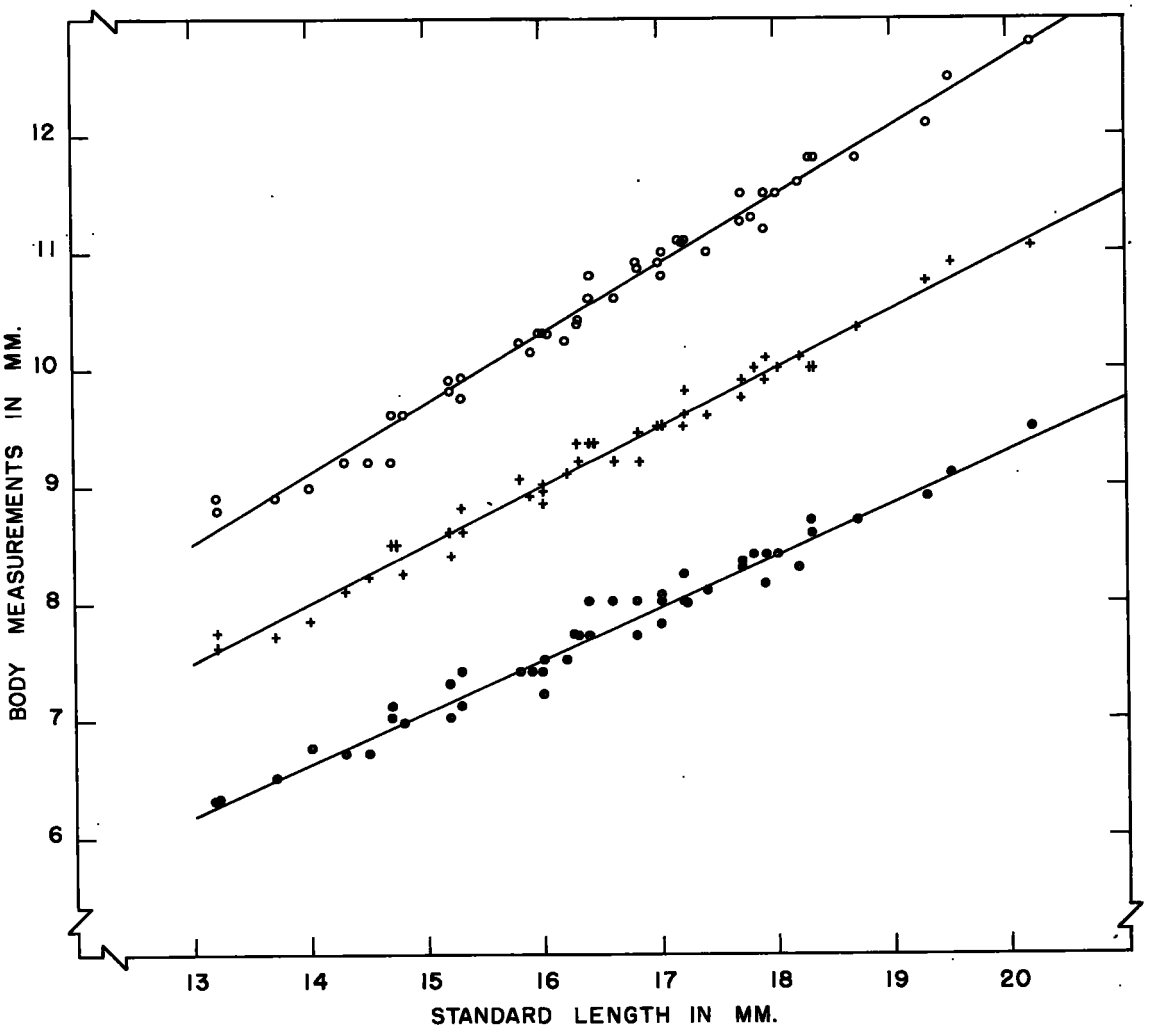

FIGURE 11.—Regression on standard length of the distance from snout to anus (open circles), from snout to the origin of dorsal fin (+), and from snout to insertion of ventral fins (closed circles) of the postmetamorphic stage of *Vinciguerria lucetia*. The lines are fitted by the method of least squares (see table 3).

almost identical. Although there is little increase in length, there is no evidence of an actual decrease (shrinking) in total length during metamorphosis. A decrease in length of *V. poweriae* and *V. attenuata* during metamorphosis has been claimed by Sanzo and by Jespersen and Tåning.

Juveniles and adults.—The rate of growth of body parts appears to be the same during the juvenile and adult stages (figs. 12 and 13), hence these two stages have been combined in our morphometric studies. During metamorphosis, three proportions increased relative to standard length (head length, eye diameter, and body depth), and three decreased (distances from snout to ventrals, snout to dorsal base, and snout to anus). The growth rate of the head during the juvenile and adult stages is about the same as during postmetamorphosis—an increase of slightly over 0.26 millimeter for each 1.0-millimeter increase in standard length. The depth of body also increases at a rate that is similar to that found for postmetamorphosing individuals—0.174-millimeter increase in depth for each 1.0-millimeter increase in standard length.

We have not attempted to fit a curve to the eye measurements, but the size-on-size plot is markedly curvilinear. The eye diameter in larger adults is proportionately less than in juveniles. Hildebrand (1946) has emphasized the proportionately smaller eye diameter in his description of *Vinci-*

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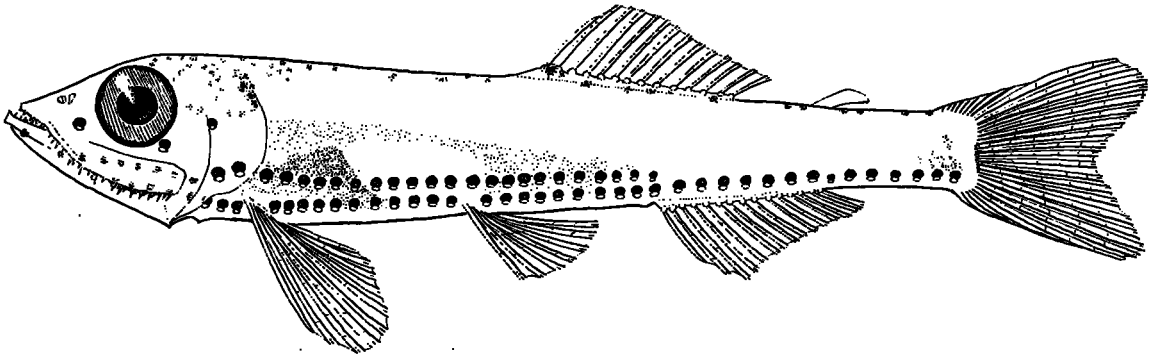

FIGURE 12.—Early juvenile of *Vinciguerria lucetia*, 19.5 mm. long, from off Point Abreojos, Baja California (station 130.35).

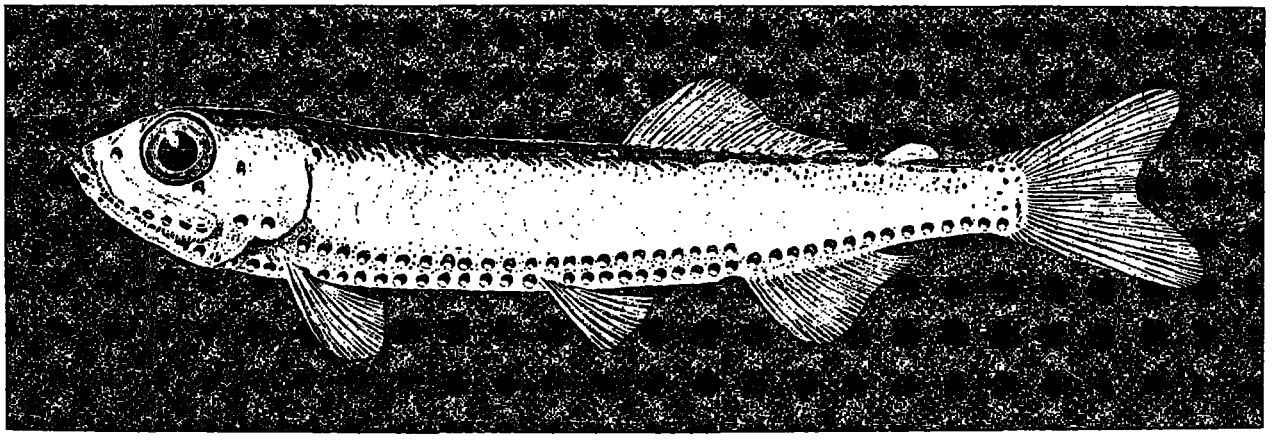

FIGURE 13.—Adult of *Vinciguerria lucetia*, 43.5 mm. long, from off Guadalupe Island.

guerria pacifici, based on large adult specimens, but this apparent difference from *V. lucetia* has not held up.

The distance from snout to anus increases 0.71 millimeter per 1.0 millimeter of growth—only slightly less than during the larval period. The distance from snout to origin of the dorsal fin, which showed a proportionate decrease during metamorphosis, again increases at a rate which is similar though slightly higher than that determined for the larval period. The same applies to the distance from snout to ventral fin bases (fig. 14).

The body parts that showed an increase in growth rate relative to standard length during metamorphosis, retained the higher rate during the juvenile and adult stages. The three measurements that showed a decrease in growth rate during metamorphosis did not continue at the decreased rate during later life, but reverted to a rate that was similar to that obtaining during the larval period.

Changes in pigmentation during development

Larval pigmentation.—The pigmentation of newly hatched larvae (approximately 2.0 mm. in length) and of larvae up to about 4.0 millimeters in length (fig. 3, *a*) differs markedly from that in larger larvae. At time of hatching, pigmentation is similar to that described for late-stage eggs, i. e., the principal feature is a line of dorsolateral pigment spots on either side of the body. In addition, there are a few ventral spots posterior to the anus and often 2 or 3 streaks of pigment in the caudal fin-fold. In larvae between 2.0 and 4.0 millimeters in length, the pigment migrates ventrally and the number of discrete pigment spots markedly decreases. For example, in yolk-sac larvae between approximately 2.0 and 2.5 millimeters in length there are 10 to 12 lateral spots between the head and anus, 2 or 3 ventral spots behind the anus, as well as streaks of pigment in the caudal fin-fold. Thereafter, until about 4.0 millimeters in length, the number of lateral spots is gradually reduced, after which size none is to be observed. If lateral spots represent migrat-

ing pigment, which is likely, the migration must occupy a considerably longer time than similar pigment movements in the larvae of the sardine, jack mackerel, Pacific mackerel, and other species that we have observed. At about 4 millimeters in length, the larvae show very little pigmentation. The usual pigmentation consists of only about three inconspicuous spots: one behind the pectoral fin (postpectoral spot), one above the anus (anal spot), and the other about midway between the anus and the end of the notochord (precaudal spot).

Throughout the remainder of the larval period (fig. 3, *b–d*), the pigment is usually confined to eight spots (or patches). These are (1) prepectoral spot—near base of pectoral fin; (2) postpectoral spot—approximately 1 millimeter behind pectoral fin; (3) anal spot—pigment spot above anus; (4) anal-base pigment—one to three pigment spots above posterior half of anal base; (5) precaudal spot—a lateral pigment spot midway between anus and end of notochord (or base of caudal fin); (6) caudal spot—located approximately 1 millimeter before end of notochord (or immediately before caudal base after flexion of notochord); (7) pigment at base of upper caudal rays; and (8) pigment at base of lower caudal rays.

A detailed study was made of the pigmentation of 79 specimens of larvae that measured between 4.3 mm. and 17.3 mm. in standard length. Pigmentation of a selected group of these larvae is given in table 6. The eight pigmented areas were never observed on any one individual, and only about 10 percent of the specimens examined had more than five of the pigmented areas developed.

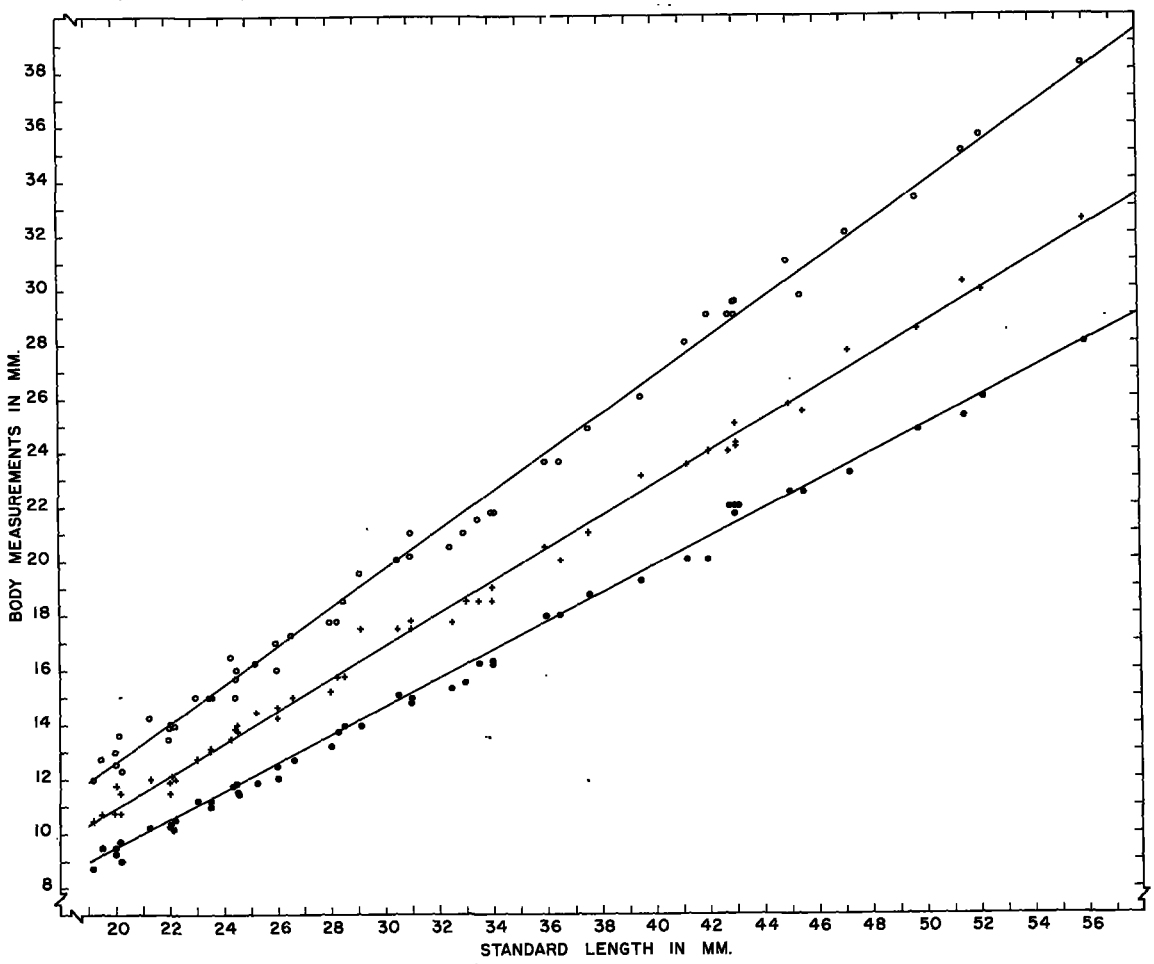

FIGURE 14.—Regressions on standard length of the distance from snout to anus (open circles), from snout to the origin of dorsal fin (+), and from snout to insertion of ventral fins (closed circles), of juveniles and adults of *Vinciguerria lucetia*. The lines are fitted by the method of least squares (see table 3).

Three of the pigment spots occurred only on larvae smaller than 9.0 millimeters. These were the postpectoral, anal, and precaudal spots. The anal spot was observed on only 8 individuals, the postpectoral spot on 14, and the precaudal spot on 24. The caudal spot was the only one found on larvae of all sizes. Seventy-six of the 79 individuals examined had this spot. The prepectoral spot was not observed on any larva smaller than 6.2 millimeters, was found on approximately half those between 6.2 and 9.0 millimeters, and on nearly all those longer than 9.0 millimeters. The pigmentation above the base of the anal fin usually was not present until after fin formation, however it was found on all larvae of more than 7.5 millimeters in length. At first formation, only a single pigment spot was present in this area; the number increased to 2, 3, or occasionally 4 spots on older larvae. The pigment at the base of the caudal fin rays formed initially soon after caudal-fin formation in the upper part of the caudal fin. Pigment along the base of the lower part of the fin was not consistently present until larvae were more than 8.5 millimeters in length. The pigment on the caudal fin consisted of elongated dashes rather than spots.

TABLE 6.—*Location of pigment area in* Vinciguerria lucetia *larvae of more than 4 millimeters standard length*

Standard length	Prepectoral	Pectoral	Anal	Anal-fin base [1]	Precaudal	Caudal	Pigmentation at base of caudal rays	
							Upper	Lower
4.3 mm					X	X		
4.8 mm					X			
5.3 mm		X	X		X	X		
5.6 mm			X		X	X		
6.3 mm		X		1	X	X	X	
6.8 mm	X	X			X	X	X	
7.3 mm	X		X	2		X	X	X
7.8 mm	X	X		1	X	X	X	
8.3 mm	X	X		2		X	X	
9.2 mm	X			2		X	X	X
9.7 mm	X			2		X	X	X
10.6 mm	X			2		X	X	X
11.5 mm	X			3		X	X	X
12.5 mm	X			2		X	X	X
13.3 mm	X			2		X	X	X
15.3 mm	X			3		X	X	X
16.2 mm	X			5		X	X	X
17.3 mm	X			4		X	X	X

[1] Number of discrete pigment spots above anal-fin base.

The caudal pigment spot, located just anterior to the end of the notochord before caudal-fin formation and just anterior to the base of the caudal fin after caudal formation, is perhaps the most diagnostic pigmentation in *Vinciguerria* larvae. The location of the caudal spot is of taxonomic value in separating the species: in *V. attenuata* and *V. poweriae* the caudal spot is on the lateral midline, whereas in *V. lucetia* and *V. nimbaria* the spot is close to the ventral margin.

Pigmentation changes during metamorphosis.—Pigmentation in the three stages of metamorphosis is separately discussed.

Prometamorphic stage: At the initiation of metamorphosis, when photophores are in the white or colorless stage, the pigmentation remains the same as in larger larvae (fig. 8).

Midmetamorphic stage: The principal augmentation of pigment during the period of rapid change in body proportion is in two areas, the head and the peritoneal wall. The pigment on the head is embedded on the back of the cerebellum and some extends over the crown. During this stage there is a rapid increase in the depth of the body cavity and the simultaneous appearance of considerable peritoneal pigment, particularly in the dorsal wall and in the posterior portion of the abdominal cavity. By the end of the stage there is a light stippling of pigment between the ventral photophores, a streak of pigment on the border of the eye just above the posterior ocular photophore, and a few pigment spots on the operculum.

Postmetamorphic stage: During this stage there is a marked increase in body pigmentation, particularly along the back from the head to the tail. On postmetamorphosing individuals, various stages in the development of dorsal pigmentation have been observed. The dorsal pigment appears just behind the head (fig. 9) and then gradually extends back. It usually is not developed along the entire length of the back until the very end of this stage. Simultaneously, there is an increase in the pigmentation on the crown of the head, a spread of pigment laterally on the nape, an augmentation of the peritoneal pigment, including a lateral spreading, and an increase in the stippling of pigment between the ventral photophores (IV and VA groups). The caudal pigment spot is still observable during this stage and embedded pigment appears in this region. The line of pigment at the base of the caudal rays intensifies and some pigment extends distally a short distance between the rays.

Juvenile and adult pigmentation.—The pigmentation described here for juveniles and adults was observed on preserved specimens that had lost their scales. Obviously, it will not apply to living specimens. The basic pattern of pigmentation is

laid down during postmetamorphosis, and subsequent pigmentation mostly serves to intensify this pattern. However, during the juvenile and adult stages various minor but characteristic pigment marks appear. Several of these are on the head; 2 spots appear on the snout between the 2 anterior ocular photophores, a dash appears on the lower jaw just anterior to each SO photophore, and stippling forms along the premaxillary and anterior border of the maxillary. There is a spread of the pigment bordering the eye, and an increase in the amount of pigment on the crown and operculum. From the nape the pigment spreads to below the midline, but along the caudal portion of the body it does not spread below the midline. However, embedded pigment can be observed on some specimens above the anal base and the amount of embedded pigment in the vicinity of the urostyle and ultimate vertebra increases in juveniles and adults. On adults, pigment has been observed extending between and outlining the principal caudal rays, but no pigmentation of the other fins has been observed.

Sequence of calcification

As noted previously, our study was made on cleared and stained material. Bone material stains red with alizarin, hence the sequence of calcification can be readily followed.

Calcification proceeds more slowly in *Vinciguerria* larvae than in most other species we have studied in detail. During much of the larval period, the only structures that show ossification, other than the unpaired fins, are parts of the head, the pectoral girdle, and the structures associated with the urostyle. The cleithrum takes the stain almost immediately in the newly hatched larva. The mouth parts and the head bones gradually differentiate during the larval period. The uroneurals first stain in larvae about 7.5 millimeters long, but no ossification of vertebral centra or spines is discernible until the larvae are approximately 11 millimeters or more in length.

Vertebral development.—The uroneurals and hypurals associated with the urostyle develop considerably earlier than the remainder of the vertebral column. The uroneurals take stain in some specimens about 7.5 millimeters long, and the hypurals form soon after. As pointed out later, there are at first 7 hypural elements, but these are subsequently reduced by fusion to 5.

The vertebral column does not begin to ossify until near the end of the larval period. Ossification of vertebrae is also delayed in other deep-sea fishes (*Leuroglossus stilbius*, for example) but not in most fishes.

The centra of vertebrae ossify before the neural or haemal spines. The first vertebral centra to ossify are some distance back of the head. They appear in about the center of the precaudal group and ossification of centra then proceeds in both directions. The complete group of precaudal centra sometimes ossifies before any of the caudal centra, but usually the anterior 1 or 2 centra form after some caudal centra can be distinguished. Differentiation of the caudal group, with the exception of the urostyle, proceeds posteriorly. Before the ultimate centrum forms, its haemal spine can be distinguished. Differentiation of haemal and neural spines, unlike that of the centra, begins at the ultimate centrum and proceeds forward. A centrum does not ossify along its entire length at initial formation, rather, a narrow band of each centrum forms first and ossification then gradually spreads throughout its length.

The size of larvae at which the vertebrae ossify varies with locality. In areas where metamorphosis begins at about 13 or 14 millimeters the vertebrae begin to ossify at about 11 millimeters. In localities where metamorphosis begins at larger sizes (16 to 19 mm.), vertebral development is correspondingly delayed. Initial ossification of centra is usually complete by the prometamorphic stage, but the neural and haemal spines form during metamorphosis.

The range in number of vertebrae, including urostyle, is from 39 to 42. The number of precaudal vertebrae varies from 22 to 24. The total number of vertebrae shows a definite latitudinal variation which parallels a variation in number of photophores (table 7).

The average number of vertebrae is 41.2 for areas where photophores average 83 per side, while in areas with low average photophore counts (between 80.1–80.6 per side) the average number of vertebrae is 40.3, approximately 1 vertebra fewer.

Gill rakers.—Gill rakers were counted on both stained and unstained material, but more readily on the stained material, especially during the larval period. Gill rakers are more difficult to count on *Vinciguerria* than on fishes that attain a larger

TABLE 7.—*Number of vertebrae in 89 specimens of* Vinciguerria lucetia, *by area of capture*

Area	Number of specimens with—				Total number of specimens	Average number of vertebrae	Average number of photophores per side
	39 vertebrae	40 vertebrae	41 vertebrae	42 vertebrae			
30°–35°N., 122°–134°W	------	2	17	5	24	41.1	83.0
27.5°–30°N., 119°–129°W	------	1	19	8	28	41.2	83.2
25°–27.5°N., 115°–117°W	------	------	2	------	2	41.0	81.3
20°–25°N., 124°W	------	------	3	2	5	41.4	83.1
20°–25°N., 111°–118°W	3	6	10	1	20	40.4	80.6
10°–15°N., 103°W	1	8	1	------	10	40.0	80.1
All specimens	4	17	52	16	89	40.9	82.2

size. The anterior rakers on the lower limb are especially difficult to get into position for counting on juveniles and adults, and, as a consequence, we may have undercounted the rakers on some specimens. The full complement consists of 8 to 10 rakers on the upper limb, and 18 to 23 on the lower.

Gill rakers form on the lower limb during the larval period, but do not appear on the upper limb until metamorphosis. Nubbins were first observed on larvae approximately 8 millimeters long. A group of rakers, usually about 10, differentiates simultaneously. Two or three are still lacking at the posterior end of the lower limb, and between 7 to 10 at the anterior end. Fifteen or sixteen rakers are formed on the lower limb by the close of the larval period, when only the anteriormost rakers have not formed (see table 30).

The rakers were counted on a number of prometamorphosing specimens. The lowest count was 0+16, the highest 4+22. Most individuals had either 2 or 3 rakers developed on the upper limb and 17 or 18 on the lower.

Midmetamorphosing individuals usually had 3 to 5 rakers on the upper, and 17 to 21 on the lower limb; postmetamorphosing specimens usually had 6 to 9 on the upper limb, 18 to 23 on the lower. All juveniles or adults counted had either 8, 9, or 10 rakers on the upper limb, 18 to 23 on the lower.

No geographical variation was noted in numbers of gill rakers in juvenile and adult specimens of *Vinciguerria lucetia.*

Development of teeth.—Larval teeth (table 8) form first on the maxillaries, which are the first jaw bones to ossify. One or two maxillary teeth per side were observed on larvae just under 5 millimeters in length. Subsequently, teeth are gradually added along the maxillaries until there are approximately 13 per side at metamorphosis. Most of the maxillary teeth are straight and needlelike. The posterior teeth are usually a little longer than the anterior ones.

TABLE 8.—*Development of teeth in larval* Vinciguerria lucetia

Standard length	Number of specimens	Average number of teeth per side			
		Maxillary	Premaxillary	Mandibular	
				Outer	Inner
4–4.9 mm	3	1.3	0	0	0
5–5.9 mm	7	2.5	0	0	0
6–6.9 mm	8	4.1	0	0	0
7–7.9 mm	6	5.3	0	0.8	0
8–8.9 mm	10	7.6	0	2.8	0
9–9.9 mm	9	7.7	0	3.4	0
10–10.9 mm	5	9.4	0	4.2	0
11–11.9 mm	15	10.2	0	4.2	0
12–12.9 mm	7	11.1	0	4.6	0.6
13–13.9 mm	6	11.5	1.9	4.3	1.3
14–14.9 mm	1	11.0	3.0	5.0	2.0
15–15.9 mm	2	13.0	2.5	5.0	1.0
17–17.9 mm	1	12.5	4.0	5.0	2.0

The mandibular teeth form in two rows. Those in the outer row form first; they are directed laterally along the anterior part of the lower jaw. They can be observed in larvae of about 7 millimeters standard length and increase in number to 3 to 5 teeth (averaging 3.4) per side in 9-millimeter larvae. During the late larval period, the average number increases to 5, with a range of 4 to 6. The mandibular teeth of the inner row form on the anterior part of the dentaries and are directed at right angles to those of the lateral row. They first form on specimens of about 12 millimeters standard length, and 1 to 3 inner teeth are developed per side before metamorphosis. They are short, wide-based, and of unequal size.

The premaxillaries calcify late and the teeth are observed soon after, when the larvae are about 13 millimeters long. About 3 or 4 unevenly spaced teeth per side usually form before metamorphosis.

During prometamorphosis, the teeth do not differ from those described for larvae, but by late postmetamorphosis the dentition is similar to that of juveniles and adults. During metamorphosis, therefore, a marked increase in the number of teeth on the maxillary, premaxillary, and mandible occurs, as well as changes in the shape and arrangement of the teeth (refer to comments under *V. poweriae*, page 404, for a discussion of changes that occur in maxillary teeth during midmetamorphosis). The increase in number of teeth at

TABLE 9.—*Number of teeth present at various stages in development of* Vinciguerria lucetia

Stage	Number of specimens	Number of teeth per side		
		Premaxillary	Maxillary	Mandibular
Late larval	8	1–4	11–13	5–7
Prometamorphic	14	4–6	12–16	5–9
Postmetamorphic	8	11–18	14–28	13–30
Juvenile	4	13–15	26–32	25–30
Adult	5	12–17	50–65	38–48

different stages in the development of *V. lucetia* is summarized in table 9.

In late-metamorphosing individuals, juveniles, and adults the teeth develop as follows:

Premaxillary teeth apparently do not increase in number after metamorphosis. The highest number found, 17 on one side and 18 on the other, was on a postmetamorphosing individual. Premaxillary teeth are moderately wide based, sharply pointed, unequal in size and uneven in spacing. Usually 5 or 6 are longer and heavier than the others. The premaxillary teeth are uniserial and curve inward at their tips.

Maxillary teeth apparently increase in number throughout life, and adults have twice as many as postmetamorphosing individuals. Maxillary teeth are in a single row. There are two principal kinds of maxillary teeth: (1) straight teeth, set perpendicular to the jaw and curved slightly inward at their tips, and (2) oblique teeth, directed forward at an angle of about 45° and shaped somewhat like a flattened S. An anterior group of straight teeth precede the insertion of the first oblique tooth and the number in this group increases markedly between the postmetamorphic and adult stages. Postmetamorphosing individuals have an anterior group of 4 to 14 straight teeth, while the adult specimens examined had from 26 to 34 teeth in this group (fig. 15). The oblique teeth are interspersed singly between groups of 2 to 5 straight or nearly straight teeth. A group of 3 or 4 straight teeth ends the series; one to three of the teeth in this group are not in line with other maxillary teeth, but originate laterally on the maxillary rather than on its lower surface. The number and

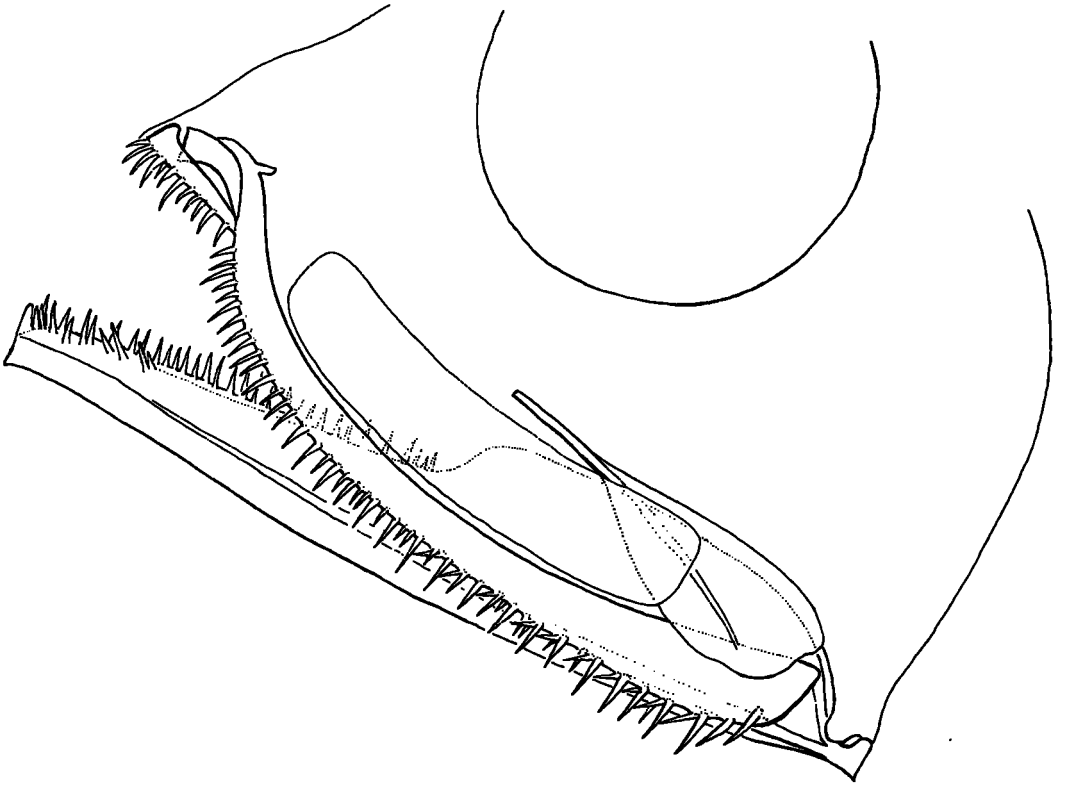

FIGURE 15.—Jaws of specimen of *Vinciguerria lucetia*, 42 mm. in length, collected off Guadalupe Island.

TABLE 10.—*Comparison of maxillary teeth on selected specimens of* Vinciguerria lucetia, *by stage of development*

Standard length	Number of straight teeth in anterior group		Number of oblique teeth		Total number of teeth	
	Left side	Right side	Left side	Right side	Left side	Right side
Postmetamorphic:						
16.75 mm	5	4	4	4	17	16
17.25 mm	3	4	5	4	15	14
17.55 mm	5	4	4	4	16	15
20.20 mm	10	13	6	5	24	26
Juvenile:						
19.50 mm	13	11	6	8	30	31
21.25 mm	10	7	7	7	26	28
24.45 mm	18	16	5	5	33	31
24.70 mm	16	16	5	6	30	32
Adult:						
29.20 mm	28	26	10	10	56	55
41.50 mm	33	32	10	10	65	63
43.00 mm	29	33	9	7	55	52
43.00 mm	28	31	7	7	50	52

arrangement of teeth vary on the two sides of the jaw (table 10).

Mandibular teeth also increase in number during growth from juvenile to adult. Mandibular teeth in the anterior part of the jaw are in two obliquely divergent rows. Teeth of the inner row are fewer and usually more uniform in size and spacing than are those of the outer row, where the teeth may be either evenly spaced or grouped in clusters of 2 or 3 teeth. The teeth in the posterior part of the lower jaw are uniserial and are more closely and uniformly spaced than the anterior group of teeth.

The palatine teeth form during the postmetamorphic stage. A specimen 16.75 millimeters long had 1 tooth on one side and 2 on the other, while a late postmetamorphosing individual, 20.2 millimeters long, had the full complement of 4 to 5 palatine teeth. The posteriormost tooth is largest, and the teeth decrease in size anteriorly.

The vomerine teeth, 1 on a side, also form during the postmetamorphic stage.

Branchiostegals.—Branchiostegals form during the late larval period just before metamorphosis. The size at which they form depends directly on the size the larva attains before metamorphosis. In some regions, branchiostegals are developed in larvae of about 12 millimeters, while in other areas they are not formed until the larvae are at least 16 millimeters long. The full complement of branchiostegals is 12, and all metamorphosing individuals had the full complement. As pointed out elsewhere, the first branchiostegal precedes the anterior branchiostegal photophore. The rays and photophores then alternate, except that the last four branchiostegals are posterior to the last photophore.

Fins.—The number of rays in fully developed fins is shown in table 11. The dorsal fin of *V. lucetia* has 13 to 16 rays (average, 14.59) and the anal fin has 13 to 17 (average, 15.14). In each fin the first ray is unsegmented, the second is segmented but unbranched, and the others are segmented and branched. We are following Jespersen and Tåning (1926) in counting the posterior two rays as separate. The bases of these rays are closer together than the bases of other rays, but they are always distinctly separated and have separate interneurals and interhaemals.

TABLE 11.—*Variation in number of rays in fully developed, unpaired fins of* Vinciguerria lucetia

Number of rays	Dorsal fin	Anal fin	Caudal fin		
			Principal rays	Dorsal secondary	Ventral secondary
4					65
5					1
7				5	
8				39	
9				20	
10				2	
13	3	1			
14	42	11			
15	48	62			
16	7	25			
17		1			
19			66		
Number of specimens	100	100	66	66	66
Average number of rays	14.59	15.14	19.00	8.29	4.02

In all specimens studied, each pectoral fin has 10 rays; the ventral (pelvic) fin has 7 rays. The uppermost ray and the lowermost ray in the pectoral are unbranched, all others are branched. All rays in the ventral fins are usually branched.

The caudal fin has 19 principal and 11 to 14 secondary rays. The principal rays are segmented, 17 are branched. The secondary (procurrent) rays are unsegmented and unbranched. Hollister (1936:259) applies the term "raylets" to such secondary rays. The secondary rays are unequally developed on the two parts of the tail, dorsal secondaries numbering 7 to 10 (average, 8.29), ventral secondaries 4 or 5 (average, 4.02).

We will discuss fins in the order of their formation: (1) Larval pectoral (without rays); (2) caudal; (3) dorsal; (4) anal; (5) ventrals (pelvics); and (6) pectoral (with rays).

Larval pectoral fins: The larval pectoral fins form almost immediately after hatching in larvae less than 2.5 millimeters in length. The fleshy base of the fin is narrow, and the membrane without rays is fan-shaped. Rays do not appear in the pectoral fins until metamorphosis (see below).

Caudal fin: The caudal fin of *V. lucetia* is a typical homocercal tail, and the development is essentially similar to that of many other isospondylous fishes.

The tail fin of isospondylous fishes typically has 19 principal rays (17 branched and the adjacent on either side unbranched). The rays are sharply divided into two groups: 10 upper and 9 lower. All 19 principal rays are ventral in origin, and all are associated with the urostyle except the lower unbranched ray in some species, in which it is attached to the haemal spine of the ultimate vertebra. This description applies to clupeids, engraulids, salmonids, osmerids, argentinids, et cetera.

The caudal fin is first evident as a ventral thickening forward of the tip of the notochord. The thickening has been observed on larvae as small as 4.5 millimeters. As usual, the first rays to form are always the central principal rays, and differentiation proceeds both anteriorly and posteriorly from this center; the rays which will constitute the upper group of 10 principal rays differentiate posteriorly, while those which will constitute the lower group of 9 principal rays differentiate anteriorly. The central caudal rays can be observed on larvae more than 5.5 millimeters long, and the full complement of 10+9 principal rays is found on larvae of more than 6.5 millimeters. The flexure of the posterior portion of the urostyle, bringing the rays into a terminal position, occurs almost simultaneously with principal-ray differentiation.

The secondary, or procurrent, caudal rays differentiate much more slowly than the principal rays. None were observed on larvae under 8.0 millimeters, and they are absent on some larvae approximately 8.5 millimeters long. The secondary rays form on either side of the principal rays, and differentiation proceeds anteriorly. The dorsal secondary rays are the only caudal rays that have a dorsal origin. The secondary rays form slowly. By the end of the larval period, 4 or 5 (occasionally 6) dorsal and 4 ventral secondary rays differentiate. This is the full complement of ventral secondary rays, but little more than half of the dorsal rays (there are 7 to 10 dorsal secondaries in the fully developed tail). Prometamorphosing individuals occasionally have the full number of dorsal secondary rays, but most of these lack 1 to 3 rays. Most midmetamorphosing individuals have the caudal secondary rays fully formed. Many isospondylous fishes with ventral light organs have fewer ventral secondary caudal rays than dorsal, hence this condition in *V. lucetia* is not unique.

The fully developed caudal fin is associated with the last three vertebrae. The development of the supporting skeletal structures for the caudal fin is discussed in a section following fin formation (p. 384).

Dorsal fin: The base of the dorsal fin can be seen on some larvae under 6.0 millimeters long, and rays are found on most larvae of more than 6.5 millimeters. Initially, a group of rays, usually six, in the central portion of the fin, differentiate at the same time, and differentiation then proceeds in both directions. The full complement of dorsal rays is 13 to 16, and the usual number is 14 or 15. Some individuals as small as 10.5 millimeters have 14 dorsal rays, and all of more than 12.0 millimeters in length have at least 14 rays; hence, dorsal-fin formation is completed during the larval period. Dorsal rays on larvae are unbranched.

Anal fin: Rays are not differentiated in the anal fin until larvae attain a length of at least 8.0 millimeters. As in the dorsal fin, the first rays to form are the median ones. Four or more rays appear simultaneously and differentiation then proceeds in both directions. The full complement of anal rays, 14 to 17, is found on all larvae longer than 13.0 millimeters.

Ventral fins: The buds of the ventral or pelvic fins can be seen on 11.0-millimeter larvae, but fin formation is not completed until metamorphosis, usually during the prometamorphic stage (table 12). The number of rays when fully formed is invariably 7.

Pectoral fins (with rays): Rays do not form in the pectoral fin until metamorphosis. Prometamorphosing specimens have from 0 to 6 rays in each fin. Since the complete complement is found on most midmetamorphosing individuals, we assume that ray formation is completed during the

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early part of midmetamorphosis. When fully formed, the number of pectoral rays is invariably 10 (table 12).

TABLE 12.—*Number of rays in pectoral and ventral fins of larval and metamorphosing specimens of* Vinciguerria lucetia

Stage	Number of rays									Total number of specimens
	0	1	3	4	5	6	7	8	10	
Larval:										
Pectoral fin	100	----	----	----	----	----	----	----	----	100
Ventral fin	100	----	----	----	----	----	----	----	----	100
Prometamorphic:										
Pectoral fin	10	1	2	2	1	4	----	----	----	20
Ventral fin	1	----	----	----	1	2	15	----	----	19
Midmetamorphic:										
Pectoral fin	----	----	----	----	----	----	2	1	22	25
Ventral fin	----	----	----	----	----	----	25	----	----	25
Postmetamorphic:										
Pectoral fin	----	----	----	----	----	----	----	----	25	25
Ventral fin	----	----	----	----	----	----	25	----	----	25

Adipose fin: The adipose fin is not evident on larvae, but can be observed on prometamorphosing individuals and is well-developed by the end of metamorphosis. The position and dimensions of this fin on adults is illustrated by morphometric measurements of three selected individuals:

Standard length	Snout to origin of dorsal	Snout to insertion of dorsal	Snout to adipose	Width of adipose at base	Length of adipose
Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
26.2	14.7	19.8	22.1	0.3	1.5
40.6	23.1	30.2	34.3	0.6	2.3
56.0	32.5	42.5	48.0	0.8	3.8

The adipose fin has a moderately narrow base. The fin is directed obliquely backward, has a curved upper (anterior) margin and a fairly straight lower margin, and ends in a blunt point.

Supporting structures for dorsal and anal fins: The number of interneural spines associated with the dorsal fin is identical with or one less than the number of rays. In specimens having 1 less ray, the anterior interneural usually comprises 2 fused elements. Most of the interneurals in the anterior half of the fin are bifurcate at their proximal ends.

There are 13 to 15 free interneurals anterior to those associated with the dorsal fin. The first free interneural precedes the first neural spine, the second one lies between the 1st and 2d neural spines, and each remaining interneural is usually situated between two neural spines. There are no free interneurals posterior to the dorsal fin.

Interhaemal spines are similar to interneurals in having the anterior spines bifurcate at their proximal ends, and in having a similar relationship with fin rays. There are no free interhaemals either anterior or posterior to the anal fin.

Supporting structures for the caudal fin: We have taken a particular interest in the caudal fin and its supporting structures as an aid in the identification of larval fish. Surprisingly, there are more marked differences among gonostomatids in the supporting elements associated with the urostyle than in any family of which we have knowledge. In *Diplophos*, for example, the primitive and complete complement of 7 hypurals and 3 epurals persists. This is the basic number in many families of isospondylous fishes. In *Cyclothone*, on the other hand, the supporting structures are reduced to two hypurals and no epurals. *Vinciguerria* is intermediate, having five hypurals and a single epural.

It is interesting to note, however, that during formation of the caudal supporting structures in *V. lucetia*, 7 hypurals initially develop, which are subsequently reduced to 5 by fusion of elements. The uroneurals ossify before any other part of the vertebral column, and the hypurals form soon after, usually on larvae between 8 and 9 millimeters long. The elements that fuse are the 2 hypurals above and the 2 below the midpoint of the caudal fin. The beginning of fusion of the elements can be observed on some larvae 11.0 millimeters long, and fusion is completed before the end of the larval period. It is an interesting point that the outer hypurals, which remain separate, ossify before the inner ones.

The caudal fin is associated with the last three vertebrae, i. e., the urostyle and the two vertebrae with normal centra, anterior to the urostyle, which are designated "ultimate" and "penultimate." The neural spines are modified on the latter two vertebrae. They are wider than ordinary spines and truncate at their distal ends. The haemal spine is always truncate on the ultimate vertebra, but is ordinarily pointed on the penultimate. Several vertebrae anterior to the penultimate also have truncate neural spines, but normally pointed haemal spines. The condition found in 13 specimens examined for these characters is given in table 13.

The specimen illustrated in figure 16 has truncate neural spines on the last 4 vertebrae anterior

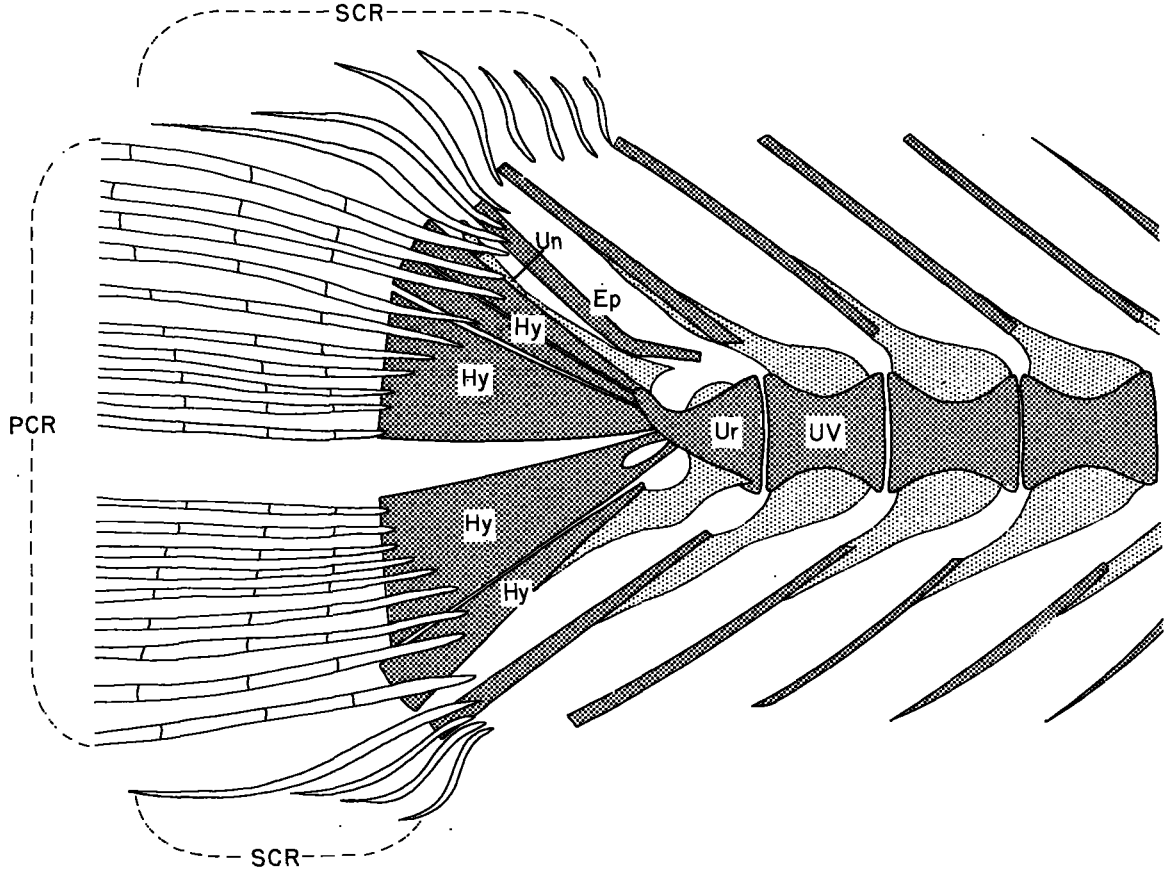

FIGURE 16.—Caudal portion of vertebral column, showing the supporting skeletal structures of the caudal fin. (Ep—epural; Hy—hypurals; PCR—principal caudal rays; SCR—secondary caudal rays; Un—uroneural; Ur—urostyle; UV—ultimate vertebra.)

TABLE 13.—*Types of neural and haemal spines on last six caudal vertebrae anterior to urostyle in* Vinciguerria lucetia

[Based on 13 specimens]

Vertebra	Number of specimens with spines—		
	Both truncate	Neural, truncate; haemal, pointed	Both pointed
I (ultimate)	13		
II (penultimate)	2	11	
III (antepenultimate)		13	
IV		9	4
V		1	12
VI			13

to the urostyle and truncate haemal spines on the last 2. As shown in table 13, the majority of specimens examined have 4 truncate neural spines, but only 2 individuals out of 13 have more than a single truncate haemal spine.

Scale formation

The scales of *Vinciguerria* are highly deciduous, so much so that specimens taken in plankton hauls or trawls seldom possess scales. As a consequence we have not been able to study scale formation. Some postmetamorphosing individuals showed scale pockets over the body, hence we assume that scales are laid down during metamorphosis. No attempt is made to show scales on our drawings. Some specimens dip netted off Guadalupe Island still retained a few scales.

Photophore development

The photophores of *Vinciguerria* are striking in appearance. The number and arrangement of these organs easily distinguish the genus from other gonostomatids. In live specimens taken by dip net at Guadalupe Island, Baja California, the organs gave off a luminescent, blue light when the specimens were held or stimulated. In adults, each photophore consists of a black base and a grayish-silver lens, which is directed downward.

Several methods of classifying photophores have been used (cf., Jespersen and Tåning, 1926;

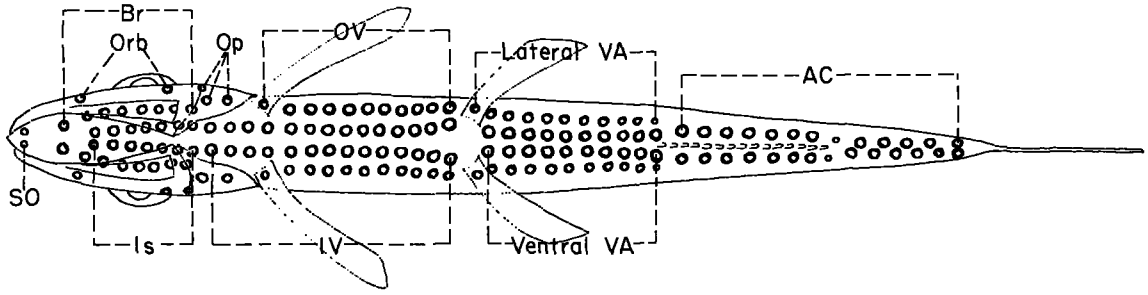

FIGURE 17.—Ventral view of juvenile *Vinciguerria lucetia*, showing the arrangement of photophore groups. (SO—symphyseal pair: Orb—orbital photophores; Op—opercular photophores; Br—branchiostegal photophores; Is—isthmian photophores; OV—lateral photophore group extending from operculum to ventral fin; lateral VA—lateral group extending from ventral fin to origin of anal fin; IV—ventral body photophores between isthmus and ventral fins; ventral VA—ventral group between ventral fins and origin of anal fin; AC—group between origin of anal fin and base of caudal fin.)

Horsburgh 1935). We are using a classification that differs slightly from previous classifications, but appears to us to be a natural system for grouping photophores in *Vinciguerria*.

The photophores have been grouped into 10 categories (see fig. 17). Five of these are used to classify the photophores on the head, 2 for lateral photophores on the body, and 3 for ventral body photophores. The head photophores are grouped as follows: (1) Symphyseal (SO)—one pair placed anteriorly on the underside of lower jaw; (2) orbital (Orb)—2 per side, 1 in front of eye, the other just under posterior portion of eye; (3) opercular (Op)—3 per side, 1 behind center of eye, 2 about on level with lateral row of photophores; (4) branchiostegal photophores (Br)—8 per side, spaced between anterior 9 branchiostegals; (5) isthmian photophores (Is)—7 per side, spaced along isthmus.

Head photophores seldom vary in number after development is complete. Less than 1 percent of the specimens examined had other than 8 branchiostegal photophores per side; 1 specimen had 9, 2 specimens had 9 photophores on one side and 8 on the other, and 1 specimen had 7 photophores on one side and 8 on the other. Only 3 individuals had other than 7 isthmian photophores per side; 2 specimens lacked a photophore on one side (7–6), the other had an additional photophore on one side (7–8).

The body photophores are alined on each side in two rows, a lateral row and a ventral row. The photophores in the lateral row are in two groups, one anterior to the ventral fins (OV), the other between the ventral and anal fins (VA). The OV group contains between 10 and 13 photophores (average, 11.34) and the VA group, when fully formed, contains 9 to 12 photophores (average, 10.88). The IV group of photophores (isthmus to ventral fins) in the ventral row is continuous with the isthmian group. The IV group contains 13 to 16 photophores (average, 14.34) on each side. The ventral series is interrupted by the ventral fins. The VA group of photophores in the ventral row begins just behind the ventral fins and extends to the origin of the anal fin; on each side there are 8 to 12, usually 9 or 10, photophores (average, 9.89). The anal-caudal (AC) group, situated between the origin of the anal fin and the base of the caudal fin, is intermediate in level between the lateral and ventral series; there are 12 to 16, usually 13 or 14, photophores on each side (average, 13.86).

Unlike the head photophores, the body photophores vary in number. The extent of this variation is shown for 586 specimens in table 14.

There is not only variation in the number of photophores per group on different individuals, but at times in the number of photophores per group on the two sides of the same individual. This asymmetry (different number per side) is more marked in the AC group than in the other body groups. The percent of individuals having asymmetry in photophore pairings is given in table 15.

The OV group of photophores in the lateral series is situated above the IV group of ventral-row photophores. The IV group extends farther

TABLE 14.—*Variation in number of body photophores, in 586 specimens of* Vinciguerria lucetia

[See text, p. 386 for explanation of symbols]

Number of photophores	Lateral row		Ventral row		AC group
	OV group	VA group	IV group	VA group	
8-9				2	
9-9		1		67	
9-10		1		45	
9-11				1	
10-10	5	70		438	
10-11	8	40		16	
11-12	369	441		16	
11-11	13	16		1	
12-12	178	17			
12-13	5				7
12-14					3
13-13	8		6		94
13-14			10		118
13-15					8
14-14			364		233
14-15			16		80
14-16					1
15-15			176		38
15-16			6		2
16-16			8		
Total number of specimens	586	586	586	586	584
Average number of photophores per side	11.34	10.88	14.34	9.89	13.86

TABLE 15.—*Asymmetry in photophore pairing in various photophore groups in* Vinciguerria lucetia

[Based on 586 specimens of table 14]

Photophore group	Frequency of specimens with photophore numbers—		Percentage of specimens with asymmetrical pairng of photophores
	Same on two sides of body	Different on two sides of body	
Head	580	6	1.0
Lateral OV	560	26	4.4
Ventral IV	553	33	5.6
Lateral VA	529	57	9.7
Ventral VA	521	65	11.1
Anal-caudal (AC)	365	219	37.5

forward than the OV group; the three anterior pairs of IV photophores have no counterparts in the OV group. Otherwise, the 2 series usually correspond photophore for photophore and the organs of the 2 series are regularly alined transversely. When asymmetry occurs, it is usually in both the IV and OV groups. Of 33 specimens that had asymmetry in the IV group, 26 showed asymmetry in the OV group as well. On the other 7 specimens, the OV group was symmetrical while the IV group had an uneven number on the two sides. Such asymmetry in the ventral IV group that is not shared by the lateral OV group is usually in the anterior three photophores. A similarly close relation obtains between the lateral VA and ventral VA series of photophores when photophore formation is complete. As is noted in the following section, a group of the lateral VA photophores is late-forming. The lateral VA group, when completely formed, averages one photophore per side more than the ventral VA group. The anterior pair of photophores of the lateral VA group, situated above the ventral fins, has no counterpart in the ventral VA group. Otherwise, the two groups have identical numbers of photophores. When asymmetry occurs, it is usually found in both groups. On only nine individuals was asymmetry in the ventral VA group not found in the lateral VA group as well. Asymmetry in the VA groups is more frequent than in the OV and IV groups, but is much less frequent than in the AC group. Hence, frequency of asymmetry seems to be definitely related to position of the photophore group on the body: least in the photophores associated with the head, and increasing posteriorly.

Late-forming photophores.—Most photophores appear simultaneously at the beginning of the transformation stage. At first formation, photophores are colorless, but the base soon becomes pigmented. Six, occasionally seven, photophores per side form late: the upper opercular, the 3 (or occasionally 4) posterior photophores of the lateral VA group, the symphyseal, and a median photophore of the AC group.

Upper opercular photophores: The pair of upper opercular photophores (Op) is usually the first of the late-forming light organs to appear, and the only ones that consistently develop during the midmetamorphic stage. These photophores are found on about 25 percent of the midmetamorphosing specimens and on all classed as postmetamorphosing. The largest individual lacking them was 19.0 millimeters long.

Posterior photophores of the lateral VA group: Three to four pairs of photophores of the posterior lateral group are lacking when the photophores initially appear. Approximately 10 percent of the specimens examined lacked 4 photophores on each side; the remainder lacked 3 photophores. Because of the relation between numbers of photophores in the lateral and ventral VA groups, it is possible to determine the number of "missing" photophores exactly. At formation, late-forming photophores are colorless and are smaller than the adjacent, earlier-formed ones.

Even when they become pigmented, they can be distinguished readily from those initially formed.

The late-forming photophores of the lateral VA group develop mainly during the postmetamorphic stage. On about 10 percent of the midmetamorphosing individuals examined, a single late-forming VA photophore or a pair of VA photophores had appeared. One pair of the lateral photophores almost always develops before the symphyseal pair, and the other 2 (or 3) pairs are added gradually. There is some variation in the sequence in which the late-forming AC pair of photophores appears in relation to the VA photophores (to be discussed later). Usually the posterior pair of lateral VA photophores is the last to form.

The largest specimen studied in which the photophores had not all formed was 22.3 millimeters in length; it lacked a VA and an AC photophore on one side. The smallest specimen with complete photophores measured 17.5 millimeters. We consider that metamorphosis terminates when the photophores are all laid down and the late-forming photophores are pigmented.

Symphyseal photophores: The pair of symphyseal (SO) photophores does not appear until the postmetamorphic stage. Of the 75 postmetamorphosing individuals used to trace photophore development, 26 still lacked these photophores. The largest individual that lacked symphyseal photophores was 19.0 millimeters long; the smallest specimen on which they were developed was 12.5 millimeters. In sequence of formation, symphyseal photophores are usually the third pair of late-forming photophores to appear.

Symphyseal photophores have been used as a diagnostic character in separating species of *Vinciguerria: lucetia* and *nimbaria* develop this pair, while *attenuata* and *poweriae* do not. However, owing to the circumstance that symphyseal photophores are late-forming, this character must be used with caution when dealing with metamorphosing individuals.

Anal-caudal photophores: The anal-caudal (AC) photophores are separated into two groups during most of the metamorphic period, but eventually become a continuous series by the addition of a pair of photophores between the two groups. The photophores in the two groups differ in spacing. In the anterior group, situated above the anal fin, the photophores of the two sides are rather widely separated and are arranged in pairs opposite one another; in the posterior group, the photophores of the two sides are too closely approximated to lie side by side, and alternate regularly, except for the posteriormost pair, or occasionally the last two pairs, which again show the transverse alinement (fig. 17). The anterior group of AC photophores usually consists of 6 or 7 photophores on a side (average, 6.78), the posterior group has 5 to 7 (average, 6.13).

The numbers of photophores in the two AC groups, based on 215 metamorphosing individuals, are given in table 16.

TABLE 16.—*Variation in number of photophores in the anterior and posterior anal-caudal groups during metamorphosis, in 215 specimens of* Vinciguerria lucetia.

[On both sides of body]

Number of photophores	Anterior group	Posterior group
5–5		8
5–6	2	38
6–6	36	86
6–7	37	58
7–7	126	25
7–8	8	
8–8	5	
8–9	1	
Average, per side	6.78	6.13

There is some variation in the sequence of development of the late-forming AC pair in relation to late-forming VA photophores; this is shown in table 17, based on 106 postmetamorphosing individuals. Usually the pair of late-forming AC photophores develop before the last pair of lateral VA photophores; 9 individuals having the AC light organs on both sides of the body still lack 1 or more pairs of VA photophores. On the other hand, 2 individuals with all VA photophores still lack the pair of AC light organs.

TABLE 17.—*Sequence of development of late-forming photophores of the lateral VA and the AC groups, in 106 specimens of* Vinciguerria lucetia

[On both sides of body]

Number of lateral VA photophores lacking	Number of AC photophores lacking		
	1–1	0–1	0–0
4–4	1	0	0
4–3	2	0	0
3–3	25	3	0
3–2	9	3	0
2–2	33	7	1
2–1	3	0	1
1–1	6	1	7
0–1	0	2	0
0–0	2	0	0
Total number of specimens	81	16	9

DISTRIBUTION OF *VINCIGUERRIA LUCETIA* IN THE EASTERN PACIFIC

Our data on the distribution of *Vinciguerria lucetia* have been derived from two sources: the survey cruises conducted by the California Cooperative Oceanic Fisheries Investigations (CCOFI), from which we have been able to derive detailed information on its distribution off California and Baja California, and the less frequent but wide-ranging cruises and expeditions that have covered much of the eastern North Pacific, such as "Norpac," "Northern Holiday," "Shellback," and "Eastropic" expeditions of the Scripps Institution of Oceanography and several tuna longline cruises conducted by the California Department of Fish and Game. Most of the material has been obtained from plankton-net collections, supplemented by an examination of collections obtained from midwater trawls, tuna stomachs, and occasionally dip netting.

DISTRIBUTION AND ABUNDANCE IN CCOFI SURVEY AREA

We shall first discuss the distribution and abundance of *V. lucetia* larvae and adults off California and Baja California, and then present such information as we have on the more extensive distribution of this wide-ranging species.

The distribution of larvae of this species in the CCOFI area in 1951 and 1952 is shown in figures 18 and 19. In each of these, the cruises extended only as far north as the California-Oregon State line. The area off northern California (station lines 40–57) was surveyed on two cruises each year: during July and August in 1951, and June and July in 1952. The area between San Francisco and Point San Juanico, Baja California (station lines 60–137) was surveyed on most cruises. The waters still farther south (station lines 140–157) were not routinely surveyed; the area was covered on three cruises in 1951 (March, June, and September), but only during the February cruise in 1952, and then only partially.

The northern extent of the distribution of *V. lucetia* has been fairly well delimited. There was only a single occurrence of larvae to the north of Point Conception in both 1951 and 1952—at station 60.80 in May 1951, and at station 77.55 in November 1952. In 1949, however, larvae were taken in several collections off central and northern California. The northernmost collection of larvae was at station 509 (37°21′ N. latitude, 130°36′ W. longitude); the northernmost collection of metamorphosing individuals was at station 704 (34°54′ N. latitude, 124°04′ W. longitude). Even so, the occurrences to the north of Point Conception have been sporadic, and the number of specimens obtained has been few.

The area off southern Baja California, unfortunately, cannot be completely compared in 1951 and 1952, owing to the fragmentary coverage in the latter season. This area appears to be the richest for *V. lucetia* of any in the CCOFI region. In 1951, when cruises extended to Cape San Lucas on three occasions, more than 50 percent of the larvae of this species were obtained on the station lines (140–157) off southern Baja California. The data are summarized in table 18.

TABLE 18.—*Census estimates of abundance (in billions of larvae) of* Vinciguerria lucetia *during three cruises in the CCOFI survey area in 1951*

Station lines	Cruise and month			Total estimated number of larvae	Percent of total
	5103 March	5106 June	5109 September		
60–77	0	0	0	0	0
80–93	139	163	68	370	3.33
97–107	28	188	639	855	7.69
110–120	700	194	1,273	2,167	19.49
123–137	116	1,193	457	1,766	15.88
140–157	1,040	1,716	3,205	5,961	53.61
Total	2,023	3,454	5,642	11,119	100.00

In the area regularly covered (station lines 60 to 137), the cumulative census estimates of larvae for comparable cruises during the 2 years (December 1951 was omitted, since there was no December cruise in 1952) are quite similar: 18,384 billion as compared to 19,020 billion (table 19). As explained in a previous publication (Ahlstrom and Counts, 1955), a census estimate is one that integrates standard haul estimates over area but not over time. Size is not taken into account. It is a comparative estimate of abundance, rather than an estimate of actual abundance, which must take into account size, growth rate, and other factors (Ahlstrom 1954), some of which are not known as yet for this species. However, for comparative purposes, census estimates are valid measures of relative abundance.

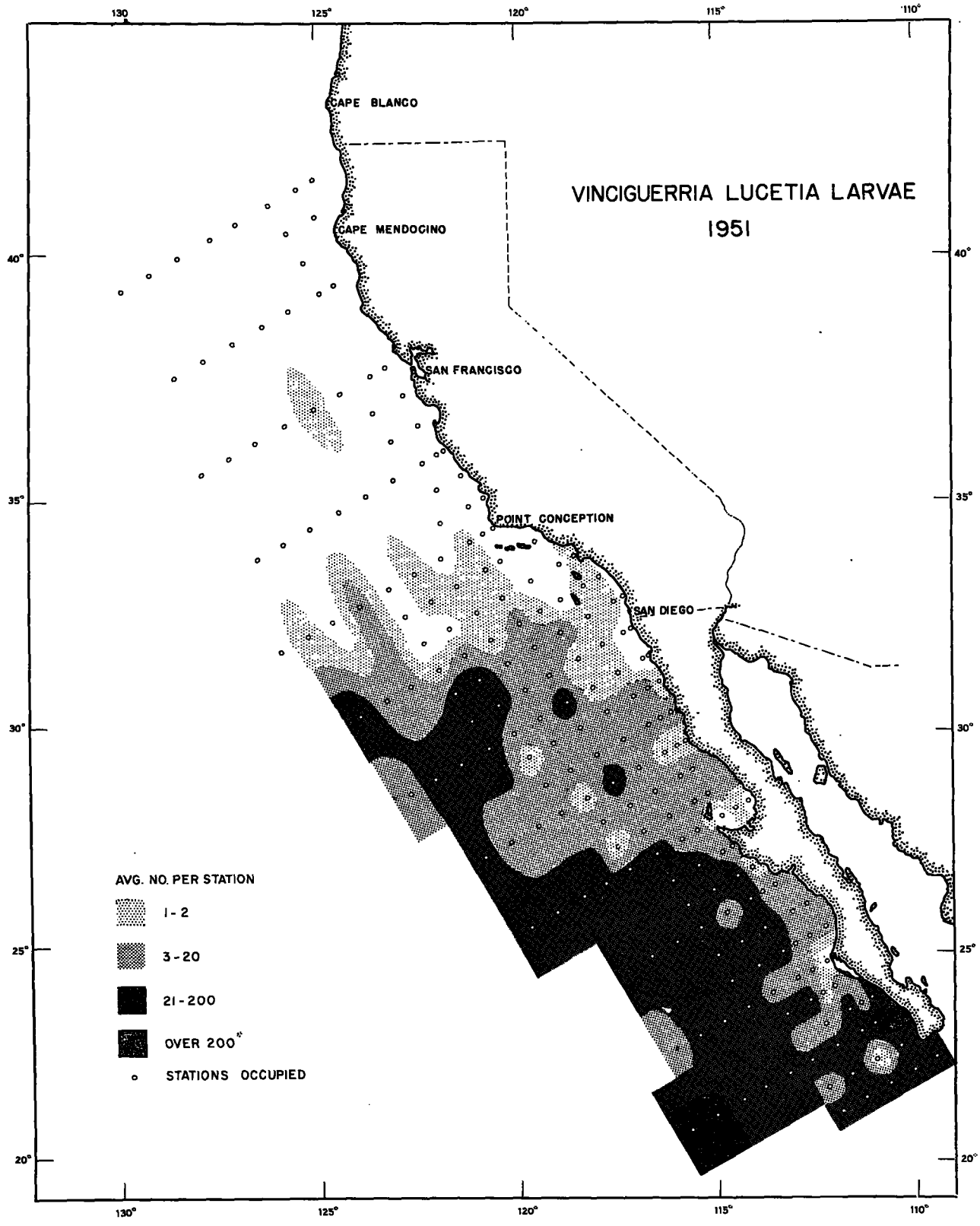

FIGURE 18.—Distribution and abundance of *Vinciguerria lucetia* larvae on survey cruises of the California Cooperative Oceanic Fisheries Investigations in 1951.

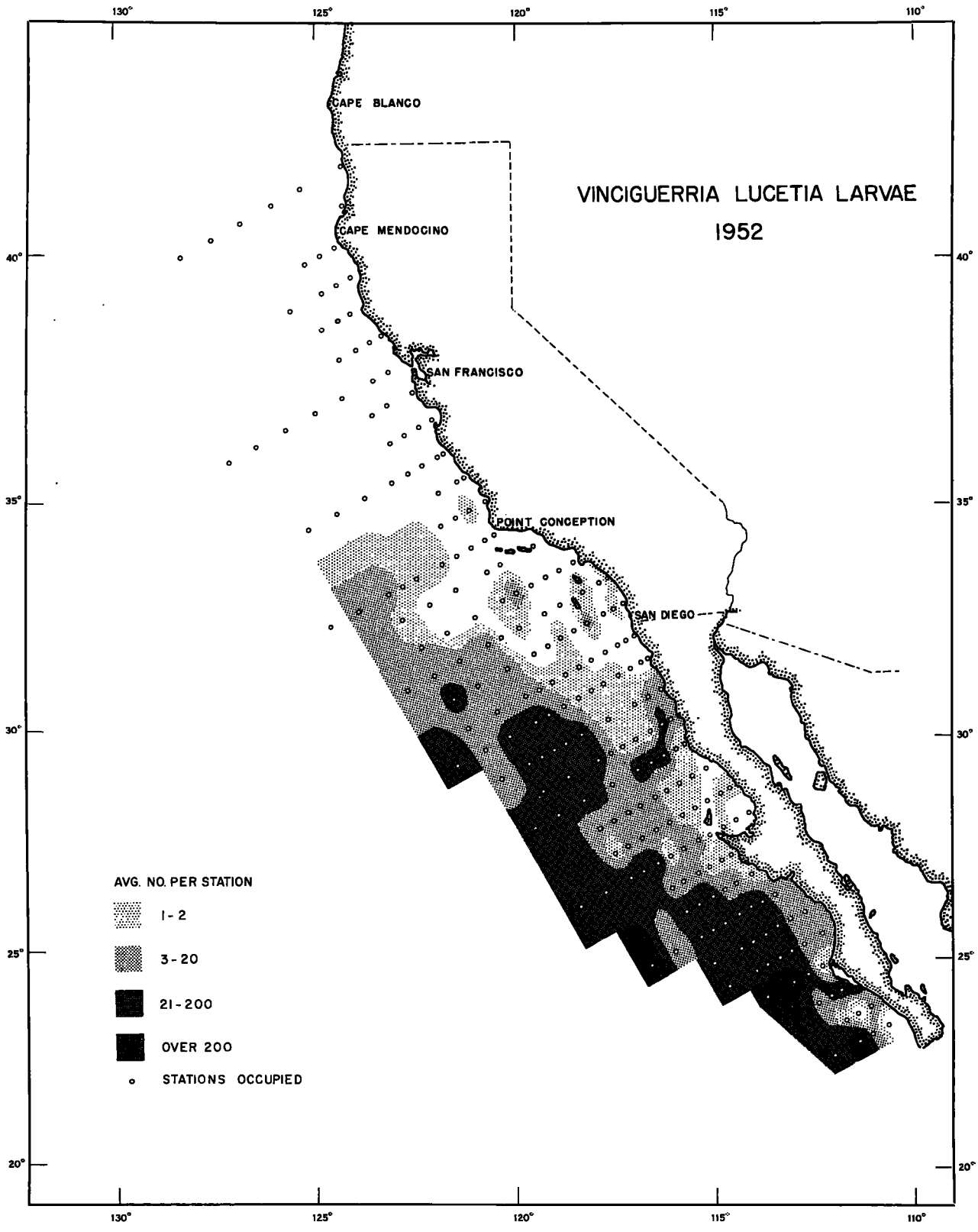

FIGURE 19.—Distribution and abundance of *Vinciguerria lucetia* larvae on survey cruises of the California Cooperative Oceanic Fisheries Investigations in 1952.

TABLE 19.—*Census estimates of abundance (in billions of larvae) of* Vinciguerria lucetia *in the CCOFI survey area during the monthly cruises of 1951 and 1952*

Station lines	Cruise and month												Total estimated number of larvae (billions)
	5101 Jan.	5102 Feb.	5103 Mar.	5104 Apr.	5105 May	5106 June	5107 July	5108 Aug.	5109 Sept.	5110 Oct.	5111 Nov.	5112 Dec.	
1951													
60–77	0	-------	-------	0	12	0	0	0	0	0	0	0	12
80–93	1	14	139	160	254	163	94	128	68	42	11	47	1,121
97–107	90	18	28	603	354	188	396	630	639	945	204	175	4,270
110–120	643	72	700	482	359	194	79	610	1,273	2,510	546	877	8,345
123–137	311	445	116	447	839	1,193	564	575	457	647	141	10	5,745
140 and below	-------	-------	1,040	-------	-------	1.716	-------	-------	3,205	-------	-------	-------	5,961
Total	1,045	549	2,023	1,692	1,818	3,454	1,133	1,943	5,642	4,144	902	1,109	25,454

Station lines	Cruise and month												Total estimated number of larvae (billions)
	5201 Jan.	5202 Feb.	5203 Mar.	5204 Apr.	5205 May	5206 June	5207 July	5208 Aug.	5209 Sept.	5210 Oct.	5211 Nov.	5212 Dec.	
1952													
60–77	-------	-------	-------	0	0	0	0	0	0	0	3	-------	3
80–93	12	1	19	52	17	48	147	177	47	145	46	-------	711
97–107	54	32	103	307	106	161	373	400	301	1,245	220	-------	3,302
110–120	536	224	265	261	874	607	1,365	616	1,303	2,152	1,553	-------	9,756
123–137	965	166	375	1,314	207	558	907	104	340	204	108	-------	5,248
140 and below	-------	474	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------	474
Total	1,567	897	762	1,934	1,204	1,374.	2,792	1,297	1,991	3,746	1,930	-------	19,494

The relative abundance of *V. lucetia* larvae in different parts of the CCOFI survey area is shown in table 20. The regular survey area has been divided into five subareas, two located off California (lines 60–77 and 80–93), and three located off Baja California (lines 97–107, 110–120, and 123–137). In neither season was as much as 6 percent of the total taken off California.

TABLE 20.—*Relative abundance (in billions of larvae) of* Vinciguerria lucetia *in different sections of the CCOFI survey area, 1951 and 1952*

[Cumulative census estimates; see table 19]

Station lines	1951		1952	
	Estimated number	Percent of total	Estimated number	Percent of total
California:				
60–77	12	0.06	3	0.02
80–93	1,121	5.75	711	3.74
Baja California:				
97–107	4,270	21.91	3,302	17.36
110–120	8,345	42.81	9,756	51.29
123–137	5,745	29.47	5,248	27.59
Total	19,493	100.00	19,020	100.00

Larvae were taken throughout the year in all parts of the distribution off southern California and Baja California (table 21). They increased in numbers in late summer and early autumn, and in both years the greatest abundance occurred in October.

TABLE 21.—*Abundance (in billions of larvae) of* Vinciguerria lucetia *in the area surveyed by CCOFI (lines 60–137), by months, 1951 and 1952*

Month	1951		1952	
	Estimated number	Percent of year's total	Estimated number	Percent of year's total
January	1,045	5.36	1,567	8.24
February	549	2.82	423	2.22
March	983	5.04	762	4.01
April	1,692	8.68	1,934	10.17
May	1,818	9.33	1,204	6.33
June	1,738	8.92	1,374	7.22
July	1,133	5.81	2,792	14.68
August	1,943	9.97	1,297	6.82
September	2,437	12.50	1,991	10.47
October	4,144	21.26	3,746	19.70
November	902	4.63	1,930	10.15
December	1,109	5.69	-------	-------
Total	19,493	100.01	19,020	100.01

Although these population estimates are based solely on larvae, specimens in older stages of development (metamorphosing individuals, juveniles, and adults) were taken in all parts of the CCOFI area below Point Conception.

WIDER DISTRIBUTION IN EASTERN PACIFIC

The northern limits of the distribution of *Vinciguerria lucetia* have been adequately delimited by the CCOFI survey cruises, but the southward and westward limits have not. Information is available on the wider distribution of this species from special cruises.

V. lucetia is not only abundant off Baja California, but throughout the area between 20° N. and 14° S. latitude (the southern limit of our collections, rather than the southern limit of distribution of the species). Throughout this wide range, *V. lucetia* is taken in some stage of development in most plankton collections. It is probably the most ubiquitous and abundant species of fish in plankton collections from the eastern Pacific. It has been taken in most hauls made with midwater trawls between 35° N. and 14° S. latitude. It is occasionally taken in dip-net collections, but the only locality where it has been consistently taken by this means is Guadalupe Island, off Baja California. Some of our best adult material has been obtained from this locality.

An unusual occurrence of *V. lucetia* should be noted. On February 10, 1956, Dr. George E. Lindsay, Director of the San Diego Museum of Natural History, found large numbers of dried individuals in windrows on the beach at San Benedicto Island. It is possible that the fish were killed by subterranean volcanic action and washed ashore, as there has recently been considerable volcanic activity on these islands. A number of these specimens were examined by us. They had the usual photophore counts for individuals from that area (80–82 photophores per side), and ranged in size from 29 to 51 millimeters in standard length. The collection contained only *V. lucetia*. This occurrence parallels the mass mortality of *Tarletonbeania crenularis* reported by Aughtry (1953).

V. lucetia is abundant in the southern portion of the Gulf of California. Distribution in the gulf during cruise 5602 is shown in figure 20.

The farthest westward that we have obtained specimens of *Vinciguerria lucetia* has been about 134° W. longitude. Above 20° N. latitude, it is replaced to the west of 134° by *V. nimbaria* and *V. poweriae*, which are discussed later in this paper. Our collections below 20° N. latitude have seldom extended this far westward, so they are inadequate to delimit the westward distribution of the species in the tropical Pacific. We have a record of *V. lucetia* from 14°21′ N. latitude, 133°05′ W. longitude. The distribution of *V. lucetia*, based on collections we have examined, is shown in figure 21.

The westward distribution of the species of *Vinciguerria* in the central Pacific could be clarified from the collections made by the Pacific Oceanic Fishery Investigations. We are not including published records of *V. lucetia* from other parts of the Pacific, as it is not often possible to verify the records from figures or description. Furthermore, it is beyond the scope of this paper.

RELATION OF PHOTOPHORE NUMBER TO LATITUDE

In studying variation in photophore number in different parts of its distribution in the eastern Pacific, 586 specimens of *Vinciguerria lucetia* were examined from 162 collections obtained between 34°55′ N. and 14°00′ S. latitude and between 78°10′ and 134°25′ W. longitude.

There are marked differences in the average total number of photophores per side in different parts of the range. To show these differences, the collections have been grouped into subareas, each comprising 5 degrees of latitude and 10 degrees (or less) of longitude. The results are summarized in table 22, and illustrated in figure 22.

The average number of photophores per side of the composite material was 81.31; the range of means for the subareas was from 78.50 to 83.40, a difference of 4.90 photophores per side.

In the CCOFI area there is a marked cline of photophore number with latitude. Fish taken north of 27°30′ N. latitude average nearly 2.5 photophores per side higher than fish taken between 20° and 25° N. latitude, while those taken between 25° and 27°30′ N. latitude have an intermediate number of photophores per side. The numbers of photophores in the head and VA groups are similar in all areas; the difference in photophore number results from reduction in the number of lateral OV and ventral IV photophores by approximately 1 photophore in each group per side and of AC photophores by about 0.5 photophore per side.

It is an interesting finding that the specimens taken offshore from southern Baja California between 119° and 126° W. longitude had counts that were similar to those found in the northern portion of the distribution (average number of photophores per side, 82.94). The temperature distribution found on "Norpac" affords an explanation: surface temperatures in the offshore area were lower than off southern Baja California.

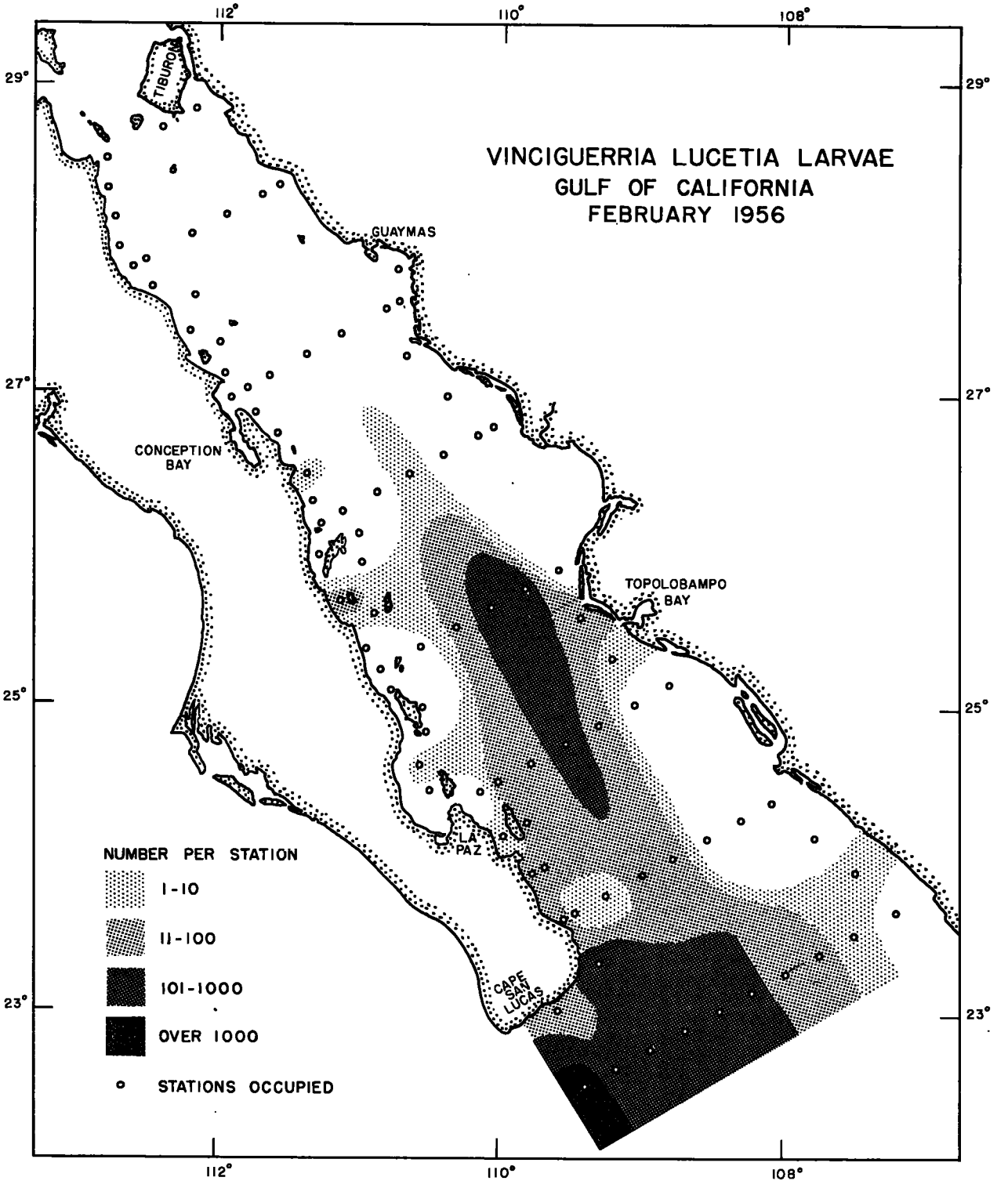

FIGURE 20.—Distribution of *Vinciguerria lucetia* larvae in the Gulf of California in February 1956 (cruise 5602).

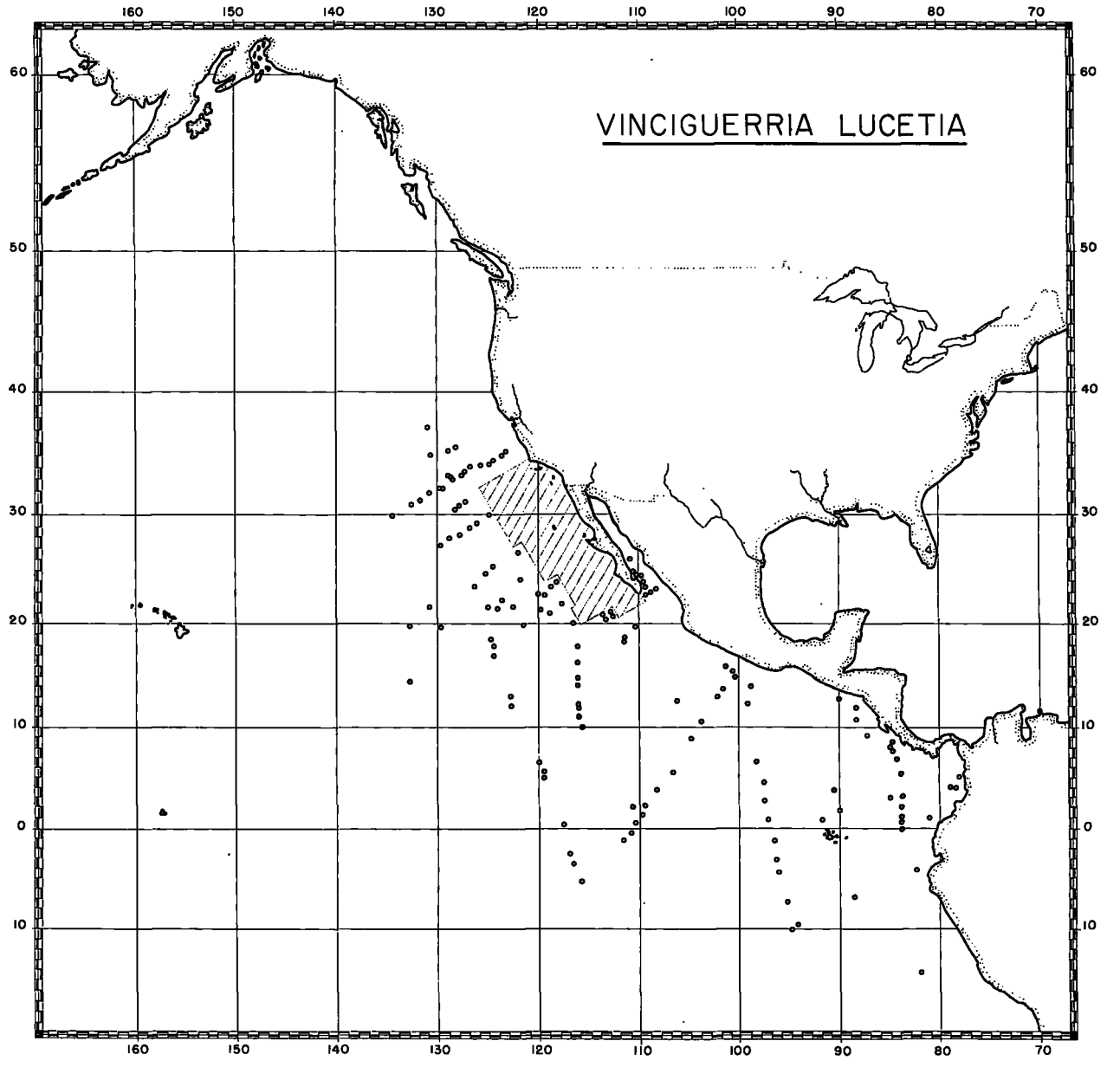

FIGURE 21.—Distribution of *Vinciguerria lucetia* larvae in the eastern Pacific. Bar shading shows the area covered by CCOFI survey cruises of 1951 and 1952 (see figs. 18 and 19).

The CCOFI survey area extends only to the tip of Baja California. Throughout the extensive area to the south, average counts are low, approximating those found off southern Baja California. The range of mean values for subareas south of 20° N. latitude was from 78.50 to 82.00 photophores per side. When the comparisons are based on all individuals taken in each 5 degrees of latitude, the results are as follows:

Latitude	Number of specimens	Average number of photophores per side
15°–20° N.	50	80.55
10°–15° N.	79	80.28
5°–10° N.	92	80.38
0°–5° N.	56	80.67
0°–5° S.	16	81.07
5°–10° S.	11	81.05
10°–15° S.	5	81.00

TABLE 22.—*Variation in number of photophores per side on* Vinciguerria lucetia *collected in the eastern Pacific*

[Area: 35° N.–14° S. lat., 78°–134° W. long.]

Area	Average number photophores per side						Total number of photophores per side	Number of specimens	Number of collections
	Head	Lateral row		Ventral row		AC group			
		OV group	VA group	IV group	VA group				
30°–35° N.:									
117°–120° W	21.0	11.83	11.00	14.83	10.00	14.20	82.86	12	6
120°–130° W	21.0	12.03	10.89	15.03	9.89	14.19	83.03	31	13
130°–134° W	21.0	12.00	10.80	15.00	9.80	14.20	82.80	5	3
27°30′–30° N.:									
117°–120° W	21.0	12.00	10.89	15.01	9.90	14.24	83.04	56	15
120°–129° W	21.0	12.04	10.94	15.04	9.94	14.44	83.40	26	11
25°–27° 30′ N.: 113°–120° W	21.0	11.26	10.96	14.26	9.95	13.85	81.28	50	18
20°–25° N.:									
109° W. and Gulf	21.0	10.91	11.00	13.91	10.00	13.72	80.54	16	5
110°–118° W	21.0	11.08	10.85	14.09	9.85	13.77	80.64	50	18
119°–126° W	21.0	11.89	10.92	14.89	9.92	14.32	82.94	31	7
15°–20° N.:									
102° W	21.0	11.00	10.00	14.00	9.00	13.50	78.50	1	1
111°–116° W	21.0	11.05	10.95	14.05	9.97	13.47	80.49	32	5
124°–125° W	21.0	11.29	10.79	14.29	9.79	13.62	80.78	17	2
10°–15° N.:									
88° W	21.0	11.06	10.96	14.06	9.94	13.75	80.77	26	2
90°–99° W	21.0	11.00	10.60	14.00	9.60	13.80	80.00	5	3
101°–106° W	21.0	11.04	10.69	14.04	9.71	13.62	80.10	26	5
115°–116° W	21.0	10.94	10.74	13.94	9.74	13.59	79.95	17	5
122° W	21.0	11.00	10.75	14.00	9.75	13.50	80.00	4	1
133° W	21.0	11.50	10.50	14.50	9.50	14.00	81.00	1	1
5°–10° N.:									
78° W	21.0	11.00	10.86	14.00	9.84	13.62	80.32	25	1
84°–87° W	21.0	11.00	10.87	13.98	9.89	13.64	80.38	59	6
105° W	21.0	11.00	10.50	14.00	9.50	13.25	79.25	4	1
119°–120° W	21.0	12.12	10.88	15.12	9.88	13.00	82.00	4	3
0°–5° N.:									
79° W	21.0	11.08	10.82	14.08	9.78	13.86	80.62	25	1
80°–90° W	21.0	11.00	11.00	13.97	10.00	13.72	80.69	16	8
92°–98° W	21.0	10.94	10.94	13.94	9.94	13.56	80.32	9	4
109°–110° W	21.0	11.00	11.00	14.00	10.00	14.25	81.25	2	2
111°–117° W	21.0	11.75	10.50	14.75	9.62	13.75	81.37	4	3
0°–5° S.:									
82° W	21.0	11.00	11.00	14.00	10.00	14.00	81.00	4	1
96°–97° W	21.0	11.25	10.92	14.25	9.92	13.58	80.92	6	2
111°–117° W	21.0	11.67	10.75	14.67	9.75	13.50	81.26	6	4
5°–10° S.:									
89° W	21.0	11.00	11.00	14.00	10.00	13.80	80.80	5	1
94°–95° W	21.0	11.12	11.38	14.12	10.38	13.88	81.88	4	3
116° W	21.0	11.00	10.50	14.00	9.50	14.00	80.00	2	1
10°–14° S.: 82° W	21.0	11.00	11.00	14.00	10.00	14.00	81.00	5	1
All areas	21.0	11.34	10.88	14.34	9.89	13.86	81.31	586	162

The lowest average counts were obtained between 10° and 15° N. latitude, but even these specimens average only about 0.4 photophore less than specimens taken off southern Baja California. Specimens obtained from south of the Equator average about 0.4 photophore higher than the material from off southern Baja California.

MOVEMENT BETWEEN AREAS

The ubiquitous distribution of *Vinciguerria lucetia* has already been commented on. Over a very extensive area, it is taken in some stage of development in most plankton hauls that we have examined. In at least a part of its range, however, it can be shown that there must be little or no interchange between the populations in not too widely separated areas. The marked difference in the average number of photophores on specimens from northern and southern Baja California has already been noted. It may be interesting to examine photophore counts from these two regions in more detail. In figure 23, the distributions of photophore counts from northern Baja California (27°30′–30° N. latitude) and southern Baja California (20°–25° N. latitude) are shown. These areas are separated from each other by about 150 miles. It will be noted that there is little overlap in the two distributions—slightly over 20 percent. Thus, only 20 percent of the specimens in the two groups have similar photophore counts. This value may be assumed to represent the maximal amount of interchange (mixing) that could take place between the two populations, at least after the photophores have formed. It is exceedingly unlikely that all the overlap in the two distributions would be the result of mixing, and it is a distinct possibility that little or no interchange actually takes place between the two.

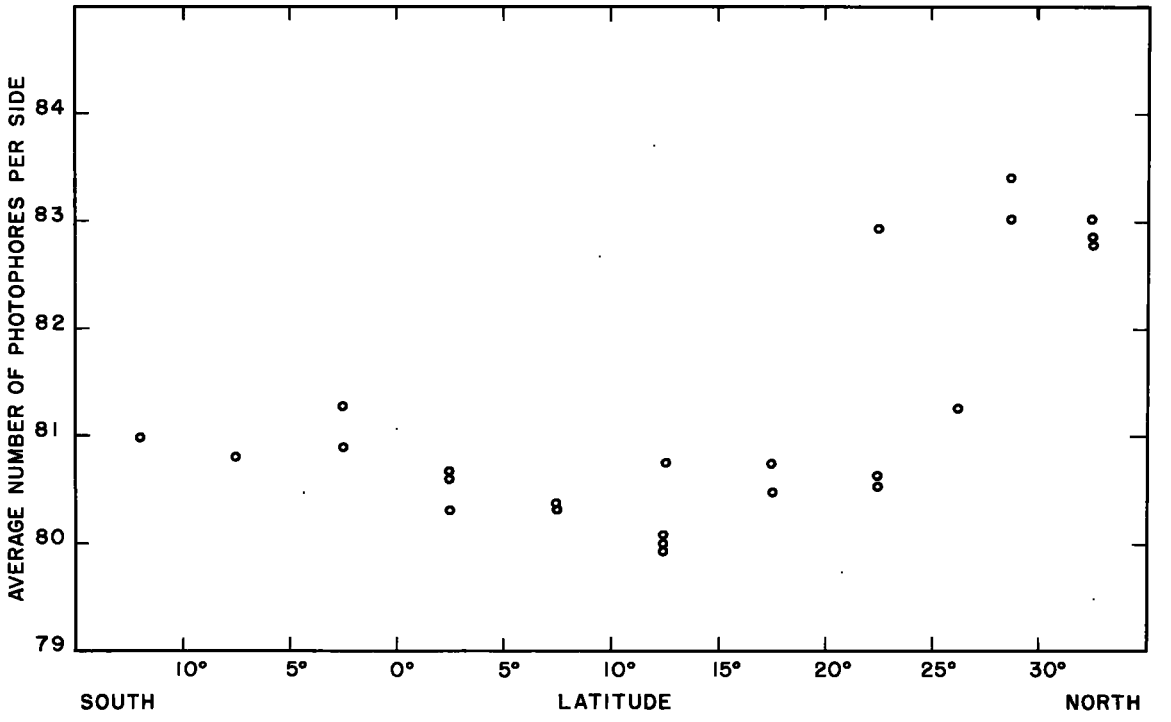

FIGURE 22.—Relation of average photophore number to latitude. This is a plot of photophore counts summarized in table 22. Only counts from areas having five or more specimens are included.

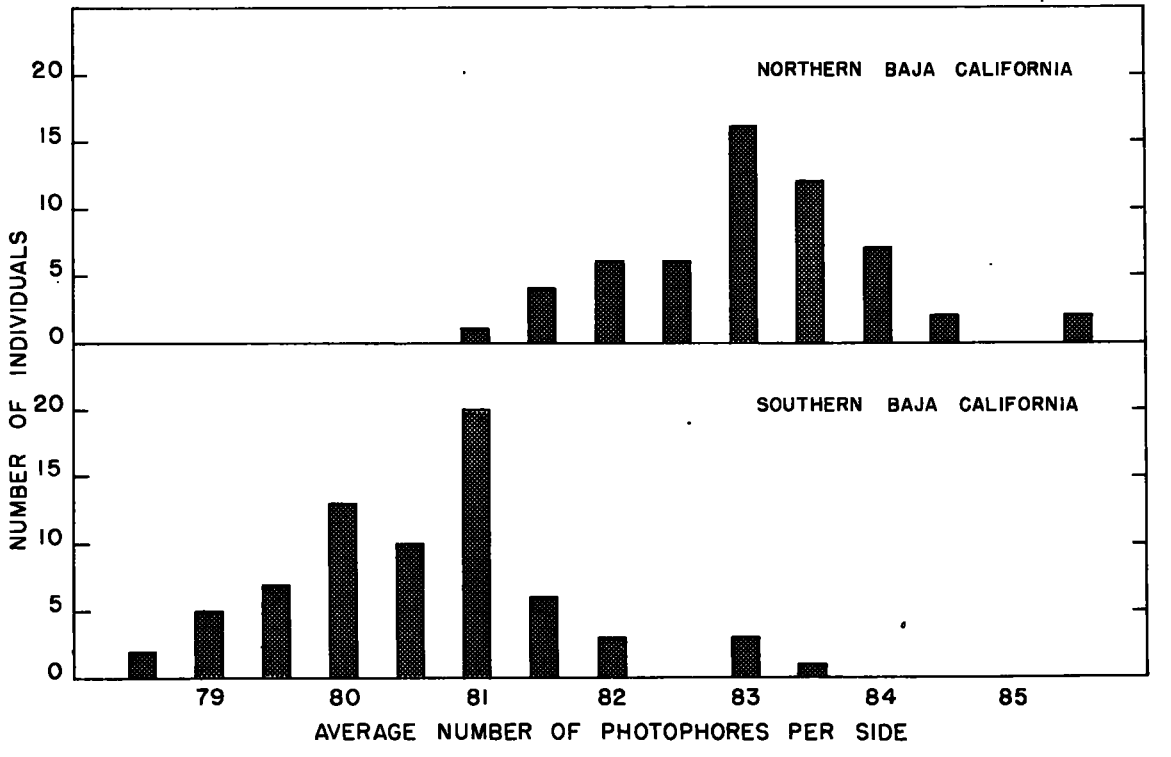

FIGURE 23.—Frequency of photophore counts per side in *Vinciguerria lucetia* from two regions: northern Baja California (27° 30′ N. to 30° N. latitude), and southern Baja California (20° to 25° N. latitude). For each individual the value plotted is the average of the photophore count on the two sides of the body.

Such a marked difference in photophore number as is shown in these two populations does not occur over much of the distribution of *V. lucetia*, hence the technique used here is applicable only to selected areas.

VERTICAL DISTRIBUTION OF EGGS AND LARVAE

Information on vertical distribution of larvae has been derived from two sources: (1) Vertical distribution series taken on cruises made especially for this purpose, and (2) deeper-level closing-net hauls taken during "Norpac."

Eggs and larvae of *V. lucetia* were taken in three series of vertically stratified horizontal net hauls made off central Baja California during April 1955, but only commonly in one series (station 130.60). The distribution of eggs and larvae at this station is shown in figure 24. This series was taken during the night. Larvae were distributed somewhat deeper in the two series taken during the daytime (stations 107.80 and 110.60), mostly between depths of 50 and 100 meters. The thermocline at all three stations was deep, between 75 and 100 meters. Obviously, these data are too sparse to permit any firm conclusions on vertical distribution of *lucetia* eggs and larvae, other than that they occur throughout the upper mixed layer, and to some extent in the thermocline.

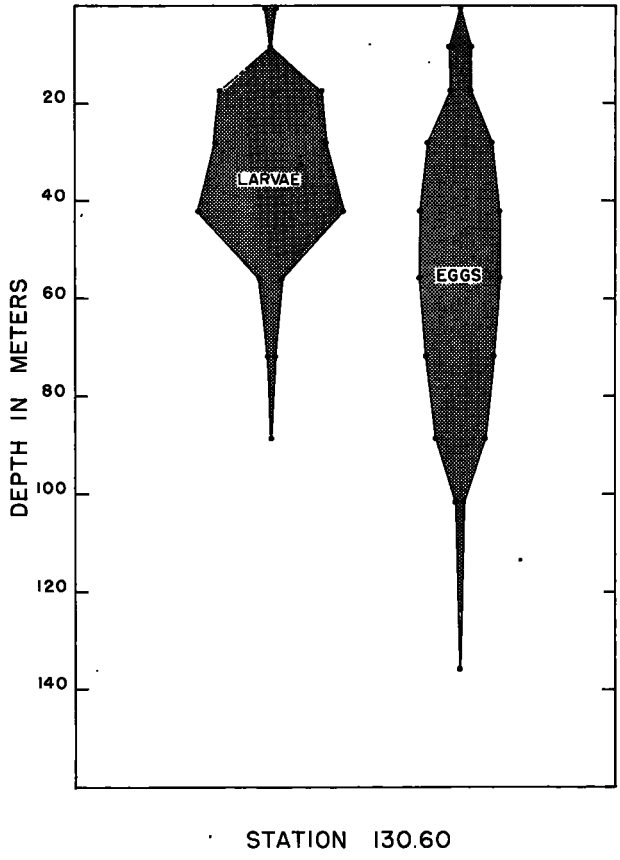

FIGURE 24.—Vertical distribution of eggs and larvae of *Vinciguerria lucetia* at station 130.60 (25°29′ N. lat., 115° 24′ W. long.) on April 21, 1955.

On "Norpac" (CCOFI cruise 5508), two net hauls were taken at most stations, an upper-net haul sampling the upper level from approximately 135 meters deep to the surface, and a closing-net haul sampling the level between approximately 270 to 135 meters deep.

Three species of *Vinciguerria* larvae were taken at 72 stations at which both nets were used. Only 1 upper-set haul in this group did not contain *Vinciguerria* larvae, while they were taken in only 12 closing-net hauls. The total number of *Vinciguerria* larvae taken in these upper-net hauls was 1,723, as compared with a total of 29 in closing-net hauls, or approximately 60 times as many. Hence, less than 2 percent of the larvae was taken by the closing net in the deeper layer sampled, which was of a thickness equivalent to the stratum sampled by the upper-net haul.

Although these results do not preclude the possibility that some *Vinciguerria* larvae may occur at depths below those sampled by the upper and closing nets, it seems unlikely that any significant quantity occurs at deeper levels.

OTHER SPECIES OF *VINCIGUERRIA* OCCURRING IN THE EASTERN PACIFIC

It should be noted that the generic name *Vinciguerria*, proposed by Jordan and Evermann (1896: 577), but first reported in Goode and Bean (1895: 513), has been accepted without a strict regard to priority. Bonaparte (1841) described a subgenus *Poweria* under *Ichthyococcus*, with *P. poweriae* as type species. Apparently this description was overlooked by Jordan and Evermann at the time they proposed the generic name of *Vinciguerria* with *V. attenuata* as the type species. However, in conformity with the principle of conservation (Hubbs 1956) adopted by the Fourteenth International Congress of Zoology for incorporation in the International Rules of Zoological Nomenclature, and in view of the fact that apparently no previous author has

adopted the name *Poweria*, it seems permissible and proper to retain the familiar name *Vinciguerria*.

Norman (1930), in his monograph of the family Gonostomatidae, has listed six species of *Vinciguerria*, of which two were considered doubtful. The 4 species considered valid were the following: *attenuata*, *poweriae*, *sanzoi*, and *lucetia;* the 2 doubtful ones were *nimbaria* and *raoulensis*. As Horsburgh (1935) has shown, *sanzoi* is identical with *nimbaria*.

The species described by Waite (1910) under the name of *Gonostoma raoulensis* may be a synonym of *V. nimbaria*—the original description is inadequate. The fin formula was given as D. 10; A. 10; V. 6; P. 11; C. 8+15. These counts, if accurate, would set this species apart from all other species of *Vinciguerria*, which never have fewer than 13 dorsal, 12 anal, 7 ventral, and 19 principal and 11 to 14 secondary (procurrent) caudal rays. The caudal count given by Waite is obviously inaccurate, and we assume that little more reliance can be placed on the counts of other fins. The characters of *G. raoulensis* that suggest a close relationship to *nimbaria* are the following: (1) Gill rakers, 5+13 on first arch; (2) presence of a symphyseal pair of photophores; and (3) number of body photophores, especially a high IV number (16).

Vinciguerria pacifici, described by Hildebrand (1946) from off northern Peru, does not appear to us to be distinct from *lucetia*.

Narooma benefica Whitley (1935) is probably a synonym of *V. lucetia*. The description is based on a specimen that was washed ashore in southern New South Wales, Australia, and slightly attacked by beach crustacea before collection. The counts of rays in the dorsal (8+?) and anal (12) fins are probably incomplete. The total photophore number is approximately 80 on each side. The grouping as given by Whitley is probably inaccurate since he lists 6 isthmian, 16 ventral IV, and 12 lateral OV photophores on a side. However, *Vinciguerria* characteristically has 7 isthmian photophores and 3 less lateral OV than ventral IV photophores, hence the grouping probably should be 7 isthmian, 15 ventral IV, and 12 lateral OV photophores on a side. A symphyseal photophore is present. Gill rakers are described as slender and numerous, but an exact count is not given.

The four species of *Vinciguerria* fall naturally into two groups, which are easily separated both as larvae and as adults. One group contains *attenuata* and *poweriae*, the other group contains *lucetia* and *nimbaria*.

The two groups are easily distinguishable in the embryonic stage. The eggs of *attenuata* and *poweriae* have an oil globule, which is lacking in the eggs of *lucetia* and *nimbaria*.

The simplest character separating late-larval and early-metamorphic stages of the two groups is pigmentation, especially in the position of the caudal pigment spot. The spot has a mediolateral position in *attenuata* and *poweriae*, whereas it is just above the ventral margin in *lucetia* and *nimbaria*. There are other differences in pigmentation between the two groups. In *lucetia* and *nimbaria* the pigment at the base of the caudal fin usually consists of 2 dashes above and 1 below the midline. Also, there are generally 2 or 3 melanophores above the anal fin. Both of these pigment groups are lacking in *attenuata* and *poweriae*.

The two groups are readily separated in the adolescent and adult stages by the presence or absence of the symphyseal pair of photophores. This photophore group is developed in *lucetia* and *nimbaria* and lacking in *poweriae* and *attenuata*.

Sanzo (1913, 1931) and Jespersen and Tåning (1926) have called attention to several characters that are useful in separating the larvae of *poweriae* from *attenuata*. Both have the conspicuous axial caudal pigment spot, but this is the only pigmentation on larvae of *poweriae*. *V. attenuata*, on the other hand, has pigment above the air bladder and sometimes has a small melanophore on the anal papilla.

An important difference between larvae of these two species is in the distance from snout to anus. The proportion is shorter in *attenuata* than in any of the other species of *Vinciguerria*, being less than 70 percent of the standard length. In larvae of *poweriae*, the distance from snout to anus averages about 75 percent of the standard length (range, 73–79 percent).

Larvae of *poweriae* have a "peculiar spot" (quoting Jespersen and Tåning, 1926) above the anal papilla. Both Sanzo and Jespersen and Tåning have called attention to this spot. It is not a pigment area, but a small, conspicuous oval structure that may be a part of the urinary system.

Three species of *Vinciguerria* occur in the east-

ern Pacific: *lucetia*, *poweriae*, and *nimbaria*. Brief descriptions of the developmental stages of the latter two species are given in following sections.

Vinciguerria poweriae (Cocco)

Gonostomus poweriae Cocco, 1838, Nuovi Ann. Sci. Nat. II, p. 167 (original description).

Ichthyococcus poweriae Bonaparte, 1841. Icon. Fauna Ital., F. 27, p. 138, fig. 8.

Maurolicus poweriae Günther, 1864. Cat. Fish., vol. 5, p. 390 (brief description).

Vinciguerria poweriae Sanzo, 1913. Mem. R. Com. Talassogr. Ital., vol. XXXV, pp. 3–7, figs. 6–9 (description of larvae). Sanzo, 1931. Fauna e Flora del Golfo di Napoli, Monogr. 38, pp. 71–75, figs. 50–53 (description of eggs and larvae). Jespersen and Tåning, 1919. Vidensk. Medd. Dansk Naturh. Foren., vol. 70, pp. 218–220, figs. 1 and 4 (prometamorphic stage and adult figured). Jespersen and Tåning, 1926. Rept. Danish Ocean. Exped., 1908–1910, vol. 2 (Biology), A 12, pp. 22–37, figs. 13–1, 14–1, 15–1, 16–1, 17–1 (comparison of *V. poweriae* with three other species).

The *poweriae* material available from the eastern Pacific consisted of eggs, larvae, and metamorphosing individuals. We obtained no material of either juveniles or adults. The distribution (occurrences) of the species on "Norpac" is shown in figure 25. Eggs from 21 localities were measured (table 23).

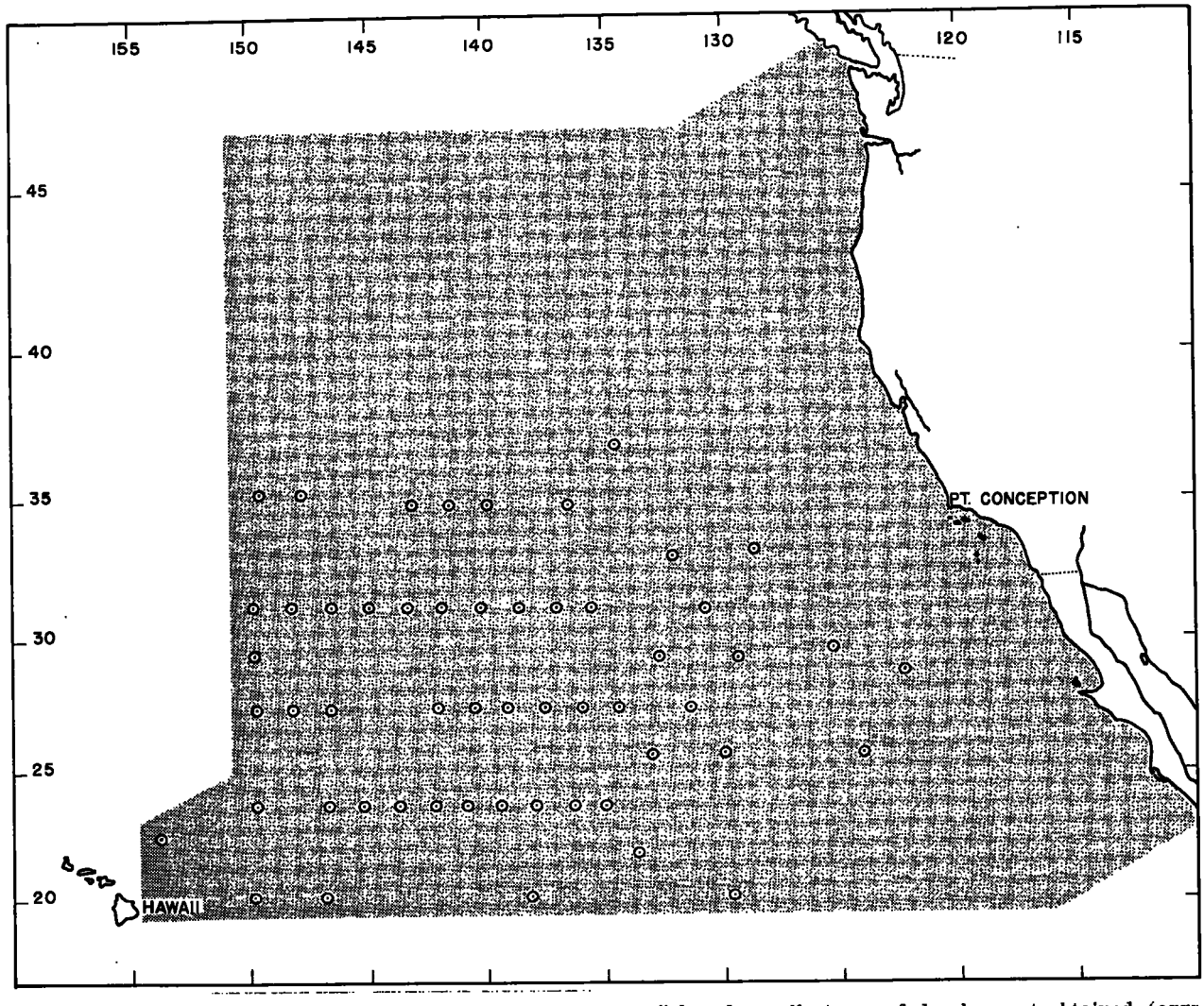

FIGURE 25.—Distribution of *Vinciguerria poweriae* on "Norpac," based on all stages of development obtained (eggs, larvae, metamorphosing individuals). Shading indicates the total area covered by agencies cooperating in the California Cooperative Oceanic Fisheries Investigations.

TABLE 23.—*Measurements of eggs of* Vinciguerria poweriae *collected at 21 stations in the eastern Pacific, in 1955*

Norpac station	North latitude	West longitude	Date	Number of eggs measured	Egg diameter (mm.)	
					Mean	Range
No. 59	34°53′	143°23′	VIII-17	20	0.813	0.76–.85
No. 60	35°08′	148°00′	VIII-23	11	.817	.78–.85
No. 61	35°07′	149°40′	VIII-23	9	.807	.79–.82
No. 68	33°02′	132°15′	VIII-21	18	.797	.75–.82
No. 78.5	31°11′	138°54′	VIII-28	8	.808	.78–.85
No. 79	31°09′	140°29′	VIII-28	5	.799	.76–.83
No. 79.5	31°10′	142°02′	VIII-27	5	.800	.78–.82
No. 81.5	31°10′	148°24′	VIII-26	7	.809	.80–.82
No. 89	29°34′	125°40′	IX-3	10	.803	.77–.83
No. 90	29°17′	129°45′	IX-1	5	.802	.78–.82
No. 91	29°17′	132°57′	VIII-31	7	.797	.76–.83
No. 101	27°26′	134°45′	VIII-19	18	.790	.76–.82
No. 101.5	27°28′	136°14′	VIII-19	14	.803	.78–.83
No. 102.5	27°26′	139°16′	VIII-20	14	.784	.75–.82
No. 126	23°43′	135°11′	VIII-20	14	.808	.78–.83
No. 127	23°40′	138°16′	VIII-21	5	.786	.77–.80
No. 127.5	23°40′	139°41′	VIII-21	24	.795	.76–.83
No. 128	23°40′	141°06′	VIII-22	9	.797	.76–.82
No. 128.5	23°38′	142°22′	VIII-22	5	.789	.76–.81
No. 129.5	23°46′	145°30′	VIII-23	9	.795	.76–.84
No. 130	23°48′	146°56′	VIII-23	10	.796	.78–.83

Measurements and meristic counts were made on 26 larvae, ranging in size from 8.3 to 18.5 millimeters in length (table 24), and on 12 metamorphosing specimens (table 25). Four stages of eggs are illustrated in figure 26, and a midmetamorphosing specimen is shown in figure 27.

The *poweriae* material obtained in the eastern Pacific differs in several respects from that collected in the Mediterranean, as characterized by Jespersen and Tåning (1926). The points of agreement, however, are more numerous and trenchant than the differences. We shall discuss three differences and then point up seven pertinent points of agreement between our material and that described by Jespersen and Tåning.

1. *Size at metamorphosis.*—We have studied six specimens of prometamorphosing *V. poweriae.*

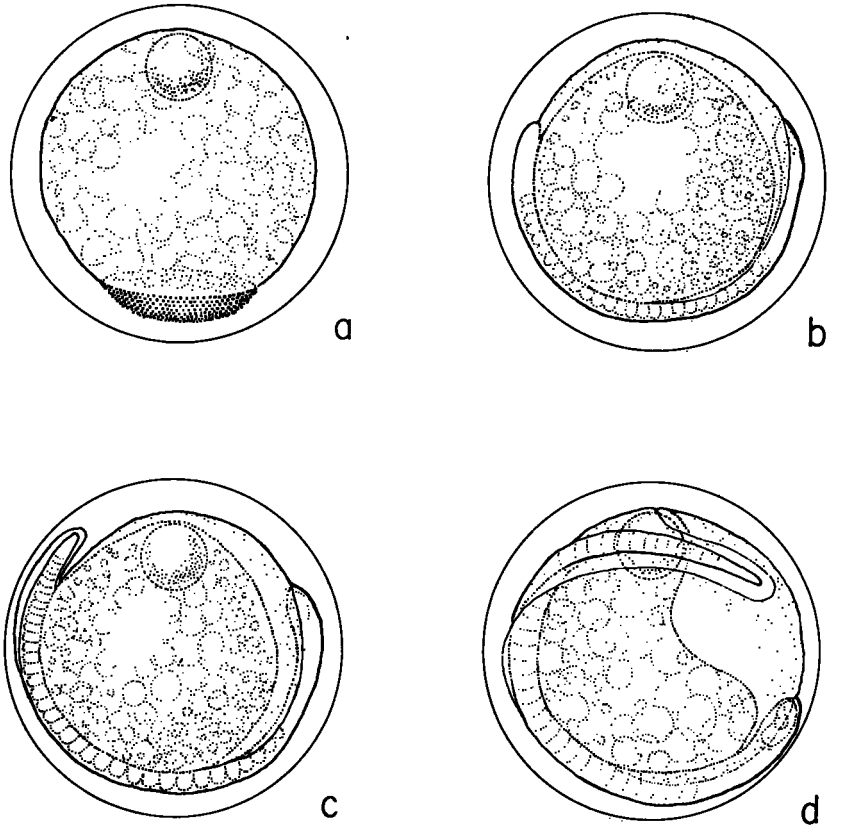

FIGURE 26.—Development of the egg of *Vinciguerria poweriae: a*, early stage, at development of blastodermal cap; *b*, middle stage, soon after blastopore closure; *c*, middle stage, with tail separating from yolk but still in same plane as embryo; *d*, late stage.

These ranged in size from 19.7 to 22.3 millimeters standard length. The size range given by Jespersen and Tåning for early metamorphosing individuals of this species was between 16 and 20 millimeters standard length.

2. *Number of vertebrae.*—The average number of vertebrae in Pacific material was 40.0, with a range of 39 to 41 vertebrae in 12 specimens. Jespersen and Tåning reported 38 or 39 vertebrae for Mediterranean material.

3. *Number of photophores.*—Photophore counts are given in table 26 for 12 specimens of metamorphosing *V. poweriae* collected from the eastern Pacific. There is close agreement in photophore counts between the material from the Pacific and from the Mediterranean, except in the number of AC photophores. Although our material is confined to metamorphosing individuals, it is a simple matter to determine from them what the full complement of AC photophores will be: it will aver-

TABLE 24.—*Measurements and meristic counts of larval* Vinciguerria poweriae *from the eastern Pacific*

[BF—base formed; U—urostyle]

Area	Body measurements (in mm.)						Meristic counts [1]					Number of gill rakers	Number of vertebrae ossified
	Standard length	Head length	Eye width	Depth at pectoral	Snout to anus	Snout to dorsal	Dorsal	Anal	Caudal fin: Principal	Caudal fin: Secondary D	Caudal fin: Secondary V		
29°17′ N., 129°45′ W	8.3	1.54	0.28	0.52	6.20		BF	BF	11	0	0		
23°42′ N., 143°57.5′ W	9.1	1.87	.35	.70	7.00		BF	BF	19	0	0		
29°34′ N., 125°40′ W	10.5	2.11	.38	.68	8.00		8	BF	19	0	0		
33°02′ N., 132°15′ W	10.8	2.05		.68	8.20		6	BF	19	0	0		
33°02′ N., 132°15′ W	11.5						8	BF	19	0	1		
31°09.5′ N., 148°24′ W	11.5	2.10		.79	8.80		10	6	19	1	1		
29°34′ N., 125°40′ W	12.0	2.24	.40	.79	9.50		8	BF	19	0	0		
31°09.8′ N., 142°02′ W	12.0	2.16	.40	.72	9.10		9	BF	19	0	0		
19°57.5′ N., 129°44′ W	12.4	2.29	.44	.76	9.60		11	9	19	2	1	0+7	
29°17′ N., 129°45′ W	12.5	2.39		.74	9.40		10	7	19	1	1	0+6	
27°25′ N., 150°00′ W	12.6	2.50	.51	.95	9.90		10	6	19	2	1	0+7	
34°51′ N., 136°45′ W	12.7	2.43	.39	.85	9.75	8.70							
34°51′ N., 136°45′ W	13.3	2.60	.42	.91	10.20	9.10							
31°12′ N., 137°19′ W	14.0		.42	.87	10.80	9.60							
21°52′ N., 133°51′ W	15.1	2.92	.46	.86	11.30	9.80	13	11	19	2	1	0+8	
29°17′ N., 132°57′ W	15.7	3.02		1.18	11.70		12	11	19	2	1	0+8	12+U
27°30.5′ N., 140°49′ W	15.9	3.03	.58	1.14	12.30	10.60	12	10	19	2	1	0+9	14+U
31°09.5′ N., 148°24′ W	16.0	2.89	.47	1.05	12.00	10.60	12	10	19	2	1	0+8	
34°51′ N., 136°45′W	16.1	2.80	.51	1.14	12.00	10.25							
25°34.5′ N., 124°21′ W	16.2	2.97	.47	1.26	12.50	10.80	12	9	19	2	1	0+9	8+U
23°40′ N., 141°06′ W	17.0						15	14	19	3	2	0+12	40
31°08.5′ N., 130°59′ W	17.0	3.02	.63	1.16	12.60	10.90	13	12	19	2	1	0+9	21+U
29°34′ N., 125°40′ W	17.1	3.20	.60	1.19	12.90	11.40	13	12	19	3	2	0+10	18+U
31°11′ N., 145°10′ W	17.2	3.13	.52	1.18	12.95	11.10	12	12	19	5	3	0+10	
31°08.5′ N., 130°59′ W	17.9	3.28		1.34	13.50	11.50	14	12	19	3	2	0+11	31+U
29°17′ N., 129°45′ W	18.5	3.69	.66	1.37	13.50	11.90	14	13	19	3	2	0+11	[2] 39

[1] No pectoral or ventral rays are formed during larval period. Larval pectorals are present on all specimens and ventral buds are developed on specimens over 15 mm. long.

[2] Penultimate vertebra still lacking; total number of vertebrae will be 40.

TABLE 25.—*Measurements and meristic counts in metamorphosing stages of* Vinciguerria poweriae *from the eastern Pacific*

Area	Body measurements (in mm.)							Meristic counts							Number of gill rakers	Number of vertebrae
	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus	Dorsal	Anal	Pectoral	Ventral	Caudal: Principal	Caudal: Secondary D	Caudal: Secondary V		
Prometamorphic:																
31°12′ N., 150°07′ W	19.7	3.87	0.79	1.76	10.2	12.1	14.6	15	14	1	6	19	7	4	2+12	40
32°03′ N., 130°21′ W	21.1	4.00	.79	1.70	10.6	13.2	15.9	14	14	4	7	19	8	4	2+12	40
31°12′ N., 137°19′ W	21.2	3.85	.60	1.65	10.8	13.6	15.8	15	13	0	Rays?	19	6	4	0+12	41
31°12′ N., 137°19′ W	21.8	4.00	.86	1.87	10.9	13.3	15.7	15	13	0	5	19	9	4	2+12	40
31°08.5′ N., 130°59′ W	22.1	4.20		1.76	11.0	13.5	15.5	14	14	0	6	19	8	4	1+12	39
29°21′ N., 126°13′ W	22.3	4.25	.86	1.80	11.0	13.7	16.2	14	14	2/3	7	19	8	4	1+12	40
Midmetamorphic:																
32°38′ N., 172°21′ W	17.2		1.12	2.47	8.5	10.4	11.8									
20°07′ N., 138°22.5′ W	19.8	4.38	.89	2.08	10.6	12.2	14.3	14	12	10	7	19	7	4	2+12	41
29°21′ N., 126°13′ W	20.2	4.35	1.20	2.60	9.5	11.0	13.2	15	15	10	7	19	7	4	3+12	40
26°53′ N., 121°39′ W	22.9	4.30	.90	2.23	11.5	14.1	15.6	13	14	10	7	19	7	4	3+12	
Postmetamorphic:																
32°53′ N., 134°13′ W	17.9	4.25	1.43	2.94	8.9	9.8	12.0	14	14	10	7	19	8	4	3+12	39
32°52′ N., 131°58′ W	18.2	4.50	1.35	3.25	9.0	10.0	12.5	15	14	10	7	19	8	4		40

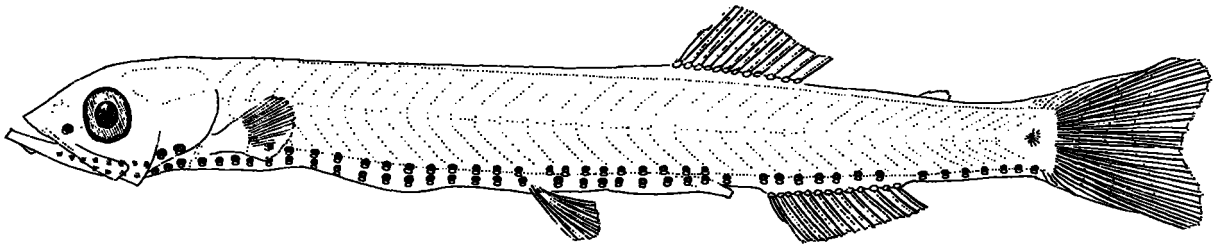

FIGURE 27.—Midmetamorphosing specimen of *Vinciguerria poweriae*, 22.9 mm. in standard length, from "Norpac" station 112D (26°53′ N., 121°39′ W.)

age 14.10 per side (range, 13–15), as compared to an average of 13.00 per side (range, 12–14) for Mediterranean specimens. Jespersen and Tåning did not report any variation in the number of ventral IV photophores (always 16) but did indicate variation in the number of lateral OV photophores (12 or 13). It is likely that variation in the number of IV photophores was overlooked by these workers, as we have found no specimen of this or of any other species of *Vinciguerria* in which there is variation in the number of photophores in the OV group but not in the IV group. The OV group averages three photophores less on a side than the IV group. The anterior three pairs of IV photophores have no counterparts in the OV group, but otherwise the two groups usually correspond photophore for photophore. In the material of *V. poweriae* we have studied, the lateral OV photophore group invariably had three photophores less on a side than the IV group. We found 15 to 17 photophores per side in the IV group (average, 15.96) and 12 to 14 photophores per side in the OV group (average, 12.96). Data on range and average counts of photophore groups in Pacific material of *V. poweriae*, *V. nimbaria*, and *V. lucetia* are given in table 27.

The points of agreement of *V. poweriae*, as described by Jespersen and Tåning from Mediterranean material, with our material from the eastern Pacific are rather numerous. We will call attention to seven:

1. *Eggs.*—The eggs of *V. poweriae* have been characterized by Sanzo (1931) as having an oil globule and being similar to the eggs of *V. attenuata*. We have had no difficulty in identifying the eggs of *V. poweriae* from the Pacific. The size range and average diameter of eggs from 21 localities were summarized in table 23. The range in size is from 0.75 to 0.85 millimeters. Eggs taken in the northern part of the distribution tend to be slightly larger than those taken farther south, but the difference is not as marked as that shown for *V. lucetia*. The single oil globule measures 0.17 to 0.19 millimeters in diameter. There is no evidence of the thin inner shell membrane that is found in eggs of *V. lucetia* and *V. nimbaria*.

TABLE 26.—*Number of photophores in metamorphosing stages of* Vinciguerria poweriae *from the eastern Pacific*

[Both sides of body given]

Station	North latitude	West longitude	Standard length	Head				Lateral row		Ventral row		Anal-caudal (AC group)	Number of incomplete photophores	Total number of photophores
				Orb and Op	SO	Br	Is	OV group	VA group	IV group	VA group			
Prometamorphic:			*Mm.*											
Norpac 82D	31°12′	150°07′	19.7	4-4	0	8-8	7-7	13-13	8-8	16-16	9-9	6+7-6+7	4-4	82-82
5009-70.175D	32°03′	130°21′	21.1	4-4	0	8-8	7-7	13-13	9-9	16-16	9-9	6+7-6+8	3-3	82-83
Norpac 78	31°12′	137°19′	21.2	4-4	0	8-8	7-7	13-14	9-8	16-17	10-9	? ?	4-4	----------
Norpac 78D	31°12′	137°19′	21.8	4-4	0	8-8	7-7	13-13	8-8	16-16	9-9	5+7-6+7	4-4	81-82
Norpac 76D	31°08.5′	130°59′	22.1	4-4	0	8-8	7-7	12-13	8-7	15-16	9-8	6+7-6+7	4-4	80-80
5304-90.152	29°21′	126°13′	22.3	4-4	0	8-8	7-7	13-13	9-9	16-16	9-10	6+8-5+7	3-4	83-83
Midmetamorphic:														
Chinook 14	32°38′	172°21′	17.2	4-4	0	8-8	7-7	13-13	9-9	.6-16	9-9	6+7-6+6	3-3	81-82
Norpac 153D	20°07′	138°22.5′	19.8	4-4	0	8-8	7-7	13-13	9-9	16-16	9-9	6+7-7+7	3-3	82-83
5304-90.152	29°21′	126°13′	20.2	5-5	0	8-8	7-7	13-13	9-9	16-16	9-9	14-6+8	1-2	82-83
Norpac 112D	26°53′	121°39′	22.9	4-4	0	8-8	7-7	12-13	9-8	15-16	9-8	7+7-7+7	3-3	81-81
Postmetamorphic:														
N. Holiday 64	32°53′	134°13′	17.9	5-5	0	8-8	7-7	13-13	9-9	16-16	9-9	13-14	1-1	81-82
N. Holiday 65	32°52′	131°58′	18.2	5-5	0	8-8	7-7	13-13	8-8	16-16	9-9	? ?	2-2	----------

TABLE 27.—*Full complement of photophores per side in three species of* Vinciguerria *from eastern Pacific*

[Figures in parentheses indicate range]

Photophore group	*V. poweriae*		*V. nimbaria*		*V. lucetia*	
	Range	Average	Range	Average	Range	Average
Orb and Op	5	5.00	5	5.00	5	5.00
SO	0	0	1	1.00	1	1.00
Br	8	8.00	8	8.00	7- 9	8.00
Is	7	7.00	7	7.00	6- 8	7.00
Lateral:						
OV	(12–14)	12.96	(13–14)	13.08	(10–13)	11.33
VA	(9–11)	10.00	(10–12)	10.92	(9–12)	10.88
Ventral:						
IV	(15–17)	15.96	(16–17)	16.08	(13–16)	14.33
VA	(8–10)	9.00	(9–11)	9.92	(8–12)	9.89
AC	(13–15)	14.10	(12–15)	13.35	(12–16)	13.86
Total number of photophores per side	(81–84)	82.02	(84–87)	84.35	(78–86)	81.29

2. *Pigmentation of larvae.*—In both localities, larval pigment is confined to the centrally placed caudal pigment spot.

3. *Supra-anal structure.*—The structure or spot above the anal papilla was present in the material from both areas.

4. *Low number of maxillary teeth.*—Jespersen and Tåning called attention to the fact that *V. poweriae* has a lower number of maxillary teeth than other species of *Vinciguerria* of corresponding sizes. We have found the same situation in Pacific material. No larva of *V. poweriae* has been examined that had more than 10 maxillary teeth. Prometamorphosing individuals have only 8 to 12 maxillary teeth; the few midmetamorphosing individuals studied have had 8 or 9 maxillary teeth. It is characteristic of the development of maxillary teeth for marked changes to occur during midmetamorphosis. The oblique teeth first appear during this stage, and the remaining teeth are unequal in size, not subequal as in late larvae. This difference is even more marked in *V. nimbaria* than in *V. poweriae*. Some or most of the larval maxillary teeth must be resorbed or shed, to account for the reduction in number at a time when oblique teeth and small straight teeth are being added to the maxillary. The number of maxillary teeth in late larvae and metamorphosing stages of the three Pacific species of *Vinciguerria* are summarized in table 28.

The greater ranges in maxillary teeth shown for the late stages of *V. lucetia* probably reflect the greater abundance of material of this species. If more specimens of the other two species were available, the ranges would undoubtedly be greater.

TABLE 28.—*Comparison of the number of maxillary teeth in three species of* Vinciguerria *from the eastern Pacific*

Stage	*V. poweriae*	*V. nimbaria*	*V. lucetia*
Late larval	7–10	13–15	10–13
Prometamorphic	8–12	14–19	12–16
Midmetamorphic	8–9	11–13	12–20
Postmetamorphic	13–14	12–19	14–28

5. *Low anal-ray count.*—The anal-ray count in *V. poweriae* is the lowest of any of the four species of *Vinciguerria*, and this species is the only one in which the average number of anal rays is lower than the average number of dorsal rays. The ray counts of the Pacific material of *Vinciguerria* are summarized in table 29.

TABLE 29.—*Comparison of fin-ray counts in three species of* Vinciguerria *from the eastern Pacific*

Fin	*V. poweriae*		*V. nimbaria*		*V. lucetia*	
	Range	Average	Range	Average	Range	Average
Dorsal	14–15	14.50	14–15	14.09	13–16	14.59
Anal	12–15	13.70	14–15	14.64	13–17	15.14
Pectoral	10	10.00	10	10.00	10	10.00
Ventral	7	7.00	7	7.00	7	7.00

6. *Low gill-raker count.*—The Pacific specimens of *V. poweriae* have identical gill-raker counts with those reported by Jespersen and Tåning for Mediterranean material. The raker counts are much lower for comparable stages of development than the counts obtained from specimens of *V. nimbaria* and *V. lucetia* (table 30). It will be noted that *V. poweriae* obtains its full complement of rakers at an earlier stage of development than do the other Pacific species. The full complement of 12 rakers on the lower limb is developed before the end of the larval period, and the small group (three) on the upper limb is developed by midmetamorphosis. The full complement of gill rakers was not found on the lower limb of *V. nimbaria* until midmetamorphosis or on the upper limb until postmetamorphosis. The development of the full set of gill rakers on the upper limb of *V. lucetia* is even more delayed.

TABLE 30.—*Number of gill rakers on the first branchial arch in three species of* Vinciguerria *from the eastern Pacific*

Stage	*V. poweriae*	*V. nimbaria*	*V. lucetia*
Late larval	0+9–12	0+12–13	0+15–16
Prometamorphic	0–2+12	2–3+13–14	0–4+16–22
Midmetamorphic	2–3+12	3–4+13–15	3–5+17–21
Postmetamorphic	3+12	5+15	6–9+18–23
Juvenile and adult	No data [1]	5+15	8–10+18–23

[1] Jespersen and Tåning (1926) report 3 to 4+11 to 12 gill rakers for juvenile and adult material of *V. poweriae* from the Mediterranean.

TABLE 31.—*Number and location of late-forming photophores per side in four species of* Vinciguerria

[Figures in parentheses indicate range]

Location of late-forming photophores	Number of late-forming photophores in—									
	V. poweriae				*V. attenuata* [1]		*V. nimbaria* [2]		*V. lucetia* [2]	
	Eastern Pacific		Mediterranean [1]		Average number	Range	Average number	Range	Average number	Range
	Average number	Range	Average number	Range						
Opercular	1		1		1		1		1	
Symphyseal	0		0		0		1		1	
Lateral VA	1.70	(1–2)	2.05	(1–3)	3.93	(3–6)	3	(3)	3.10	(3–4)
Anal-Caudal	1		1		1		1		1	
Total	3.70		4.05		5.93		6		6.10	

[1] From Jespersen and Tåning (1926).
[2] From eastern Pacific.

7. *Late-forming photophores.—V. poweriae* has the lowest number of late-forming photophores of any species of *Vinciguerria*. Available information on late-forming photophores is summarized in table 31.

At the initial formation of the photophores *V. poweriae* usually lacks only four photophores on a side, while the other three species usually lack six. There is a slight, but probably not a significant, difference between the Pacific and Mediterranean material of *V. poweriae* in the number of late-forming photophores: 3.7 as compared with 4.05.

Differences in pigmentation between *poweriae* and *attenuata* on the one hand and *lucetia* and *nimbaria* on the other have already been commented on. Aside from pigmentation, the larva of *poweriae* is quite similar in appearance to that of *lucetia;* however, the larvae of the two species differ somewhat in body proportions. The differences are not marked, yet are greater than those between larvae of *lucetia* and *nimbaria*. Statistics describing the regressions of body proportions on standard length for *poweriae* larvae are given in table 32. In addition to standard length, measurements were made of five body parts: head length, depth at pectoral, width of eye, distance from snout to anus, and distance from snout to origin of dorsal fin. The body proportions of larvae of *poweriae* differ from those of larvae of *lucetia* in the following principal ways: (1) The head is about 10 percent shorter (fig. 28); (2) the body is more slender; depth at pectorals is about 15 percent less than in *lucetia* larvae of the same standard length; and (3) the eye is smaller, at least in width (the dimension taken).

TABLE 32.—*Statistics describing regression of body measurements on standard length for larvae of three species of* Vinciguerra

Body proportion	Size range	$\bar{x}$	$\bar{y}$	n	b	a	$sy{\cdot}x$
Head length:	*Mm.*						
lucetia	2.2–18.2	8.15	1.73	100	0.214	0.012	0.1219
nimbaria	5.4–16.0	10.34	2.08	30	.199	.022	.1140
poweriae	8.3–18.5	14.00	2.64	24	.180	.125	.1245
Body depth:							
lucetia	2.2–18.2	8.22	0.67	97	.098	−.137	.0727
nimbaria	5.4–16.0	10.32	0.89	32	.103	−.173	.1060
poweriae	8.3–18.5	14.00	0.97	25	.082	−.177	.0933
Eye diameter:							
lucetia	2.2–18.2	8.50	0.34	91	.039	.007	.0340
nimbaria	5.4–16.0	10.95	0.43	27	.040	−.011	.0440
poweriae	8.3–18.5	14.08	0.47	20	.031	.035	.0497
Snout to dorsal:							
lucetia	6.6–18.2	11.08	7.01	57	.565	.739	.1887
nimbaria	10.1–16.0	12.90	8.17	16	.574	.764	.1281
poweriae	12.7–18.5	15.90	10.47	14	.539	1.896	.1725
Snout to anus:							
lucetia	2.2–18.2	8.15	6.00	100	.734	.020	.2044
nimbaria	5.4–16.0	10.30	7.77	31	.731	.242	.1417
poweriae	8.3–18.5	14.00	10.62	25	.725	.468	.1893

Vinciguerria nimbaria (Jordan and Williams)

Zalarges nimbarius Jordan and Williams, *in* Jordan and Starks, 1896. Proceed. California Acad. Sci., Ser. 2, vol. 5, p. 793, pl. 76 (original description).

Vinciguerria nimbaria Gilbert, 1908. Mem. Mus. Compar. Zool., vol. 26, p. 237 (description emended). Horsburgh, 1935. Proceed. California Acad. Sci. (Ser. 4), vol. 21, pp. 230–231 (description emended, *sanzoi* placed in synonymy).

Vinciguerria sanzoi Jespersen and Tåning, 1919. Vidensk. Medd. Dansk Naturh. Foren., vol. 70, pp. 218–220, figs. 2, 5 (original description). Jespersen and Tåning, 1926. Rept. Danish Ocean. Exped., 1908–1910, vol. 2 (Biology), A12, pp. 23–29 (*V. sanzoi* compared with other species of *Vinciguerria*).

?*Gonostoma raoulensis* Waite, 1910. Trans. New Zealand Inst., vol. 42, p. 373, pl. 35, fig. 1 (original description).

Gilbert (1908) first called attention to an inaccuracy in the original description by Jordan and Williams of *Zalarges nimbarius* with regard to the

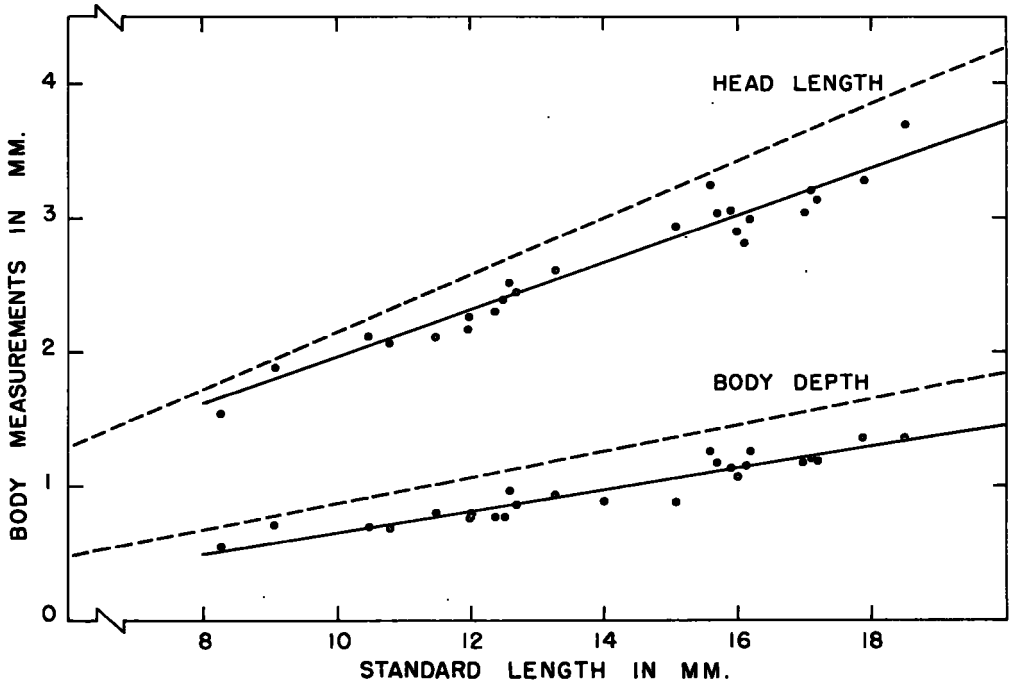

FIGURE 28.—Regressions of head length and body depth on standard length of larvae of *Vinciguerria poweriae*. Regression lines (solid) were fitted by the method of least squares (see table 32 for statistics describing the regressions). The broken line above each regression is the comparable regression line for *V. lucetia* larvae (see figs. 4 and 5).

number of dorsal rays, and Horsburgh (1935) reexamined the original material and further amended the description by pointing out the presence of an adipose fin and a pair of vomerine teeth. Horsburgh also examined material of *V. sanzoi* and concluded that it was identical with *V. nimbaria*. We concur in this disposition of *V. sanzoi*, as the Pacific material of *V. nimbaria* examined by us agrees in all particulars with the detailed descriptions of larvae, metamorphosing individuals, and adults of *V. sanzoi*, as described by Jespersen and Tåning.

V. nimbaria is closely related to *V. lucetia*, from which it can be rather readily separated after photophore formation, but the eggs and younger larval stages of the two species are practically identical.

In the eastern Pacific, *V. nimbaria* is an oceanic species, occurring mainly to the west of 133° W. longitude. The distribution of metamorphosing individuals, juveniles, and adults is shown in figure 29. One specimen (H50–104, Scripps Institution) was taken by explosives in the Scripps Submarine Canyon, near La Jolla, another at station 100.80 (30°01′ N., 120°07′ W.), but these are the only individuals thus far taken within the area routinely surveyed on CCOFI cruises. No attempt has been made to plot the distribution of eggs and larvae of *V. nimbaria*, because of the uncertainty of distinguishing them from *V. lucetia*. However, as no specimens of *V. lucetia* have been taken to the west of 134° W. longitude, there seems to be little overlap in the actual distributions of the two species.

We have assumed that eggs and larvae occurring in the area where later stages of *V. nimbaria* are found also belong to this species. Several collections contained larvae in various stages of development together with metamorphosing individuals and juveniles of *V. nimbaria*. This material has been carefully examined to determine characters that can be used to separate the eggs and larvae of *lucetia* and *nimbaria*. Measurements and meristic counts on 34 specimens identified as *V. nimbaria* larvae are given in table 33. Unfortunately, the only valuable diagnostic characters do not appear until near the end of the larval period. The eggs of the two species are almost identical in appearance and size, and both lack an oil globule. One tenuous difference is in the amount of

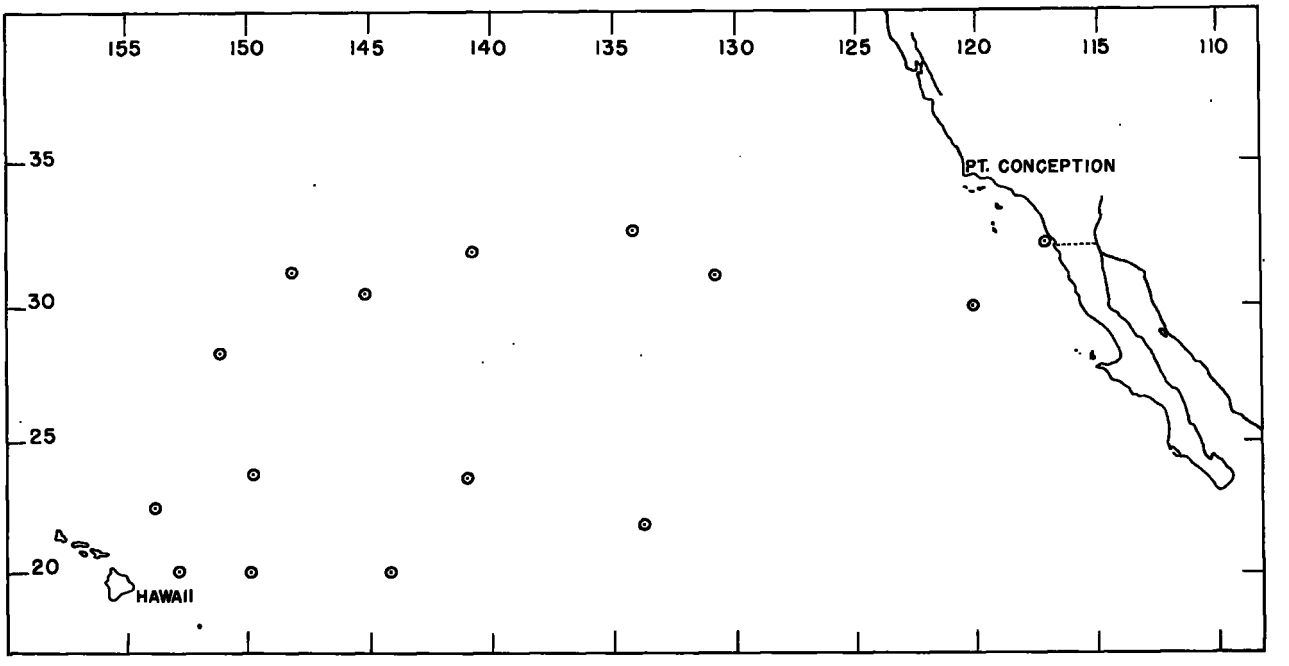

FIGURE 29.—Distribution (occurrences) of metamorphosing, juvenile, and adult *Vinciguerria nimbaria*, based on material studied from the eastern Pacific.

TABLE 33.—*Measurements and meristic counts of* Vinciguerria nimbaria *larvae from the eastern Pacific*

[BF—base formed; U—urostyle]

Area	Body measurements (in mm.)						Meristic counts [1]					Number of gill rakers	Number of vertebrae ossified
									Caudal fin				
	Standard length	Head length	Eye width	Depth at pectoral	Snout to anus	Snout to dorsal	Dorsal	Anal	Principal	Secondary D	Secondary V		
31°09.5′ N., 148°24′ W	5.4	1.07	0.18	0.40	4.00				0	0	0		
23°45′ N., 150°00′ W	5.4	0.94		.28	4.10				0	0	0		
20°03′ N., 150°01.5′ W	6.0	1.19		.44	4.70		BF		10	0	0		
19°57.5′ N., 144°15′ W	6.9	1.45	.26	.52	5.20		7		19	0	0		
23°45′ N., 150°00′ W	7.1	1.49	.32	.56	5.35		8	BF	19	0	0		
23°45′ N., 150°00′ W	7.3	1.38		.51	5.40		8	BF	19	0	0		
20°03′ N., 150°01.5′ W	7.3	1.59	.24	.72	5.50		10	BF	19	0	0		
32°53′ N., 134°13′ W	7.6	1.55		.68	6.00		6	BF	19	0	0		
31°11′ N., 145°10′ W	8.0	1.40	.30	.60	6.05		7	BF	19	0	0		
20°03′ N., 150°01.5′ W	8.2	1.77	.32	.65	6.40		11	BF	19	0	0		
20°03′ N., 150°01.5′ W	8.3	1.75		.66	6.40		10	BF	19	0	1	0+8	
20°03′ N., 150°01.5′ W	8.5	1.79	.35	.82	6.50		10	7	19	1	1	0+8	
23°45′ N., 150°00′ W	8.8	1.77	.35	.70	6.50		10	BF	19	1	1	0+8	
31°09.5′ N., 148°24′ W	9.1	1.24	.32	.72	7.05		10	BF	19	1	1		
23°45′ N., 150°00′ W	9.2	1.84	.38	.79	7.05		11	4	19	1	1	0+8	
31°11′ N., 145°10′ W	9.4						12	8	19	1	1	0+8	
23°40′ N., 141°06′ W	10.1	2.11	.38	.79	7.90	6.70	12	9	19	1	1	0+10	
19°57.5′ N., 144°15′ W	10.7	2.18	.42	1.05	8.10	6.95	14	13	19	3	2	0+11	
28°06.5′ N., 151°25′ W	10.7	2.28	.53	1.10	8.20	6.90	13	11	19	3	1	0+10	
20°03′ N., 150°01.5′ W	10.8		.44	.96			12	12	19	3	2	0+10	
23°45′ N., 150°00′ W	11.0	2.11	.36	.82	8.30	7.00	13	11	19	3	2	0+9	
31°11′ N., 145°10′ W	11.6	2.24	.47	.95	8.85	7.40	13	13	19	2	2	0+10	
20°03′ N., 150°01.5′ W	12.5	2.50	.51	1.21	9.20	8.00	13	14	19	4	3	0+11	27+U
28°06.5′ N., 151°25′ W	13.0	2.80	.54	1.28	9.50	8.00	13	12	19	4	3	0+12	31+U
31°09.5′ N., 148°24′ W	13.1	2.50	.51	1.21	9.85	8.20	13	12	19	4	2	0+11	22+U
31°11′ N., 145°10′ W	13.3	2.53	.49	1.08	9.90	8.50	13	14	19	3	2	0+10	
23°40′ N., 141°06′ W	13.6	2.71	.46	1.16	10.05	8.65	14	14	19	2	3	0+12	29+U
23°40′ N., 141°06′ W	13.7	2.80	.52	1.11	10.20	8.50	14	14	19	4	4	0+12	25+U
23°45′ N., 150°00′ W	14.1	3.00	.53	1.18	10.35	8.75	14	13	19	6	3	0+13	34+U
30°25′ N., 145°08′ W	14.2	3.00	.60	1.53	10.50	9.10	13	14	19	5	4	0+13	38+U
31°09.5′ N., 148°24′ W	14.2	2.71	.49	1.14	10.85	9.00	14	13	19	4	3	0+13	35+U
19°57.5′ N., 144°15′ W	14.5						15	15	19	6	4	2+13	42
28°06.5′ N., 151°25′ W	14.5	2.98	.66	1.53	11.00	8.90	13	15	19	6	4	0+13	42
31°09.5′ N., 148°24′ W	16.0	3.08	.63	1.39	11.95	10.10	14	14	19	5	4	0+13	42

[1] No pectoral or ventral rays are formed during larval period. Larval pectorals are present on all specimens and ventral buds are developed on most specimens over 10 mm. in length.

TABLE 34.—*Comparison of number of gill rakers in larvae of* Vinciguerria nimbaria *and* V. lucetia *from the eastern Pacific*

Standard length	*V. nimbaria*			*V. lucetia*		
	Number of specimens	Number of gill rakers		Number of specimens	Number of gill rakers	
		Range	Average		Range	Average
6–6.9 mm	4	0	0	5	0	0.
7–7.9 mm	3	0 or nubs	0 or nubs	5	0	0.
8–8.9 mm	4	0+8	0+8	4	nubs or 0+10	0+10.
9–9.9 mm	3	0+8	0+8	4	nubs	nubs.
10–10.9 mm	4	0+9–0+11	0+9.9	2	0+11	0+11.
11–11.9 mm	3	0+9–0+10	0+9.7	5	0+11–0+13	0+12.
12–12.9 mm	1	0+11	0+11	1	0+12	0+12.
13–13.9 mm	4	0+10–0+12	0+11.3	3	0+13–0+15	0+13.7.
14–14.9 mm	3	0+13–2+13	.7+13	4	0+13–0+15	0+13.8.
15–15.9 mm				2	0+14–0+17	0+15.2.
16–16.9 mm	1	0+13	0+13	2	0+16	0+16.
17–17.9 mm				1	0+16	0+16.

pigmentation developed in late egg stages; in the material examined, *V. nimbaria* has less pigment on late-stage embryos. The size range of eggs identified as *V. nimbaria* is from 0.64 to 0.72 millimeter in diameter.

The pigmentation of larvae of the two species is so similar that we have found no diagnostic differences. All of the pigment areas described for *V. lucetia* also develop on larvae of *V. nimbaria*. Since Jespersen and Tåning (1926) have also described the pigmentation of larvae of *V. sanzoi* (=*nimbaria*), there can be no question about the accuracy of this observation. In both species the caudal spot is near the ventral margin. Both species develop several pigment spots above the anal fin, and also along the base of the caudal fin rays. Morphometric measurements have not shown any clear-cut differences in body proportions. Two characters are useful in separating late-stage larvae: gill rakers and teeth. As noted previously, only the gill rakers on the lower limb of the first branchial arch develop during the larval period; rakers were developed on the upper limb of only one specimen that we have examined. The number of gill rakers on the lower limb in late stage larvae of *V. nimbaria* is 12 or 13, as compared with 15 or 16 on late-stage larvae of *V. lucetia* (table 34). *V.* lucetia usually has two more gill rakers at initial formation during the larval period and three more at the beginning of metamorphosis than *V. nimbaria*.

There are more maxillary and mandibular teeth on larvae of *V. nimbaria* than on larvae of comparable size of *V. lucetia* (tables 8 and 35). Larger larvae of *V. nimbaria* usually have about 2 more maxillary teeth and 1 more mandibular tooth per side than do comparable-sized larvae of *V. lucetia*.

TABLE 35.—*Number of teeth per side in larval* Vinciguerria nimbaria

Standard length	Number of specimens	Maxillary		Mandibular lateral		Premaxillary	
		Range	Average	Range	Average	Range	Average
5–5.9 mm	2	2–3	2.5	0	0	0	0
6–6.9 mm	4	3–6	4.8	0	0	0	0
7–7.9 mm	3	6	6.0	1–3	1.4	0	0
8–8.9 mm	4	7–8	7.5	2–4	3.0	0	0
9–9.9 mm	3	7–9	8.2	3–5	3.8	0	0
10–10.9 mm	4	10–13	11.0	3–5	4.4	0	0
11–11.9 mm	3	11	11.0	5–6	5.2	0	0
12–12.9 mm	1	13	13.0	5–6	5.5	0	0
13–13.9 mm	4	11–13	12.2	4–8	6.0	0–2	1.0
14–14.9 mm	3	12–15	13.3	6–8	6.8	2–4	2.8
16–16.9 mm	1	13	13.0	5–6	5.5	2	2.0

Metamorphosing and older individuals of *V. nimbaria* are readily separable from specimens of *V. lucetia* on the basis of measurements and meristic counts (table 36), and especially of photophore counts (table 37). In addition to differences in number of gill rakers, there are differences in the number of IV and OV photophores. Specimens of *V. nimbaria* have 16 (rarely 17) photophores in the ventral IV group and 13 (rarely 14) in the adjacent OV group. Occasionally, *V. lucetia* may have as many as 16 ventral IV photophores and 13 OV photophores (8 specimens out of 586 studied), but the average numbers in these groups are only 14.34 and 11.34 photophores, respectively. The few specimens of the two species that have identical numbers of IV and OV photophores may be separated by examining the gill rakers (table 30). The full complement of gill rakers in *V. nimbaria* is 5–6+15 in the material examined, while in *V. lucetia* the range is from 8–10+18–23. It will be noted that *V. nimbaria* and *V. lucetia* have identical numbers of lateral VA and ventral VA photophores (table 27). Both species average about one photophore more per side in the VA

groups than *V. poweriae*. *V. nimbaria* has a somewhat lower average AC photophore count than *V. lucetia:* 13.35, as compared to 13.86. This difference is even more marked if the comparison is confined to individuals of *V. lucetia* having 15 or more ventral IV photophores per side; the average AC count on these specimens is approximately 14.25 photophores per side.

The number and location of late-forming photophores are identical in *V. nimbaria* and *V. lucetia*.

V. nimbaria averages nearly 1 vertebra more than *V. lucetia*. Of 16 cleared and stained specimens of *V. nimbaria* that had the vertebral column developed, 12 individuals had 42 vertebrae, 1 had 43, and 3 had 41, for an average of 41.9 vertebrae. The range in vertebral numbers in *V. lucetia* is from 39 to 42, with an average of 40.9 vertebrae.

Differences in body proportions between *V. nimbaria* and *V. lucetia* are too slight to be of use in separating the two species.

TABLE 36.—*Measurements and meristic characters in metamorphosing, juvenile, and adult stages of* Vinciguerria nimbaria *from the eastern Pacific*

Area	Body measurements (in mm.)							Meristic counts							Number of gill rakers	Number of vertebrae
	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus	Dorsal	Anal	Pectoral	Ventral	Caudal				
												Principal	Secondary			
													D	V		
Prometamorphic:																
20°06.5′ N., 153°06′ W	14.2		0.65					14	13	0	Bud	19	6	4	2+13	42
19°57.5′ N., 144°15′ W	14.8	3.18	.60	1.66	7.7	9.0	11.0	14	14	0	Bud	19	6	4	1+13	42
31°09.5′ N., 148° 24′ W	15.1	3.28	.69	1.37	8.1	9.6	11.3	13	14	0	5	19	7	4	2+13	42
20°03′ N., 150°01.5′ W	15.3	3.28	.66	1.43	8.2	9.8	11.4	14	15	0	6	19	7	4	2+13	42
23°45′ N., 150°00′ W	15.3	3.23	.63	1.44	8.0	9.7	11.3	13	15	0	Bud	19	6	4	2+14	42
28°06.5′ N., 151°25′ W	15.6	3.30	.77	1.77	7.9	9.3	11.5	15	15	0	7	19	8	4	3+14	42
32°02′ N., 140°55′ W	17.5							14	15	1	7	19	8	4	2+14	43
31°08.5′ N., 130°59′ W	19.4	3.66	.74	1.74	9.9	12.2	14.2	14	14	1	7	19	7	4	2+13	42
Midmetamorphic:																
22°34′ N., 154°01′ W	17.3	4.05	1.14	2.36	8.2	9.7	11.4	14	15	10	7	19	8	4	4+15	42
23°45′ N., 150°00′ W	17.6	4.00	1.10	2.48	8.5	10.0	11.6	14	15	10	7	19	8	4	4+14	42
32°53′ N., 134°13′ W	17.9	3.92	1.03	2.28	8.8	10.2	12.4	14	14	7	7	19	7	4	3+14	41
Postmetamorphic:																
22°34′ N., 154°01′ W	17.2	4.41	1.36	2.82	8.2	9.7	11.5	14	15	10	7	19	8	4	5+15	42
23°40′ N., 141°06′ W	18.2	4.55	1.19	2.63	8.5	10.0	12.0	14	15	10	7	19	8	4	5+15	42
Juvenile and adult:																
19°57.5′ N., 144°15′ W	24.1	6.60	2.34	4.90	12.0	14.0	16.5	14	14	10	7	19	8	4	5+15	41
20°03′ N., 150°01.5′ W	24.5	6.50	2.23	5.10	12.0	13.9	15.9	14	14	10	7	19	8	4	5+15	41
21°52′ N., 133°51′ W	30.0														5+15	
Scripps Canyon	48.0	13.25	3.50	8.10	25.0	28.8	33.5	14	15	10	7				6+15	

TABLE 37.—*Number of photophores in metamorphosing, juvenile, and adult stages of* Vinciguerria nimbaria *from the eastern Pacific*

[Both sides of body given]

Station	North latitude	West longitude	Standard length	Head				Lateral row		Ventral row		Anal-caudal (AC group)	Number of photophores incomplete	Total number of photophores
				Orb and Op	So	Br	Is	OV group	VA group	IV group	VA group			
Prometamorphic:			*Mm.*											
Chinook 14	32°38′	172°21′	14.0	4-4	0	8-8	7-7	13-13	8-8	16-16	10-10	6+5-6+6	6-6	83-84
Norpac 81.5	31°09.5′	148°24′	15.1	4-4	0	8-8	7-7	13-13	8-9	16-16	10-11	5+6-5+6	6-6	83-85
N. Holiday 56	28°06.5′	151°25′	15.6	4-4	0	8-8	7-7	13-13	8-8	16-16	10-10	6+6-7+6	6-6	84-85
N. Holiday 61	32°02′	140°55′	17.5	4-4	0	8-8	7-7	13-13	8-8	16-16	10-11	7+7-6+7	6-7	86-87
Norpac 76D	31°08.5′	130°59′	19.4	4-4	0	8-8	7-7	14-14	7-7	17-17	9-9	6+7-7+6	6-6	85-85
Midmetamorphic:														
Norpac 131.5	22°34′	150°01′	17.3	5-5	0	8-8	7-7	13-13	8-8	16-16	10-10	6+6-7+5	5-5	84-84
Norpac 131D	23°45′	150°00′	17.6	4-4	0	8-8	7-7	13-13	8-8	16-16	10-10	6+6-6+6	6-6	84-84
N. Holiday 64	32°53′	134°13′	17.9	4-4	0	8-8	7-7	13-13	8-8	16-16	10-10	6+6-6+6	6-6	84-84
Postmetamorphic:														
Norpac 131.5	22°34′	150°01′	17.2	5-5	1-1	8-8	7-7	13-13	9-9	16-16	10-10	6+6-6+7	3-3	84-85
Norpac 128D	23°40′	141°06′	18.2	5-5	0	8-8	7-7	13-13	9-8	16-16	10-10	6+6-6+7	4-5	84-85
Juvenile and adult:														
Norpac 155D	19°57.5′	144°15′	24.1	5-5	1-1	8-8	7-7	13-13	11-11	16-16	10-10	13-13		84-84
Norpac 157D	20°03′	150°01.5′	24.5	5-5	1-1	8-8	7-7	13-13	10-11	16-16	9-10	14-13		83-84
Norpac 141D	21°52′	133°51′	30.0	5-5	1-1	8-8	7-7	13-13	11-11	16-16	10-10	13-13		84-84
Scripps Canyon	32°53′	117°17′	48.0	5-5	1-1	8-8	7-7	13-13	10-11	16-16	9-10	14-12		83-83

SUMMARY

The development of *Vinciguerria lucetia*, family Gonostomatidae, is described from the embryonic to the adult stages. *V. lucetia* is one of the most abundant pelagic forage fishes in the eastern north Pacific.

The pelagic egg is moderately small (0.58–0.74 mm.), spherical, lacks an oil globule, has segmented yolk and a double shell membrane. There is an apparent cline in egg size with latitude.

Postembryonic development has been divided into six stages: larval, prometamorphic, midmetamorphic, postmetamorphic, juvenile, and adult. In dealing with changes in body form, each stage has been treated separately. Six dimensions have been studied in addition to standard length: head length, body depth, eye width, distance from snout to insertion of ventral fins, distance from snout to dorsal origin, and distance from snout to anus. Rectilinear regressions of size on size have been derived for each body dimension.

The threadlike, nearly colorless larvae are similar in appearance to larvae of the sardine and anchovy. The range in standard length of larvae studied was 2.2 to 18.2 mm.

Marked changes take place in body proportions and body structures during metamorphosis with little or no increase in standard length. The head length increases about 20 percent between the larval stage and postmetamorphic, the eye diameter and also body depth increase approximately 80 percent. On the other hand, there is approximately a 10-percent decrease in distance from snout to insertion of ventral fins and from snout to dorsal origin, and a somewhat greater decrease in the distance from snout to anus.

Specimens of *V. lucetia* metamorphose at a smaller size in the area south of 25° N. latitude than in the northern part of the range.

Ossification of the vertebral column occurs immediately before metamorphosis. The centra of vertebrae ossify before the neural or haemal spines. The range in number of vertebrae is from 39 to 42. The total number of vertebrae shows a definite latitudinal variation.

Gill rakers form on the lower limb during the larval period, but do not appear on the upper limb until metamorphosis. Gill-raker formation is completed by the end of metamorphosis.

Tooth development is traced from the larval period through to the adult. Maxillary, premaxillary, and mandibular teeth first form in the larval stage, but palatine and vomerine teeth do not appear until postmetamorphosis.

The caudal, dorsal, and anal fins form during the larval period, but procurrent caudal-ray formation is not completed until metamorphosis. Rays do not form in either the pectoral or ventral fins until metamorphosis.

Photophores develop during metamorphosis, at first as white photophores (prometamorphic stage) then as pigmented functional organs. Six or seven pairs of photophores form late; two pairs are usually added during the midmetamorphic stage, the remainder during the postmetamorphic stage. Photophore formation is completed and all photophores are pigmented by the end of metamorphosis. Marked differences were found in the average total number of photophores per side in different parts of the range between 35° N. and 14° S. in the eastern Pacific. Specimens from 30° to 35° N. averaged nearly 83 photophores per side, while specimens obtained between 5° and 15° N. averaged less than 80.5 photophores per side.

Abundance and distribution of larvae within the California Cooperative Oceanic Fisheries Investigations survey area are estimated and illustrated for 1951 and 1952. Based on more extensive collections, *V. lucetia* has been obtained between 35° N. and 14° S. latitude and 78° and 134° W. longitude.

Two other species of *Vinciguerria* have been found to occur in the eastern Pacific: *V. nimbaria* and *V. poweriae*. Both occur on the fringes of the area routinely surveyed on CCOFI cruises, but both were well represented in the extensive coverage obtained on "Norpac." Characters used to separate the three species at different stages of development are given.

V. poweriae is readily separated in the adolescent and adult stages by the absence of the symphyseal pair of photophores, which is developed in *lucetia* and *nimbaria*. The simplest character for separating late-larval, and early-metamorphic stages of *V. poweriae* from the two other species is pigmentation, especially the mediolateral position of the caudal pigment spot. Measurements and meristic counts are given for larvae and metamorphosing stages of *V. poweriae* and for all stages in the development of *V. nimbaria*.

V. nimbaria can be rather easily separated from *V. lucetia* after photophore formation, but the eggs and younger larval stages of the two species are practically identical. Two characters are useful in separating late-stage larvae: gill rakers and teeth. There are more maxillary and mandibular teeth and fewer gill rakers on larvae of *V. nimbaria* than on larvae of *V. lucetia* of comparable size.

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APPENDIX

Measurements of individual specimens of *Vinciguerria lucetia* are given in the following five tables. The different stages of development are presented in separate tables with the exception of juvenile and adult stages, which are combined in one table.

APPENDIX TABLE 1.—*Measurements (in mm.) of larvae of* Vinciguerria lucetia *from the eastern North Pacific*

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5106-107.40	30°23′	116°46′	2.24	0.38	0.10	0.14			1.35
5106-120.110	25°38′	119°44′	2.37	.43	.12	.16			1.66
5106-120.110	25°38′	119°44′	2.42	.43	.12	.18			1.65
5106-127.40	26°40′	114°31′	2.45	.38	.12	.18			1.66
5106-120.110	25°38′	119°44′	2.47	.43		.18			1.80
5106-120.110	25°38′	119°44′	2.47	.43		.18			1.69
5106-127.40	26°40′	114°31′	2.60	.50	.10	.21			1.60
5106-127.40	26°40′	114°31′	2.60	.50	.12	.14			1.69
5106-107.40	30°23′	116°46′	2.62	.49	.14	.18			1.70
5106-127.40	26°40′	114°31′	2.75	.49	.10	.16			1.80
5105-137.60	24°21′	114°40′	3.00	.61		.19			2.05
5106-107.40	30°23′	116°46′	3.00	.61	.14	.18			2.05
5106-107.40	30°23′	116°46′	3.05	.63	.14	.21			2.08
5105-137.60	24°21′	114°40′	3.50	.70		.23			2.55
5106-120.110	25°38′	119°44′	3.50	.70	.16	.21			2.47
5106-107.35	30°31′	116°25′	3.51	.61	.14	.18			2.47
5106-120.110	25°38′	119°44′	3.70	.79	.18	.26			2.75
5106-127.40	26°40′	114°31′	3.75	.79	.14	.23			2.70
5106-120.110	25°38′	119°44′	4.00	.70	.16	.26			2.54
5106-107.35	30°31′	116°25′	4.05	.70	.14	.18			2.90
5106-107.40	30°23′	116°46′	4.10	.88	.18	.33			2.95
5106-130.90	24°27′	117°18′	4.25	.79	.18	.26			3.15
5106-107.40	30°23′	116°46′	4.25	.89	.18	.26			3.20
5103-120.110	25°33′	119°44′	4.60	.88	.18				3.30
5106-127.40	26°40′	114°31′	4.75	.91	.19	.39			3.55
5106-127.40	26°40′	114°31′	4.75	.92	.18	.35			3.50
5106-130.90	24°27′	117°18′	4.75	.95	.18	.35			3.65
5106-130.90	24°27′	117°18′	4.90	1.00	.18	.35			3.60
5103-120.110	25°33′	119°44′	5.00	1.00					3.75
5106-127.40	26°40′	114°31′	5.00	.95	.18	.34			3.75
5106-130.90	24°27′	117°18′	5.15	1.15	.21	.35			4.05
5106-130.90	24°27′	117°18′	5.25	1.14	.21	.40			3.85
5106-130.90	24°27′	117°18′	5.35	1.20	.23	.35			4.10
5106-127.40	26°40′	114°31′	5.45	1.15		.31			4.00
5009-70.145	33°06′	128°20′	5.80	1.40		.40			4.35
5105-137.60	24°21′	114°40′	5.80	1.22	.21	.43			4.35
5009-70.160	32°40′	129°24′	5.85	1.36		.39			4.45
5106-127.40	26°40′	114°31′	5.95	1.28	.23	.39			4.35
5106-130.90	24°27′	117°18′	6.00	1.45	.28	.49			5.25
5105-137.60	24°21′	114°40′	6.25	1.30	.24	.46			4.65
5106-130.90	24°27′	117°18′	6.25	1.35	.23	.47			4.60
5106-107.35	30°31′	116°25′	6.50	1.30	.26	.43			4.90
5106-120.110	25°38′	119°44′	6.65	1.50	.26	.47		4.50	5.00
5106-130.90	24°27′	117°18′	6.85	1.50	.28	.52		4.50	5.20
5106-130.90	24°27′	117°18′	7.25	1.50	.28	.52		5.00	5.60
5106-123.40	27°18′	114°52′	7.30	1.53	.28	.52			5.55
5106-130.90	24°27′	117°18′	7.40	1.60	.26	.50		5.00	5.60
5009-70.145	33°06′	128°20′	7.45	1.70	.32	.54		5.00	5.55
5106-107.40	30°23′	116°46′	7.50	1.60	.30	.52		5.00	5.50
5105-137.60	24°21′	114°40′	7.60	1.55	.30	.63		5.00	5.90
5106-93.90	30°50′	121°34′	7.70	1.60	.30	.52		5.00	5.60
5106-107.35	30°31′	116°25′	7.75	1.65	.30	.52		5.00	5.85
5009-70.160	32°40′	129°24′	8.10	1.80		.55		5.25	6.50
5009-70.160	32°40′	129°24′	8.25	1.95	.30	.65		5.45	6.20
5009-70.145	33°06′	128°20′	8.30	2.00	.35	.70		5.75	6.25
5106-130.90	24°27′	117°18′	8.45	1.85	.32	.70		5.75	6.35
5106-93.90	30°50′	121°34′	8.45	1.95	.35	.74		5.30	6.50
5106-93.90	30°50′	121°34′	8.50	1.85	.35	.66		5.50	6.35
5106-107.40	30°23′	116°46′	8.75	2.02	.30	.70		5.50	6.30
5106-93.90	30°50′	121°34′	8.80	1.95	.37	.68		5.60	6.35
5106-107.40	30°23′	116°46′	8.90	2.00	.32	.70		5.75	6.55
5009-70.145	33°06′	128°20′	9.15	2.15	.38	.78		6.30	7.00
5106-93.90	30°50′	121°34′	9.30	2.20	.37	.79		5.80	6.75
5106-93.90	30°50′	121°34′	9.50	2.05	.35	.80		6.25	7.25
5103-120.110	25°33′	119°44′	9.60	1.87	.35	.79		6.25	7.15
5106-93.90	30°50′	121°34′	9.65	2.20	.40	.79		6.25	7.05
5009-70.145	33°06′	128°20′	10.15	2.40	.40	.85		6.55	7.70
5105-93.80	31°10′	120°54′	10.35	2.25	.35	.88		6.50	7.50
5009-70.145	33°06′	128°20′	10.50	2.50	.40	1.00		6.75	7.95
5011-133.60	24°53′	115°10′	10.65	2.40	.47	1.05	5.50	6.60	8.00
5106-93.90	30°50′	121°34′	11.25	2.40	.50	.96		6.95	8.35
5009-70.160	32°40′	129°24′	11.30	2.55	.47	.91		7.75	8.50
5009-70.160	32°40′	129°24′	11.35	2.60	.50	1.00		7.25	8.40
5106-93.90	30°50′	121°34′	11.35	2.60	.50	1.05		7.00	8.60
5106-93.90	30°50′	121°34′	11.35	2.35	.52	.89		7.30	8.25

APPENDIX TABLE 1.—*Measurements (in mm.) of larvae of* Vinciguerria lucetia *from the eastern North Pacific*—Continued

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5106-107.40	30°23′	116°46′	11.55	2.30	0.42	.80	----------	6.75	7.85
5009-70.145	33°06′	128°20′	11.60	2.50	.50	.95	----------	7.25	8.55
5106-107.35	30°31′	116°25′	11.60	2.35	.42	.91	----------	7.25	8.35
5106-107.35	30°31′	116°25′	11.70	2.39	.40	.80	----------	7.50	8.60
5009-70.160	32°40′	129°24′	11.75	2.70	.50	1.00	----------	7.35	8.65
5009-70.160	32°40′	129°24′	11.90	2.70	.57	1.05	----------	7.40	9.00
5009-70.145	33°06′	128°20′	12.05	2.75	.50	1.15	6.25	7.75	9.00
5106-107.35	30°31′	116°25′	12.20	2.60	.49	.96	6.00	7.25	9.00
5106-107.80	28°54′	119°18′	12.80	2.70	.49	.96	6.50	8.00	9.40
5011-130.110	23°57′	118°33′	13.20	2.89	.65	1.30	----------	8.05	9.20
5011-133.60	24°53′	115°10′	13.30	2.90	.51	1.17	----------	8.20	9.65
5009-70.145	33°06′	128°20′	13.40	2.75	.50	1.20	6.75	8.40	10.00
5106-93.90	30°50′	121°34′	13.50	2.75	.52	1.14	7.00	8.40	10.00
4909-81.107	32°22′	124°13′	13.60	2.86	.52	1.10	----------	8.30	9.80
5009-70.145	33°06′	128°20′	13.75	3.00	.60	1.35	6.90	8.50	10.05
5011-133.60	24°53′	115°10′	14.35	3.10	.55	1.30	7.35	9.00	10.70
4909-102.74	29°53′	119°29′	14.70	3.20	.65	1.40	----------	9.00	10.60
4909-71.85	34°54′	124°06′	14.80	3.07	.63	1.54	----------	8.90	10.50
4909-81.107	32°22′	124°13′	14.80	2.88	.61	1.40	----------	9.30	10.80
4909-81.107	32°22′	124°13′	14.80	2.94	.60	1.28	----------	9.10	11.00
5011-133.60	24°53′	115°10′	15.20	3.20	.56	1.30	7.80	9.00	11.10
4909-70.95	34°42′	124°48′	15.50	3.10	.60	1.50	7.60	9.50	11.20
4909-102.74	29°53′	119°29′	16.20	3.43	.66	1.60	----------	10.20	11.65
4909-80.147	31°10′	127°08′	17.20	3.30	.60	1.60	----------	10.40	12.50
4909-70.115	34°19′	126°18′	18.20	3.60	.65	1.60	9.00	11.25	13.10

APPENDIX TABLE 2.—*Measurements (in mm.) of prometamorphic-stage specimens of* Vinciguerria lucetia *from the eastern North Pacific*

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5103-157.30	21°53′	110°35′	13.2	2.75	0.56	1.28	6.1	8.0	9.4
510s-140.60	23°50′	114°14′	13.8	3.00	.60	1.66	7.1	8.4	10.0
5103-157.30	21°53′	110°35′	14.2	2.97	.58	1.42	8.1	8.8	10.3
5103-150.60	22°04′	113°18′	15.2	3.25	.58	1.69	8.0	9.7	11.2
5103-157.10	22°33′	109°23′	15.5	3.15	.55	1.50	7.5	9.5	11.0
Shellback 13	18°06′	124°14′	16.0	3.50	.70	1.40	7.5	9.8	11.2
5011-133.60	24°53′	115°10′	16.0	3.25	.75	1.50	8.1	9.8	11.2
5011-133.60	24°53′	115°10′	16.1	3.30	.58	1.25	8.1	10.0	11.7
5011-130.110	23°57′	118°33′	16.5	3.76	.79	1.95	8.4	10.1	11.8
5205-110.90	28°01′	119°36′	17.0	3.60	.65	1.40	8.0	10.0	11.8
4909-102.74	29°53′	119°29′	17.0	3.68	.68	1.70	8.4	10.6	12.2
4909-71.85	34°54′	124°06′	17.2	3.82	.70	1.87	8.8	10.7	12.4
4909-81.107	32°22′	124°13′	17.3	3.80	.79	1.75	8.8	10.6	12.4
5009-70.190	31°35′	131°29′	17.6	3.65	.75	1.70	8.4	10.5	12.2
4909-71.85	34°54′	124°06′	17.8	3.68	.74	1.80	9.3	10.9	12.8
4909-71.85	34°54′	124°06′	18.0	3.90	.84	1.95	9.2	11.0	12.9
4909-80.147	31°10′	127°08′	18.1	3.75	.75	2.00	9.1	11.4	13.2
4909-80.147	31°10′	127°08′	18.2	3.80	.72	1.80	9.0	11.2	13.1
4909-70.95	34°42′	124°48′	18.3	3.60	.70	1.80	9.0	11.5	13.2
4909-102.94	29°10′	120°48′	18.9	3.76	.80	1.84	9.0	11.2	13.0
4909-81.107	32°22′	124°13′	18.9	3.90	.75	1.76	9.5	11.4	13.4
N. Holiday 66	32°39′	129°41′	19.2	3.55	.80	1.70	9.3	11.5	13.2

APPENDIX TABLE 3.—*Measurements (in mm.) of midmetamorphic-stage specimens of* Vinciguerria lucetia *from the eastern North Pacific*

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
Shellback 13	18°06′	124°14′	13.5	3.15	0.56	1.60	6.6	8.2	9.6
Do	18°06′	124°14′	13.8	3.25	.66	1.77	6.5	8.1	9.1
Do	18°06′	124°14′	13.8	3.35	.66	1.67	6.8	8.4	9.5
5011-153.50	21°47′	112°14′	14.1	3.34	.72	1.33	6.8	8.5	9.5
5011-140.60	23°46′	114°18′	14.2	3.46	.75	2.02	6.7	8.2	9.4
5106-157.10	22°33′	109°23′	14.3	3.41	.77	2.10	6.8	8.2	9.5
5401-143.30	24°13′	112°04′	14.3	3.51	.72	2.11	6.8	8.4	9.4
5106-157.40	21°32′	111°14′	14.6	3.30	.61	1.61	7.0	8.6	9.9
5011-153.50	21°47′	112°14′	14.8	3.35	.60	1.77	7.2	8.8	10.0
5106-157.10	22°33′	109°23′	15.0	3.40	.72	1.72	7.0	8.8	10.0
5011-140.70	23°25′	114°55′	15.0	3.23	.64	1.75	7.0	8.8	10.0
5401-143.30	24°13′	112°04′	15.1	3.36	.66	1.85	7.0	8.8	10.0
5106-157.10	22°33′	109°23′	15.2	3.41	.70	1.85	7.0	8.9	10.0
5106-157.50	21°12′	111°52′	15.3	3.55	.70	2.13	7.2	8.7	10.0
5011-137.50	24°39′	114°02′	15.4	3.51	.68	2.05	7.5	9.1	10.5
5112-120.60	27°13′	116°32′	15.5	3.33	.65	1.82	7.4	9.2	10.5
5106-157.50	21°12′	111°52′	15.6	3.64	.70	2.05	7.2	9.0	10.2
5106-157.40	21°32′	111°14′	15.7	3.36	.58	1.80	7.2	9.4	10.4
Shellback 13	18°06′	124°14′	15.8	3.55	.78	1.95	7.5	9.2	10.4
5106-157.40	21°32′	111°14′	16.0	3.38	.61	1.82	7.5	9.5	10.7
5202-140.40	24°26′	113°02′	16.4	3.46	.61	1.82	7.9	9.9	11.2
5112-120.60	27°13′	116°32′	16.5	3.64	.74	2.10	8.0	10.0	10.9

APPENDIX TABLE 3.—*Measurements (in mm.) of midmetamorphic-stage specimens of* Vinciguerria lucetia *from the eastern North Pacific*—Continued

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5011-133.60	24°53′	115°10′	16.6	3.75	0.80	1.95	7.9	9.8	10.9
5106-157.40	21°32′	111°14′	16.7	3.55	.61	1.82	8.2	10.0	11.9
5104-100.100	29°20′	121°28′	16.9	4.00	.91	2.36	7.8	9.5	10.9
5202-120.60	27°13′	116°32′	17.2	3.55	.99	1.87	8.0	10.4	10.7
5009-90.145	29°32′	125°40′	17.2	3.64	.70	1.82	8.0	9.9	11.6
4911-92.137	29°34′	124°52′	17.3	3.90	.79	1.80	8.2	10.1	11.5
4911-80.147	31°11′	127°03′	17.4	4.00	.88	2.16	8.4	10.1	----------
4911-123.63	26°40′	116°28′	17.5	4.29	1.00	2.24	8.2	9.9	11.5
4910-70.115	34°07′	126°17′	17.6	3.80	.84	2.08	8.4	10.0	11.8
5108-100.60	30°41′	118°48′	17.7	4.00	.77	2.39	8.6	10.5	12.0
4911-80.137	31°29′	126°20′	17.7	4.00	.89	2.26	8.6	10.1	11.8
4909-80.147	31°10′	127°08′	17.8	4.00	.88	2.20	8.5	10.5	11.7
5011-133.70	24°35′	115°40′	17.9	3.85	.70	1.95	8.0	10.6	12.2
4911-80.137	31°29′	126°20′	17.9	4.02	.96	2.34	8.5	10.0	11.8
4911-102.74	29°56′	119°29′	17.9	3.95	.82	1.85	8.2	10.8	12.2
Shellback 13	18°06′	124°14′	17.9	4.00	.86	1.95	8.6	10.4	12.0
4909-80.147	31°10′	127°08′	18.0	3.90	.88	2.30	8.8	10.6	12.2
5009-70.190	31°35′	131°29′	18.0	3.80	.85	2.30	8.4	10.5	12.0
4908-123.75	26°16′	117°03′	18.2	4.00	.68	2.08	8.9	11.0	12.3
4909-80.147	31°10′	127°08′	18.2	3.75	.88	2.26	8.8	10.4	12.1
5110-107.40	30°08′	116°48′	18.4	4.10	.77	2.13	9.0	11.0	12.5
4911-80.137	31°29′	126°20′	18.4	4.03	.79	2.26	8.9	10.8	12.3
4909-80.147	31°10′	127°08′	18.6	3.90	.80	2.18	9.1	11.1	12.8
4909-80.147	31°10′	127°08′	18.7	4.00	.86	2.30	9.0	11.1	12.8
4909-80.147	31°10′	127°08′	18.7	3.90	.80	2.10	9.1	11.5	13.0
4909-80.147	31°10′	127°08′	19.0	3.90	.82	2.20	9.3	11.5	13.1
5110-107.40	30°08′	116°48′	19.2	4.10	.77	2.21	9.2	11.4	13.0

APPENDIX TABLE 4.—*Measurements (in mm.) of postmetamorphic-stage specimens of* Vinciguerria lucetia *from the eastern Pacific*

Station	Latitude	Longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5103-157.10	22°33′N.	109°23′W.	13.2	3.50	0.90	1.92	6.3	7.8	8.9
5110-127.50	26°24′N.	115°08′W.	13.2	3.46	.90	2.05	6.3	7.6	8.8
5011-150.100	20°41′N.	115°40′W.	13.7	3.55	.97	2.20	6.5	7.7	8.9
5011-140.70	23°25′N.	114°55′W.	14.0	3.90	1.15	2.35	6.8	7.8	9.0
5201-137.50	24°41′N.	114°02′W.	14.3	3.90	1.06	2.21	6.7	8.1	9.2
5011-157.30	21°52′N.	110°38′W.	14.5	3.80	1.07	2.21	6.7	8.2	9.2
Shellback trawl 16	12°07′N.	106°03′W.	14.7	4.05	1.17	2.65	7.1	8.5	9.2
5011-153.50	21°47′N.	112°14′W.	14.7	3.79	1.18	2.31	7.0	8.5	9.6
5106-153.20	22°48′N.	110°22′W.	14.8	3.87	1.00	2.13	7.0	8.2	9.6
5011-140.70	23°25′N.	114°55′W.	15.2	4.00	.95	2.15	7.0	8.4	9.9
5011-150.110	20°21′N.	116°17′W.	15.2	4.15	1.30	2.45	7.3	8.6	9.8
Shellback trawl 16	12°07′N.	106°03′W.	15.3	4.35	1.40	2.60	7.4	8.8	9.9
5011-137.40	25°00′N.	113°23′W.	15.3	3.95	1.08	2.30	7.1	8.6	9.8
5106-153.20	22°48′N.	110°22′W.	15.8	3.97	1.00	2.18	7.4	9.0	10.2
5401-147.30	23°38′N.	111°47′W.	15.9	3.97	1.13	2.60	7.4	8.9	10.2
5011-157.20	22°13′N.	110°00′W.	16.0	4.08	1.04	2.39	7.2	9.0	10.3
5011-Sp	24°18′N.	112°30′W.	16.0	4.18	1.10	2.64	7.4	8.8	10.3
Shellback 88	04°12′S.	96°07′W.	16.0	4.05	1.11	2.50	7.5	9.0	10.3
5011-153.50	21°47′N.	112°14′W.	16.2	4.05	1.18	2.54	7.5	9.1	10.2
5011-150.25	23°12′N.	115°40′W.	16.3	4.25	1.28	2.56	7.7	9.4	10.4
5011-137.40	25°00′N.	113°23′W.	16.3	4.20	1.23	2.55	7.7	9.2	10.4
5011-157.20	22°13′N.	110°00′W.	16.4	4.20	1.07	2.60	7.7	9.4	10.6
5010-70.130	33°33′N.	127°16′W.	16.4	4.41	1.21	2.64	8.0	9.4	10.8
4910-124.83	25°51′N.	117°37′W.	16.6	4.40	1.43	3.10	8.0	9.2	10.6
5011-Sp	24°18′N.	112°30′W.	16.8	4.25	1.15	2.59	7.7	9.2	10.8
5501-117.35	28°39′N.	115°17′W.	16.8	4.38	1.21	2.54	8.0	9.4	10.9
Shellback 13	18°06′N.	124°14′W.	17.0	4.35	1.35	2.70	8.0	9.5	11.0
4910-82.87	32°57′N.	122°47′W.	17.0	4.35	1.10	2.36	8.0	9.5	10.8
Shellback 83	00°53′N.	97°12′W.	17.0	4.35	1.29	2.70	7.8	9.5	10.9
5401-130.35	26°19′N.	113°48′W.	17.2	4.45	1.31	2.55	8.0	9.6	11.1
4910-102.84	29°35′N.	120°08′W.	17.2	4.45	1.22	2.90	8.0	9.5	11.1
5009-70.235	30°02′N.	134°23′W.	17.2	4.23	1.03	2.51	8.2	9.8	11.1
5002-110.80	28°16′N.	118°58′W.	17.4	4.75	1.20	2.69	8.1	9.6	11.0
5401-130.35	26°19′N.	113°48′W.	17.7	4.90	1.46	2.95	8.4	9.8	11.2
5401-137.40	21°40′N.	119°41′W.	17.7	4.60	1.44	2.90	8.3	9.9	11.5
Shellback trawl 11	08°09′N.	84°58′W.	17.8	4.95	----------	3.10	8.4	10.0	11.3
5109-110.60	28°56′N.	117°39′W.	17.9	4.85	1.33	2.80	8.2	9.9	11.2
4911-92.137	29°34′N.	124°52′W.	17.9	----------	1.08	2.44	8.4	10.1	11.5
Shellback 13	18°06′N.	124°14′W.	18.0	4.75	1.38	3.00	8.4	10.0	11.5
5401-130.35	26°19′N.	113°48′W.	18.2	4.80	1.46	3.00	8.3	10.1	11.6
5401-110.50	29°14′N.	117°01′W.	18.3	4.90	.91	3.05	8.7	10.0	11.8
5106-153.20	22°48′N.	110°22′W.	18.3	4.90	1.36	3.00	8.6	10.0	11.8
5401-130.35	26°19′N.	113°48′W.	18.7	5.05	1.55	2.95	8.7	10.4	11.8
4902-92.117	30°11′N.	123°37′W.	19.3	5.05	1.46	3.05	8.9	10.8	12.1
5404-123.50	26°58′N.	115°30′W.	19.5	5.10	1.49	3.15	9.1	10.9	12.5
4911-113.127	26°14′N.	121°44′W.	20.2	5.25	1.66	3.50	9.5	11.0	12.8

APPENDIX TABLE 5.—*Measurements (in mm.) of juvenile and adult specimens of* Vinciguerria lucetia *from the eastern Pacific*

Station	North latitude	West longitude	Standard length	Head length	Eye width	Depth at pectoral	Snout to ventral	Snout to dorsal	Snout to anus
5201-137.50	24°41′	114°02′	19.2	5.15	1.70	3.20	8.8	10.5	12.0
5011-143.60	23°10′	113°56′	19.5	5.00	1.60	3.65	9.5	10.8	12.8
Shellback 63	12°20′	102°38′	20.0	5.10	2.15	4.00	9.5	11.8	13.0
5401-130.35	26°19′	113°48′	20.0	5.15	1.55	3.05	9.2	10.8	12.5
5103-157.10	22°33′	109°23′	20.2	5.50	1.75	3.80	9.8	11.5	13.6
5009-90.160	29°07′	126°30′	20.2	5.25	1.80	3.75	9.0	10.8	12.2
5203-137.50	24°40′	114°02′	21.2	5.70	1.65	4.10	10.2	12.0	14.2
5112-110.50	29°17′	117°02′	22.0	5.90	1.85	3.85	10.4	11.9	13.9
5401-140.50	24°08′	113°41′	22.0	5.90	2.00	3.90	10.2	11.5	13.5
5009-90.160	29°07′	126°30′	22.1	5.65	1.90	4.55	10.2	12.1	14.0
5011-133.70	24°35′	115°40′	22.2	5.80	1.95	3.75	10.5	12.0	14.0
5201-110.80	28°18′	118°54′	23.0	6.35	2.10	4.25	11.2	12.8	15.0
5110-127.50	26°24′	115°08′	23.5	6.25	2.00	4.10	11.0	13.1	15.0
5103-120.45	27°41′	115°33′	23.5	6.20	2.00	4.15	11.2	13.1	15.0
5003-120.60	27°14′	116°32′	24.3	6.60	2.50	5.00	11.8	13.5	16.5
5009-90.160	29°07′	126°30′	24.4	6.50	2.20	4.80	11.9	13.8	16.0
4911-112.88	27°48′	119°14′	24.5	6.50	2.30	4.75	11.5	14.0	15.8
5202-110.60	28°58′	117°40′	24.5	6.50	2.15	4.35	11.5	13.8	16.0
4911-112.88	27°48′	119°14′	25.2	6.50	2.35	4.90	11.9	14.4	16.2
5202-123.50	27°01′	115°32′	26.0	6.50	2.45	5.25	12.5	14.6	17.0
5105-90.120	30°26′	124°01′	26.0	7.00	2.30	4.50	12.0	14.2	16.0
4911-112.88	27°48′	119°14′	26.6	6.95	2.40	5.15	12.8	15.0	17.2
5302-120.50	27°34′	115°52′	28.0	7.50	2.50	5.10	13.2	15.2	17.8
4903-111.58	28°47′	117°21′	28.2	7.75	2.65	4.90	13.8	15.8	17.8
5205-110.90	28°01′	119°36′	28.5	8.00	2.70	5.50	14.0	15.8	18.5
4802-Sp.	26°30′	113°52′	29.1	8.35	2.90	5.60	14.0	17.5	19.5
5003-110.50	29°15′	116°59′	30.5	8.50	2.95	5.40	15.1	17.5	20.0
4911-103.111	28°31′	121°52′	31.0	8.50	2.60	5.50	15.0	17.5	20.2
5203-117.60	27°49′	116°51′	31.0	8.40	2.85	5.90	14.8	17.8	21.0
5510-120.90	26°15′	118°28′	32.5	9.00	3.05	6.00	15.4	17.8	20.5
5011-Sp.	24°18′	112°30′	33.0	9.00	2.75	5.75	15.5	18.5	21.0
4908-112.98	27°36′	119°52′	33.5	9.25	3.10	6.00	16.2	18.5	21.5
5302-110.60	28°56′	117°39′	34.0	9.00	3.05	6.15	16.3	18.5	21.8
5205-110.90	28°01′	119°36′	34.0	9.50	3.05	6.35	16.2	19.0	21.8
5004-90.90	31°25′	121°59′	36.0	10.00	3.20	6.40	18.0	20.5	23.6
5005-120.60	27°20′	116°33′	36.5	10.00	3.10	6.40	18.0	20.0	23.6
4904-112.98	27°21′	119°52′	37.6	10.15	3.35	7.00	18.8	21.0	24.8
5007-100.70	30°21′	119°32′	39.5	10.50	3.45	6.70	19.2	23.1	26.0
Off Guadalupe Is.	29°15′	118°20′	41.2	11.00	3.55	7.50	20.0	23.5	28.0
Do.	29°15′	118°20′	42.0	11.50	3.75	8.00	20.0	24.0	29.0
Do.	29°15′	118°20′	42.8	12.00	3.70	8.00	22.0	24.0	29.0
Do.	29°15′	118°20′	43.0	11.40	3.50	8.00	21.8	24.3	29.0
Do.	29°15′	118°20′	43.0	11.75	4.05	8.25	22.0	25.0	29.5
Do.	29°15′	118°20′	43.0	11.60	3.85	8.00	22.0	24.2	29.5
Do.	29°15′	118°20′	45.0	12.05	3.90	8.25	22.5	25.8	31.0
5205-110.90	28°01′	119°36′	45.5	12.20	3.90	7.90	22.5	25.5	29.8
SIO-51-91	25°52′	114°40′	47.2	13.00	3.65	7.50	23.2	27.7	32.0
SIO-54-214	29°15′	118°20′	49.8	12.85	3.75	9.00	24.8	28.5	33.3
SIO-51-91	25°52′	114°40′	51.5	13.35	3.60	8.90	25.3	30.2	35.0
SIO-54-214	29°15′	118°20′	52.2	13.00	3.90	9.30	26.0	29.9	35.6
SIO-54-214	29°15′	118°20′	56.0	14.00	4.10	10.10	28.0	32.5	38.2

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

ANNOTATED BIBLIOGRAPHY ON THE CUTTHROAT TROUT

BY OLIVER B. COPE

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ABSTRACT

Publication of articles on the cutthroat trout began before the turn of the century, after explorations in the Intermountain Region had brought several forms of the cutthroat to the attention of fishery workers. The present compilation brings together 135 abstracts of papers which deal with the biology, culture, distribution, and management of the cutthroat. Twenty-seven zoological names proposed for the cutthroats are listed, and 70 vernacular names, taken from the literature, are presented.

ANNOTATED BIBLIOGRAPHY ON THE CUTTHROAT TROUT

By Oliver B. Cope, *Fishery Research Biologist*, Bureau of Sport Fisheries and Wildlife

The cutthroat trout, *Salmo clarki* Richardson, was the subject of technical fishery articles before the turn of the century. Explorers and fishery workers first became acquainted with the inland forms of this species at the time of the opening of the Intermountain Region, where the cutthroat was the only native trout. Early explorations and the beginnings of fish culture in the Rocky Mountains were the occasions for the first writings on the cutthroat in fishery journals.

As the years passed, articles on the cutthroat appeared sporadically, while most of the attention of trout researchers and managers who reported in the journals was on the rainbow, brown, and brook trouts. In recent years, interest in the cutthroat has been revived, owing in part to the need for information about management of the species in the face of increasing fishing pressure, reduced water supplies, and the trends toward encouragement of native species in western waters and planting of catchable-size fish. The literature of the past 10 years has enjoyed an upsurge in number of papers dealing with the cutthroat, and the species has attained added importance as a subject for biological investigations. The present bibliography has been prepared to bring together the scattered references on the cutthroat to guide fishery workers concerned with this species.

SCOPE

Articles included here are those considered as adding something to our knowledge of the biology, culture, management, or distribution of the cutthroat. Many papers which mention the species very briefly and check lists or routine planting and distribution reports are omitted from treatment here. Original descriptions of species and subspecies are not necessarily included. In general, the abstracts cover published papers, although a few administrative reports are included because of the value of their data and conclusions. When abstracts or summaries have been included in papers, I have transcribed them here; otherwise I have written the abstracts.

NOTE.—Approved for publication Sept. 3, 1957. Fishery Bulletin 140.

NAMES FOR THE CUTTHROAT

A list of names for the cutthroat has been included in this compilation. Perhaps to no other species of trout have so many names, zoological and common, been applied. The species has occupied a variety of waters and has hybridized to produce various genetic mixtures, races, and color phases which have prompted the creation of new names for the many forms. Miller (1935) recognizes 1 species with 11 subspecies. The literature contains the following specific and subspecific names for the cutthroat; some of them are now in synonymy, and some of the forms are probably extinct: *Salmo alpestris* Dymond, *bathoecetor* Meek, *beardslei* Jordan and Seale, *bouvieri* Bendire, *brevicauda* Suckley, *carinatus* Cope, *clarki* Richardson, *declivifrons* Meek, *eromogenes* Evermann and Nichols, *gairdneri* Jordan and Beardslee, *gibbsi* Suckley, *henshawi* Gill and Jordan, *jordani* Meek, *lewisi* Girard, *macdonaldi* Jordan and Evermann, *mykiss* Jordan and Evermann, *pleuriticus* Cope, *purpuratus* Bendire, *seleniris* Snyder, *spilurus* Cope, *stellatus* Girard, *stomias* Cope, *tahoensis* Jordan and Evermann, *tsuppitch* Girard, *utah* Suckley, and *virginalis* Girard. *Salmo evermanni* Jordan and Grinnell is listed by Miller as being in the cutthroat series.

The following vernacular names for cutthroat trout appear in the literature: Alaska cutthroat, Arkansas trout, black trout, black-speckled trout, black-spotted trout, blueback, bluenose trout, Bonneville Basin trout, brook trout, Clark's salmon, coastal cutthroat, Colorado cutthroat, Colorado River trout, Columbia River trout, Columbia salmon-trout, Crab Creek cutthroat, Cranbrook

trout (cutthroat x Kamloops hybrid), cutthroat trout, cutthroat trout of Utah Lake, flat trout, Gibbs' salmon, great trout of Lake Tahoe, green-back trout, harvest trout, Jordan's trout, Lahontan cutthroat, Lake Tahoe trout, lake trout, Lewis' trout, long-headed trout of Crescent Lake, mountain cutthroat, mulefish (cutthroat x rainbow hybrid), native trout, Piute cutthroat, Piute trout, Platte cutthroat, pogy, porgy, Pyramid Lake trout, redfish, red trout, red-bellied trout, red-sided cutthroat, red-throated trout, Rio Grande cutthroat, Rio Grande trout, river trout, Rocky Mountain trout, salmon trout of Lake Southerland, San Gorgonio trout, short-tailed trout, silver trout, silvery-white salmon-trout, Snake River cutthroat, Southern Rocky Mountain trout, snipe, speckled trout, speckled mountain trout, spotted trout of Lake Southerland, spring trout, tommy, Truckee trout, Utah cutthroat, Waha Lake trout, white salmon, winter trout, yellow-belly, yellowfin trout, Yellowstone trout, Yellowstone cutthroat, and various Indian names.

ANNOTATED BIBLIOGRAPHY

BALL, ORVILLE P.

1955. Some aspects of homing in cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett., 32: 75–80.

Very little previous work has been done to measure the homing instinct in adfluvial fish. The U. S. Fish and Wildlife Service studied homing in the cutthroat in Yellowstone Lake from 1949 to 1955. Immatures in streams were fin-clipped, and spawners in streams were tagged with Petersen disks. Results from immatures were not conclusive, but only 6 out of 280 repeat spawners returned to streams other than those in which they were originally tagged.

BANGHAM, RALPH V.

1951. Parasites of fish in the Upper Snake River drainage and in Yellowstone Lake, Wyoming. Zoologica, 36, Part 3(16): 213–217.

Parasites of 291 Yellowstone cutthroat are listed; 278 of the fish examined were infested. Sixteen species of parasites are named, and the incidences of several are noted in discussions.

BARRETT, I.

1951. Fertility of salmonoid eggs and sperm after storage. Jour. Fish. Res. Bd. Can., 8 (3): 125–133.

Effects of storage on fertility of salmonoid eggs have been studied. Mature eggs and sperm were stripped into dry sterile jars and stored for varying periods at low temperatures before testing their fertility with fresh genital products. Eggs of the chum salmon, *Oncorhynchus keta*, were stored at temperatures of 2.5° to 5.8° C. for 108 hours with an average infertility of less than 20 percent. The sperm of this species shows a wide variation in its reaction to storage, but may be retained for 36 hours in sterile jars with an average of less than 10 percent infertility. Cutthroat eggs stored 36 hours were 18 percent infertile. Kamloops and cutthroat confirmed the applicability of the technique of transporting eggs and sperm stored together in the absence of water.

BEAN, TARLETON H.

1894a. Life history of the salmon. Bull. U. S. Fish Comm., 12: 21–38.

The red-throated trout, *Salmo mykiss*, is called Clark's trout and Rocky Mountain trout. Discussion of distribution, food-habitat preferences, and habits is given.

1894b. Bibliography of the Salmonidae of Alaska and adjacent regions. Bull. U. S. Fish Comm., 12: 39–49.

Lists several very early papers pertaining to cutthroat trout.

BILTON, T. H.

1952. The creel census of cutthroat trout at Lakelse Lake, 1952. Prog. Reports of the Pacific Coast Stations, Fish. Res. Bd. Can., No. 92, October: 18–20.

Three years of creel-census data were accumulated for cutthroat in the lake and river fishery in the Lakelse drainage. Lake fishing was best in July, during mayfly hatches. The river fishery had moved to the lake by this time. In August and September the majority of fishing was in the lake.

The fishery was probably exploiting less than 10 percent of the catchable stock annually. A heavier fishery would obtain a higher yield, probably over a long period of years.

BILTON, T. H., and M. P. SHEPARD.

1955. The sports fishery for cutthroat trout at Lakelse Lake, British Columbia. Prog. Reports of the Pacific Coast Stations, Fish. Res. Bd. Can., No. 104, November: 38–42.

Since 1950 the Fisheries Research Board of Canada has kept records on cutthroat in Lakelse Lake and Lakelse River. Notes on feeding and spawning are given. The sport fishery is described. About 2,000 cutthroat are taken annually by this fishery. Age III and IV trout have predominated in the catch each year.

Figures on the catch per unit of effort indicate that no severe depletion has occurred in the lake population, but the catches on the river have declined since 1950.

Anglers have removed an average of 7 percent of the lake population anually, and 18 to 31 percent of the river population.

BJORNN, TED C.

1957. A survey of the fishery resources of Priest and Upper Priest Lakes and their tributaries, Idaho. Idaho Fish and Game Dept., Completion Report. 176 pp.

In 1955 a survey of the fishery resources of Priest and Upper Priest Lakes and their tributaries was initiated to determine the factors causing the decline in the number of cutthroat in the lake.

Streams running into the lakes provided adequate spawning sites for both cutthroat and Dolly Varden trout. In streams where brook trout have become abundant, competition for food and space between brook trout and cutthroat is very intense. Competition is less in the lakes.

Of the 93,300 fish caught in 1955 from these lakes, 10 percent were cutthroat, and of the estimated total catch of 111,400 in 1956, 5 percent were cutthroat.

The average rate of catch for cutthroat in the upper lake was 1.02 fish per boat per hour, compared with 0.70 in Priest Lake. The average-size cutthroat caught in 1956 was between 11.1 and 11.2 inches. The body-scale relation appeared to be approximately linear.

Juvenile cutthroat spawned from fish migrating from the lakes were found to spend an extended period of time in the streams before migrating to the lakes. Of the fish collected from Priest Lake in 1956, 38 percent spent 2 years in the streams before migrating, 57 percent 3 years, and 5 percent 4 years. For the upper lake, 6 percent migrated after their first year, 35 percent after their second, and 58 percent after their third. The spawning season begins in April and generally ends July 1. Cutthroat in the Priest Lakes mature predominantly during their fifth year of life. Only a very small number of fish ever spawn a second time.

Diet of the cutthroat consists mainly of insects and some plankton.

An average of nearly 500,000 cutthroat a year, mostly fry, have been planted in the Priest Lake drainage for at least the last 10 years, but less than 1 percent have been returned to the creel.

BLACK, EDGAR C., and ISADORE BARRETT.

1957. Increase in levels of lactic acid in the blood of cutthroat and steelhead trout following handling and live transportation. Can. Fish. Cult., Issue 20, pp. 13–23.

Alterations in the blood levels of lactic acid were investigated in hatchery-raised coastal cutthroat and steelhead trout in the following conditions: (*a*) After transferring from outside ponds to troughs inside the hatchery 60 yards (54.9 meters) away; (*b*) sham transportation run for 2 hours in tank truck; (*c*) holding cutthroat for 40 hours, steelhead for 16 hours, in hatchery troughs before transportation of 2 hours 50 minutes.

The following results were noted: (1) Significant increases in blood lactic acid in both species as a result of minimal handling, i. e., in transporting the fish from outside ponds to inside hatchery troughs; (2) very significant increase in blood levels of lactic acid following sham transportation run for 2 hours in a tank truck, and levels were higher in both species than those observed for lake trout and Kamloops trout in 1955; (3) storage of cutthroat for 40 hours resulted in significant lowering of blood level of lactic acid (range 0.8–17.5 mg. percent) following transportation run of 2 hours 50 minutes. Storage of steelhead trout for 16 hours before the same transportation run of 2 hours 50 minutes resulted also in a lower blood level of lactic acid (range 9.5–88 mg. percent).

BONHAM, KELSHAW, and R. WALTER WILLIAMS.

1948. Effect of population pressure upon rate of growth and food conversion of fingerling cutthroat trout. Prog. Fish-Cult., 10 (1) : 15–18.

Fingerling cutthroat trout in 80-gallon aquariums were fed equal amounts of food per fish; two tanks had 28 fish each, two had 280 fish each. Lengths and weights were determined on four occasions. Crowded fish did not differ significantly from uncrowded ones in growth rate or food-conversion rate.

BROWN, C. J. D., and JACK E. BAILEY.

1952. Time and pattern of scale formation in Yellowstone cutthroat trout, *Salmo clarkii lewisi*. Trans. Amer. Micros. Soc., 71 (2) : 120–124.

Scales from adult and immature Lake Yellowstone cutthroat were studied, and three kinds of scale development noted: (1) Fish completely scaled before their first winter and with annuli on all scales; (2) fish partially scaled before the first winter, some scales without annuli; (3) fish without scales in their first winter, and with no annuli at the end of the first growing season.

BROWN, C. J. D., and CHARLES BUCK, JR.

1939. When do trout and grayling fry begin to take food? Jour. Wildl. Mgt., 3 (2) : 134–140.

Experiments on time of initial feeding were done for grayling and several trouts, including cutthroat. Some cutthroat fry were feeding 14 days after hatching, and all were feeding 23 days after hatching. Little uniformity between species was shown; rainbow began first, brook trout last. Size or presence of yolk sac showed no correlation with initial feeding time.

CALHOUN, A. J.

1944a. Black-spotted trout in Blue Lake, California. Calif. Fish and Game, 30 (1) : 22–42.

Upper Blue Lake is an oligotrophic lake at 8,130-foot elevation in the California Sierra Nevada. The lake has black-spotted trout which spawn in five tributary streams. Spawning time, size of spawners, and age of spawners are discussed.

In 1941 a significant number of the trout which matured sexually failed to ascend a stream to spawn.

Marked trout showed that growth did not take place after spawning, and few spawned a second time.

Heavy annual plants of small fingerlings, coupled with closure to fishing, over a 6-year period, did not increase the number of fish in the spawning runs. It seemed to lead to an overpopulation of fish and a depletion of food.

It appears undesirable to return spent spawners to a lake like Blue Lake.

1944b. The food of the black-spotted trout (*Salmo clarkii henshawi*) in two Sierra Nevada lakes. Calif. Fish and Game, 30 (2) : 80–85.

The black-spotted trout in Upper Blue Lake, a deep granite basin at 8,130-foot elevation, subsisted largely on chironomid larvae and pupae. They failed to utilize the rather abundant population of the minnow, *Rhinichthys oscula*, which competes with young trout for food.

The trout of Heenan Lake, a former grazing meadow at 7,000-feet transformed by a dam into a 25-foot-deep reservoir, subsisted largely on plankton crustacea (daphnia and copepods). The extremely abundant bottom fauna of the littoral zone provided only 17 percent of their food (scuds of the *Gammarus* type); immature chironomids, plentiful in bottom samples, provided less than 9 percent.

Heenan Lake trout were in much better condition than those of Blue Lake, reflecting the relative richness of the two lakes.

CALIFORNIA DEPARTMENT OF FISH AND GAME.

1956. Cutthroat nursery. Outdoor Calif., 17 (6):6–7, 11.

Heenan Lake, on the east slope of the Sierra Nevada in California, was built in the late twenties and stocked with cutthroat (*Salmo clarkii henshawi*) from Alpine County. The fish grew well and egg-taking was initiated. California and Nevada have taken 19 million cutthroat eggs from Heenan Lake for stocking elsewhere. California is attempting to reestablish the cutthroat in its former waters on the east slope.

CARLANDER, KENNETH D.

1950. Handbook of freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 281 pp.

Contains life history and biological measurements reported in many papers on cutthroat.

1953. Handbook of freshwater fishery biology with the first supplement. Wm. C. Brown Co., Dubuque, Iowa. 429 pp.

Contains life history and biological measurements reported in many papers on cutthroat.

CODE, MARK R.

1950. Cutthroat trout without dorsal fins. Prog. Fish-Cult., 12 (2): 85–86.

Cutthroat without dorsal fins were found in South Fork of Sheep Creek in the Ashley National Forest in Utah in 1936. The coloring of the abnormal fish was darker than that of normal cutthroat in the same stream. Some fish with deformed dorsal fins were found in the same stream.

COPE, E. D., and H. C. YARROW.

1875. Report upon the collections of fishes made in portions of Nevada, Utah, California, New Mexico, and Arizona during the years 1871, 1872, 1873, and 1874. Zoology of the Wheeler Survey, 5: 637–700.

Life history account of *Salmo virginalis*, called lake trout, brook trout, and speckled trout, with account of spawning, feeding, and movements. Angling methods are discussed. A discussion of Rio Grande trout, *Salmo spilurus* and *Salmo pleuriticus*, is presented.

COPE, OLIVER B.

1953a. Chloretone as an anaesthetic for adult cutthroat trout. Prog. Fish-Cult., 15 (1): 35.

Chloretone was successfully used for anaesthetizing adult cutthroat at Yellowstone Lake in 1952. Stock solution was prepared in the laboratory, diluted in the field, and used on cutthroat at a strength of 1: 2,000. Cost of the chloretone is slightly higher than that of urethane.

1953b. Length measurements of Lake Yellowstone trout. U. S. Fish and Wildl. Serv., Spec. Sci. Rept.—Fish. No. 103. 17 pp.

Conversion factors and tables are given for total length, fork length, and standard length of cutthroat from Yellowstone Lake. Comparisons from year to year of average total lengths from the fishery and from spawning runs show that declines in size took place from 1950 to 1952 in the northern part of the lake, where fishing was heaviest.

1955. The future of the cutthroat in Utah. Proc. Utah Acad. Sci., Arts, and Lett., 32: 89–93.

The original cutthroats in Utah, the Utah cutthroat and the Colorado cutthroat, have been replaced by the Yellowstone cutthroat. Three factors threaten the cutthroat in Utah and in other Rocky Mountain States. Construction of dams has blocked spawning runs, and more dams are planned. Rainbow are being planted in cutthroat waters and replacing the cutthroat. Importation of cutthroat eggs from Yellowstone Park has been stopped, eliminating about 45 percent of the supply to Utah.

1956. Some migration patterns in cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett., 33: 113–118.

Migrating cutthroat trout spawners in Arnica Creek, Yellowstone National Park, were counted, day and night, in 1951. Five-sixths of the total count for the season entered the stream between the hours of 6 p. m. and 7–8 a. m. This nocturnal migration is unusual for salmonid spawners, and is explained by the response of spawners to evening freshets that occur during the season of melting snows.

Lakeward-migrating fry in the same stream were counted, and it was found that 88 percent of the total count from August 1 to 15 moved downstream at night. Nocturnal movements of fry have been observed in other trouts and in salmon, and have been attributed to a negative phototropism.

1957a. Six years of catch statistics on Yellowstone Lake. Trans. Amer. Fish. Soc., 85: 160–179.

Catch statistics on cutthroat in Yellowstone Lake are reported for the years 1950–55. This fishery has only one species, the Yellowstone cutthroat. Hourly distribution of fishing is unusual in that there is practically no fishing before 7 a. m. and there are three peak periods of fishing throughout the day. There is an unusual uniformity of fishing effort among days of the week. Characteristics of the various components of the fishery are described.

Reduction of the daily catch limit from 5 to 3 fish in 1953 did little toward reducing total catch, but a shortened season had a decided effect on reduction of catch.

1957b. Races of cutthroat trout in Yellowstone Lake. U. S. Fish and Wildl. Serv., Spec. Sci. Rept.—Fish. No. 208. pp. 74–84.

Yellowstone cutthroat in tributaries to Yellowstone Lake and in Yellowstone River were studied to determine the existence of races. Tagging showed the association of groups of fish with particular spawning streams, and suggests that each tributary studied has its own race of cutthroat. Migrational patterns in the lake after spawning are quite constant from year to year. Mixing of races takes place in the lake, and each part of the lake appears to contain about the same mixture each year.

Times of migration into 5 streams were examined for 5 years, and 5 different patterns were perceived. The patterns were very constant from year to year.

Differences in mean total length of fish in spawning runs were measured, and significant differences found between streams. The differences may be due to differences in age composition or in growth rate, but are racial, since the same relations occur year after year.

Sizes of eggs and numbers of eggs per female were compared in relation to sizes of fish. Counts and measurements do not suggest that the fish are all of the same race.

1957c. The choice of spawning sites by cutthroat trout. Proc. Utah Acad. Sci., Arts, and Lett., 34: 73–79.

Several environmental factors were examined in stream surveys on six Yellowstone Lake tributaries used by cutthroat trout for spawning. Attempt was made to relate distribution of redds in each stream with factors known to sometimes influence choice of spawning sites. Distribution of the best gravel and presence of waterfalls, log jams, and chemical barriers can account for distribution of nests in most of the streams. No explanation is at hand, with our limited knowledge, to reveal why more spawning did not take place in upstream areas in Chipmunk Creek: spawners shunned what seemed to be ideal spawning territory in middle stretches and used lower sections.

Influences of forest cover and stream gradient on distribution of spawning in streams were studied, but no effects were apparent.

A theory applying to use by migrating spawners of headwater areas by the first part of the migration and downstream sections by the later parts of the run was examined in the light of experience with cutthroat in these streams. Arnica, Chipmunk, and probably Pelican Creek fish support the theory; Clear Creek fish were the only ones appearing to refute the hypothesis.

CRAMER, FREDERICK K.

1940. Notes on the natural spawning of cutthroat trout (*Salmo clarkii clarkii*) in Oregon. Proc. Sixth Pacific Sci. Congress, 3:335–339.

This study at Alsea Hatchery in Oregon was concerned primarily with spawning activities of coastal cutthroat. Time of spawning: spawning migrations were counted from December 5, 1938, to February 17, 1939, indicating a peak in late November and early December. Time of hatching: eggs hatch in 45–50 days. Nature of gravels and nests: eggs were 4–7 inches deep in pea-size gravel. Spawning activity: spawning day and night. Spawning was completed in 2 days. More than one nest per female was built. Eggs removed from nest: proportion of fertile live eggs 90 percent and better at stages up to 17 days. Egg counts: 2-year-old hatchery trout averaged 372.5 eggs per female. Small, wild, resident cutthroat averaged 480, and large, sea-run cutthroat averaged 1,170 eggs per female. Sex ratio: 52 males to 48 females in the spawning run.

DANIELS, T. W.

1952. Two-Ocean Pass, Wyoming. Wyo. Wildl., 16 (6): 4–8.

Two-Ocean Pass, on the Continental Divide in Wyoming, is described geographically, and historical significance of fishing studies there is discussed. This was the route used by cutthroat to enter Yellowstone Lake from the Snake River, according to the author, who cites Evermann.

DAVIS, H. S.

1947. Care and diseases of trout. U. S. Fish and Wildl. Serv., Res. Rept. 12, Third Rev. 98 pp.

Care of trout at the hatchery, including care of ponds and raceways, is treated at some length. This is followed by general discussion of trout foods and methods of feeding, special attention being paid to use of dry products for supplementing fresh meat in the diet. Some consideration is given improvement of brood stock and its practical value.

General discussion of parasites and diseases of trout and their control is followed by detailed account of each disease, including characteristic symptoms, etiology, pathology, and methods of control. Figures include drawings and photomicrographs of the most important organisms that cause trout diseases and their effects on tissues.

Numerous examples of care and diseases of cutthroat trout are used in this report.

1953. Culture and diseases of game fish. Univ. of Calif. Press, Berkeley and Los Angeles. x+332 pp.

Cultural methods applicable to cutthroat and other trouts are discussed, and diseases and parasites, some of which occur in cutthroat, are taken up in detail.

DEWITT, JOHN W., JR.

1954. A survey of the coast cutthroat trout, *Salmo clarki clarki* Richardson, in California. Calif. Fish and Game, 40(3): 329–335.

Distribution of coastal cutthroat in California, morphology, life-history notes, and age distribution are discussed.

DIMICK, R. E., and FRED MERRYFIELD.

1945. The fishes of the Willamette River system in relation to pollution. Oreg. St. Coll. Eng. Exp. Sta. Bull. 20. 58 pp.

Details of distribution of coastal cutthroat in this drainage are given. Two biological phases of the cutthroat are reported for the Willamette system. One is nonmigratory and does not get down to the main stem. The other is migratory and gets at least down to the main stem, and perhaps to the ocean. Migratory fish are larger, growing to 18–20 inches. Spawning and feeding habits are discussed. Relations to pollution are treated.

DIMICK, R. E., and DON C. MOTE.

1934. A preliminary survey of the food of Oregon trout. Oreg. St. Agr. Exp. Sta. Bull. 323. 23 pp.

Insects are the dominant food organisms of cutthroat and rainbow trout in Oregon. Aquatic insects form the bulk of the food. Terrestrial insects are prominent in diet in spring, summer, and fall. Crayfish, small fish, and pieces of dead salmon are important to large trout, while immatures of blackflies and midges are important to small trout in streams. Small trout in lakes eat mainly immature midges and water fleas. Fresh-water shrimps are important to Oregon trout in lakes. Table II has detailed analysis of food of 326 cutthroat trout.

DONALDSON, LAUREN R., and FRED J. FOSTER.

1938. A summary table of some experimental tests in feeding young salmon and trout. Trans. Amer. Fish. Soc., 67: 262–270.

Tables contain many references to diets fed to cutthroat, and effects on the fish.

DONALDSON, LAUREN R., DONALD D. HANSLER, and TERRY N. BUCKRIDGE.

1957. Interracial hybridization of cutthroat trout, *Salmo clarkii*, and its use in fisheries management. Trans. Amer. Fish. Soc., 86: 350–360.

Two races of coastal cutthroat trout (*Salmo clarkii*) were hybridized and resultant first-generation hybrids were compared with parent races. In both laboratory and field studies the hybrids showed evidence of hybrid vigor. Catch of sport fishermen, during two seasons at Echo Lake in Washington, where both parent and hybrid trout were planted, was composed of 3 to 6 times as many fish of hybrid stocks as of parent races.

DYMOND, J. R.

1928. The trout of British Columbia. Trans. Amer. Fish. Soc., 58: 71–77.

Description of cutthroat is given, with notes on distribution. Suggestions for management are advanced.

1931. Description of two new forms of British Columbia trout. Contr. Can. Biol. Fish. N. S., 6 (16): 391–395.

Kamloops and cutthroat trout found at high altitudes in British Columbia differ in so many respects from those occurring at lower levels that it has been found advisable to recognize them as subspecifically distinct. Two new subspecies are therefore described, viz., *Salmo kamloops whitehousei* and *Salmo clarkii alpestris*.

1932. The trout and other game fishes of British Columbia. Can. Dept. Fish., Ottawa. 51 pp.

Structural and color details of cutthroat in British Columbia are described in detail. *Salmo clarkii clarkii*, *S. c. lewisi*, and *S. c. alpestris* are subspecies treated, and a hybrid between Kamloops and cutthroat is briefly discussed. Excellent color plates of coastal and Yellowstone cutthroats are included. Descriptions and life histories include colorations, morphologies, migrations, spawning, and game-fish qualities. Comparisons with steelhead are made for the coastal form.

ECHO, JOHN B.

1956. Some ecological relationships between yellow perch and cutthroat trout in Thompson Lake, Montana. Trans. Amer. Fish. Soc., 84: 239–248.

Relation between yellow perch and cutthroat trout in Thompson Lakes in Montana was investigated in summers of 1952 and 1953. These lakes originally contained cutthroat trout and were later planted with yellow perch. Spawning time of yellow perch was in early May, of cutthroat trout in late May. The population of yellow perch was large, and growth was very slow. Although number of cutthroat trout was small, growth rate for this species was about average. Food of yellow perch was largely immature aquatic insects and plankton, while that of cutthroat trout was mostly mature aquatic insects and small perch. Yellow perch were commonly distributed along lake margins, and concentrations of perch fry and adults were found in these areas in spring. During this period the salmonid fishes were predominantly in deep water. Spot poisoning of yellow perch concentrations practically destroyed all fish in the treated area. Management suggestions are given.

ELLIS, MAX.

1914. Fish of Colorado. Univ. Colo. Studies, 11 (1): 1–136.

General discussion of trouts in Colorado; specific treatments of distributions and appearances of *Salmo c. spilurus*, *S. c. pleuriticus*, *S. c. stomias*, and *S. c. macdonaldi*.

EVERMANN, BARTON W.

1893. A reconnaissance of the streams and lakes of western Montana and northwestern Wyoming. Bull. U. S. Fish Comm., 11: 3–60.

Deals with natural-history features of trout streams and distribution of fishes, as well as requirements for fish-cultural stations. Distributional and descriptive notes on *S. mykiss* are given.

EVERMANN, BARTON W., and E. L. GOLDSBOROUGH.

1907. The fishes of Alaska. Bull. U. S. Bur. Fish., 26: 219–360.

Discussion of distribution of cutthroat trout in Alaska, description of the fish and comparison with rainbow, and fishing methods. Excellent colored plate.

FISH, FREDERIC F.

1934. Ulcer disease of trout. Trans. Amer. Fish. Soc., 64: 252–258.

Lesions of a type like furunculosis were noted on fingerling cutthroat, brook, rainbow, and lake trout and were caused by *Proteus hydrophilus*. Gross and microscopic pathology are described, and control is discussed. Photographs of lesions on cutthroat.

FLEENER, G. G.

1952. Life history of the cutthroat trout, *Salmo clarki* Richardson, in Logan River, Utah. Trans. Amer. Fish. Soc., 81: 235–248.

This study of cutthroat trout in Logan River, Utah, was based on 306 specimens collected during 1948 and 1949 with an alternating-current electric shocking machine. Cutthroat trout comprised 24 percent of the anglers' catch in 1948 and 31.5 percent in 1949. The greatest numbers were found in areas with a high stream gradient. An estimated minimum number of 43.6 pounds of cutthroat per acre and 565 fish per mile was obtained from a series of shocking operations in 1949. Scale analysis was employed in determining age of the fish. With a scale magnification of 50×, the body-scale (L/S) relation of cutthroat trout can be described as a curvilinear regression line, and expressed by the equation

$$L=3.411\ S^{1.2906}$$

Smallest average annual growth increment was 53 millimeters. This was based on a growing season of approximately 200 days. Growth began in latter part of March and extended to early October.

Relation between standard length and weight was expressed mathematically as

$$W=4.344\times10^{-5}L^{2.8253}$$

where W equals weight in grams and L equals standard length in millimeters. Coefficient of condition decreased as length of fish increased. Male cutthroat trout had slightly more weight per unit of length than females. Of 142 fish marked with jaw tags, 15 were recovered; 9 moved out of the 0.1-mile area where they were released. Spawning period of cutthroat trout in this area lasted from early April to middle of August, but most fish spawned before middle of July. Adult females ranged in size from 11 inches downward. Slightly more females were present in a total of 35 separate collections.

Insects were the main item in diet of Logan River cutthroat trout. Ephemeroptera, Trichoptera, and Diptera were principal aquatic orders taken, while most important terrestrial order was Coleoptera. Small numbers of fish eggs eaten indicated that survival was not affected. Only two occurrences of fish were found in the entire food habits study. Small size of cutthroat trout in this area is in part attributable to almost total absence of forage fish in upper Logan River.

FOSTER, FRED J.

1933. Life histories and environmental needs of native and introduced fish. In "Game Management Developments and Needs." Misc. Pub. No. 10, Utah State Agr. Coll., pp. 5–9.

Relations between cutthroat in Utah and introduced yellow perch are discussed. Kinds of cutthroat present in Utah, spawning conditions, characteristics of eggs and hatching habits of fry are presented. Causes of mortality are listed as nonfertilization, high water, and natural enemies. Life history of yellow perch is briefly discussed. Environmental needs of cutthroat are noted—character of water, food, and proper spawning conditions.

GEE, MERLE A.

1940. Report on the Upper Pecos River creel census, Santa Fe National Forest. Trans. Fifth N. A. Wildl. Conf., pp. 207–217.

A creel census was conducted in 1939 in the Upper Pecos River. Brown, rainbow, and Yellowstone cutthroat were the species caught. Brown trout, naturally reproduced, were the most abundant in the creel. Rainbows, stocked and naturally reproduced, were next in numbers in the creel. Cutthroat, planted and naturally reproduced, comprised only 9.18 percent of the catch. The cutthroat catch peaked in August, possibly as a result of midsummer recruitment. The 6- to 8-inch size class of cutthroat was the most important class.

1942. Success of planting legal-sized trout in the southwest. Trans. Seventh N. A. Wildl. Conf., pp. 238–245.

Plants of legal-sized rainbow and cutthroat trout were made from 1939 to 1941, and in spring, summer, fall, and winter plantings. Returns for the two species were generally comparable, with returns from 37.3 to 58.8 percent from spring and summer plantings. Best returns were from releases just before opening of fishing season and during the season. Overwintering of planted fish was poorer than with wild fish.

GILBERT, CHARLES H., and BARTON W. EVERMANN.
1894. A report upon investigations in the Columbia River Basin, with descriptions of four new species of fishes. Bull. U. S. Bur. Fish., 14:169–204.
Discusses morphology of various subspecies of cutthroat in this drainage and others.

GRASSE, JAMES E.
1949. Beaver and trout. Wyo. Wildl., 13 (11):4–13, 34.
Review of work on beaver-trout relations is given. Beaver in Wyoming are discussed, and place of cutthroat and brook trout in relation to these species is treated. Author concludes that beaver ponds are beneficial to trout in Wyoming, and that brook trout is beaver-pond trout in that state.

GREENE, WILLIAM S., JR.
1937. Colorado trout. Colo. Museum of Nat. Hist., Popular Series, No. 2. 48 pp.
Contains sections on *Trutta pleuriticus*, *T. virginalis*, *T. macdonaldi*, and *T. stomias*, with treatments on identification, distribution, and biology.

GRIFFITHS, FRANCIS P., and ELDEN D. YOEMAN.
1940. A comparative study of Oregon coastal lakes from a fish management standpoint. Proc. Sixth Pacific Sci. Congress, 3:323–333.
Oregon Game Commission studied certain coastal lakes in Oregon to compare productivity and to find a brood lake for coastal cutthroat. Geographical and climatological features of the lakes are discussed, fish faunas of 10 lakes are listed, and their limnology treated. Food of cutthroat of the lakes is composed mostly of insects. Condition factors ranged from 41.67 to 69.47. Suggestions for management of the lakes are presented.

HAIG-BROWN, RODERICK L.
1939. The western angler—an account of Pacific salmon and western trout. Derrydale Press, N. Y. 200 pp.
Good account in nontechnical language of biologies and life histories of cutthroats in British Columbia. Chapter on coastal cutthroats describes migrations in detail, and another on nonmigratory cutthroat contains a great deal of valuable material on habits.

HALL, E. RAYMOND.
1924. Pelicans versus fishes in Pyramid Lake. Condor, 27:147–160.
Importance of cutthroat trout of Pyramid Lake is discussed, and decline of commercial and sport fisheries is described. Investigation of white pelicans in relation to cutthroat was begun in 1924. Food habits of pelicans and their feeding behavior in herding trout are treated. Red suckers, lake minnows, lake chubs, carp, Sacramento perch, and catfish were taken by the pelicans, as well as cutthroat up to 8 pounds. Trout were considered accidental food items. It is concluded that white pelican is not detrimental to fishing industry, although local people believe it eats large numbers of cutthroat. Decline of trout is blamed on depletion of water, as well as on a dam, diversions, and pollution.

HALL, MAURICE C.
1930. Report on parasites of pelican and trout investigations at Yellowstone Lake, 1930. Unpublished report in Yellowstone Museum. 10 pp.
Studies on tapeworms in cutthroat and pelicans featured postmortem examination of pelicans for parasites and antihelminthic treatment of pelicans. Pelicans are freed from tapeworms with kamala. Relation between fish size and parasitism is discussed, as is relation between parasitism and reduced cutthroat egg production. Antihelminthic treatment of pelicans is recommended as control for tapeworms in Yellowstone Lake cutthroat.

HATTON, S. ROSS.
1932. The fish fauna of Utah Lake. Master's Thesis, Brigham Young University, Provo, Utah. 64 pp.
Synonymy, description, and habits of *Salmo utah* are given. Historical importance of this fish in Utah Lake is discussed. Gradual disappearance of species from Great Basin is described.

HAZZARD, A. S.
1932. Preliminary report of a biological survey of the streams and lakes of Grand Teton National Park and Jackson Lake, Wyoming. Unpublished rept. to U. S. Bur. Fish. 94 pp.
Cutthroat is treated at some length. Average size and condition factors are given for many waters. Spawning habits and distribution are described for Teton area. Average condition factor for all lakes was 1.345, for all streams 1.328.

HAZZARD, A. S., and M. J. MADSEN.
1933. Studies of the food of the cutthroat trout. Trans. Amer. Fish. Soc., 63:198–207.
Food studies of *S. lewisi* from Jackson Lake, Wyoming, Glacier Park, Montana, and other lakes and streams in Teton Park, Wyoming, were conducted over three seasons. Diet of smallest fingerlings is diversified, midges being most important item. Considerable variation in diet was seen from stream to stream and from lake to lake. Change in diet at 11½ inches was noted in Jackson Lake fish from crustacea toward fish. A variety of fish species was utilized. Large (11¾–14½ inches) cutthroat from Strawberry Reservoir, Utah, had only midge larvae and pupae in their stomachs. Stomachs of *Salmo gibbsii* from Middle Fork of Salmon River in Idaho had great numbers of snails, with fish, fish eggs, caddis, and stoneflies. Cutthroat diets are similar to those of other trouts.

HENSHALL, JAMES A.

1902. Food and game fishes of the Rocky Mountain region. Trans. Amer. Fish. Soc., 31: 74–88.

Several common names for cutthroat in Rocky Mountain region are given. Distribution and habits are discussed.

1906. A list of the fishes of Montana. Bull. Univ. of Mont., No. 34. 13 pp.

Red-throat trout is discussed with reference to distribution, color patterns, and habits.

HILDEBRAND, SAMUEL F., and IRVING L. TOWERS.

1927. Food of trout in Fish Lake, Utah. Ecology, 8 (4): 389–399.

Contents of 181 stomachs of brook, lake, rainbow, and cutthroat trout were studied with reference to physical conditions and plant and animal life of Fish Lake, Utah. *Daphnia*, amphipods, insects, and *Nostoc* colonies were chief organisms found. Lesser numbers of fish eggs, *Pisidium*, snails, and certain higher plants were found.

HUEY, WILLIAM S.

1956. New Mexico beaver management. N. Mex. Dept. of Game and Fish, Bull. No. 4. 49 pp.

During summer of 1955, studies were conducted to determine beaver-trout relations. Two inventories were made in each of six experimental sections of upper Red River in Taos County. Three of these contained beaver ponds and three did not. Each section had 50 yards of stream. Cutthroat, brook, and rainbow trout and white suckers were in the experimental area. Average trout population in beaver sections was 154 in June and 180 in August, as opposed to 33 in June and 47 in August for nonbeaver sections. Trout from beaver ponds were slightly larger than those from nonbeaver sections. Food production was significantly higher in beaver sections and trout growth appeared to be faster in these sections.

HUEY, WILLIAM S., and WILLIAM H. WOLFRUM.

1956. Beaver-trout relations in New Mexico. Prog. Fish-Cult., 18 (2): 70–74.

Effect of beaver activity on trout production in Red River, New Mexico, was studied. Cutthroat, rainbow, and brook trout were present: cutthroat and brook amounted to 98–99 percent of the trout.

Production was increased in beaver ponds. Ponds produced more trout than undisturbed stream areas, and growth was faster. Cutthroat were apparently not prevented from spawning because of beaver activity.

IDYLL, CLARENCE.

1942. Food of rainbow, cutthroat, and brown trout in the Cowichan River System, B. C. Jour. Fish. Res. Bd. Can., 5 (5): 448–458.

Stomach contents of 293 rainbow, 160 cutthroat, and 113 brown trout were examined and analyzed according to species, size groups (5 cm.), and habitat (river or lake). For rainbows of both river and lake (4 to 50 cm. in length), insects, chiefly Trichoptera and Simuliidae, were predominant in all size groups. Fish constituted a small fraction of the food except in winter when salmon eggs were available. River cutthroat subsisted chiefly on insects (Trichoptera) up to 15 cm., on insects and fish (*Gasterosteus*) up to 30 cm., thereafter largely on fish. Lake cutthroat did not eat fish in any number until 41 cm. long. Brown trout ate chiefly insects (Trichoptera) up to 45.5 cm., thereafter turning more definitely to a fish (salmonid) diet. Cutthroat were more piscivorous than brown trout. Definite selection of food by the trout was indicated.

IRVING, ROBERT B.

1953. Ecology of the cutthroat trout, *Salmo clarkii* Richardson, in Henrys Lake, Idaho. Master's Thesis, Utah State Agr. Coll., 101 pp.

Cutthroat trout of several stocks live in Henrys Lake with rainbow and brook trouts, whitefish, bullhead, and silverside minnow. Limnological data suggest high productivity. Growth is rapid, and body-scale relation is 21.59 mm. $+6.879\ S_l + 0.03874\ S_l^2$. Only 2 percent of cutthroat reach 5 years of age; 2 percent of rainbow and cutthroat hybrids reach 7 years of age. Length-weight relation of cutthroat is $\text{Log } W = -4.6353 + 2.9529 \text{ Log } L$. Average female cutthroat has 2,703 eggs. Average total length of spawners is 18.5 inches for male and 19 inches for female. Sex ratio in 1951 was 96 males to 100 females.

Potential harvest is estimated at 89.2 pounds per surface acre. In 1951 the lake yielded 5.1 pounds per surface acre. Cutthroat in the creel averaged 2.5 pounds.

1956. Ecology of the cutthroat trout in Henrys Lake, Idaho. Trans. Amer. Fish. Soc., 84: 275–296.

Henrys Lake in eastern Idaho is a shallow, fertile lake, with an estimated 606 pounds of bottom and plant-inhabiting fauna in 1951. *Salmo clarki*, *Cottus bairdi semiscaber*, and *Prosopium williamsoni* are the native fish; *Salmo gairdneri*, *Salvelinus fontinalis*, and *Richardsonius balteatus hydrophlox* are introduced species. Rainbow-cutthroat hybrids were rare in the catch. Body-scale relation in cutthroat was $L = 21.59 + 6.879\ R + 0.03874\ R^2$. Male cutthroat in 1951 matured at ages II and III, females at ages III and IV. Severe mortality subsequent to spawning is reported for 1951. Variation in growth is attributed to differences between time spent in streams and in the lake, seasonal variation of environmental conditions, and different ages at maturity. Rates of female to male cutthroat in catch decreased with age and progress of season. Ninety percent by number and 74 percent by volume of food were midges, shrimp, and damselflies. Pathogenic bacteria infected mature fish in 1950, 1951, and 1952 spawning migrations. Asphyxiation was cause of mortalities at mouths of streams in January 1952. The population is short-lived owing to disease, asphyxiation, predation, angling, and spawning mortality.

JORDAN, DAVID STARR.

1890. The fishes of the Yellowstone Park. Zoe, 1 (2): 38–40.

Discussion of native fishes of Yellowstone Park. Describes historical geology of area and suggests that *Salmo mykiss* entered Yellowstone Lake and River from Pacific Creek in Snake River drainage.

1891a. Report of explorations in Colorado and Utah during the summer of 1889, with an account of the fishes found in each of the river basins examined. Bull. U. S. Fish Comm., 9: 1–40.

Discussions of distribution, appearance, and biology of *S. m. macdonaldi*, yellow-finned trout; *S. m. stomias*, green-backed trout; *S. m. clarki*, cutthroat trout; *S. m. pleuriticus*, Colorado River trout; *S. m. spilurus*, trout of the Rio Grande; *S. m. virginalis*, trout of Utah Lake; *S. m. bouvieri*, Waha Lake trout; *S. m. henshawi*, Lake Tahoe trout; *S. m. lewisi*, trout of the Upper Missouri.

1891b. A reconnaissance of the streams and lakes of the Yellowstone National Park, Wyoming, in the interest of the United States Fish Commission. Bull. U. S. Fish Comm., 9: 41–63.

Discusses distribution of each drainage. Much detail is given on distribution of *S. mykiss* and infestation by *Dibothrium* worms. Classified list of waters suitable for *S. mykiss* is presented.

1907. The trout and salmon of the Pacific Coast. State Bd. Fish Comm. of Calif., Rept. (1905–1906): 77–92.

Describes discovery of cutthroat in Oregon by Clark. Movements of trout species in northern hemisphere are described; movement of cutthroat from Alaska southward is traced. Color patterns are given. Tahoe trout and Crescent trout are treated separately.

1920. The trout of the Rio Grande. Copeia, No. 85, pp. 72–73.

Nomenclature of cutthroat is discussed. *Salmo virginalis* is the Rio Grande trout, and *S. utah* is the Bonneville Basin trout.

1928. The distribution of fresh-water fishes. Annual Report of Smithsonian Institution for 1927, pp. 355–385.

Principles of zoogeography are discussed, including methods of distribution of fishes. Geographic barriers throughout world are described, with their influence on groups of fishes. Dispersal of fresh-water fishes is discussed in general terms, and movement of cutthroat over Two-Ocean Pass in Wyoming is treated in detail. Speciation in cutthroat in Great Basin is described.

JORDAN, DAVID STARR, and BARTON W. EVERMANN.

1902, 1934. American food and game fishes. Country Life Press, Garden City, N. Y., pp. 175–179.

Keys to species of cutthroat are given. Discussion of distribution, biology, and habits of *S. clarki*, *S. lewisi*, *S. gibbsii*, *S. henshawi*, *S. tahoensis*, *S. utah*, *S. jordani*, *S. bathoecetor*, *S. declivifrons*, *S. virginalis*, *S. pleuriticus*, *S. bouvieri*, *S. stomias*, and *S. macdonaldi* is presented.

JORDAN, DAVID STARR, and H. W. HENSHAW.

1879. Report upon the fishes collected during the years 1875, 1876, and 1877, in California and Nevada. Report of the Chief of Engineers, Part 3, Appendix NN, Appendix K, pp. 1609–1622. Executive Documents, 3d Sess., 45th Cong., 1878–79, vol. 5.

Contains detailed descriptions of *S. tsuppitch* Richardson (black trout), *S. henshawi* Gill & Jordan (silver trout) and *S. pleuriticus* Cope (Rio Grande trout), with notes on distributions and biologies.

JUDAY, CHAUNCEY.

1907a. Notes on Lake Tahoe, its trout and trout-fishing. Bull. U. S. Bur. Fish., 26: 133–146.

Description of Lake Tahoe, its vegetation, and its plankton is given. Account of *Salmo henshawi* (Lake Tahoe trout, Truckee trout, pogy, and snipe) and *Salmo tahoensis* (silver trout) is presented. Gives distribution, breeding habits, hatchery operation, food habits, angling methods, shipments of trout from the lake, and their commercial value ($6,819 in 1906).

1907b. A study of Twin Lakes, Colorado, with especial consideration of the food of the trouts. Bull. U. S. Bur. Fish., 26: 147–178.

Describes physical characteristics of the lakes, aquatic vegetation, plankton, and fishes, including *Salmo macdonaldi* (yellow-fin trout) and *Salmo stomias* (green-back trout). Importance of study of fish food is discussed, and details of analyses of fish stomachs are given. *S. stomias* stomachs contained fish remains, insects, crustaceans, and vegetable fragments. Importance of plankton crustacea as fish food is discussed at length.

KEMMERER, GEORGE, J. F. BOVARD, and W. R. BOORMAN.

1924. Northwestern lakes of the United States; biological and chemical studies with reference to possibilities in production of fish. Bull. U. S. Bur. Fish., 49: 51–140.

Physical and biological surveys were made in many northwestern lakes for comparisons with each other and with Wisconsin lakes, and to determine suitability for trout. Cutthroat trout found in Bear Lake, Idaho, Henry Lake, Idaho, Coeur d'Alene Lake, Idaho, Hayden Lake, Idaho, Payette Lake, Idaho, Pend Orielle Lake, Idaho, Priest Lake, Idaho, and Spirit Lake, Idaho. Food habits are discussed.

KENDALL, W. C.

1915. The fishes of the Yellowstone National Park. Rept. U. S. Comm. Fish for 1914, App. VIII, pp. 1–28.

Fishing for cutthroat and other species is described for major waters of Yellowstone Park. Tapeworm parasite of cutthroat of Yellowstone is discussed. Detailed distribution of cutthroat is given for Yellowstone Park. Distribution from hatchery is listed.

LAAKSO, MARTIN.

1955. Variability in scales of cutthroat trout in mountain lakes. Proc. Utah Acad. Sci., Arts, and Lett., 32: 81–87.

Some cutthroat trout in mountain lakes fail to establish a year mark during first year of life and have scales designated as "retarded." Fry which are more advanced in their first fall have year marks corresponding to each year of life and are called "normal." Frequency of normal scales was found to be closely correlated (r.=.79) with growth index (quotient of mean length divided by mean age for each sample) in total of 12 areas.

1956. Body-scale regressions in juvenile cutthroat from Yellowstone Lake. Proc. Utah Acad. Sci., Arts, and Lett., 33: 107–111.

The body-scale regressions of juvenile cutthroat trout from different areas in Yellowstone Lake showed significant differences in slope. Curves plotted for fingerlings captured near the outlet of Yellowstone Lake exhibited steeper slopes, showing that scale growth was relatively faster than in fish collected along the lakeshore and in two small tributaries.

LAAKSO, MARTIN, and OLIVER B. COPE.

1956. Age determination in the Yellowstone cutthroat trout by the scale method. Jour. Wildl. Mgt., 20 (2): 138–153.

Fishery studies on cutthroat trout in Yellowstone Lake have required investigation into technique of age determination. Scales exhibit growth characteristics different from those of same species in other waters at lower altitudes. Present studies have centered around identification of scales on which first annulus failed to form.

Cutthroat trout in Yellowstone Lake ascend spawning streams from May to late July. Fry emerge from late June to early September. Scale formation is initiated when fish are 41 to 44 millimeters in length. Late-hatched fry may not attain this length before interruption of growth in October, and thus may overwinter without scales or with only a few small scales. As a result, three developmental types of fry occur in the population: (1) fry overwintering in a fully scaled state; (2) fry passing the winter partially scaled; and (3) fry overwintering without scales.

Annulus development after first growing season occurred on scales of fingerlings whose scale growth had reached 4-circulus stage. Late-hatched fry with rudimentary scales failed to establish a year mark during their first fall and winter period. These fish with "retarded" scales exhibit annulus formation following their second growing season. Term "retarded scale" is proposed to designate a scale that does not exhibit an annulus after first growing season, and "normal" is applied to a scale which did establish a year mark after 1 season's growth. Structural criteria have been established for identification of the two types of scale development. Bases for differentiating the types are (1) numbers of circuli before first annulus, (2) size of focus, or first circulus, and (3) shape and density of first one or two circuli.

Annulus formation begins before May 1 and is usually complete by middle of June. Spawners appear to initiate scale growth before nonspawners.

Fingerlings taken late in season and presumed to be in first year of life included 35 percent fully scaled individuals, unscaled comprised 22 percent, partially scaled made up 42.7 percent. Adults sampled from 1951, 1952, and 1953 fisheries averaged 40 percent normal.

LAND, S. E.

1913. The black-spotted mountain trout. Trans. Amer. Fish. Soc., 42: 183–198.

Salmo stomias Cope and *Salmo spilurus* Cope are discussed as to distribution and handling.

LEACH, GLEN C.

1923. Artificial propagation of brook trout and rainbow trout, with notes on three other species. Rept. U. S. Comm. Fish. for 1923, App. VI, pp. 1–74.

Describes places where cutthroat trout have been cultured. Spawning season, growth, and egg production are noted. Quotes articles relating to biology of this species. Tapeworm parasite at Yellowstone is discussed.

LINTON, EDWIN.

1891a. On two species of larval dibothria from the Yellowstone National Park. Bull. U. S. Fish Comm., 9: 65–79.

A collection of *Salmo mykiss* and suckers from Yellowstone Park were examined for parasites. Larval cestodes were found in both fishes. Detailed descriptions of anatomies of the tapeworms are given, and figures are presented. *Dibothrium cordiceps* Leidy is the worm found in the cutthroat.

1891b. A contribution to the life history of *Dibothrium cordiceps* Leidy, a parasite infesting the trout of Yellowstone Lake. Bull. U. S. Fish Comm., 9: 337–358.

Discussions of larval and adult stages of *D. cordiceps* from *Salmo mykiss* in various waters of the Yellowstone, and an account of distribution and anatomy and of pelican hosts. Author accounts for abundance of parasitized trout in Yellowstone Lake and migration of parasite into muscular tissue of its host.

1893. On fish entozoa from Yellowstone National Park. Rept. U. S. Comm. Fish. 17: pp. 545–564.

This paper treats all internal parasites found in a collection of trout, suckers, and chubs from Yellowstone Park. Parasites from *Salmo mykiss* were: tapeworm *Dibothrium cordiceps* Leidy, fluke *Distomum laureatum* Zeder, acanthocephalan *Echinorhynchus globosus* Rud. and nematode *Dacnitis globosa* Dujardin. Details of life history and biology are given for some of these parasites.

LOCKE, S. B.
1929. Whitefish, grayling, trout, and salmon of the intermountain region. Rept. U. S. Comm. Fish. for 1929, App. V, pp. 173–190.

Identification and description of salmonids in intermountain region are treated. Cutthroat is discussed in the various forms reported for drainages in this region.

LORD, RUSSELL F.
1930. Rearing a brood stock of blackspotted trout. Trans. Amer. Fish. Soc., 60: 164–166.

Sources of blackspotted trout eggs are suffering a decline in abundance, and it seems necessary to rear new brood stocks of this species. Attempts in 1920–22 at Springville, Utah, were unsatisfactory. Experiments at Pittsford, Vermont, beginning in 1926, resulted in an egg take of 115,000 eggs in 1930. An 8.6-percent loss was suffered up to the eyed stage. Shipments were made and fry were feeding nicely at latest report.

MCCONNELL, WILLIAM J., WILLIAM J. CLARK, and WILLIAM F. SIGLER.
1957. Bear Lake, its fish and fishing. Utah Dept. Fish and Game, Idaho Dept. of Fish and Game, Wildl. Mgmt. Dept., Utah State Agr. Coll. 76 pp.

The cutthroat is one of three important game fish of Bear Lake. Methods of catching cutthroat are discussed, as well as importance of cutthroat in the fishery. Gill-netting showed cutthroat to be most abundant between shore and 75-foot contour throughout year. Life history of cutthroat in Bear Lake is treated, and calculated total lengths to seventh year are given. Creel census showed that 900 to 1,000 cutthroat were caught annually from 1953 to 1956. History of planting cutthroat in Bear Lake is given. Length frequencies of cutthroat taken in creel are figured. It is concluded that present cutthroat population is only slightly exploited, and that if population density were increased, shore fishermen would probably not enjoy greatly increased success.

MADSEN, DAVID H.
1936. Protection of native fishes in the National Parks. Trans. Amer. Fish Soc., 66: 395–397.

Planting policies in National Parks are discussed, and rainbow-cutthroat hybridization through planting is described. Importance of this trend in Rocky Mountains is stressed. Policy for management of cutthroat and other native species in National Parks is presented.

MADSEN, M. J.
1940. Report on age and growth of the cutthroat trout (*Salmo lewisi*) of Yellowstone Lake, Wyoming. Unpublished rept. U. S. Fish and Wildl. Serv. 12 pp.

Studies on scales collected from Yellowstone Lake in 1938 and 1939 showed age group III to dominate the fishery, followed by age groups IV, II, and V. Sexes in catch were 54.8 percent males and 45.2 percent females in 1938; in 1939, percentages were 67.4 and 32.6, respectively.

Condition factors were calculated as 1.2271 for 1938 and 1.3027 for 1939. Condition factors for males were higher than for females.

Weight-length relations are presented.

Observations on parasitism by tapeworms were made, showing that in 1938, 31.8 percent of the fish examined were parasitized; in 1939 the percentage was 45.7. Parasitized fish had lower condition factors than did nonparasitized ones.

MERRIMAN, DANIEL.
1935. The effect of temperature on the development of the eggs and larvae of the cutthroat trout (*Salmo clarkii clarkii* Richardson). Jour. Exp. Biol., 12 (4): 297–305.

Eggs of coastal cutthroat were raised from fertilization through hatching at constant temperatures of 11.3°, 8.25°, and 6.35° C. Temperature is not limiting factor in determining length of hatching period. Average size of cutthroat embryos at hatching was smaller at higher temperatures and larger at lower temperatures. Maximum increment of growth occurred about 41st day at 8.25° C. and about 28th day at 11.3°. Percentage of dry weight of cutthroat embryos showed a steady decrease from about 25 to 14 percent, while that of yolks showed an increase from about 46 to 55 percent. Embryos absorbed water from the yolk, and at a faster rate from the environment, both before and after hatching.

MILLER, RICHARD B.
1952. Survival of hatchery-reared cutthroat trout in an Alberta stream. Trans. Amer. Fish. Soc., 81: 35–42.

Gorge Creek, typical small mountain trout stream in southwestern Alberta, was divided by fish-tight screens into two sections, each about three-quarters of a mile in length. The number of native trout in these was determined by marking and recapture. One section was left as a control. Into the other, 199 3-year-old and 201 2-year-old hatchery-reared cutthroat trout were liberated. Each of the planted trout was weighed and given a numbered Petersen tag before planting. Fish that died were removed daily and weighed. Daily angling was carried on to recapture, weigh, and again release as many as possible. One-third of the 3-year-old fish died, mainly in the first 2 weeks following planting. All lost weight for 40 days, apparently through inability to compete with the native population. By fall (about 100 days after planting) the survivors had regained their planted weights. All, or nearly all, of the 2-year-old fish died, apparently from a combination of shock and starvation. Native trout in experimental section gained weight all summer, and by fall were in as good condition as native trout in control section.

Plans for planting hatchery-reared trout in sections of stream free of native trout and for transplanting native trout into sections containing native trout are described.

1954a. Movements of cutthroat trout after different periods of retention upstream and downstream from their homes. Jour. Fish. Res. Bd. Can., 11 (5) : 550–558.

A homing experiment of cutthroat trout (*Salmo clarki*) was carried out in Gorge Creek, a small trout stream more or less typical of streams of eastern slopes of Rocky Mountains in Alberta. A half-mile portion of the stream was screeened off and, into the enclosure thus formed. 105 trout were transferred from above and 104 from below. Each of these was given a numbered tag and the home locality was recorded. Transfers were made from June 24 to August 13. On August 15 the screens were removed; September 3 to 5, most of the experimental area was poisoned with Fish Tox and the localities of tagged fish recorded. It was found that most of the trout that had been confined for 30 or more days remained in the enclosure area, i. e., they had adjusted to new homes. Exceptions appear to be result of random movements. Trout of upstream origin, confined for less than 30 days, move toward their original home territory. Trout of downstream origin, confined for less than 30 days, show very much less ability to move toward or to find their homes. Hypothesis is that trout are guided by smell in finding home.

A few observations on size of home territory suggest that it is small, perhaps not more than 20 yards of stream. Trout may inhabit same area of stream for at least 3 years.

1954b. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Trans. Amer. Fish. Soc., 83 : 120–130.

Gorge Creek, typical small mountain trout stream on eastern slope of Rocky Mountains, was used in test to measure survival and weight changes in hatchery-reared cutthroat trout (*Salmo clarki*). Resident population of this species exists in the stream. Experimental procedure was to introduce groups of trout into enclosures one-half to three-fourths of a mile long: each trout in a group was given a numbered Petersen tag and weighed before planting. Recapture by angling and reweighing was carried out throughout the season of planting and also in later summers. In this way six lots of pond-reared, one lot of stream-reared, and one lot of transplanted wild cutthroat trout were studied. Pond-reared fish exhibited very low survivals over first (0 to 4.9 percent) and second (0 to 3.1 percent) winter. Survival was largely independent of age. Transplanted, wild trout showed survivals of 46.0 to 29.0 percent to second and third summers, respectively. Stream-reared hatchery fish gave an intermediate value (17.2 percent to second summer).

All lots of trout lost weight for some 30 to 40 days when superimposed on a resident population. This loss was more severe and was regained more slowly in pond-reared trout than in transplanted wild trout.

It is held that low survivability of hatchery fish is due to absence of natural selection at early stages in life history.

1955. Trout management research in Alberta. Trans. Twentieth N. A. Wildl. Conf., pp. 242–252.

Experiments were conducted in Gorge Creek in South Saskatchewan River system to learn what happened to hatchery-reared cutthroat trout released in the stream.

With pond-reared cutthroat planted in an area with wild trout, there was an early, heavy mortality, followed by a period in which survivors lost weight. With wild cutthroat transplanted to an area with other wild cutthroat, the wild fish had lower mortalities and less weight loss than the pond fish.

Partially stream-reared cutthroat planted in the stream with wild fish suffered greater mortality than the wild, transplanted fish, but less than the pond-raised fish.

Hatchery-reared cutthroat planted in a stream with no resident population survived well and immediately began to gain weight. All groups showed low survival over first winter.

MILLER, ROBERT RUSH.

1950. Notes on the cutthroat and rainbow trouts with the description of a new species from the Gila River, New Mexico. Ann Arbor, Michigan: Univ. Mich. Press. Occasional Papers, Mus. Zool., No. 529. 42 pp.

Salmo gilae, a new species, is described. It resembles *S. gairdnerii* in some respects and *S. clarkii* in others. Status of trouts of western North America is reviewed. Comparisons between rainbow and cutthroat series are presented and discussed. Origins of *S. clarkii* are discussed.

MILLER, ROBERT R., and J. R. ALCORN.

1946. The introduced fishes of Nevada, with a history of their introduction. Trans. Amer. Fish. Soc., 73 : 173–193.

History and distribution of *Salmo clarkii henshawi*, *S. c. lewisi*, and *S. c. utah* are described in detail for Nevada. Rainbow-cutthroat hybrids are also discussed, and stocking these species in the same water is discouraged.

MOORE, H. L., O. B. COPE, and R. E. BECKWITH.

1952. Yellowstone Lake trout creel censuses, 1950–1951. U. S. Fish and Wildl. Serv., Spec. Sci. Rept.—Fish. No. 81. 41 pp.

Two years of cutthroat trout creel census on Yellowstone Lake gave estimates of catch, effort, numbers of fishermen, and catch per hour for each unit of the fishery. Variances were calculated for catch and effort estimates, and mathematical basis for shoreline census method is described.

Catches of 1950 and 1951 were 199,993 and 207,860 for Yellowstone Lake. Catches per hour ranged from 0.16 to 2.12, depending on the unit of the fishery.

MOTTLEY, C. McC.

1934. The origin and relations of the rainbow trout. Trans. Amer. Fish. Soc., 64: 323–327.

Rainbow and cutthroat forms of trout were evolving from a single salmonine stock in the last interglacial period after having been separated from progenitors of Pacific salmon by previous glaciation. Salmonine stocks were forced southward at last glaciation and then moved north again as ice melted. Cutthroats came into British Columbia from glacial Lake Bonneville and are found at higher elevations and farther from sea than rainbows.

MUTTKOWSKI, RICHARD A.

1925. The food of trout in Yellowstone National Park. Roosevelt Wild Life Bull., 2 (4): 471–497.

The cutthroat and its environment, water food and surface food, feeding habits, and hints to anglers are discussed.

1929. The ecology of trout streams in Yellowstone National Park. Roosevelt Wild Life Annals, 2 (2): 155–240.

Contains detailed descriptions and classification of Yellowstone trout streams, with lists of flora and fauna. A little about biology of cutthroat itself is given.

NEAVE, FERRIS.

1949. Game fish populations of the Cowichan River. Fish. Res. Bd. Can., Bull. No. 84. 32 pp.

Some habits and life history of cutthroat in this British Columbia stream are described. Cutthroat are very widely distributed in this system. They spawn in winter and spring. Immatures may remain up to 2 years in spawning streams. Cutthroat move randomly in streams in winter, aside from movements connected with reproduction. Growth rate is variable. First spawning is usually at 3 or 4 years of age. Spawning more than twice is exceptional.

NEEDHAM, PAUL R., and F. K. CRAMER.

1943. Movement of trout in Convict Creek, California. Jour. Wildl. Mgt., 7 (2): 142–148.

A 2-way fish trap was used in Convict Creek to study movements of brown, cutthroat, brook, and rainbow trout. Numbers of cutthroat trapped were small, and did not conclusively show migration patterns.

OLIVE, JOHN R.

1953. A bibliography of the limnology and fishery biology of Colorado. Mimeo. Publ., Colo. Game and Fish Dept., 34 pp.

Contains references to many reports and papers on cutthroat in Colorado.

PAUTZKE, CLARENCE F.

1938. Studies on the effect of coal washings on steelhead and cutthroat trout. Trans. Amer. Fish. Soc., 67: 232–233.

Effects of coal washings in Cedar River in Washington were measured on steelhead and cutthroat. Cutthroat, 1 to 2 inches, died in 30 minutes, while the control was unaffected. Steelhead, 6 inches long, died in 1½ hours.

PECHACEK, LOUIS S.

1950. Harvest of wild and stocked fish from the Logan River drainage. Master's Thesis, Utah State Agr. Coll. 103 pp.

In this study of harvest of cutthroat, brook, brown, and rainbow trouts and mountain whitefish in Logan River in 1949, it was determined that cutthroat comprised 31.5 percent of the catch, rainbows 34 percent (25.5 percent were marked rainbows).

PLATTS, WILLIAM S.

1957. The cutthroat trout. Utah Fish and Game Magazine. 13 (10): 4, 10.

This account of the cutthroat in Utah describes history and range of Utah cutthroat and Colorado cutthroat. Management of cutthroat in Utah is discussed in relation to environmental changes. Habitat, life history, spawning habits, and development of immature cutthroat are treated. Future for this fish in Utah is felt to be poor.

PURKETT, CHARLES A., JR.

1951. Growth rate of trout in relation to elevation and temperature. Trans. Amer. Fish. Soc., 80: 251–259.

A study of 758 trout from West Gallatin River indicated that growth was greater at lower elevations where water was warmer. Rainbow trout from upper and lower sections of West Gallatin River showed following differences in length at end of each year: 0.3 inch first year, 1.3 inches second year, 2.1 inches third year, 2.5 inches fourth year, and 4.0 inches fifth year. Growth rates of cutthroat and hybrid trout showed similar trend. Average summer difference in water temperature (early morning), between upper and lower stations of West Gallatin River, was 9.6° F. Condition factors did not show significant variations between sections.

Total of 184 trout from Bridger-Spring Creek did not show significant differences in growth rate. Water temperatures in stream did not vary greatly.

RASMUSSEN, DELBERT H.

1956. A creel census and fisherman expenditure study on Snake River, Wyoming. Wyo. Game and Fish Comm., Fish. Tech. Rept. No. 4. 26 pp.

A 40-mile section of Snake River was censused in 1955. Snake River cutthroat comprised 92 percent of catch and average 11 inches in length. Length frequencies and length-weight relations are given. Catch

per hour for bank fishermen was 0.74, for boat fishermen 0.64.

RASMUSSEN, D. I.

1941. Beaver-trout relationship in the Rocky Mountain region. Trans. Fifth N. A. Wildl. Conf., pp. 256–263.

Area in Wasatch National Forest containing 620 miles of stream inhabited by cutthroat, almost 200 miles of which was stocked with beavers, was studied to learn effects beavers had on cutthroat. Physical and chemical measurements and bottom fauna counts suggested that beaver did not produce adverse effects on trout. Beaver dams obstructed trout movement to some extent.

RICH, WILLIS H.

1924. Destruction of trout by pelicans in Yellowstone National Park. Rept. U. S. Comm. Fish. for 1923, App. VII, pp. 1–27.

In 1922, U. S. Bureau of Fisheries began investigation of pelicans in Yellowstone National Park, with Dr. H. B. Ward doing the work. He found that breeding period of white pelican in the park is synchronized with that of cutthroat trout. The pelican colony was 500–600 adults, and produced 200 young. Each pelican ate about 350 fish in the season. Control of pelicans by destruction of eggs was recommended.

ROBERTSON, O. H.

1947. An ecological study of two high mountain trout lakes in the Wind River Range, Wyoming. Ecology, 28 (2) : 87–112.

This study sought to explain difference in sizes of cutthroat trout from two adjacent, similar lakes. Life spans were about equal, but growth was faster in one lake. This lake had a better food supply, and its trout had food volumes in their stomachs thrice those of the smaller trout. No differences between the lakes were found in plankton counts, temperature, pH, O_2, dissolved Ca, or HCO_3. The richer lake had higher concentrations of phosphates, iodine, and organic matter.

ROUNSEFELL, GEORGE A.

1957. Fecundity of North American Salmonidae. U. S. Fish and Wildl. Serv. Fish. Bull., No. 122, vol. 57, pp. 451–468.

Measurements of egg diameters of cutthroat trout are compared with those of other salmonids. Measurements on number of eggs per female are given in relation to size of female, as well as other measures of egg size.

SCHNEIDER, PHILLIP W., and FRANCIS P. GRIFFITHS.

1943. Production of trout in a small artificial pond in western Oregon. Jour. Wildl. Mgt., 7 (2) : 148–154.

Stocking of trout in Cronemiller Pond resulted in no reliable survival data on rainbows and brown trout. Later stocking of cutthroat fingerlings with wild rainbow fry resulted in survival of 71.3 percent after 14.5 months for the cutthroat. Production was 46.5 pounds per surface acre.

SCHULTZ, LEONARD P.

1934. Species of salmon and trout in the northwestern United States. Proc. Fifth Pacific Sci. Congress (Can.), 5 : 3777–3782.

Contains brief discussion and keys, in which cutthroat is included.

1936. Keys to the fishes of Washington, Oregon, and closely adjoining regions. Univ. Wash. Pub. Biology, 2 (4) : 103–228.

Contains keys to cutthroats.

1941. Fishes of Glacier National Park, Montana. U. S. Dept. Interior, Fish and Wildl. Serv., Conservation Bull. 22. 42 pp.

Has an account of distribution, keys to species, abundance, appearance, and habits of fishes of Glacier Park. Two forms of cutthroat, *S. c. lewisi* and *S. c. clarkii*, are treated. Detailed distributional tables for park waters and fishes are presented.

SIMON, JAMES R.

1935. A new species of nematode, *Bulbodacnitis scotti*, from the trout, *Salmo lewisi* (Girard). Univ. of Wyo. Pub. 2 (2) : 11–15.

Contains description of new nematode from intestine and other viscera of *Salmo lewisi* in Yellowstone Lake.

1939, 1953. Yellowstone fishes. Yellowstone Library and Museum Assoc., pp. 1–39.

Fish-cultural practices for cutthroat in Yellowstone, parasites of cutthroat in the park, and natural predators on cutthroat are discussed. Description of Yellowstone cutthroat is given with notes on habits and distribution in Yellowstone.

1946. Wyoming fishes. Wyo. Game and Fish Dept., Bull. No. 4. 129 pp.

Keys to identification of cutthroat are given, and sections on *S. clarki lewisi*, cutthroat-rainbow hybrids, *S. c. pleuriticus*, and *S. c. stomias* cover distribution in Wyoming, biology, and fishing. Illustrations of cutthroat and hybrids are included.

SMITH, HUGH M., and WILLIAM C. KENDALL.

1921. Fishes of the Yellowstone National Park. Rept. U. S. Comm. Fish. for 1921, App. III, pp. 1–30.

Cutthroat is listed as one of indigenous species in Yellowstone. Hatchery operations with cutthroat are described. Section on cutthroat gives detailed distribution within Yellowstone Park, discusses fishing, and gives something on tapeworm parasite of fish in these waters.

SMITH, OSGOOD R.

1941. The spawning habits of cutthroat and eastern brook trouts. Jour. Wildl. Mgt., 5 (4) : 461–471.

Spawning cutthroat were studied in Convict Creek, California, and observations made on distribution of

fish and spawning periods, numbers of eggs retained by females, spawning activities, night spawning, egg predation, guarding completed redd, and damage to eggs by overlapping of redds. Contains excellent photographs of spawning.

1947. Returns from natural spawning of cutthroat trout and eastern brook trout. Trans. Amer. Fish. Soc. 74: 281–296.

Experiments were conducted over three seasons to determine number of fingerlings or fry produced by natural spawning of cutthroat (*Salmo clarkii henshawi*) and eastern brook trout (*Salvelinus fontinalis*). Returns were secured by inducing wild trout to spawn in controlled and screened section of stream. Resulting fingerlings were collected by diverting water and pumping pools dry.

Cutthroat spawned in May and fingerlings were recovered in September each year.

During first summer, horizontal screens, acting as fish traps, were used below cutthroat spawning areas so that some fry were trapped soon after emerging from gravel. Other fry remained in the section and were recovered in September. Minimum survival was about 17 percent of estimated number of eggs laid. Data were obtained on fry migration and growth of fry spawned at same time.

Vertical screens were used in all other experiments so that all survivors were collected in September. Survivals of cutthroat ranged from nothing to about 6 percent of estimated number of eggs in 4 trials, each trial section containing 1 to 3 female spawning trout.

SMITH, S. B.

1955. The relation between scale diameter and body length of Kamloops trout, *Salmo gairdneri kamloops*. Jour. Fish. Res. Bd. Can. 12 (5): 742–753.

The scale-body relation for Kamloops trout is very close to direct proportion for fish larger than 4.5 cm. fork length. Observations on steelhead trout, *Salmo gairdneri gairdneri*, and on coastal cutthroat trout, *Salmo clarki clarki*, suggest that an isometric scale-body relation may exist among those species also. McMynn and Vernon have shown relation in cutthroat to be linear with a log-log regression-line slope of 1.019, compared with 1.024 for Kamloops and 1.010 for steelhead.

SNYDER, J. O.

1917. Fishes of the Lahontan system of Nevada and Northeastern California. Bull. U. S. Bur. Fish., 35: 31–86.

In this account of all fishes in this basin, *Salmo henshawi* is given a long treatment. Details of color patterns from different drainages are given, as well as counts of spots on body areas. Very detailed measurements of specimens from different waters, of both sexes, and of different size groups are shown in tables. Migrations of cutthroat are discussed. The famous large cutthroat of Pyramid Lake are described. Methods of fishing and types of gear used are discussed.

1940. The trouts of California. Calif. Fish and Game, 26 (2): 96–134.

Descriptions of morphology, distributions, and biologies and life histories of *Salmo clarki*, *Salmo henshawi*, *Salmo seleniris*, and *Salmo pleuriticus* are given in this treatment of trouts in California.

SUCKLEY, GEORGE.

1874. On the North American species of salmon and trout. Rept. U. S. Comm. Fish. for 1872–73. pp. 91–160.

This catalog of North American Salmonidae classifies the genus *Salmo*, with anadromous salmons and trouts separated from nonanadromous species. Each species is individually treated with discussion of nomenclature, morphological characteristics, colors, diagnostic features, habitat, life-history notes, and taxonomic relations. Cutthroats treated are *Salmo tsuppitch* Richardson, *Salmo clarkii* Richardson, *Salmo virginalis* Girard, *Salmo lewisi* Girard, *Salmo stellatus* Girard, *Salmo gibbsii* Suckley, and *Salmo brevicauda* Suckley.

SUMNER, FRANCIS H.

1940. The decline of the Pyramid Lake fishery. Trans. Amer. Fish. Soc., 69: 216–224.

History of Pyramid Lake (Nevada) cutthroat trout (*Salmo henshawi* Gill and Jordan) fishery, conducted by reservation Indians, shows a rapid decline in catch within last few years. While the Indian is blamed for overfishing, the white man's demand for trout, the dams and diversions that he built along the Truckee River where the trout have spawned, the pollutants that he has dumped into the river, the spawn that he has taken, the competing species of fish that he has introduced, and principally the large amounts of water that he has diverted to another watershed, have led to a condition which has prevented the trout from reproducing its kind. Revival of the fishery is made doubtful by an agreement concerning use of Truckee River's flow, expense of hatching and rearing a stock of Pyramid Lake trout (not to mention questionable availability of its eggs), and inadequate regulation of the fishery. The Pyramid Lake cutthroat trout fishery appears to be doomed.

1948. The coast cutthroat trout. Oreg. State Game Comm. Bull., 3 (12): 1, 6–8.

Study on a coastal stream, Sand Creek, was begun in 1946, with upstream-downstream traps. "Blueback" trout, (salmon-trout, harvest trout) appear in coastal streams in October in many color phases. Upstream mortality was around two-thirds. Sand Creek cutthroat spend 1 to 5 years in the stream before migrating to the ocean, most doing so at 3 years of age. In the 1946 spawning run, 19.2 percent had spawned once before, 7.0 percent twice, and 1.5 percent three times. Some may spawn without ever having gone to the ocean.

1953. Migrations of salmonids in Sand Creek, Oregon. Trans. Amer. Fish. Soc., 82: 139–150.

Upstream and downstream fish traps were maintained on Sand Creek, a small Oregon trout stream, during 4 upstream and 3 downstream fish runs (1946–49), and a smaller trap was operated on a tributary during part of 1947. Two trouts, *Salmo clarki clarki* and *Salmo gairdneri gairdneri*, and two salmons, *Oncorhynchus kisutch* and *Oncorhynchus keta*, made spawning runs in fall and winter; downstream migrations of fry and fingerlings occurred in the spring.

Water temperatures and information on occurrence and magnitude of freshets were taken. Records on fish trapped included numbers of salmonids, lengths, weights, sex ratios, loss in weight after spawning, and survival rates.

Cutthroat upstream migrants ranged from 4.0 to 10.7 inches in fork length for one size group and from 11.0 to 18.6 inches in another size group. Sex ratios of sea-run cutthroat showed predominance of females (1.00 male to 1.69 female). Weights of migrating cutthroat ranged from 0.50 to 2.94 pounds. Fork lengths of downstream migrants were from 2.7 to 10.9 inches.

Survival of cutthroat spawners averaged 32 percent. Weight loss of spawners was about one-third.

TANNER, V. M.

1936. A study of the fishes of Utah. Proc. Utah Acad. Sci., Arts, and Lett., 13: 155–184.

This treatment of fishes of Utah has keys to several forms of cutthroat, and a discussion of findings of some early explorers with regard to distribution and abundance of cutthroat in Utah waters.

TANNER, V. M., and SHELDON P. HAYES.

1933. The genus Salmo in Utah. Proc. Utah Acad. Sci., Arts, and Lett., 10: 163–164.

Two cutthroats, S. *utah* Suckley and S. *pleuriticus* Cope, are in Utah. Yellowstone and Pyramid Lake cutthroats have been introduced and have mixed with native forms. Suckley, Goode, Jordan and Evermann, and Cope are quoted with regard to cutthroats on which they worked.

TRYON, C. A. JR.

1943. The effect of covering hatchery troughs on the growth of cutthroat trout (*Salmo clarkii*). Trans. Amer. Fish. Soc., 72: 145–149.

An experiment was designed and carried out to test effect of covered troughs on growth rate of cutthroat trout at Bozeman, Montana. Analysis of data showed trout in open troughs to have significantly greater growth rate than those in covered troughs. Growth rate in open troughs was greater by 13.8 percent.

TUNISON, A. V., and C. M. MCCAY.

1933. The nutritional requirements of brook trout. Trans. Amer. Fish. Soc., 63: 167–177.

In this study on nutrition of trout a group of cutthroat trout became infested with *Octomitis salmonis*. Antiseptics were fed in liver. Control of moving forms was achieved with mercurous chloride, 0.2 percent, Hexamethylenamine, 0.5 percent, and Naphthol (beta), 0.5 percent, and partial control with carbon tetrachloride, 0.2 percent.

TURNER, C. L.

1946. A case of hermaphroditism in the cutthroat trout. Chicago Acad. Sci., Nat. Hist., Misc. No. 1, pp. 1–2.

A female cutthroat (*Salmo clarkii*) from Yellowstone Lake was examined by the author. Ovaries were normal. At the anterior end of the right ovary was a flattened oval mass, which was examined histologically. This was a small testis, with mature spermatozoa and nests of spermatogonia.

Hermaphroditism as a normal situation in other fishes is discussed.

UNITED STATES COMMISSION OF FISH AND FISHERIES.

1900. A manual of fish culture. From Rept. U. S. Comm. Fish. for 1897. 340 pp.

This manual deals with all aspects of culture of fishes raised in the United States. A small section is devoted to cutthroats.

WARD. H. B.

1923. The pelicans of Yellowstone Lake. Typewritten rept. to U. S. Bur. Fish., pp. 1–20.

Relations of the white pelican and the fish of Yellowstone Lake in 1922. Feeding habits of the pelicans were closely observed. Of the fish eaten, 98 percent were cutthroat trout. It is estimated that 350,000 cutthroat were taken by pelicans in 1922.

VERNON, E. H., and R. G. MCMYNN.

1957. Scale characteristics of yearling coastal cutthroat and steelhead trout. Jour. Fish. Res. Bd. Can., 14 (2): 203–212.

Some scale characteristics of 88 yearling coastal cutthroat trout (*Salmo clarki clarki*) and 96 yearling steelhead (*Salmo gairdneri*) were compared in some detail. Although the number of diagonal scale rows above the lateral line was significantly higher in cutthroat, counts of the two species overlap. Correlation of scale circuli counts with scale diameter was 0.94 for steelhead and 0.90 for cutthroat. At any given scale size cutthroat scales had 8 percent more circuli than steelhead scales. Measurements of lateral and longitudinal diameters and anterior radii of scales show that the anterior portions of cutthroat scales tend to be longer and narrower than those of steelhead.

Regression analyses of each scale measurement on fork length indicated that, for any given fork length, cutthroat scales are smaller than those of steelhead, the greatest difference being apparent when anterior radii are compared. Growth of scales in a dorsoven-

tral plane approximates isauxesis in relation to fork length, but scale growth in a longitudinal plane tends toward positive heterauxesis which is particularly pronounced in the anterior portions of scales.

Multiple regression analyses of scale diameter, scale row count, and fork length indicated that the smaller size of cutthroat scales is not balanced by proportionate increase in their number. When scale diameter is adjusted for scale number and fork length, cutthroat scales are 15.6 percent smaller than those of steelhead, indicating that young cutthroat are covered by their scales with less overlap.

WELSH, JAMES P.

1952. A population study of Yellowstone blackspotted trout (*Salmo clarkii lewisi* Girard). Ph. D. dissertation, Leland Stanford Jr. Univ., pp. 1–180.

A study of cutthroat populations in Arnica Creek, tributary of Yellowstone Lake, Yellowstone National Park, was made in 1950 and 1951. Sex ratio in the 1951 runs was 90 males to 102 females. Length-weight regression of Arnica Creek resident trout was calculated at Log Y=3.002 Log X—5.063. Egg counts ranged from 745 to 1,495 per female. Times of spawning runs and their variation within the season are discussed at length.

WILLOUGHBY, HARVEY.

1951. Age and growth of the cutthroat trout, *Salmo clarkii lewisi*, in Yellowstone Lake. Yellowstone Nature Notes, Yellowstone Library and Mus. Assn., 25 (3) : 29–32.

Scales were read from 523 cutthroat collected from Yellowstone Lake in 1949. Age distribution and growth rate were figured. Year class IV was best represented, followed by III, V, and VI.

WOODBURY, L. A.

1934. Parasites and diseases of the trout of Yellowstone Lake (*Salmo lewisi*). Master's Thesis, Univ. of Utah, pp. 1–60.

Treats body constants of Yellowstone cutthroat, food habits in relation to parasites, neoplasms, muscular abcess, subcutaneous abcess, gill disease, phycomycetosis, protozoan infestation, trematodes, cestodes, nematodes, acanthocephala, and copepoda.

YARROW, H. C.

1874. On the speckled trout of Utah Lake, *Salmo virginalis* Girard. Rept. U. S. Comm. Fish. for 1872–73, App. B, Ch. XII, pp. 363–368.

Life history of red-throated trout, *Salmo virginalis*, in Utah Lake, treating spawning, feeding, and movements. Maximum length was 3 feet, maximum weight 15½ pounds.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

SURFACE CIRCULATION IN THE GULF OF MAINE AS DEDUCED FROM DRIFT BOTTLES

By C. Godfrey Day

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ABSTRACT

Drift-bottle returns from 17 cruises over the Gulf of Maine and Georges Bank are compared. Seasonal and year-to-year differences in surface water circulations are noted. Wind values for 60 days following each cruise are presented in an effort to determine wind influence on surface circulation within the area.

SURFACE CIRCULATION IN THE GULF OF MAINE AS DEDUCED FROM DRIFT BOTTLES

By C. GODFREY DAY, *Research Assistant*
WOODS HOLE OCEANOGRAPHIC INSTITUTION

Between 1931 and 1956, the United States Fish and Wildlife Service made a number of cruises to the Gulf of Maine and Georges Bank as part of a study of the distribution and movement of the eggs and larvae of commercially important food fishes. On 17 of these cruises, during the years 1931, 1932, 1933, 1934, 1953, 1955, and 1956, drift bottles were launched throughout the area.[1] The seasonal coverage of these bottle seedings extends from late February through June.

Plots of drift-bottle returns showed such marked differences that a careful analysis of these data was necessary. This paper reports the results of a study of the surface circulations as deduced from bottle returns. Seasonal and year-to-year differences are noted. Daily values for surface-wind direction and force for the period of each cruise and for 60 days following have been taken from the daily weather maps in an effort to determine the effect wind may have had on the surface-water movement.

The original data, the result of studies by the United States Bureau of Fisheries and the United States Fish and Wildlife Service, are on file at the Woods Hole Oceanographic Institution, where a punchcard system is maintained and supplemented as new drift-bottle returns are received and further studies initiated.

The basic data used in the present paper are available in tabular form in Special Scientific Report: Fisheries No. 242.

BOTTLE TYPES AND DISTRIBUTION

The bottles employed were those commonly used for carbonated drinks. They were of clear glass and measured approximately 22 cm. in height and 6 cm. in diameter, with a capacity of 8 fluid ounces.

Some of the bottles released on the 1931–34 cruises were equipped with drogues and some were not. The pattern of distribution during this period was confined to Georges and Browns Banks, but otherwise it followed no clear-cut system. Usually from 5 to 15 bottles were launched at a station, but occasionally they were distributed over a short track at the rate of 2 bottles every 2 miles. (These tracks of release are not indicated in the figures as they would needlessly confuse the drawing; all returns, however, are accounted for.)

During the 1953–56 cruises, half of the bottles were ballasted with dry sand so that they would float vertically at or near the surface; the other half contained no ballast. The bottles were distributed over a grid of stations fairly evenly covering the Gulf of Maine and Georges Bank. Twelve bottles were released at each station, 6 with ballast and 6 without.

INTERPRETATION OF DRIFT-BOTTLE RETURNS

The trajectories shown in the figures which follow represent general directional trends and in no case should they be considered to indicate the actual routes followed. For each bottle there are but two knowns with which to work: the place and date of launching and the place and date of recovery.

The method by which tracks were constructed from these meager data is best illustrated by an example. To this end, figure 1—*a*, *b*, *c*, and *d*—was prepared, showing the initial treatment of data from cruise 48 of the *Albatross III*.

The first step was to select the bottles with the shortest period of drift and plot their net movement by straight lines (fig. 1, *a*). Usually, as in

[1] Walford (1938) has discussed the results of the 1931 and 1932 drift-bottle returns; the others have not previously been reported.

Note.—Approved for publication, September 30, 1957. Fishery Bulletin 141.

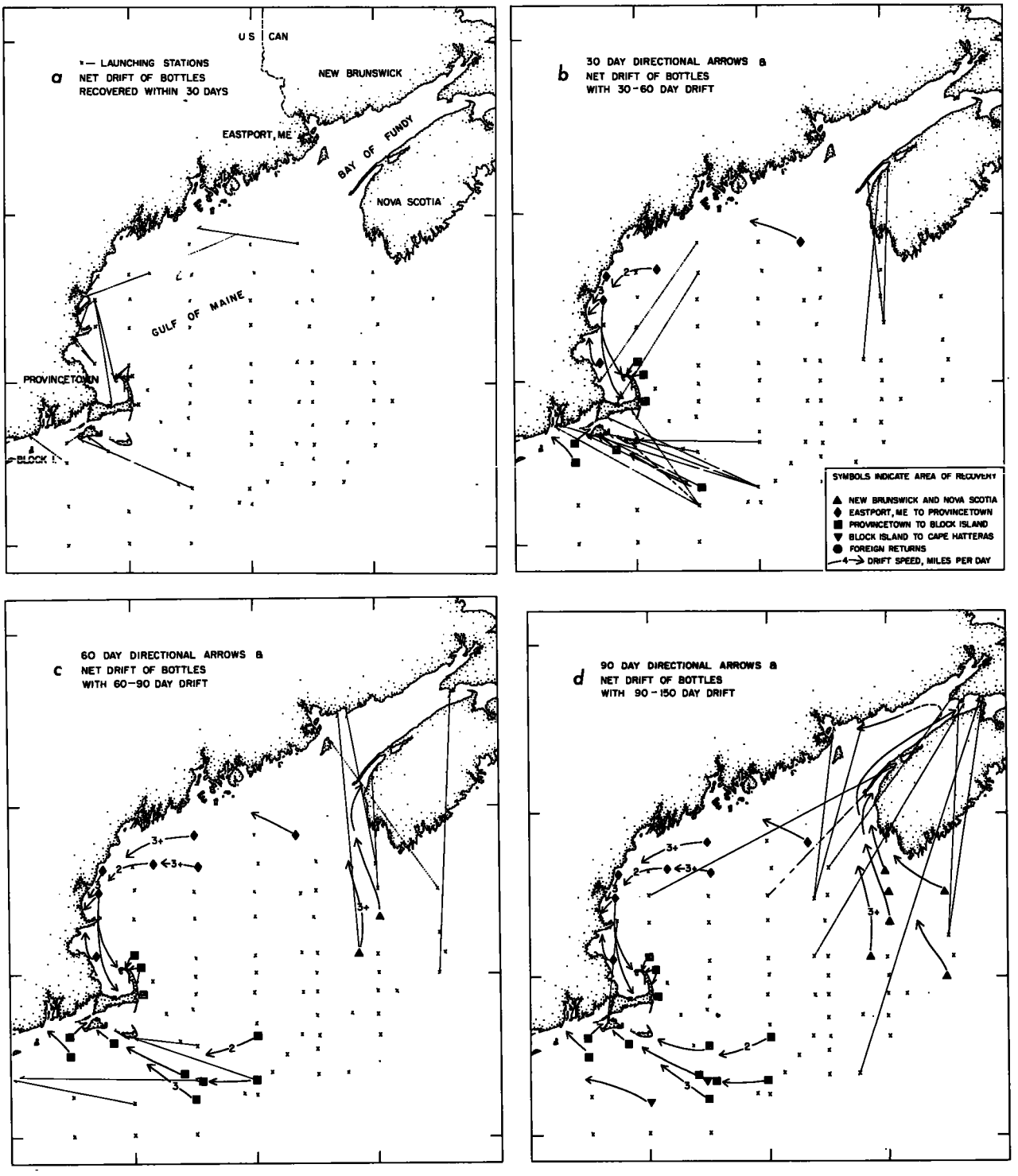

FIGURE 1.—Example of method of interpretation of bottle returns. *a*. Bottles recovered within 30 days of launching; *b*. bottles recovered within 30 to 60 days; *c*. bottles recovered within 60 to 90 days; *d*. bottles recovered within 90 to 150 days. (x indicates station of launching; arrow, direction of drift; figure on arrow, speed of drift.)

this example, enough bottles were found within 30 days of their launching to allow construction of this initial picture. It was felt that these early returns, because of time limitations, came closest to showing the actual path of drift. They came, of course, from the inshore launching stations. These straight lines were then reduced to the first few directional arrows (fig. 1, *b*), and symbols indicating areas of recovery were placed at launching points.

Similarly, the next group of bottles having drifts of from 30 to 60 days was plotted (fig. 1, *b*), showing straight line or net movement. Again, these straight lines were reduced to directional arrows, drawn to conform as nearly as possible to the first set. This process was repeated for the 60- to 90-day drifts which were superimposed as straight lines (fig. 1, *c*). The whole process was repeated (fig. 1, *d*) as often as the data required, until all returns had been accounted for.

It will be noticed that in the final chart for cruise 48 (fig. 11), a cyclonic eddy was shown in the northern Gulf of Maine. This was deduced from the pattern already established (fig. 1, *d*) and from the fact that some bottles recovered from these stations had been adrift for more than 100 days, indicating little likelihood of direct movement toward their recovery point. In addition, the period of drift for the bottle launched in the north-central part of the eddy exceeded considerably the period of drift of those bottles launched in the southern part, though all were found in the same recovery area.

In following the method of charting water movements from bottle recoveries outlined here, certain general principles have been adhered to. The first-drawn directional arrows, which were based on relatively few returns, were subject to minor modifications by subsequent, more numerous recoveries. Such changes, never radical in nature, seldom had to be made, however. Very late returns, which came in after many months or even years, were arbitrarily made to fit the previously established pattern.

Where a concentration of release stations appeared from which there were no returns, directional arrows were made to avoid this area, which was assumed to be characterized by an offshore movement. (Note the northward confinement of the Gulf eddy in figure 11.) Where alternate routes appeared possible, the one more consistent in terms of drift velocity was chosen. Where velocities have been entered, they indicate the fastest drift as being most representative, since other slower bottles may have lain undiscovered on the beach for some time. Where routes were most open to question, a dashed line was used in plotting.

Finally, it should be stated that the plots were completed before the surface wind vectors were read from daily weather maps and graphed. Thus, knowledge of wind patterns in no way influenced the assumed course of bottles.

The end result of this treatment is seen in the charts for each cruise. In referring to them it should be remembered that—

1. Arrows show directional trends, not actual routes followed.

2. A single arrow may show the trend of a number of bottles.

3. Symbols—used in figures 3 to 19—at the point of release (near the base of an arrow) indicate the general region of ultimate recovery.

4. Positions of all stations at which bottles were dropped are shown with the exception of a few instances during the 1931–34 cruises where bottles were set out in short lines of 2 bottles every 2 miles. In some instances where bottles from the same launching position stranded in different recovery areas, two or more symbols are grouped together.

For purposes of comparison, the 17 cruises considered here have been divided on a seasonal basis into five groups (table 1): Group *A*, late February and early March; group *B*, late March and early April; group *C*, late April and early May; group *D*, late May and early June; and group *E*, late June.

Each cruise is considered from the following aspects:

1. How does it agree or disagree with other cruises in the same seasonal category?

2. Are there any seasonal circulatory characteristics?

TABLE 1.—*Summary of drift-bottle releases in the Gulf of Maine, by cruise and year*

Cruise	Date	Number released	Number returned [1]	Percentage recovered
Group *A:*				
Albatross III:				
Cruise 57	Feb. 21–Mar. 2, 1955	648	34	5.2
Cruise 71	Feb. 20–Mar. 2, 1956	719	54	7.5
Group *B:*				
Albatross III:				
Cruise 46	Mar. 19–Apr. 2, 1953	801	58	7.2
Cruise 58	Mar. 19–Apr. 1, 1955	826	76	9.2
Cruise 72	Mar. 21–31, 1956	633	47	7.4
Albatross II	Apr. 4–18, 1932	737	77	10.4
Group *C:*				
Albatross II	Apr. 17–29, 1931	450	49	10.9
Atlantis: Cruise 28	Apr. 27–May 13, 1934	629	101	16.1
Albatross III:				
Cruise 48	Apr. 24–May 8, 1953	970	108	11.1
Cruise 60	Apr. 19–May 3, 1955	1,235	139	11.3
Cruise 73	Apr. 17–28, 1956	780	72	9.2
Group *D:*				
Albatross II	May 26–June 7, 1931	352	58	16.5
Albatross III:				
Cruise 50	May 25–June 2, 1953	552	39	7.1
Cruise 61	May 16–28, 1955	672	77	11.5
Cruise 75	May 16–29, 1956	1,078	119	11.0
Group *E:*				
Atlantis: Cruise 16	June 19–28, 1933	532	93	17.5
Albatross III: Cruise 76	June 11–24, 1956	1,137	90	7.9
Total		12,751	1,290	

[1] As of December 1956.

3. To what extent can differences or similarities be accounted for by the wind patterns during and immediately following each cruise?

4. How does it agree with or depart from Bigelow's (1927, fig. 207) schematic diagram of the circulation in this area?

Although figure 2, based on Bigelow's diagram of nontidal circulation is for July and August, it is used throughout this discussion as a convenient norm for comparison with each of the cruises.

Bigelow summarized the circulation in the Gulf of Maine as a general anticlockwise eddy around the basin of the Gulf. He called this the "Maine" or "Gulf of Maine" eddy. We have called it the "Gulf" eddy. He pointed out (p. 972) that—

> The eddying drift is operative throughout the year, but differs in velocity and generally in detail, from season to season. It is also complicated by subsidiary eddying movements in the Bay of Fundy, Massachusetts Bay, Vineyard Sound, around Nantucket and Nantucket Shoals, and around and over Georges Bank, which are clockwise around these shoals but counterclockwise in the bays and basins * * *.

We shall call the clockwise eddy around Georges Shoals the "Georges" eddy.

For convenience, reference is made in the discussion of cruises, which follows, to four arbitrarily defined areas within the region of study. These are superimposed on Bigelow's schematic diagram as well as on the subsequent plots.

SURFACE CIRCULATION PATTERNS IN THE GULF OF MAINE

GROUP *A* CRUISES: LATE FEBRUARY AND EARLY MARCH

Albatross III cruise 57, February 21–March 2, 1955 (Figure 3)

In area I, there is a pronounced southerly movement along the western shore of the Gulf and there are indications of a strong seaward movement east of Cape Cod through South Channel, breaking the southwestern sector of the Gulf eddy. Maximum velocities are in the order of 2 miles a day. Water movement in area II differs from Bigelow's diagram in that the northward flow from Browns Bank into the Bay of Fundy is not clearly established, two stations showing movement to southeastern Nova Scotia and one station showing a 540-day drift to Maine. Area III shows the return of 1 bottle out of 84 bottles put out at 7 stations (12 per station). At other times, returns would have been had from Long Island and the southwest as far as Cape Hatteras.

The best agreement with Bigelow, though the data are scarce, is found in area IV. On the northern edge of the Bank, the Gulf eddy is indicated by 3 returns from 1 station; 1 bottle entered the Bay of Fundy and 2 reached the western shore of the Gulf. Anticyclonic movement around Georges Bank is suggested by westward drift from two stations and pronounced seaward movement from the eastern and southern edges by the concentration of no-return stations and the scattered foreign returns.

The apparent resultant of wind vectors for 40 days following the cruise shows a dominant wind from about west-northwest. Whether one assumes a movement of surface water to the right of the wind in accordance with Ekman (1902) or a direct downwind transport, winds could well account for the departures from the norm, as taken from Bigelow.

Albatross III cruise 71, February 20–March 2, 1956 (Figure 4)

Area I, for this period, is in close agreement with area I, cruise 57, of 1955, in the pronounced southward movement of bottles toward Cape Cod and the lack of bottles returning via the Gulf eddy to northern and eastern waters. Velocities are

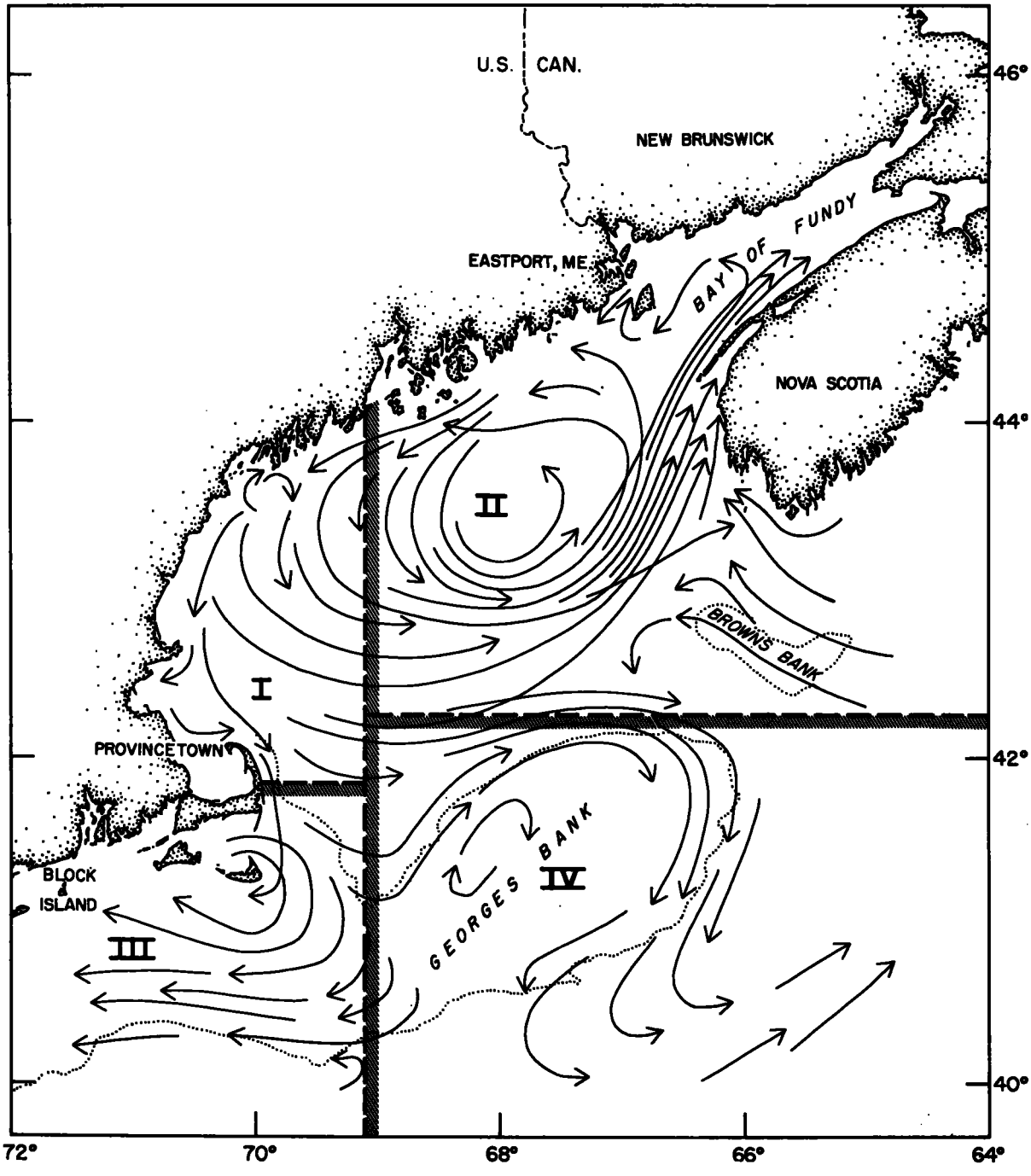

FIGURE 2.—Orientation chart based on Bigelow's diagram of water circulation during July and August in the Gulf of Maine.

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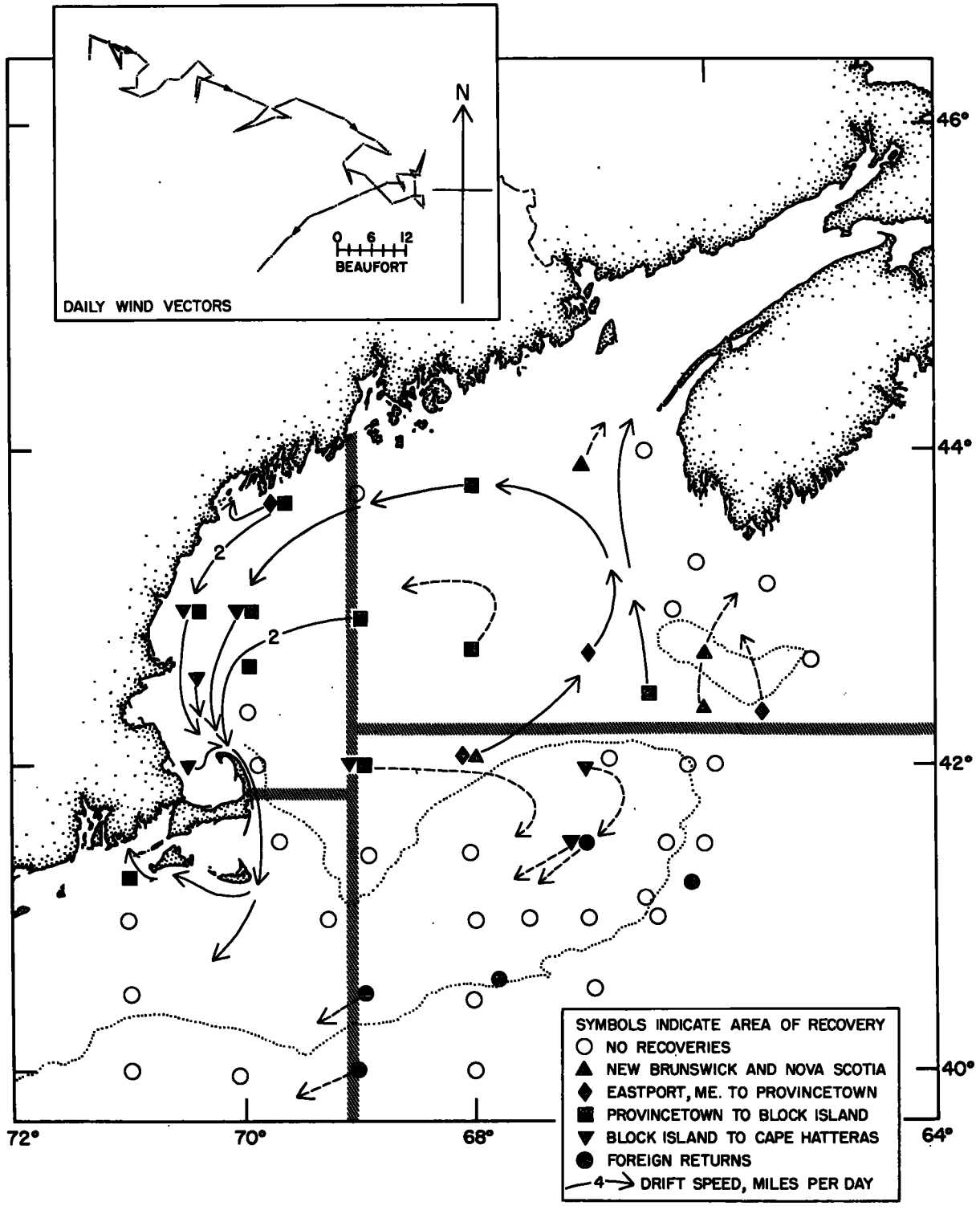

FIGURE 3.—Surface circulation in the Gulf of Maine as deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 57, February 21–March 2, 1955.

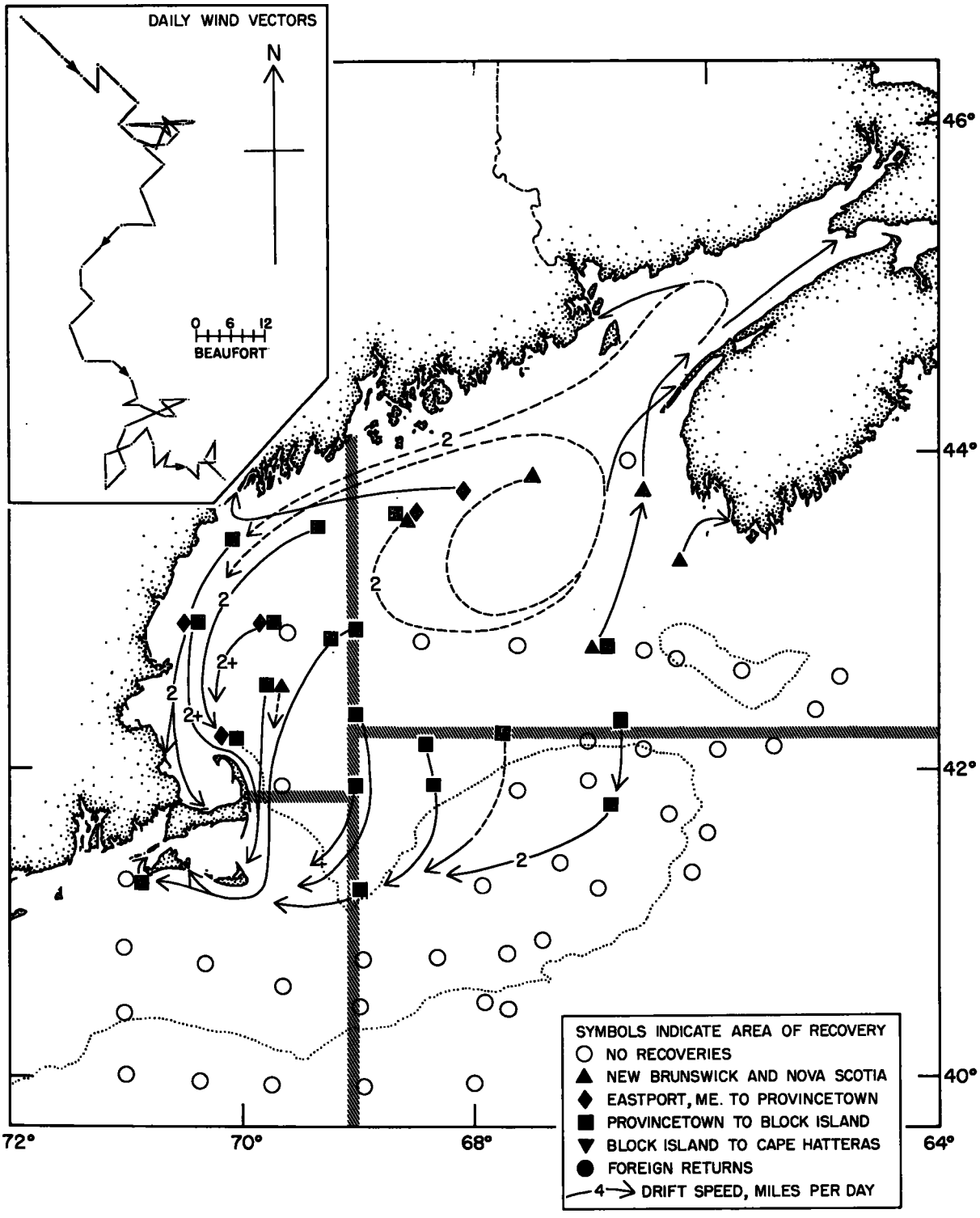

FIGURE 4.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 71, February 20–March 2, 1956.

comparable though slightly in excess of those for 1955.

In area II, three salient features appear: The Gulf eddy has been confined to the northeast; there are no returns from the Browns Bank region and the northward flow toward the bay of Fundy is singularly weak and displaced westward; and there appears no flow from northern Georges Bank toward the Bay of Fundy. The movement here is sharply toward Cape Cod and the islands.

Conditions in area III are very like those of a year earlier. Only one out of nine stations has been heard from to date, this one being close to Gay Head. No bottles have been picked up to the westward, contrary to the pattern of later seasons.

Area IV shows conditions during cruise 71 that are unique among our 17 cruises. All signs point to strong southerly movement normal to the usual easterly flow at the confluence of the Gulf and Georges eddies, along the north edge of the Bank. As was the case in cruise 57, no local United States returns have been had from stations south of 41°N. latitude.

The wind vectors following this cruise show 10 days of winds from different quarters, essentially canceling each other, and then a period of northerlies of more than usual force for 20 days. This latter period, it appears, could well account for all the features described in the four areas. That the surface waters were wind influenced is apparent from a comparison of the first and last stations for the cruise, which were made to the southwest of Gay Head. There were no returns from station 1, which was followed by 11 days of northwesterlies; there were four returns from Vineyard Sound from station 60, which was followed by 10 days of mutually negating winds.

If one may make generalizations on the basis of two cruises, it may be said that when winds from the northwest quarter prevail during late February and early March, the idealized circulation in the region will be modified thus:

1. Surface waters from the western Gulf will tend to flow southward past Cape Cod and out South Channel, thus interrupting the Gulf eddy in this area and tending to confine it to the north and east.

2. The northward movement from Browns Bank into the Bay of Fundy will be greatly diminished, some water being deflected along the southeastern coast of Nova Scotia.

3. The usual westward movement of waters south of Nantucket and Martha's Vineyard will be deflected offshore or temporarily interrupted.

4. The Georges eddy will be ill-defined and tend to disappear as winds become more northerly.

Under these conditions, the survival chances for eggs or larvae are small, unless confined to the northeastern sector of the Gulf.

GROUP *B* CRUISES: LATE MARCH AND EARLY APRIL

Albatross III cruise 46, March 19–April 2, 1953 (Figure 5)

A southerly movement of 4 miles per day generally parallel to the coast characterizes the waters in area I for this period. There is no indication from drifts for this cruise that the Gulf eddy is yet established, as there appears to be no return flow from this region to the northeast.

The northward flow from Browns Bank and the tip of Georges Bank in area II is firmly established, as is the veering to the northwest toward the coast of Maine, thus completing the eastern and northern segments of the eddy. Velocities up to 4 miles a day agree with those in area I. The picture agrees well with that of Bigelow, except in the southwestern part of the area.

The westerly drift south of Cape Cod and the islands is established in area III. Three unballasted bottles launched just east of the Cape moved northwest at 5 miles a day, driven by 5 days of wind from the southeast and east. The expected movement here is southerly.

Only three drift-bottle returns were had from Georges Bank in area IV. Two of these bottles moved westward to Long Island and Oregon Inlet at better than 2 miles a day. The third probably followed the path suggested by Bigelow, veered off the southern edge of the Banks and traveled at nearly 4 miles a day to the neighborhood of Sable Island.

The pattern of no-return stations for this cruise suggests an outflow from the Gulf across eastern Georges Bank, breaking the southern segment of the Gulf eddy. It is unusual to have a concentration of no-return stations occur so far to the north in the Gulf as it did on this cruise.

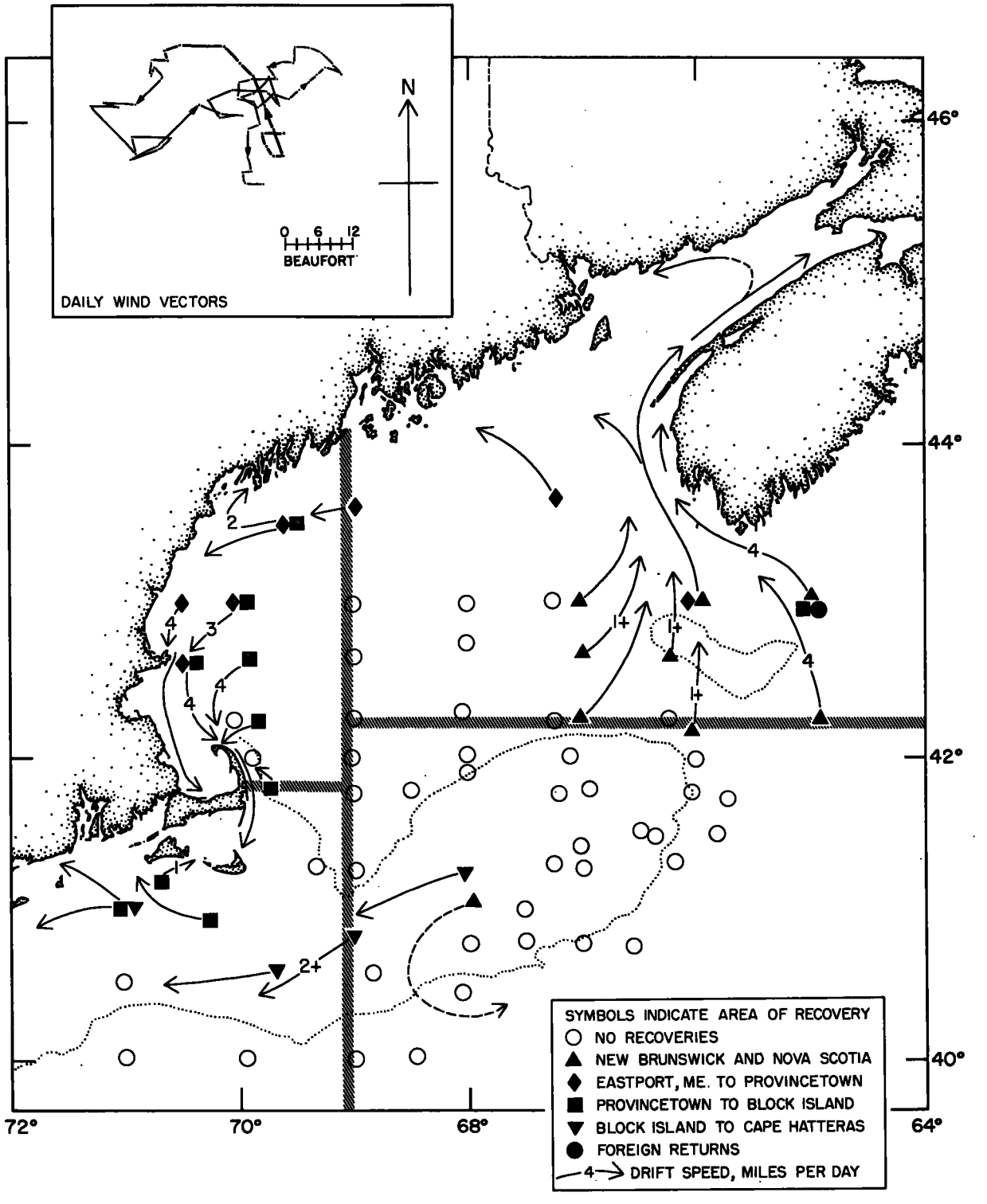

FIGURE 5.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 46, March 19–April 2, 1953.

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It is not possible to see any wind influence during this cruise except on the very short drifts we have mentioned. Wind vectors for the 60 days following the last bottle drop tend to counteract one another.

***Albatross III* cruise 58, March 19–April 1, 1955 (Figure 6)**

The net drift in area I during this period is southerly, but there appears to be a strong westward, onshore component with no sign of an eastward return of the Gulf eddy.

Circulation in area II is in general agreement with that described by Bigelow for this area, except that the southern segment of the Gulf eddy is broken.

Of 120 bottles launched in area III, only two returns were had, they being from Maryland and Virginia. This agrees with the large number of bottles from north of Cape Cod and from Georges Bank which ultimately stranded to the west.

A good number of drift-bottle returns were had from Georges Bank, all showing a southwest movement but giving little indication of an anticyclonic eddy around the Bank.

The wind vectors show the first directional dominance to be northeasterly beginning 20 days after the end of the cruise, when there were 5 consecutive days of force-5 winds from this quarter. There is little doubt that winds of this force and duration influenced surface movement, but whether they alone produced the southwesterly movement which characterizes this group of bottles cannot be stated.

***Albatross III* cruise 72, March 21–31, 1956 (Figure 7)**

Unfortunately, this cruise did not cover the northern part of the Gulf of Maine; as a result, little can be deduced about the state of the Gulf eddy at this time.

Only three bottle-drop stations were made in area I. Of the total of 36 bottles put out, 2 were recovered in area III some months later.

Area II shows surface water movement of better than 2 miles a day from western Browns Bank north into the Bay of Fundy. Stations east of Browns Bank were not heard from.

There were good returns from offshore stations in area III, which show a pronounced northerly component to the usual westward flow expected here.

Returns from Georges Bank (area IV) indicate a southwest movement, probably becoming more westerly somewhere in the vicinity of South Channel. There are no returns to indicate the existence of the Georges eddy. The tendency for bottles to move westward beyond Block Island, as in the previous cruise, is not seen here.

Vectors show winds to be more directional for this cruise than for the two other cruises in group *B*. There was a slight northwesterly set during the first 38 days following the last bottle-drop station. This gave way to southwesterlies which predominated for the next 30 days and so markedly influenced the results of the succeeding cruise (cruise 73, fig. 13). Comparison of cruises 72 and 73 indicate that the critical winds occur during the first month following a cruise. Thus, to estimate loss or survival of fish eggs and larvae, accurate knowledge as to dates and location of the heaviest spawning is essential.

The three cruises of group *B*, which cover the last 10 days of March for 3 different years, have these points in common.

1. The Gulf eddy is complete on the eastern, northern, and western segments in 1953 and 1955 (cruises 46 and 58), but appears broken on the southern segment, the movement here being either offshore or southwesterly across Georges Bank and out of the Gulf.

2. The northern sector of the Georges eddy, where it sometimes becomes confluent with the Gulf eddy, is not apparent. The surface-water movement is southwesterly across the Bank.

3. The generally westward movement south of Cape Cod and the islands appears established.

4. It would appear that surface plankton in the central and western Gulf of Maine or over Georges Bank would have been carried out of the region in a southwesterly direction in 1955 and 1956 and possibly offshore in 1953.

INTERMEDIATE CRUISE

***Albatross II* cruise, April 4–18, 1932 (Figure 8)**

This cruise is intermediate, seasonally speaking, between groups *B* and *C*, and is treated separately. Bottles were seeded only over the south-

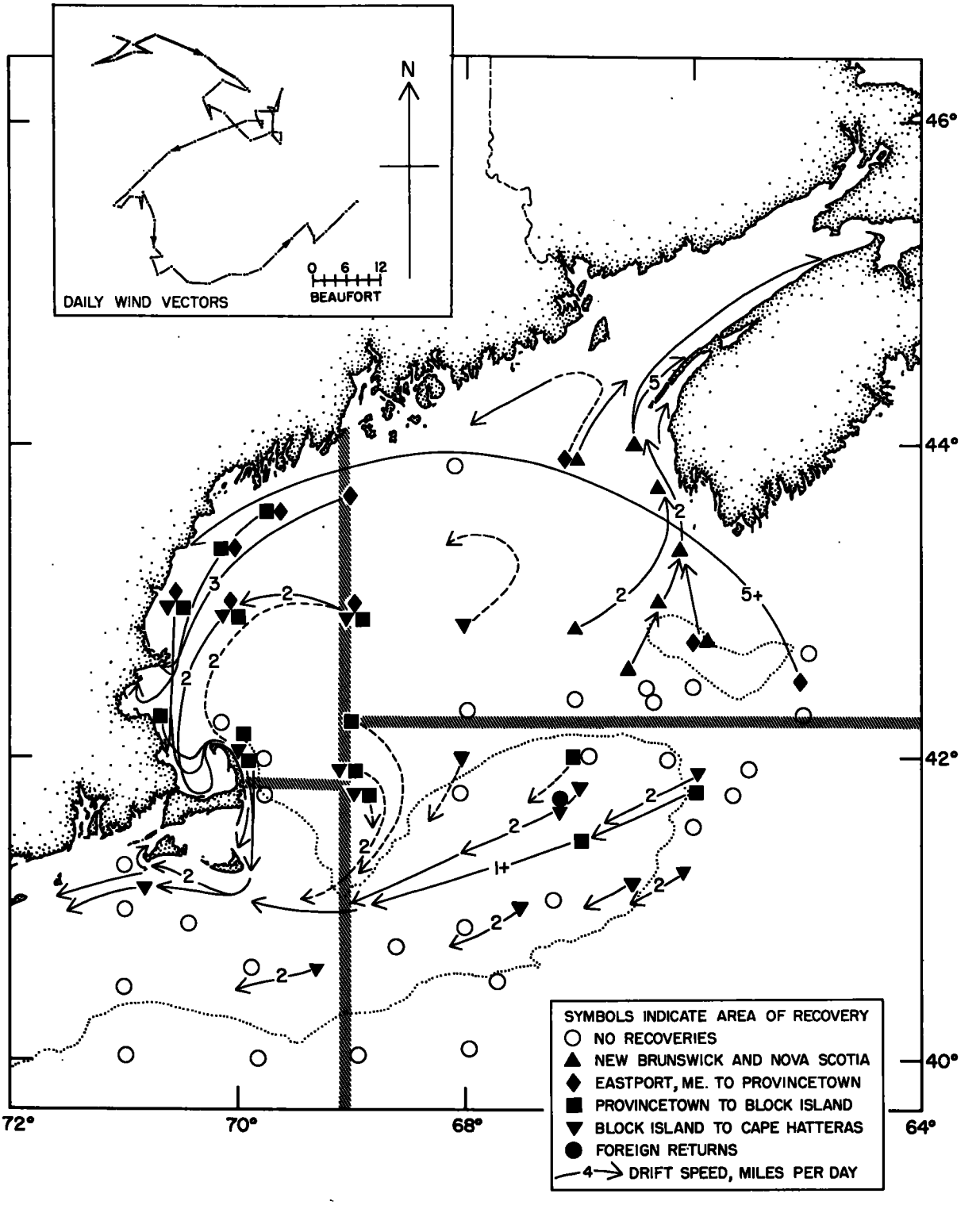

FIGURE 6.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 58, March 19–April 1, 1955.

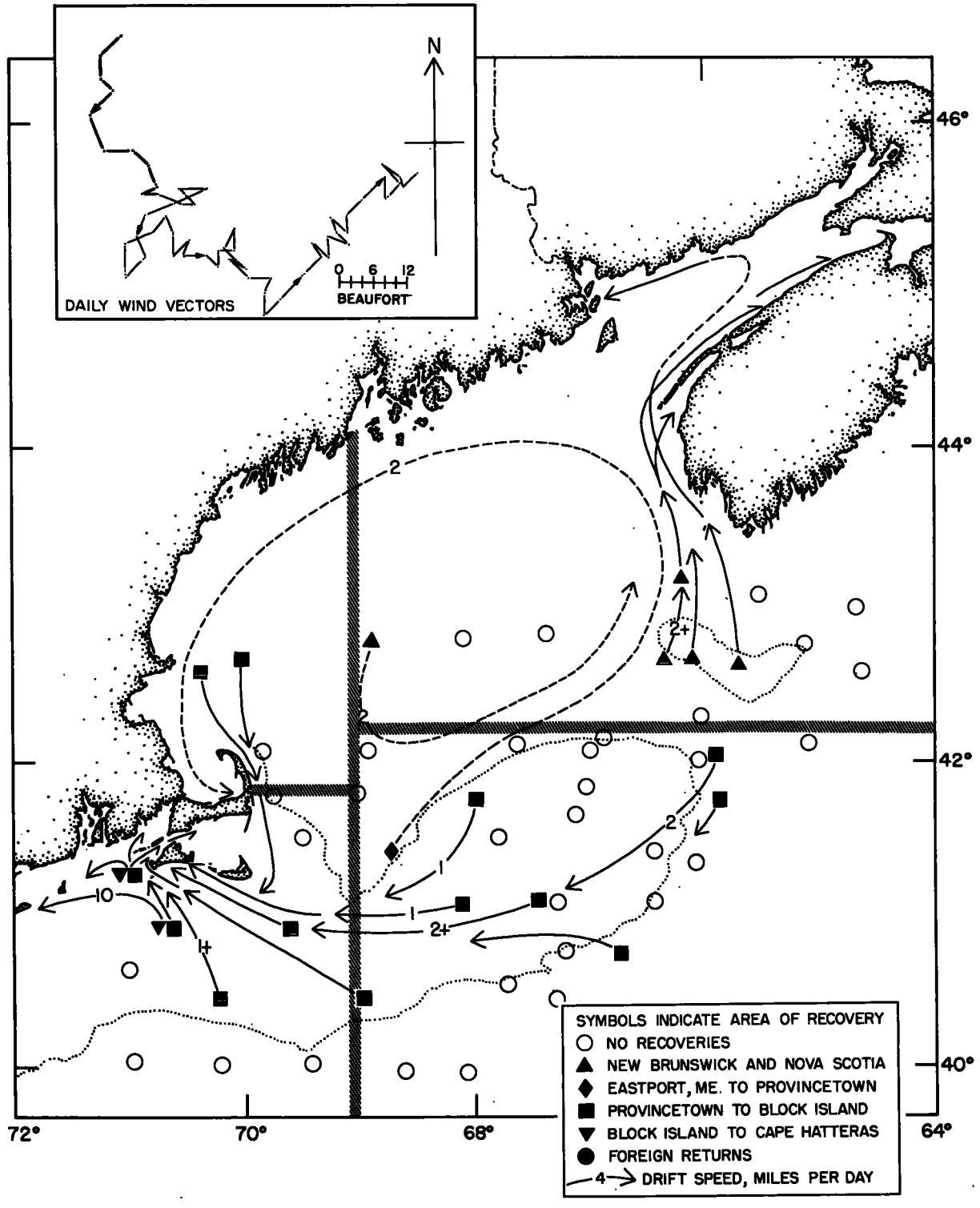

FIGURE 7.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 72, March 21–31, 1956.

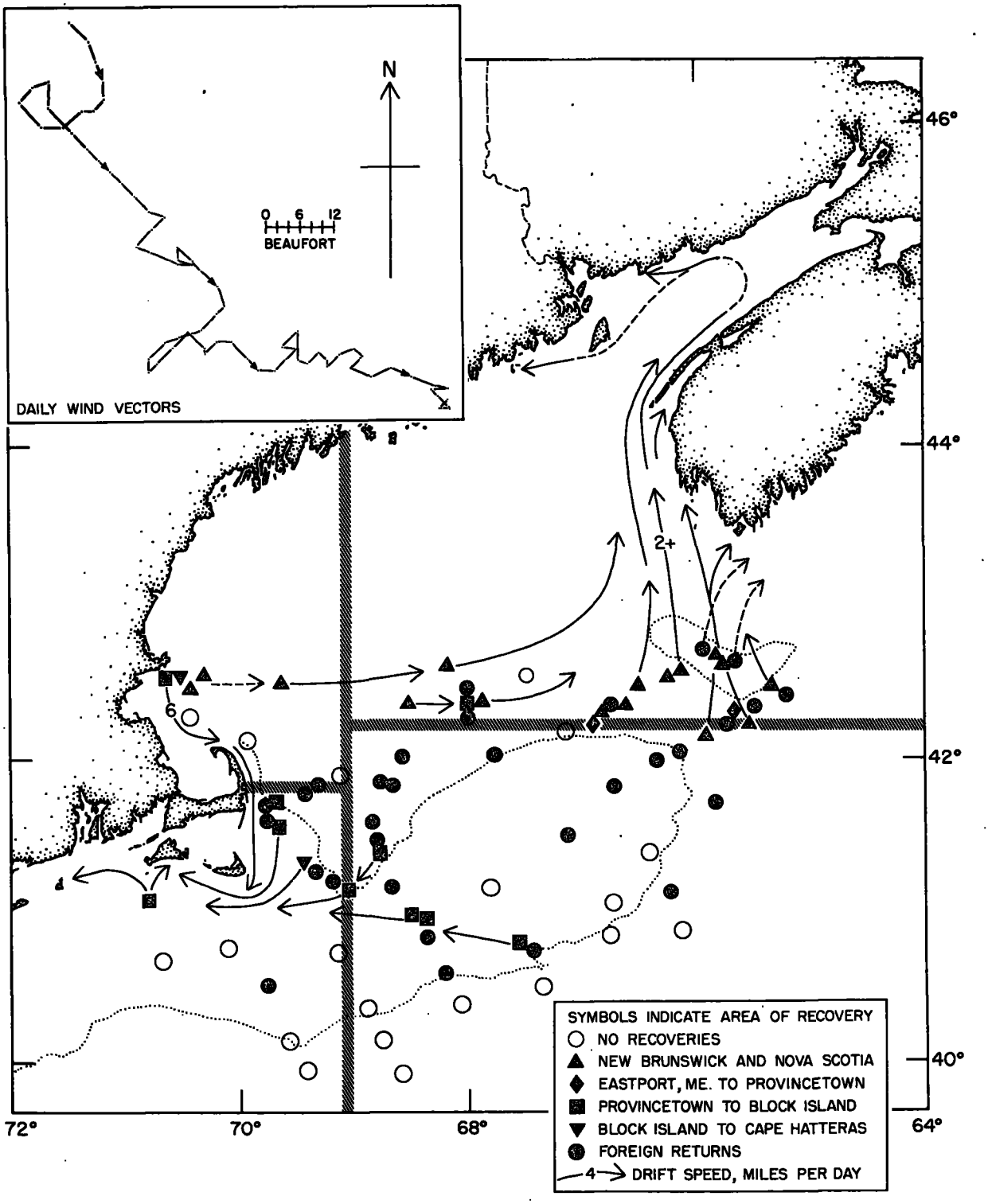

FIGURE 8.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross II*, April 4–18, 1932.

ern part of our region of study, but certain characteristics are well defined.

For the first time, seasonally speaking, the southern segment of the Gulf eddy appears clearly, with bottles seeded north of Cape Cod returning to Canadian waters. The northward movement from Browns Bank toward the Bay of Fundy is apparent.

From Georges Bank and South Channel, there is a preponderance of returns from abroad with little indication of the initial route followed by the bottles. Whether the bottles first started toward the west or traveled downwind in a southeasterly direction, it is apparent that the surface-water movement was away from the region of study. As there were more returns than normal from Newfoundland, Sable Island, and eastern Nova Scotia, and fewer than usual from Long Island, it would seem reasonable to assume that the bottles followed a downwind course in moving out of the region.

In discussing the circulation deduced from the *Albatross II* cruises (figs. 8 and 9), Walford (1938, p. 49) states: "It is evident * * * that there was a very important difference between the circulatory picture in the season of 1932 and that of the corresponding period of 1931."

Inspection of the wind vectors for these cruises appears to indicate wherein the difference lies. In 1931 they show little directional dominance, while in 1932 the offshore tendency is clearcut. That winds are often responsible for anomalies in circulation in this region cannot be denied. Better understanding is needed of how winds from different quarters may establish or modify the circulation of water depending on their force and duration.

GROUP *C* CRUISES: LATE APRIL AND EARLY MAY

Albatross II cruise, April 17–29, 1931 (Figure 9)

This cruise, confined to Georges Bank, covers areas III and IV only. The drift-bottle returns, however, indicate that the southern segment of the Gulf eddy has appeared, joining the northward-moving water over Browns Bank.

Area III shows a strong northerly set which is eventually deflected westward closer to land. This movement agrees with the clockwise eddy which is now firmly established around Georges Bank at a minimum rate of 2 miles a day. The six foreign returns were from stations along the southern edge of the Bank; they could have veered southward from the eddy in the manner suggested by Bigelow or have moved southwest toward Cape Hatteras and there entered the Gulf Stream.

Winds for 30 days following the cruise show that they probably had little effect on the surface-water movement.

Atlantis cruise 28, April 27–May 13, 1934 (Figure 10)

This cruise, also limited to the south and east, nevertheless shows the Gulf eddy as established in these areas, and it seems reasonable to assume that it was complete on the northern and western sectors as well. From Browns Bank, some bottles tended eastward and some into the Bay of Fundy, a situation which may reflect the conflicting winds which characterize the 50-day period following the cruise.

The surface movement in area III is southward out South Channel and thence westward, with none of the northerly motion noticeable in the preceding cruise. Only 1 of the 101 returns came from the Nantucket-Martha's Vineyard area, while many came ashore on Long Island and points west.

The Georges eddy in area IV is quite apparent at this time, as is the southern segment of the Gulf eddy where the two seem to meet north of the Bank. A surprising aspect is the fact that 36 of the 101 bottle returns came from overseas; stranding points were widely distributed between Norway and the Bahamas. There is nothing in the wind pattern to explain this offshore tendency. In view of the large number of recoveries between Long Island and Cape Hatteras, it may well be that the "foreign" bottles initially moved in this direction before entering the Gulf Stream near Cape Hatteras.

Albatross III cruise 48, April 24–May 8, 1953 (Figure 11)

The drift pattern in area I agrees well with Bigelow, except that the return flow of the Gulf eddy does not extend as far south as he shows it. Southward velocities along the coast are 3 miles a day.

Water movement in area II agrees almost exactly with Bigelow, as does that in area III.

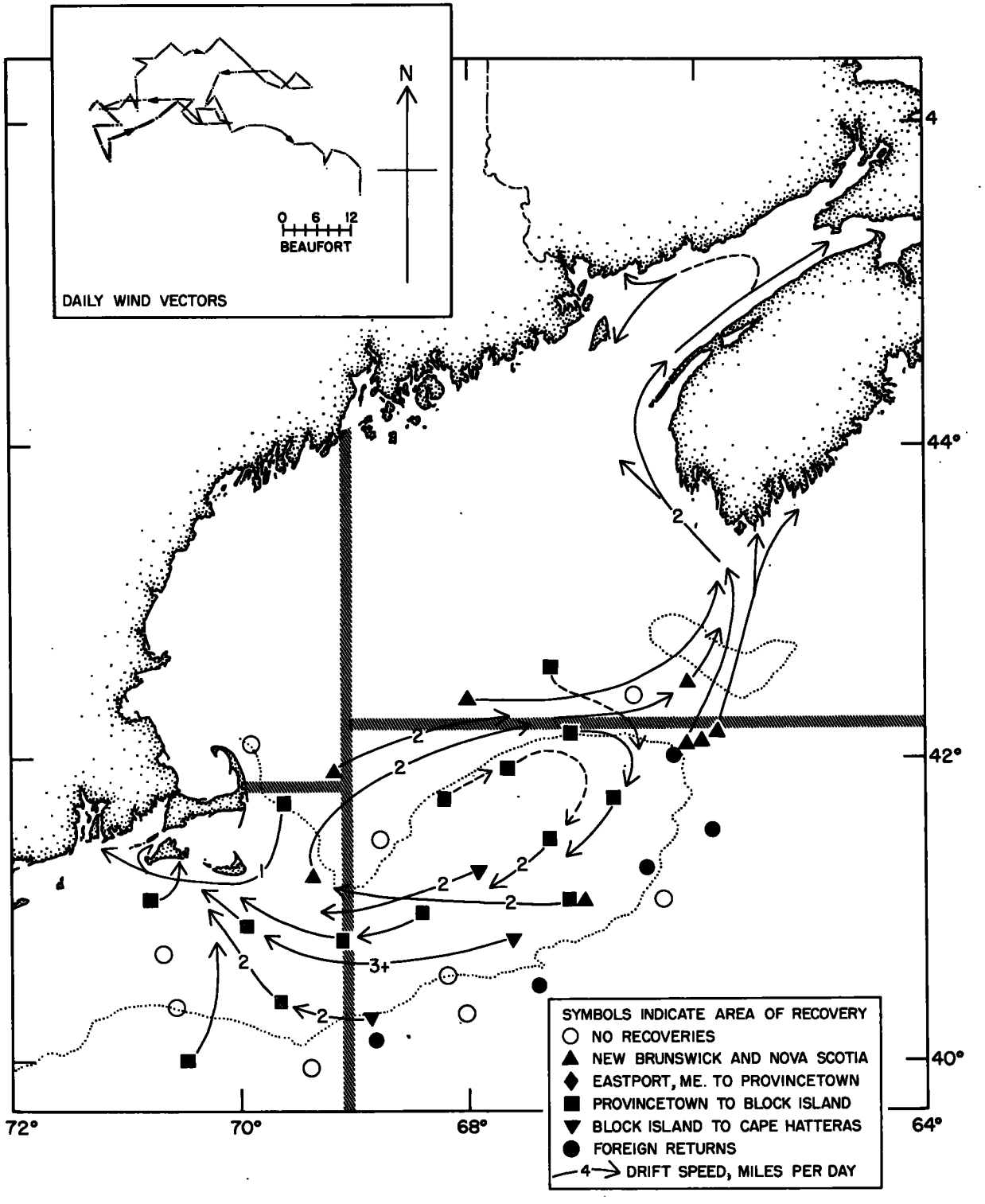

FIGURE 9.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross II*, April 17–29, 1931.

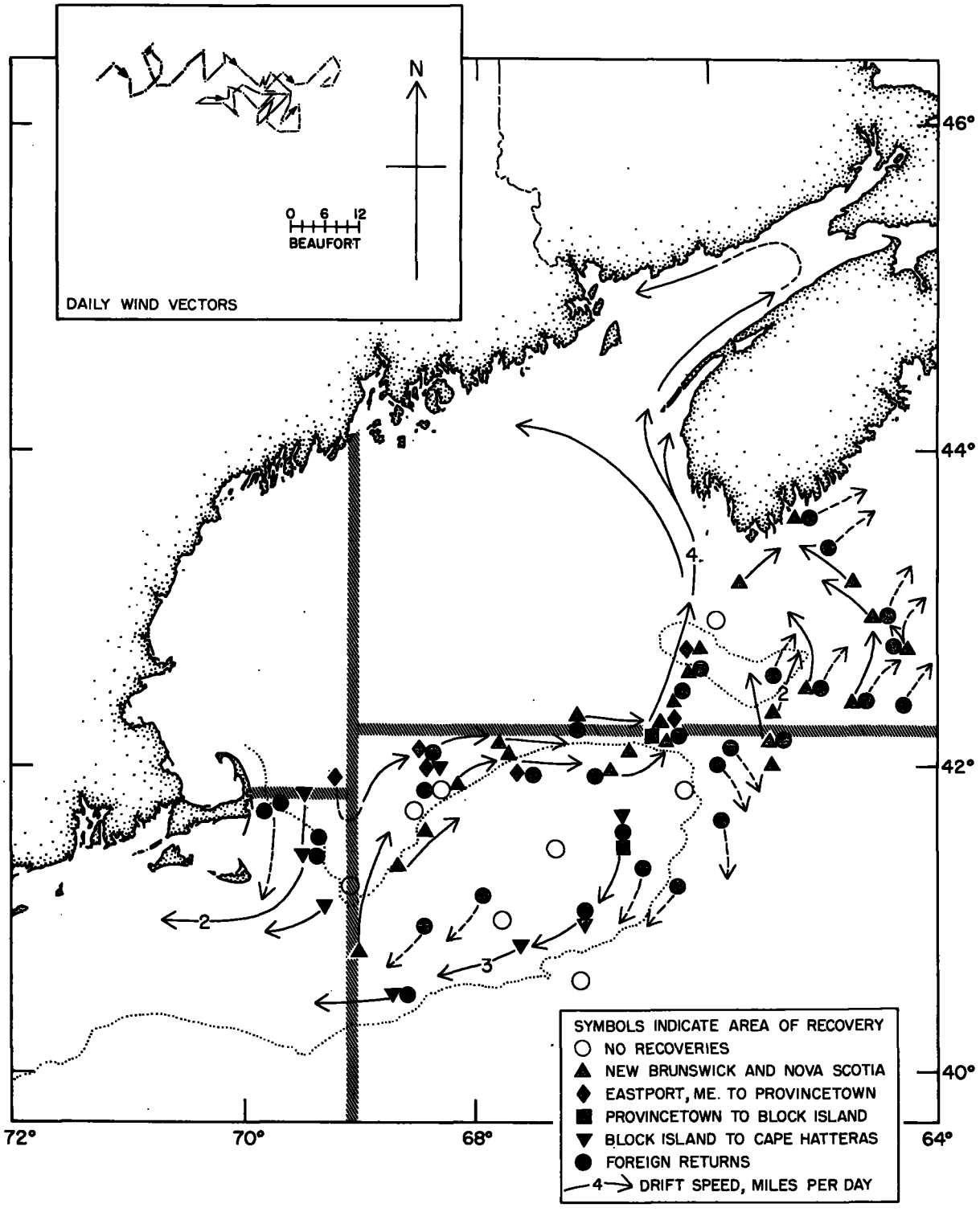

FIGURE 10.—Surface circulation deduced from recoveries of drift bottles launched by *Atlantis*, on cruise 28, April 27–May 13, 1934.

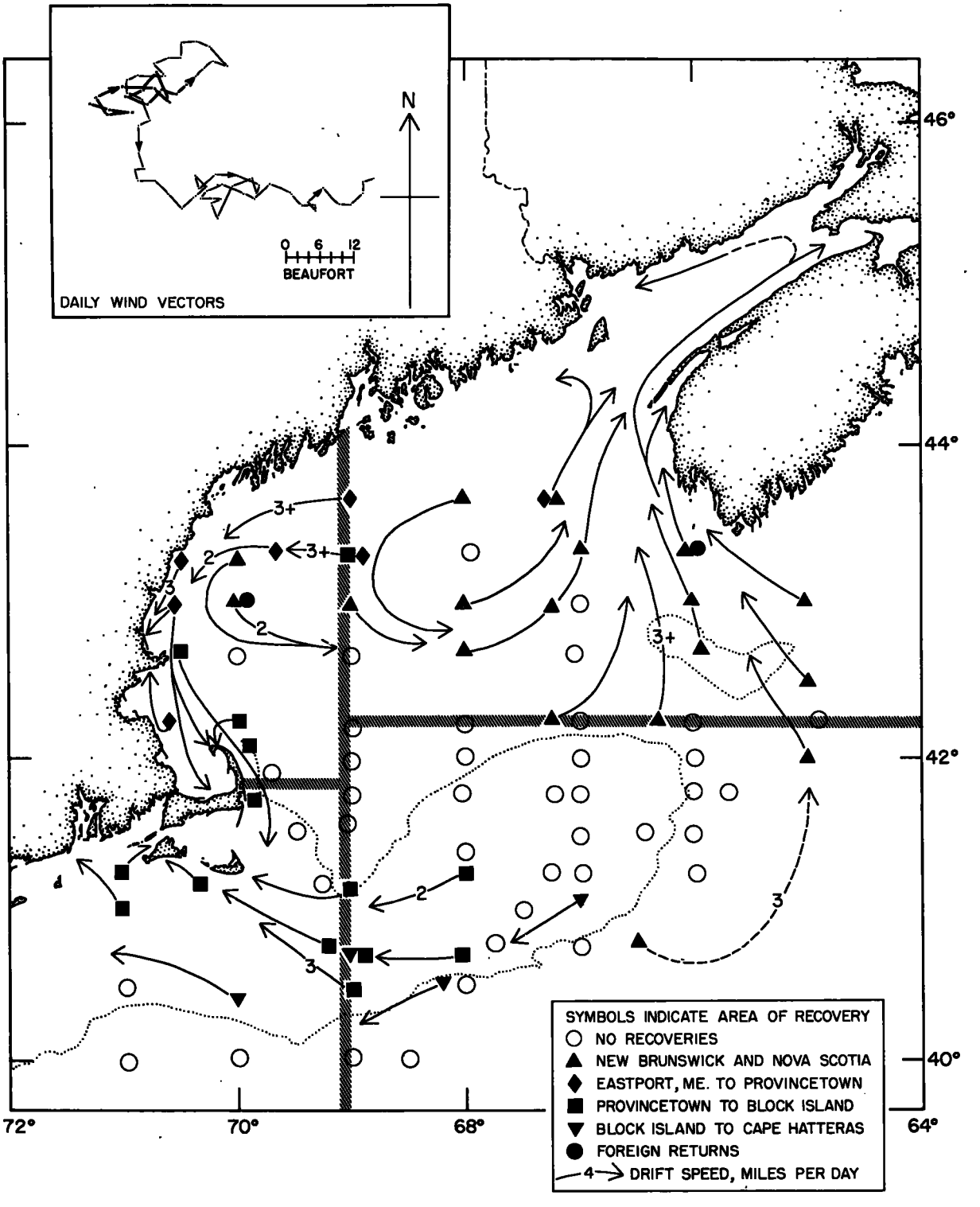

FIGURE 11.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 48, April 24–May 8, 1953.

Though bottle returns from area IV indicate no Georges eddy, the number of no-return stations in the southern Gulf and northern edge of the Bank can reasonably be assumed to show a general eastward movement through the region with a pronounced outflow off eastern Georges Bank. If this were the case, then the circulation could be said to agree very well with Bigelow's diagram.

All told, this cruise in late April and early May of 1953 is the first to agree with Bigelow in all four areas.

***Albatross III* cruise 60, April 19–May 3, 1955 (Figure 12)**

There were 21 drift-bottle returns from the five stations north of Cape Ann in area I, which show the occurrence of unusual velocities of from 8 to 12 miles a day. Thirteen of these bottles (three with and ten without ballast) came ashore before the end of the cruise on May 4 and very obviously owe their high speeds to a fair wind augmenting the usual southwesterly movement (see vectors, fig. 12). In the southern part of the area, the same winds undoubtedly account for the pronounced water movement out South Channel with no indication of easterly flow in the Gulf eddy.

The cyclonic movement around Browns Bank in area II was drawn because it best fits the wind pattern and logically explains the no-return stations immediately to the northwest. The Gulf eddy is firm on the east and north.

Surface water in area III shows marked movement out South Channel. It is to be noted that there were no local returns from stations made at the start of the cruise in the region south of the islands when winds were northeasterly for some days; but four stations in this area were heard from locally at the end of the voyage, during a time that was characterized by calms and light westerlies. Thus, wind influence on the bottles released in this area may be called "marked."

The Georges eddy on the north is confirmed by one return from the Bay of Fundy with a second possibly making the circuit before going to the west. There were many returns from southern Georges Bank, which fit well with the northwesterly movement seen in area III during this period.

As has been noted previously, the wind pattern, which is relatively clear-cut during and after the cruise, could be said to have had a marked influence on the drift of bottles released at this time.

***Albatross III* cruise 73, April 17–28, 1956 (Figure 13)**

To date, there are only 7 returns from the 84 bottles put out at 7 stations in area I during this cruise. The difference here between this cruise and the other cruises in group *C* is marked and can only be attributed to the winds prevailing at this time. With the exception of two bottles coming into the area from the east, little or no southerly movement of surface water is indicated. That there were no returns from the station immediately south of Cape Ann can only be explained by the winds.

The northward movement of water into the Bay of Fundy appears displaced slightly to the west, with velocities of 4 miles a day. The one return from south of Browns Bank shows a net movement of 75 miles in 95 days, which tells little. The northeasterly motion along the Nova Scotian side of the Bay of Fundy is accelerated to 6 miles a day.

Area III shows no southerly movement of bottles through South Channel, while south of the islands the usual westward flow is strongly deflected shoreward. The appearance and progression of this northerly deflection are apparent in the sequence of the five cruises in 1956, the deflection becoming more pronounced as the season advanced.

Two returns only were had from the entire Georges Bank region: one at Gay Head and the other in Buzzards Bay. It is hard to believe that these returns represent the dominant movement from the Bank, in view of the many no-return stations which surround the two points of release.

The first three cruises discussed under group *C* have wind patterns showing no very clear directional dominance. Thus it would appear possible to consider the deduced surface movement in these years to be fairly typical for the season. The cruises themselves agree reasonably well, and show, in general, that the idealized surface circulation as seen by Bigelow is taking shape for the first time, seasonably speaking. All three cruises show the Gulf eddy to be completed in its southern sector, a condition not noticeable in earlier cruises. The Georges eddy was clearly present in

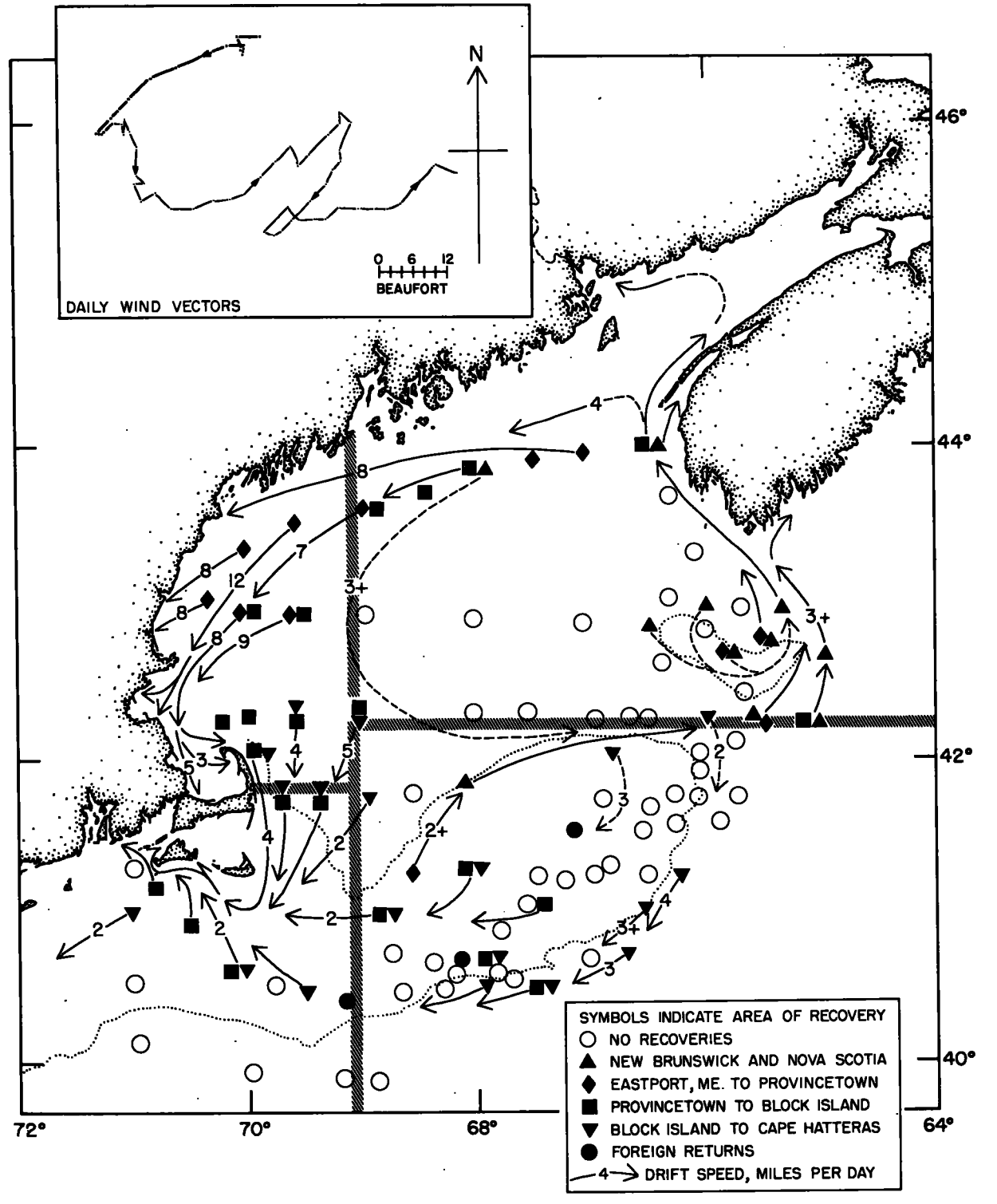

FIGURE 12.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 60, April 19–May 3, 1955.

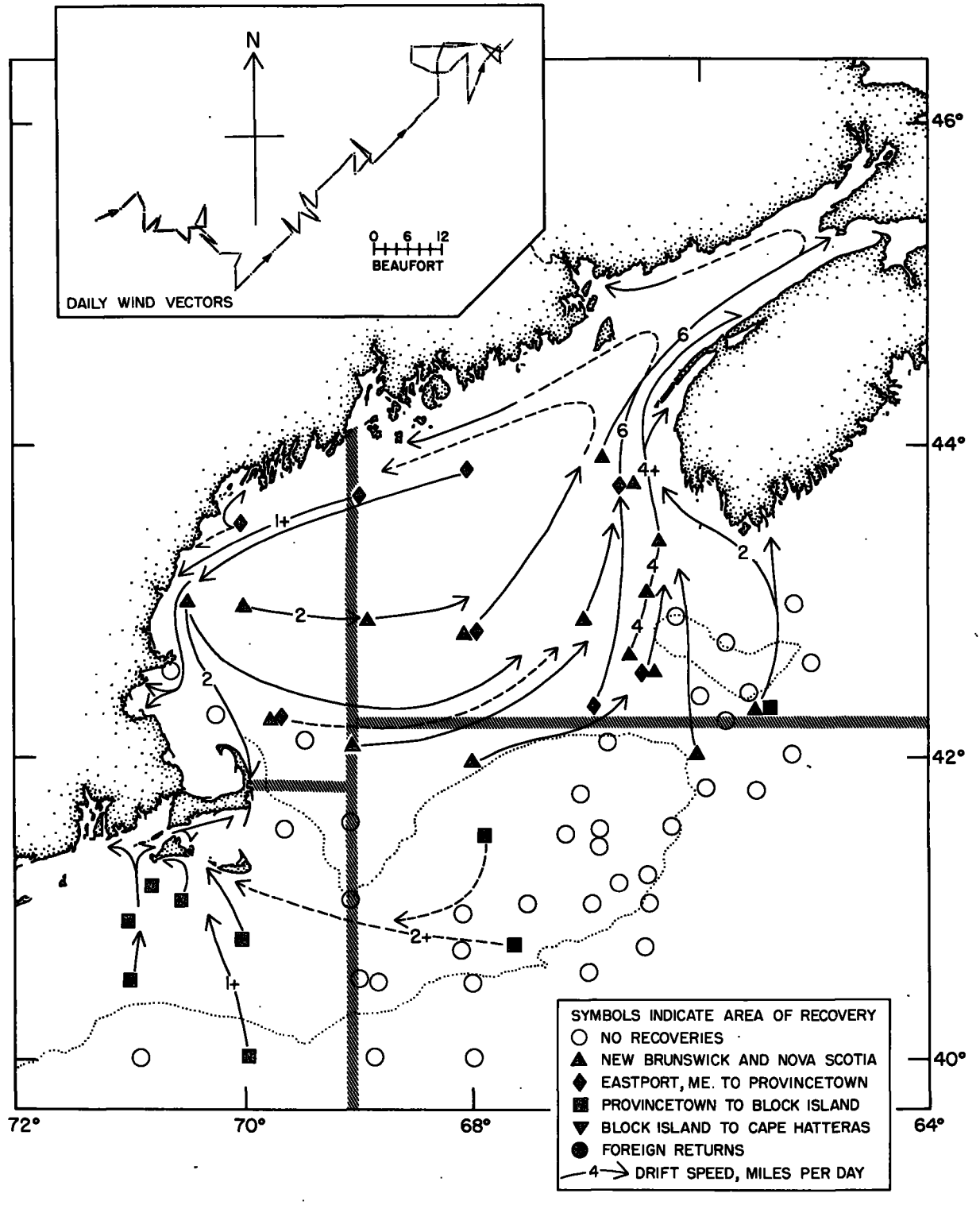

FIGURE 13.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 73, April 17–28, 1956.

1931 and 1934, while in 1953 it can be considered present except on the eastern end where movement was probably offshore.

Cruise 60, in 1955, while indicating the presence of both the Georges Bank and Gulf eddies, clearly shows the effect of winds. The continuous northeast winds during the cruise and northerly winds for the 12 days following apparently accelerated water movement along the northern and western edges of the Gulf and greatly augmented the seaward flow through South Channel. The western segment of the Gulf eddy was probably displaced eastward. The winds were not strong enough or of sufficient duration to destroy the northeastward flow of the Georges eddy, however.

Cruise 73, in 1956, shows even more wind dominance. The northwest winds during and for 10 days following the cruise appear to have lasted long enough to move bottles offshore along the western edge of the Gulf and confine the southern edge of the Gulf eddy to the north. Bottles from the eastern half of Georges Bank were moved out of the area, probably to the east, and the presence of a Georges eddy is in question. Movement south of Cape Cod and the islands has a pronounced northerly direction, probably being deflected by the southwest winds starting 11 days after the cruise (see cruises 75 and 76, p. 468).

GROUP *D* CRUISES: LATE MAY AND EARLY JUNE

Albatross II cruise, May 26–28 and June 3–7, 1931 (Figure 14)

The Georges eddy is clearly delineated here, the southwestward movement over the southern part being the most pronounced. The southerly flow out of South Channel is evident, as is the westward flow south of the islands. Winds immediately following the end of the cruise are contradictory.

Albatross III cruise 50, May 25–June 2, 1953 (Figure 15)

From the northern part of area I, the Gulf eddy carried bottles to the tip of Cape Cod at speeds of 5 miles a day and thence northeast into Canadian waters at better than 2 miles a day. From the southern stations, bottles were probably swept offshore into the Georges Bank region by the dominant northerly and westerly winds.

In area II, the southern segment of the Gulf eddy moved slightly northward, there being no returns from South Channel or northern Georges Bank. The northward flow into the Bay of Fundy is represented by returns from four stations, giving a velocity of 4 miles a day.

Area III showed a few scattered returns from stations near shore.

In area IV, cruise 50 is unique among the 17 cruises in that there were no returns from the numerous stations over Georges Bank. While it was in this year (cruises 46, 48, and 50) that some of the ballasted bottles sank (see p. 471), it is still remarkable that none of those without ballast (114 bottles seeded in area IV) have turned up locally or from abroad. The scatter of no-return stations for this cruise indicates a pronounced offshore movement of surface water from the southern Gulf and from Georges Bank to an extent that would have removed any surface eggs and larvae in those regions.

Albatross III cruise 61, May 16–28, 1955 (Figure 16)

The overall picture for this cruise agrees well with Bigelow. The southerly movement through area I and the return flow of the Gulf eddy are both present, as is the flow out South Channel.

Area II shows the eddy complete with speeds of 3 miles a day on the south and east and of 5 miles a day along the coast of Maine.

Surface water drift in area III agrees with Bigelow's diagram, except that the onshore movement south of the islands is again present.

It is probably safe to assume a northeasterly flow along the inner edge of Georges Bank and a seaward movement over the eastern end of the Bank. The southern part has a movement to the westward of 3 miles a day. Returns were had from well offshore which confirms the northwesterly movement apparent in area III.

The northerly component found in area III, and sometimes in area IV, seems to develop when winds are from the west and southwest, as they were during and after this cruise.

Albatross III cruise 75, May 16–29, 1956 (Figure 17)

Area I shows the influence of the dominant offshore wind system during this period. The return flow of the Gulf eddy is clearly marked but is dis-

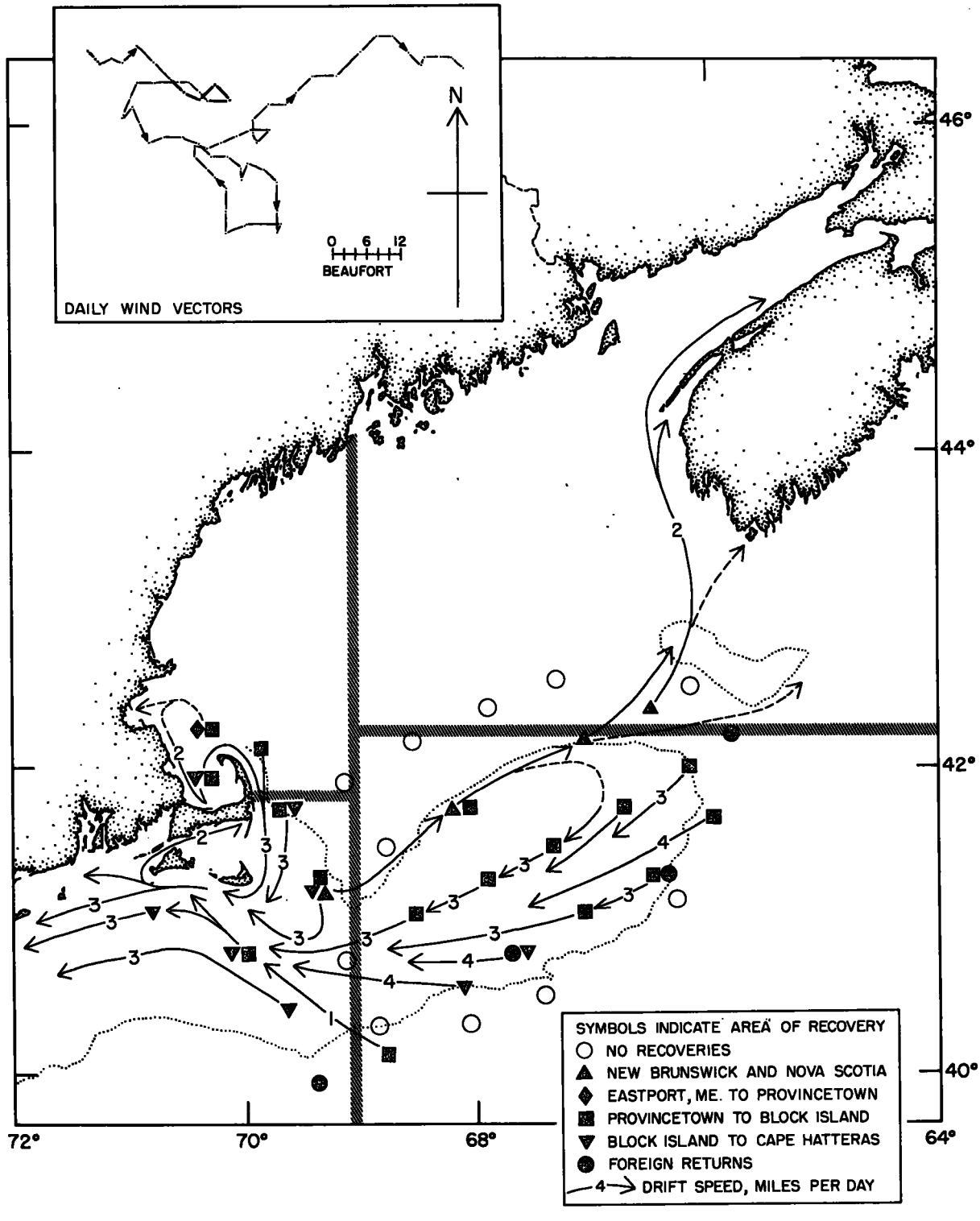

FIGURE 14.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross II*, May 26–28 and June 3–7, 1931.

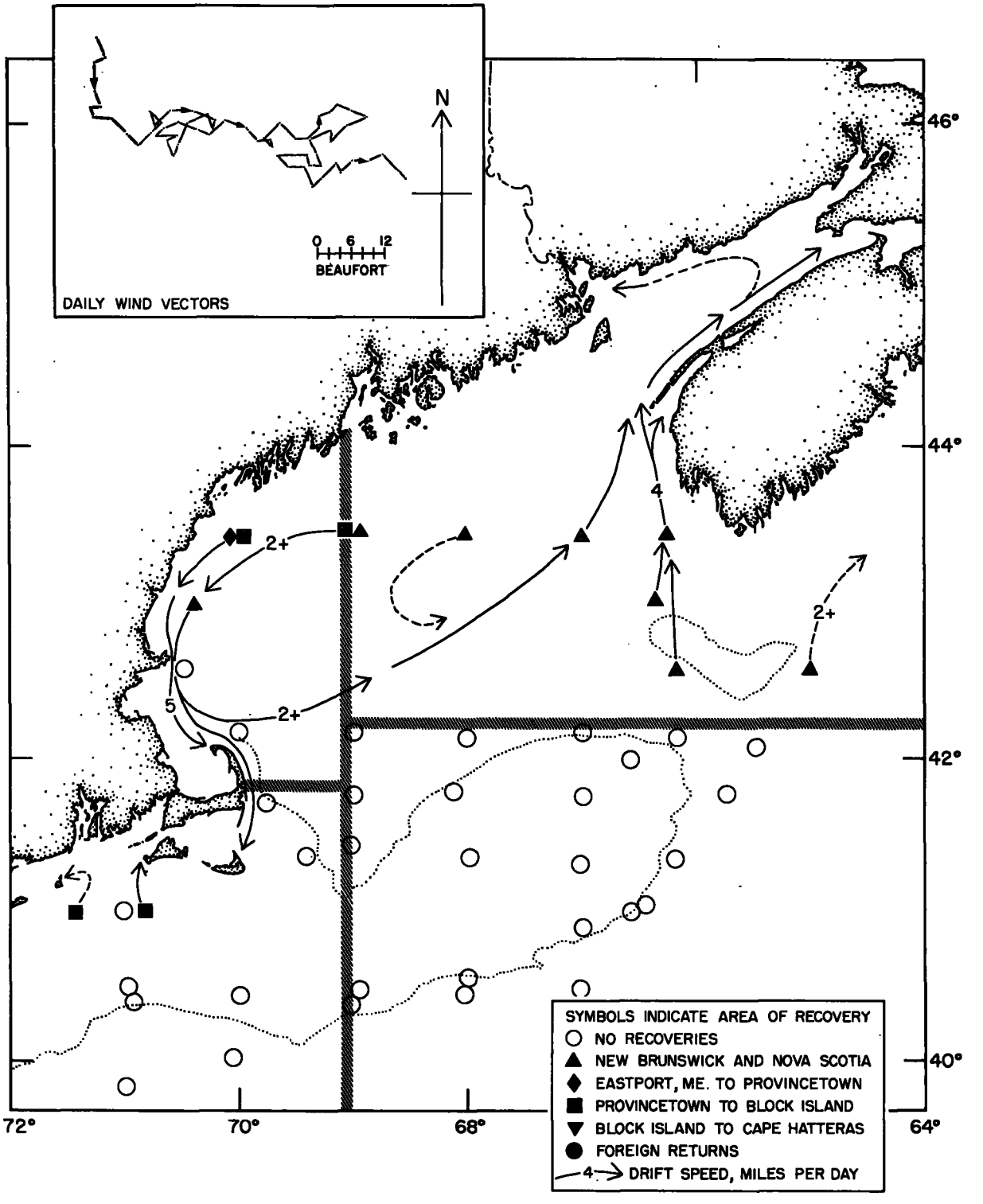

FIGURE 15.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 50, May 25–June 2, 1953.

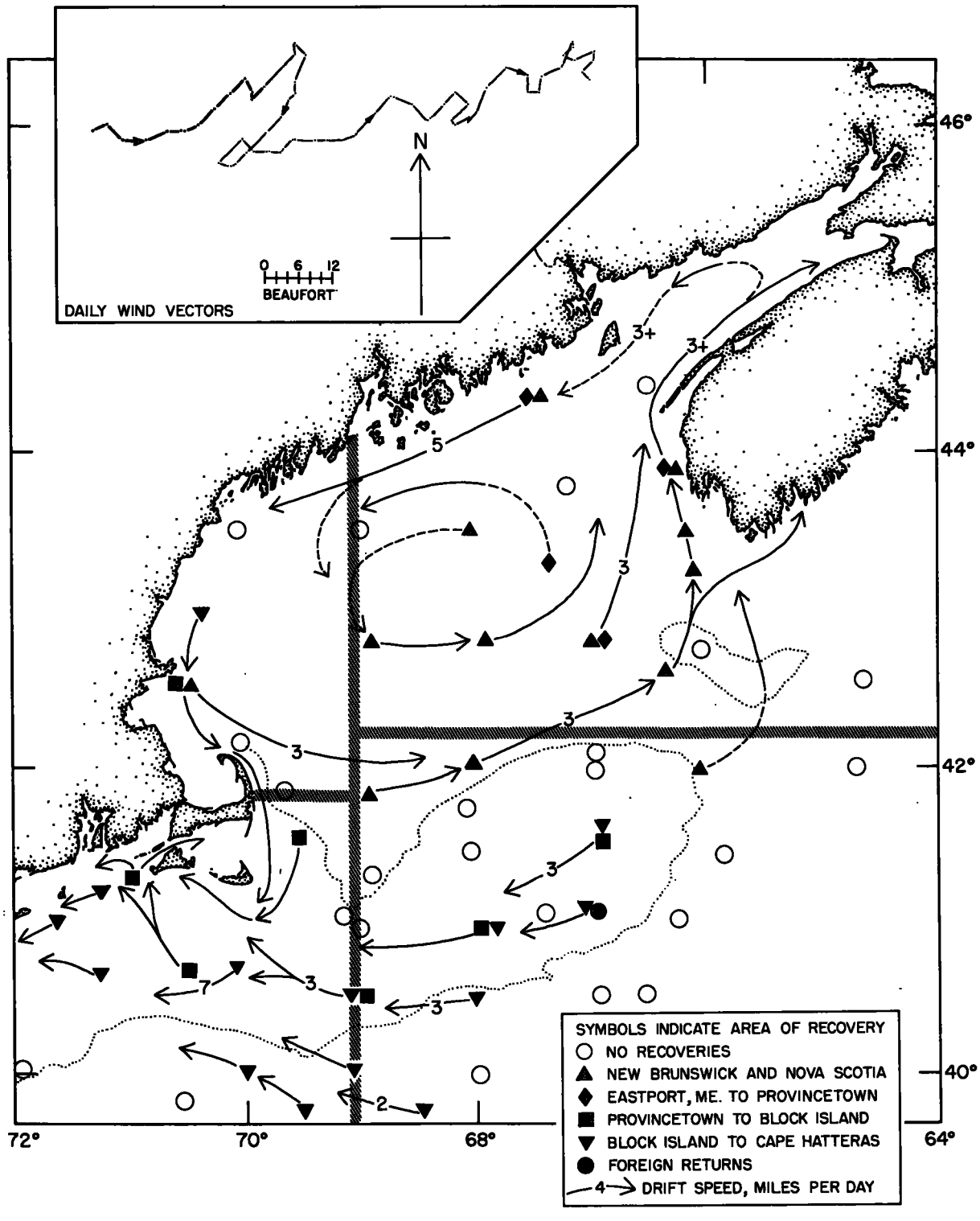

FIGURE 16.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 61, May 16–28, 1955.

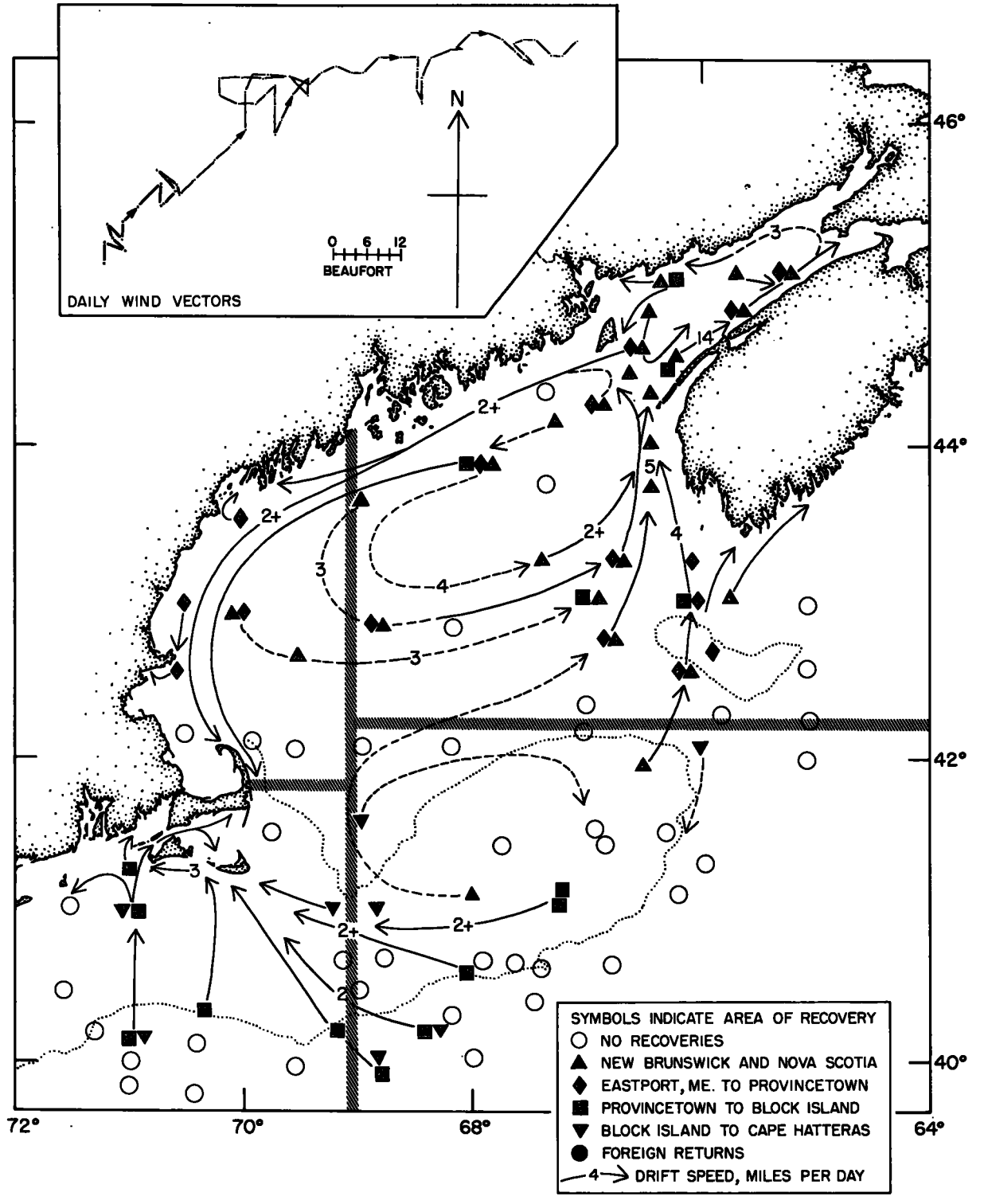

FIGURE 17.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 75, May 16–29, 1956.

placed to the north, while the movement out South Channel is not apparent.

In area II, there is a pronounced northward flow from the region of Browns Bank, with a velocity of 5 miles a day. This increased to a velocity of 14 miles a day along the southeastern shore of the Bay of Fundy. The return flow along the coast of Maine dropped to 2 miles a day.

Area III shows the westward flow pushed sharply onshore and thence, in many cases, to the northeast into Buzzards Bay and the sounds. Southerly flow out South Channel is not apparent.

In area IV, the Georges eddy does not appear. However, it seems reasonable to assume a southeasterly movement from the western and southern Gulf outward across the tip of Georges Bank. Returns from the southern half of the Bank seem to have moved westward and northward exhibiting the same onshore tendency seen in area III.

There is no doubt that the surface movement in the area of study was strongly influenced by the dominant southwest and west wind system here.

Of the four cruises in group *D*, only the first (*Albatross II*) can be considered free from wind influence. Unfortunately, bottles were put out only in the southern portion of the area of study, but from the drift characteristics of these it is fair to assume that the circulation agreed well with the Bigelow diagram. Assuming this is true and that such movement—which we saw developing in the cruises of group *C*—can be considered normal circulation at this season, the following departures from normal in the last three cruises appear:

1. The offshore winds which characterized cruise 50 confined the Gulf eddy well to the north while the Georges Bank–South Channel region was virtually swept clean.

2. Wind vectors for cruise 61 averaged slightly to the south of west and the drift pattern agreed with Bigelow's, with one exception: the westerly flow south of the islands was strongly deflected northward.

3. In 1956 winds during cruise 75 were uniformly from the southwest. They probably served to confine the Gulf eddy to the northeastern part of the Gulf of Maine, piling up water in this region. As we have seen before, winds from this direction again served to give a strong northerly component to the westerly drift from Georges Bank and south of the islands. Surface outflow from the region came from the western Gulf out across the east end of the Banks.

GROUP *E* CRUISES: LATE JUNE

Atlantis cruise 16, June 19–28, 1933 (Figure 18)

The eastern and southern regions of the Gulf of Maine covered by this cruise are in good agreement with the Bigelow norm. The Georges eddy is apparent, as is the northward movement of surface water across Browns Bank. South of the islands in area III the westerly motion lacks the northward set which appears to occur with southwest winds (cf. 1956 cruises).

Albatross III cruise 76, June 11–24, 1956 (Figure 19)

Bottles launched in area I moved eastward into Canadian waters, penetrating well into the Bay of Fundy at a rate of 4 miles a day. Among all the cruises, this cruise represents the best agreement with the Bigelow diagram in this area. The northerly flow from Browns Bank is clearly marked. Thus, the west winds appear to have closed off the Gulf circulation.

In area III, the onshore set seen earlier (cruises 72, 73, and 75) has been intensified and many bottles moved eastward into Vineyard and Nantucket Sounds. Area IV produced few returns, these being from Virginia and North Carolina and indicating, along with the no-return stations, a pronounced movement away from the region.

Of these two June cruises, the first cruise, though of limited coverage, can be said to represent normal circulation for the season and to agree well with the Bigelow diagram, being relatively uninfluenced by winds.

The second cruise, in 1956, which is characterized by fairly consistent westerlies, shows that such winds can be expected to modify the Bigelow norm in the southern portion of the area of study in that movement from Georges Bank will be generally offshore away from the area, and the usual westward flow south of Cape Cod and the islands will be deflected northward and onshore. The surface plankton from the Bank would be lost to the area, while that which may have drifted westward would be moved shoreward.

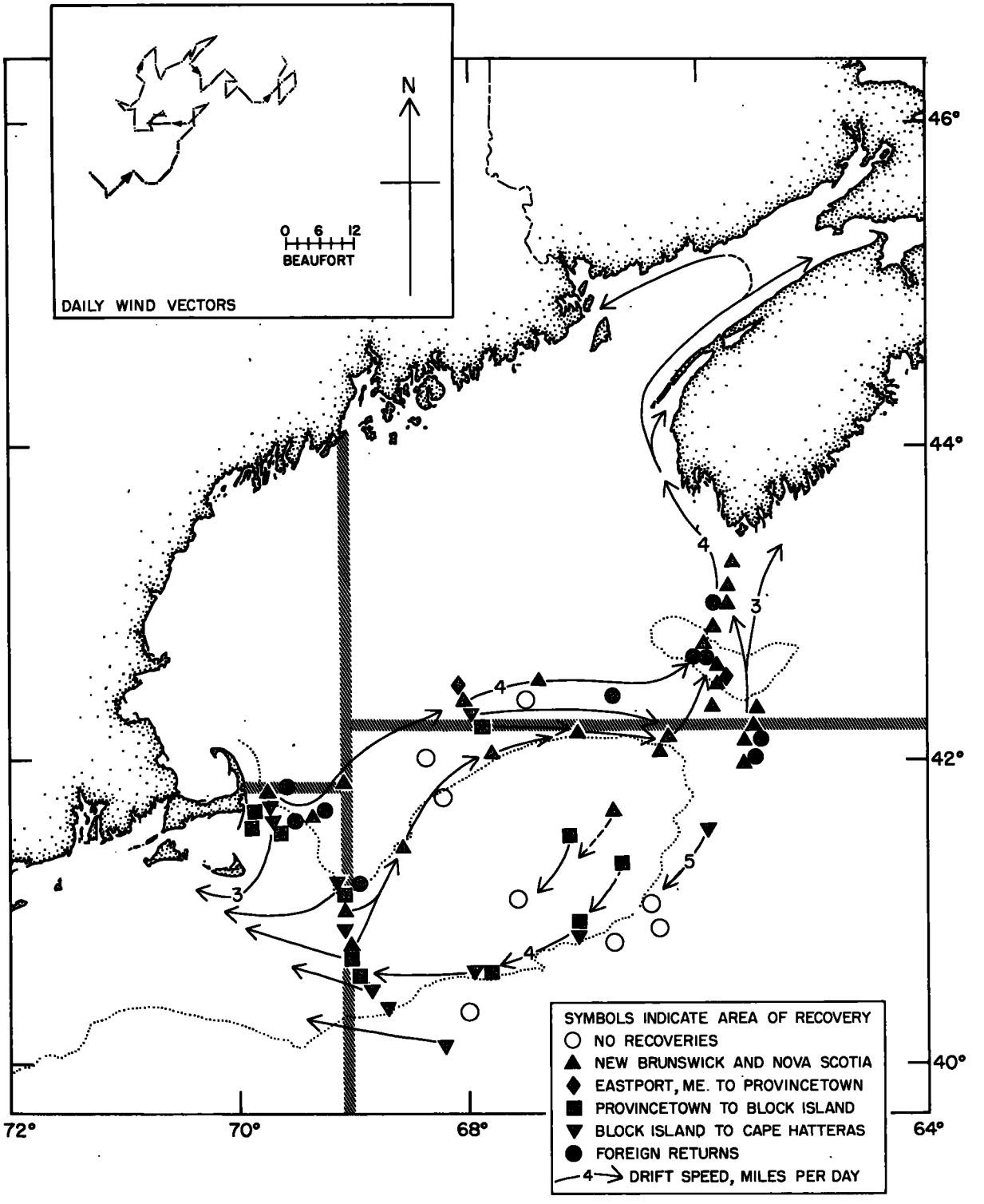

FIGURE 18.—Surface circulation deduced from recoveries of drift bottles launched by *Atlantis*, on cruise 16, June 19–28, 1933.

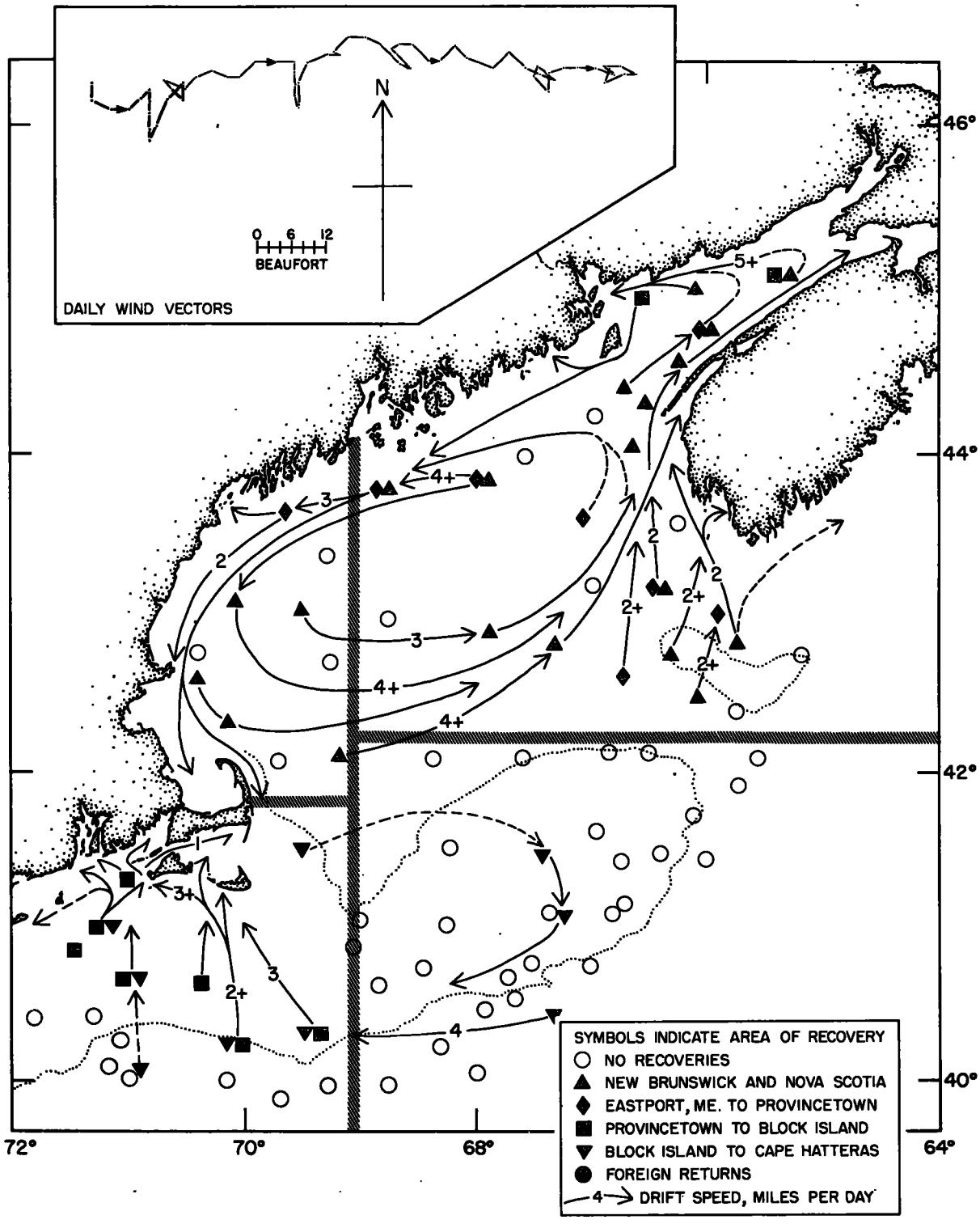

FIGURE 19.—Surface circulation deduced from recoveries of drift bottles launched by *Albatross III*, on cruise 76, June 11–24, 1956.

INDICATIONS OF BOTTOM DRIFT

An interesting and unexpected result of the drift-bottle seedings in the Gulf of Maine is found in the returns for 1953. By a fortunate accident, some of the ballasted bottles apparently sank, either because too much sand had been added or because the bottles themselves were heavier than normal.

The inference that these bottles sank seems justified. In four cases, fishermen stated that the bottles were brought up from the bottom in nets. Thus, it is thought reasonable to assume that the other ballasted bottles found at sea by fishermen also sank, as it is improbable that they could have remained afloat in the same area of swift tidal currents for periods ranging from 4 to 37 months.

The net direction and distance of drift of 12 of these bottles are shown in figure 20. In only two instances is there any indication of rate of drift: bottle No. 13339 shows a net movement of 1 mile a day and No. 13827 of 0.7 mile a day. Of interest is the uniform picture of southwesterly movement of water at the bottom along the southern edge of Georges Bank and the general southerly movement out South Channel. This, in general, fits well with the surface water movement in these areas.

CONCLUSIONS

A consideration of the 17 cruises in the Gulf of Maine from the point of view of the conditions tending to conserve or disperse planktonic forms within the region of study leads to three conclusions.

1. Bigelow's (1927, pp. 972–3) July–August pattern, a relatively closed circulation and hence highly conservative, seems to evolve with the seasons, possibly as a result of vernal warming and the consequent formation of density structure. In February and March, the Gulf eddy is ill-defined on the south as water from area I moves seaward out South Channel. The Georges eddy is not apparent, the net movement of surface water being southwest. By late April, the two counterrotating

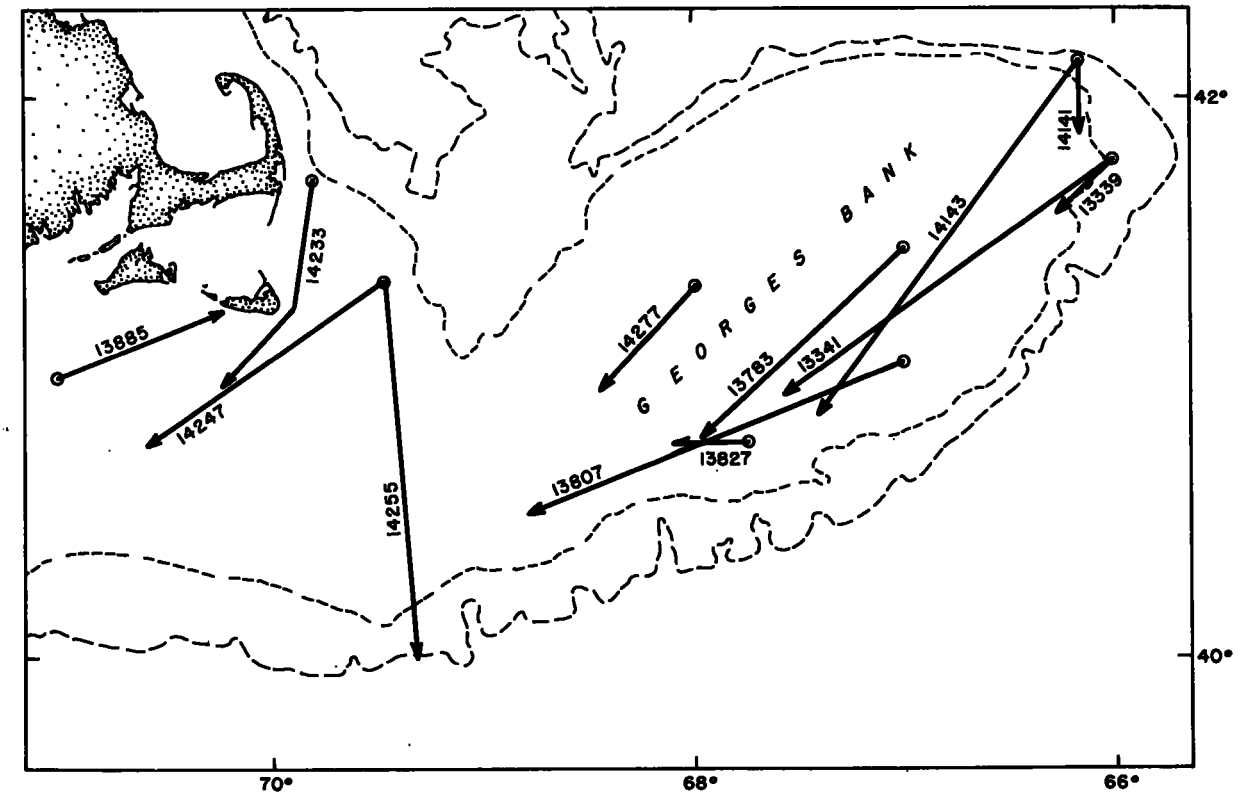

FIGURE 20.—Net movement of drift bottles which apparently sank and were recovered from the bottom by fishermen.

eddies are taking form with the appearance of a northeasterly movement along the northern edge of Georges Bank where the two eddies become confluent. After this development, plankton within the Gulf would probably be retained.

2. At any time during the seasons considered, the prevailing circulation may be strongly modified by winds. Offshore winds from the northwest quadrant have a pronounced effect on the Georges Bank region, tending to destroy the eddy (figs. 3, 4, 8, and 15). Northeasterly winds, even of short duration as during cruise 60 of the *Albatross III* (fig. 12), speed up the northern segment of the Gulf eddy and increase the flow out South Channel. Winds from the west and southwest (figs. 13, 16, 17, and 19) seem to give a strong onshore component to the waters south of Cape Cod and to accentuate the northward flow from Browns Bank into the Bay of Fundy.

3. In the region of Georges Bank, a marked difference between conditions in the 1930's and 1950's is apparent. With the exception of the April cruise of 1932 (fig. 8), when winds were uniformly offshore, the Georges eddy during the 1930's was far more pronounced than during the last few years. Though there are indications of an eddy in 1955 (fig. 12), it is markedly absent in 1953 and 1956 (figs. 4, 5, 7, 11, 13, 15, 17, and 19). Plankton on the Bank had more chance of surviving locally in the early 1930's than in 1953 and 1956.

Efforts to assess the potential of any given spawning season within the area should certainly involve accurate knowledge of the time and place of spawning and a careful consideration of wind patterns during the period of the planktonic stage of the fish in question.

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FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

ATLANTIC COAST MIGRATIONS OF AMERICAN SHAD

By GERALD B. TALBOT AND JAMES E. SYKES

FISHERY BULLETIN 142
From Fishery Bulletin of the Fish and Wildlife Service
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ABSTRACT

The returns from 17,508 American shad (*Alosa sapidissima*) tagged at various places along the Atlantic coast over a period of 19 years have been used to study the migrations of this fish. Thirty-nine percent of these tags were recovered. These recoveries disclosed that after spawning, adult shad from Chesapeake Bay to the Connecticut River migrate northward and spend the summer and fall in the Gulf of Maine. Canadian shad migrate southward to spend the same period in the Gulf of Maine. There is only slight evidence as to where shad spend the winter months, but it appears that they are scattered along the Middle Atlantic area, probably in deep water, for beginning in January or February as the spawning season approaches they move inshore and shad which spawn from Georgia to the St. Lawrence River are caught from North Carolina to Long Island. Those not caught migrate either north or south to their native streams and spawn, repeating this cycle each year if they escape natural and fishing mortalities. The young shad leave their native streams in the fall; probably spend the winters in the Middle Atlantic area, migrate to the Gulf of Maine each summer along with the adults; and when mature return to their native streams to spawn. Those shad that spawn in streams south of Chesapeake Bay and particularly south of North Carolina die after spawning. How or by what mechanism shad and other anadromous fishes are guided in their migrations has not yet been satisfactorily determined.

ATLANTIC COAST MIGRATIONS OF AMERICAN SHAD

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The study of fish migrations has long intrigued many persons. Much of the early work was inspired by scientific curiosity or undertaken as a hobby by wealthy owners of riparian rights. More recently, however, knowledge of fish migrations has been necessary for the intelligent management of some species, since many fisheries depend on congregations of migrating fish. This is particularly true of the American shad (*Alosa sapidissima*) of the Atlantic coast.

Very little has been published concerning the migrations of shad. Vladykov (1950, 1957) studied the migrations of tagged shad in the St. Lawrence River in Canada, and Vladykov and Wallace (1937: p. 64) mentioned one distant recovery of a shad tagged in Chesapeake Bay. Most of the work on anadromous fish migrations has been undertaken on the several species of salmon and much of it has revolved around three problems: (1) Do anadromous fish move long distances from the stream where they were spawned; (2) if so, do they find their "home" stream again when they become mature and return to fresh water to spawn; and (3) if they return to their home stream, how or by what mechanism do they find it.

Rutter (1902: p. 121) maintained that it was "incredible that the salmon remember their native stream," and asserted that if they did return to their native stream it was only because they never did stray from its influence; therefore, the salmon were attracted by that stream when ready to return to fresh water. Huntsman (1937) has been a proponent of Rutter's theory and stated, "It would seem that if a fish happened to get very far from this zone of the river influence. . . . It may be said to be 'lost.'" Others, however, have shown that salmon migrate long distances in the sea and yet return in a great majority of the cases to their native rivers (Calderwood 1937: p. 207; Clemens, Foerster, and Pritchard, 1939: p. 51; Davidson 1937: p. 55; Rich 1937a: p. 477, 1937b: p. 122, 1939: p. 45).

Very little has been determined as to how anadromous fish find their way back to their native rivers from great distances in the sea and then up the various tributaries to their native streams. Ward (1921a, 1921b, 1939a: p. 1, 1939b: p. 60) studied sockeye salmon of the Copper River in Alaska, and the Skagit River in Washington and concluded that when migrating up a river and presented with a choice at the fork of a stream these salmon always choose the one with the cooler water. Powers (1939), Powers and Clark (1943), and Powers and Hickman (1928) attributed the direction taken by sockeye salmon to gradients of salinity in the sea and to gradients of carbon dioxide tension in the sea and in the rivers.

In 1939, however, Scheer (p. 426) pointed out that—

> Although the suggestions made by these writers are of some value in indicating possibilities, neither has taken into consideration the fact that a run of fishes, whether in the sea or in a river, may divide, some passing into one river or tributary while others continue on their previous course.

This is particularly true in a large river system such as the Fraser where Talbot (1950) has shown that several races of sockeye salmon are migrating upstream at the same time, each passing into its own system and tributary. That each of these is a separate race has been pointed out by Thompson (1945).

More recently Collins (1952), working with *Pomolobus pseudoharengus* and *P. aestivalis*, has shown that when given a choice the majority of these fish entered the warmer channel when the

Note—Approved for publication, June 27, 1957. Fishery Bulletin 142.

temperature difference continuously exceeded 0.5° C., or the channel where the free CO_2 was lowest when the difference exceeded 0.3 p.p.m. Also, Hasler and Wisby (1951), Wisby and Hasler (1954), and Hasler (1954) have shown by careful experimentation that fishes have a remarkable olfactory sense by which they can detect a difference between streams, and that this may explain the salmon's ability to return to its parental stream. While these experiments prove without doubt that fish can differentiate between odors, temperatures, et cetera, they do not explain how the fish find their way to their home rivers from great distances in the sea, or how they find their way upstream in a large river system to the area where it is conceivable that their senses of differentiation might begin to influence their choice of tributaries, as mentioned by Scheer.

Concerning shad migrations, Stevenson (1899: p. 106) stated—

> it was formerly considered that the entire body of shad wintered in the South and started northward in a vast school at the beginning of the year . . . sending a detachment up each successive stream, this division, by a singular method of selection, being the individuals that were bred in those respective streams, the last portion of the great school entering the Gulf of St. Lawrence. ". . . the present theory [1899] is that the young shad hatched out in any particular river remain within a moderate distance off the mouth of that stream until the period occurs for their inland migration, and that the schools of fish are generally distributed off the coast at all times, entering the rivers as soon as the temperature of the water is suitable.

Bigelow and Schroeder (1953: p. 108) partially, at least, subscribe to the latter theory for they state that, "Probably the shad of the year winter near the mouths of their parent streams; the larger sizes somewhat farther out and deeper." That some shad do migrate long distances has been pointed out by Bigelow and Schroeder quoting from unpublished work by the U. S. Fish and Wildlife Service, and work by Vladykov and Wallace (1938) and Vladykov (1950).

This paper presents data from many shad tagging experiments carried out by the United States Fish and Wildlife Service during the past 19 years which illustrate the migrations of this species. The work was completed as part of an investigation of Atlantic coast shad carried out by the Service as the primary research agency of the Atlantic States Marine Fisheries Commission.

The tagging programs used as the basis of this paper were undertaken by many biologists of the United States Fish and Wildlife Service and its predecessor, the United States Bureau of Fisheries. Biologists from the New York Conservation Department, the Chesapeake Biological Laboratory, and Virginia Fisheries Laboratory have also assisted and furnished equipment on many occasions. The assistance of these agencies and biologists is gratefully acknowledged.

LIFE HISTORY

Shad are the largest members of the herring family in the United States. They are anadromous, spawning in the spring of the year in streams from the St. Johns River in Florida to the St. Lawrence River in Canada. The spawning migrations begin earliest in the south (November in the St. Johns River) and are progressively later in northward rivers depending upon the latitude. The eggs are about 3 millimeters in diameter, are nonadhesive, and are deposited loosely in the water. After absorbing water, the eggs sink to the river bottom and are carried along by the current. The number of eggs produced each season per female averages about 250,000, and not 25,000 or 30,000 as is so often quoted in the literature (U. S. Commission of Fish and Fisheries, 1898; Lehman 1953). The eggs hatch in 6 to 8 days at 17° C. The young live in the rivers during the summer and usually migrate to sea in the fall of the same year, at which time they are 3 to 5 inches in length. Shad mature and return to the rivers to spawn 3 to 6 years later—most return at 4 or 5 years of age. After spawning, if they survive natural and fishing mortalities, they return to the sea. The following year they again return to fresh water to spawn, and at this time are called "repeaters." The age of shad and number of times they spawn can be determined from their scales (Cating 1953).

TAGGING PROGRAMS

The returns from tagging 17,508 shad at many locations along the eastern coast of the United States during the years 1938 through 1956 were used in this study. These are shown in table 1. Prior to 1950 the tagging programs were of a

limited nature, carried out over a short period each year, usually in the ocean or bays, for the purpose of determining either the migration patterns of shad or the rivers to which shad were returning when intercepted by commercial fishing gear. Beginning in 1950, most of the tagging was carried out in rivers during the entire spawning season, primarily for the purpose of estimating population size and related data. Those surviving fishing and natural mortality returned to the ocean and later, when caught, gave evidence of migration patterns.

TABLE 1.—*Shad tagged and tags recovered, 1938–56*

(1) Place of tagging	(2) Date of tagging	(3) Number of fish tagged	Number of tags recovered— (4) Near tagging site	(5) Before or during spawning	(6) After spawning	(7) In following springs [1]	(8) Miscellaneous [2]
Maine:							
Mount Desert Rock	Aug. 28, 1947	242		29			
Pinkham Bay	Aug. 23-24, 1948	201		10			1
Pleasant River	Aug. 27 to Sept. 10, 1948	158		4			
Connecticut:							
Connecticut River:							
Saybrook	Apr. 14 to July 9, 1951	1,482	408	2	1	24	
Holyoke Dam	June 22, 1954	100				1	
Holyoke Dam	June 1–30, 1956	960	175		1		
New York:							
Fire Island	Apr. 12–22, 1946	97		35			
Fire Island	June 10–19, 1946	101		13	1		
Hudson River	Apr. 23 to June 16, 1950	1,289	356		8	160	12
Hudson River	Apr. 3 to June 9, 1951	2,006	718		7	52	8
Staten Island	Apr. 4 to May 21, 1956	1,054	75	402	1		
New Jersey coast:							
Sandy Hook	Apr. 22–25, 1938	146	5	107	3		
Sandy Hook	Apr. 25–26, 1939	240	4	97			1
Belford	Apr. 16 to May 1, 1940	319	43	94			
Sandy Hook	Apr. 13–14, 1942	220	17	57	1		
Belford	Apr. 22, 1943	100	3	29	1		2
Sandy Hook	Apr. 19, 1944	104	5	22			3
Belford	Apr. 26 to May 3, 1945	85	1	15			
Seaside Park	Apr. 19–20, 1945	126	6	34	1		6
Sandy Hook	Apr. 22–25, 1946	176	3	19			5
Beach Haven	Mar. 28 to May 22, 1956	943		292	4		
Point Pleasant	Apr. 19 to May 23, 1956	962	2	377	4		
Maryland–Virginia:							
Chesapeake Bay:							
Little Creek, Va	Apr. 20, 1939	338	182		2		
Little Creek, Va	Mar. 22 to Apr. 15, 1940	300	143	15			
Watts Island, Va	Apr. 2–8, 1940	118	74	2			1
Horn Harbor, Va	Mar. 27 to Apr. 10, 1940	125	84	2			
Buckroe Beach, Va	Mar. 21 to Apr. 11, 1940	242	148	2			
Cedar Point, Governors Run, Tilghman Island, Md.	Apr. 16 to May 5, 1941	229	137	1	1		
Watts Island, Va	Apr. 16, 1941	103	56	3	1		
Buckroe Beach, Va	Apr. 9, 1941	100	41	4			
New Point, Va	Apr. 21, 1942	97	43	1			
New Point Light, Va	Apr. 1, 1943	101	30	1			
Potomac River	May 22, 1950	63	8		1		
Potomac River	Mar. 13 to May 28, 1952	321	188	1	2		2
James River	Mar. 1 to Apr. 30, 1952	374	264	6			
Little Creek, Va	Mar. 18 to May 10, 1952	1,395	509	63	5		
Susquehanna Flats	Apr. 10 to May 27, 1952	449	257		2		4
Solomons, Md	Apr. 2 to June 3, 1952	420	226	2			
NorthCarolina: Neuse River	Jan. 7 to Apr. 14, 1953	377	222	1			3
South Carolina: Edisto River	Feb. 15 to Apr. 15, 1955	128	16				
Georgia: Ogeechee River	Feb. 3 to Apr. 15, 1954	235	133				
Florida: St. Johns River	Dec. 15, 1952 to Apr. 7, 1953	882	188				2
Total		17,508	4,770	1,740	49	237	50

[1] Shad tagged on spawning ground.
[2] Tags recovered in markets, homes, et cetera; no data available on area or date of recapture of fish.

In almost all cases the fish were obtained for tagging from commercial fishing gear. In Maine, shad were captured in weirs and purse seines. On the New York–New Jersey coast, Chesapeake Bay, and the Neuse River in North Carolina, shad were captured by pound nets, and in the latter two locations by haul seines also. Practically all the other fish caught in rivers were from gill nets except in the St. Johns River, Florida. Here, shad are also caught in large numbers by a special-type haul seine (locally termed "shad nets") operated by power boats. In a few cases, shad were captured by the tagging crews using gill nets and haul seines.

Fish in good condition were selected as the nets were emptied. In most cases, the fishermen would

cooperate by slowing down their operations so that the fish for tagging were out of the water a minimum of time. Where this was not possible the fish were placed in tubs or tanks of fresh water until tagged and released. Most of the fish were marked with Petersen disk tags consisting of two celluloid disks, held in place, one on each side of the back just below the dorsal fin, by a nickel pin that passes through the fish. Strap tags (modified cattle ear tags) were affixed to the gill covers of a few shad, and also a few fish were marked with cheek tags (bachelor-button-type), which consist of a plastic disk held to the outer surface of the gill cover by a rivet that passes through the gill cover (fig. 1). A return legend and serial number were printed on each tag for identification purposes and a reward was paid as an incentive to the finder to return the tag.

Some tagging experiments (including all internal belly tags) are not reported in this paper, since there either were no returns, no data with returns, or the fish were recaptured shortly after tagging near the locality of tagging and, therefore, did not illustrate migration. All of the internal belly tags returned (5 percent of the fish tagged) were from markets, homes, et cetera, or were found when the

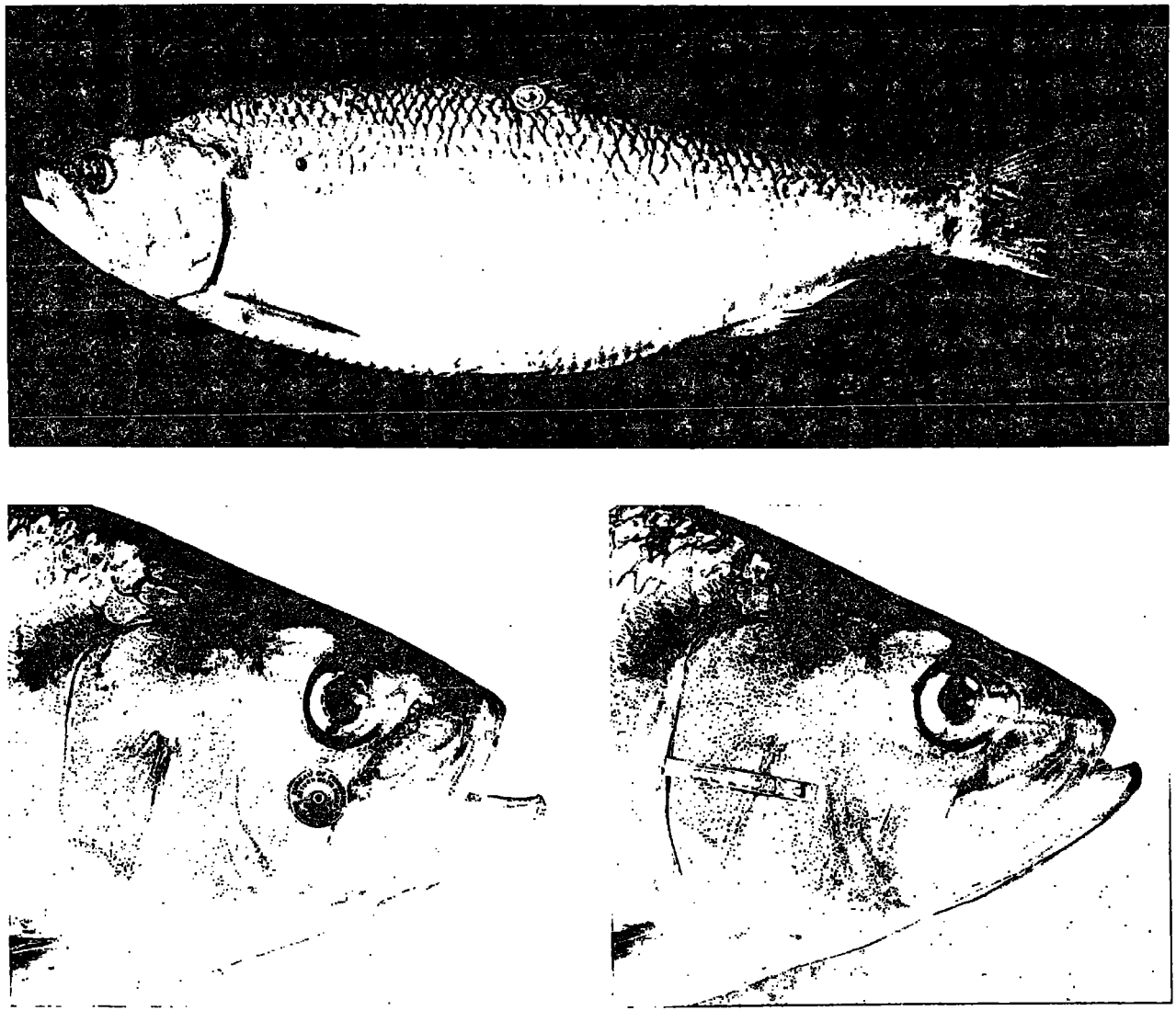

FIGURE 1.—Upper: Male shad tagged with Petersen disk tag. Lower left: Shad with cheek tag. Lower right: Shad with strap tag.

fish were being cleaned; thus, the place of recapture was doubtful in most cases.

All of the shad were tagged during spring spawning runs with the exception of those tagged in Maine during August and September. A total of 6,846 tags were recovered from these experiments. Petersen disk tags gave the highest percentage of returns (40 percent), while only 11 percent of the strap and 8 percent of the cheek-type tags were recovered. The low recovery of the tags applied to the gill covers probably resulted because they are not easily seen or because they are more easily detached from the fish than are the Petersen disk tags. In some cases Petersen disk tags have been shown to cause the fish to be more readily entangled in gill nets, and this may be partly responsible for the higher recapture rate of fish bearing this type of tag.

ANALYSIS OF TAG RETURNS

To facilitate analysis of the tagging, the 6,846 returns from the many tagging programs were classified in table 1 as follows: (1) Recoveries near the tagging site (col. 4); (2) recoveries before or during spawning, usually March through May (col. 5); (3) recoveries after spawning, June 1 or June 15 through November (col. 6); (4) recoveries of those fish tagged on the spawning ground and captured the following years during the spring (col. 7); and (5) miscellaneous, including returns from markets, homes, et cetera (col. 8), where it was impossible to determine the place and/or date of recapture. All tags recovered from the tagging experiments were assigned to the appropriate category (table 1). Tag recoveries in the first two categories were made during the same period, but only those showing movement away from the tagging site were listed as tag recoveries "before or during spawning." Tags recovered near the tagging site were not used in this study since they showed no migration, but they were listed in column 4 so that all recoveries would be accounted for.

Of the tags affixed on the spawning grounds in the Hudson and Connecticut Rivers, no difficulty was experienced in separating those recovered before or during spawning (col. 5) from those recovered after spawning (col. 6). In this case, if the tags were recovered outside the river, they were considered as having been recovered after spawning. A few tags recovered from fish tagged on the coast of New Jersey and in the Chesapeake Bay area were not so easily classified, since it was not known exactly where these fish had spawned. Shad tagged at these places were recovered from spawning areas in the Chesapeake and Delaware Bays, the Hudson and Connecticut Rivers, and in Canadian streams. However, spawning in all streams south of Long Island is virtually completed by May 31, while spawning in the Connecticut River is usually completed by June 15. In the few doubtful cases, if the tags were recovered in the ocean after May 31 south of Long Island or after June 15 off Massachusetts, Maine, or Canada, they were arbitrarily classified as having been taken after spawning. Therefore, using these criteria, a few errors in classification may have resulted, since shad tagged in Chesapeake Bay or on the coast of New Jersey and recaptured between Long Island and Canada after June 15 were classified as captured after spawning, but they could have been on their way to spawn in streams in Maine or Canada, where spawning occurs in June and even as late as July. These cases were few, and even if improperly classified they still help to illustrate the migration pattern of shad at this time of year.

Five percent of the tags used in our study of shad migrations were recovered 1 to 4 years after tagging. Of these, 55 percent were recovered on the spawning grounds and listed in column 7 of table 1. The others are listed under columns 5 or 6, regardless of year of recovery. In other words, a tag recovered from near the tagging site 1 or more years after tagging was classified under column 4. A tag recovered in the ocean after 1 or more years was classified under column 5 or column 6, the same as if it were recovered the year the fish was tagged. This was necessary since there was no way to determine where the fish bearing these tags had been during the intervening periods. The assumption in these cases was that the fish were repeating a migration pattern that they followed each year and, therefore, were properly classified.

The returns from the Gulf of Maine tagging, listed in column 5, were analyzed under a heading separate from the other tags in this column. The Maine tagging was carried out in August and September and illustrates a migration pattern different from the other tag recoveries in column 5,

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which were tagged during the spring months. The tag recoveries from Maine and those listed in table 1, columns 4, 5, and 6 are discussed in the following sections.

TAG RECOVERIES BEFORE AND DURING SPAWNING

In this group are fish recaptured on their way to the spawning grounds or on the spawning grounds that were tagged in the spring (mostly March through May) off Fire Island, New York, and the coast of New Jersey, in Chesapeake Bay, and at the mouth of the Neuse River in North Carolina. Recoveries in this group from tagging conducted at the first two locations are shown graphically in figure 2, and those from Chesapeake Bay and the Neuse River in figure 3. The broken lines showing the paths of migration in these and the following figures are not intended to give the exact routes followed by the migrating shad, but merely to indicate the tagging and recovery areas.

The tagging near Fire Island was carried out in two periods during 1946 (table 1). Those shad tagged from April 12 to 22 were mostly recaptured in the Connecticut River (26 fish), while only nine (included in the 20 shad in fig. 2) were recovered in the Hudson River. Those fish tagged from June 10 to 19 were mostly spawned-out shad from the Hudson River, for only 1 tag was recovered from the Connecticut River that year, while during the shad run of the following year 11 fish were recaptured from the Hudson River and none was recovered from the Connecticut River.

Tag recoveries indicate that most of the shad tagged on the coast of New Jersey and Staten Island were bound for the Hudson (1,377 fish recaptured) and Connecticut Rivers (120 fish recaptured) as shown in figure 2. A few were recaptured in Delaware Bay and in the spawning areas of the Maurice River, a tributary to the bay. Some also were recaptured in Chesapeake Bay and tributaries, while a few were recaptured early in the season en route to, or in, Canadian rivers. The recapture of a shad tagged in June off Fire Island was made in North Carolina the following spring.

Most of the shad tagged in Chesapeake Bay were recaptured in the near vicinity either in the bay or its tributaries, where they spawn (table 1, col. 4). The same is true of those shad that spawned in the Neuse River, where all but one of the recaptures were made either in this river or in neighboring waterways. The tagged shad which did leave the vicinity of tagging and were recovered before or during the spawning season are shown in figure 3. As with those fish tagged on the coast of New Jersey and off Fire Island, some of the shad tagged in the Chesapeake Bay area migrated long distances during this period and spawned in widely separated streams from South Carolina to Canada.

TAG RECOVERIES AFTER SPAWNING

All tags that were affixed in the Hudson and Connecticut Rivers, along the coast of New Jersey, and in Chesapeake Bay, and recovered after spawning in these areas was completed, are plotted in figure 4. Tags recovered during this period indicated a shad migration in the ocean northward from the tagging area. Recoveries off Long Island of fish tagged in the Hudson River were made from June 5 through June 25. Fish tagged in Chesapeake Bay were recaptured off Long Island from June 9 through June 17, while shad tagged on the coast of New Jersey, and which spawned predominantly in the Hudson River as previously shown, were recaptured off Long Island between June 11 and 26.

The earliest recapture off Massachusetts was on June 22 of a shad tagged at the mouth of Chesapeake Bay on April 14, and the earliest recapture in Maine was July 6 of a shad tagged in Chesapeake Bay on May 21. The earliest recovery in Canada was on July 9 near the mouth of the St. Johns River, New Brunswick. This fish was tagged off New Jersey on April 25.

Tags were recovered off Massachusetts during the months of June, July, and August, and in October and November, while in Maine, New Brunswick, and Nova Scotia, they were recovered only during the months of July, August, and September. These records indicate that the recoveries of tagged fish in June, July, and August may have been made as the shad migrated past Massachusetts on their way north to Maine and Canadian waters, while the October–November recoveries were made as the shad were on their return trip south.

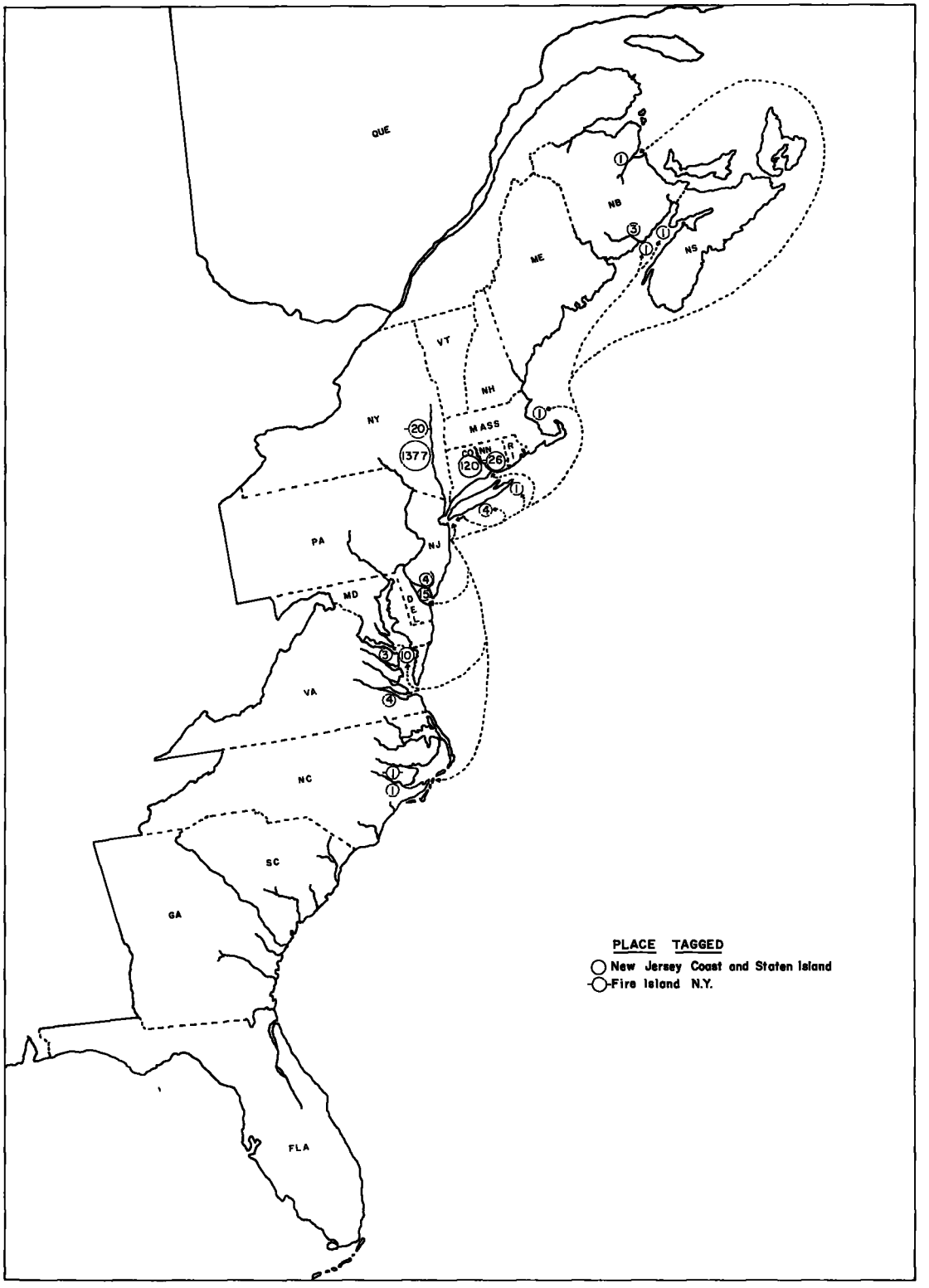

FIGURE 2.—Tags recovered before or during the spawning period (before June 1 south of Long Island and before June 15 off Massachusetts, Maine, and the Canadian Provinces) which were affixed at Fire Island and Staten Island, New York, and along the New Jersey coast during the period March through June. (The broken lines connect place of tagging with place of recapture, but do not necessarily show the migration route. The figures in circles indicate the number of tags recovered in each locality.)

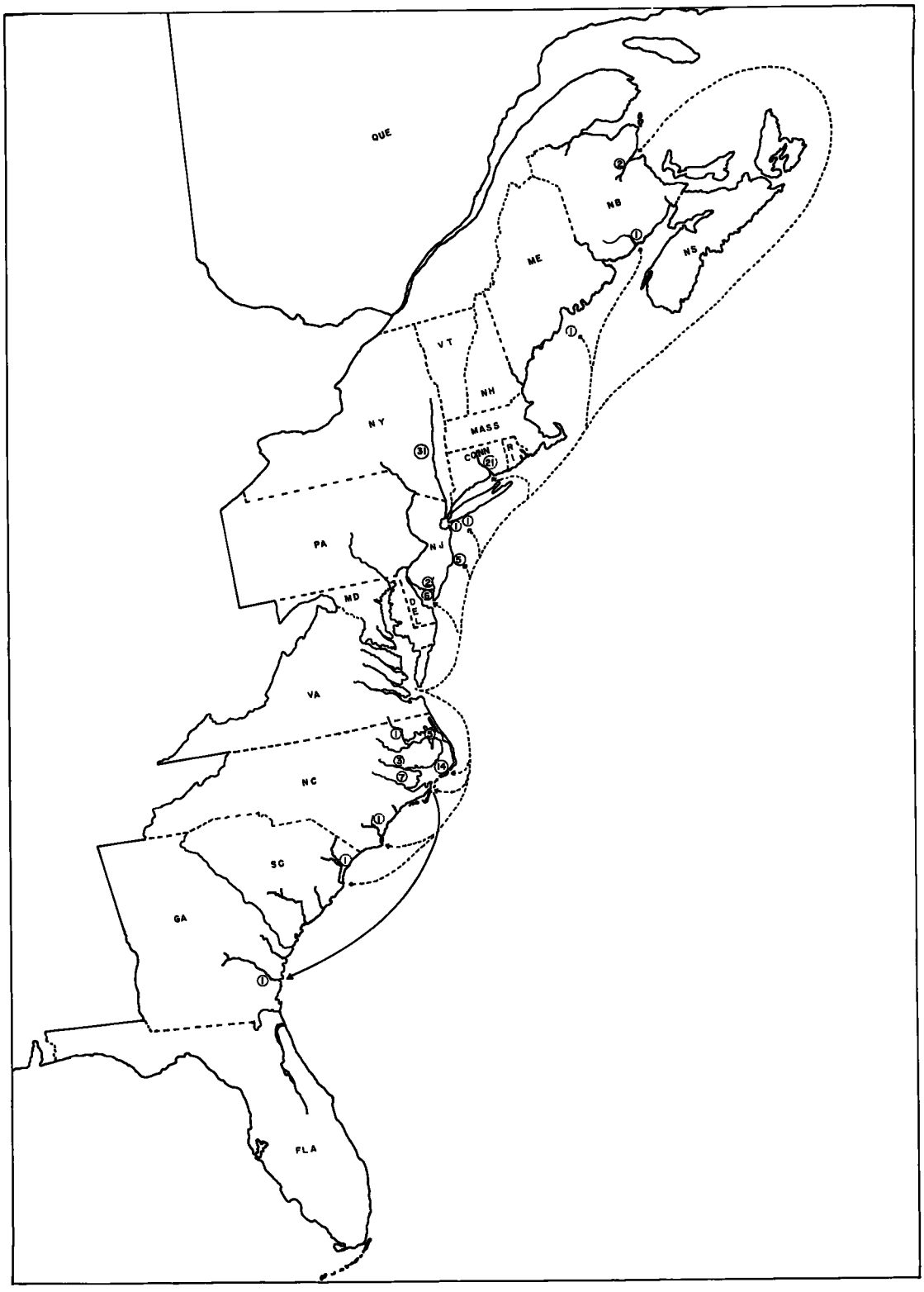

FIGURE 3.—Tags recovered before or during the spawning period (before June 1) affixed in Chesapeake Bay from March through May and at the mouth of the Neuse River from January through April. (The broken lines connect place of tagging with place of recapture, but do not necessarily show the migration route. The figures in circles indicate the number of tags recovered in each locality.)

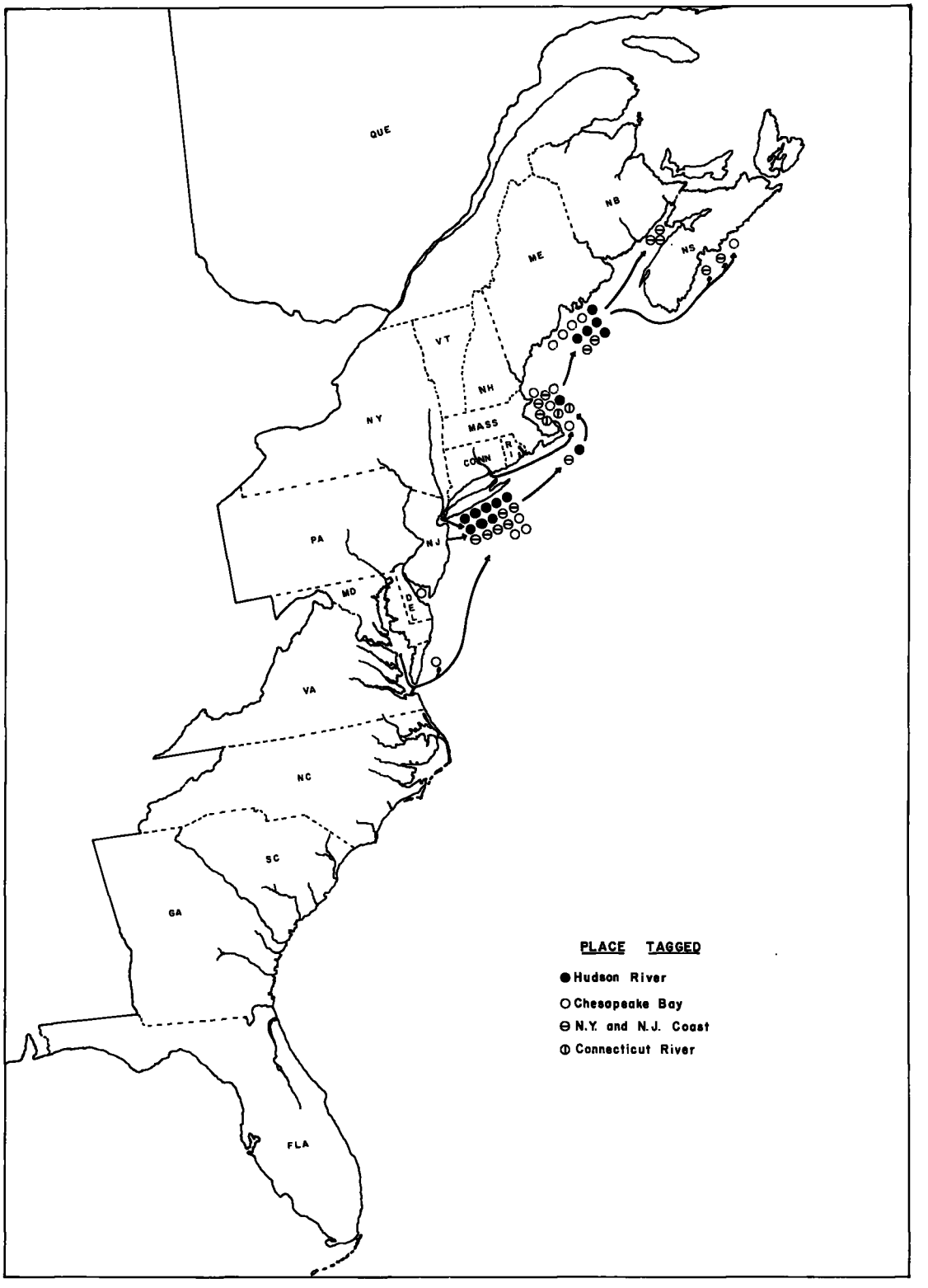

FIGURE 4.—Tags affixed in the Hudson and Connecticut Rivers, off Fire Island, New York, along the coast of New Jersey, and in Chesapeake Bay and recovered after the spawning period (after May 31 south of Long Island and after June 15 north of Long Island).

Very little evidence is available as to where shad spend the winter months. Only one tag was recovered during the period December through January. This fish was tagged in the Connecticut River during the spawning season and recaptured in the ocean off the New Jersey coast on December 13 of the following year. Sometimes when the winter is mild shad in small quantities will enter the sounds of North Carolina during November and December, but will disappear if the weather gets cold. Because shad appear in abundance all along the middle and south Atlantic coast beginning in February, it is assumed that they spend the winter months in this area, probably in deep water.[1]

RECOVERIES FROM SHAD TAGGED IN MAINE

Tagging in the Gulf of Maine was carried out during August and September (table 1) at a time when (as will be shown later) shad are abundant in this area. All the recoveries, with the exception of one tag retaken in November of the year of tagging in Massachusetts, were made the following years during the spring and summer (fig. 5). Most of the recoveries were made south of Maine during the spring in rivers from Georgia to Connecticut. A few were also taken in New Brunswick and Nova Scotia, and in the St. Lawrence River in Quebec during the same period. No Maine tags were recovered from the St. Johns River in Florida, but doubtless shad from this river also summer in the Gulf of Maine during their early years. It seems probable that additional tagging would result in recaptures in this river. If this is true, the early running shad of this river may migrate from the Gulf of Maine directly to Florida, since they enter the St. Johns River as early as November. With one exception, therefore, tag returns indicate that shad from the whole Atlantic coast range of this species can be found during the summer months in the Gulf of Maine.

[1] Evidence supporting this theory was obtained on March 3, 1958, when the U. S. Fish and Wildlife Service exploratory vessel *Delaware* caught shad in 40 to 50 fathoms off the coast of North Carolina.

SPRING RECOVERIES OF SHAD TAGGED ON SPAWNING GROUNDS

Figure 6 shows the tags recovered early in the spring of the years following the tagging of shad on their spawning grounds in the Hudson and Connecticut Rivers. These tag recoveries were made from North Carolina to Long Island during February and March, but as the time of spawning approached, the recoveries were made nearer the mouths of the rivers where the fish had been tagged and to which they were obviously returning. Although tags affixed in the Connecticut and Hudson Rivers were recovered along the Atlantic coast from North Carolina to Long Island, and in Chesapeake and Delaware Bays, not a single tagged fish was recovered from a spawning ground other than the one in which it was tagged. Of the Hudson River tags, 185 were recovered back in the Hudson River, and 23 tags affixed in the Connecticut River returned again to the Connecticut River.

RATE OF MIGRATION OF TAGGED SHAD

The speed with which shad are capable of traveling during their migrations is difficult to determine from tagging experiments, since the routes taken are not known. Furthermore, it is not known how long a shad may have delayed near the tagging site, or how long it may have been in an area before being captured. Table 2 lists a number of recaptures of shad tagged at several locations, and illustrates some of the fastest migrations found during our analysis of tagging data. The distance traveled per day ranged from 14.4

TABLE 2.—*Distance and miles per day traveled by tagged shad*

Place of tagging	Date tagged	Place recovered	Date recovered	Distance (miles)	Number of days	Miles per day
New York: Fire Island	4/18/46	St. John River, N. B	5/27/46	560	39	14.4
New Jersey:						
Beach Haven	5/12/56	Hudson River, N. J	5/17/56	72	5	14.4
Point Pleasant	5/ 5/56	Hudson River, N. J	5/ 7/56	48	2	24.0
Point Pleasant	5/11/56	St. John River, N. B	6/18/56	648	37	17.5
Point Pleasant	4/29/56	Connecticut River	5/ 7/56	192	8	24.0
Seaside Park	4/19/45	Lynnhaven, Va	4/26/45	210	7	30.0
Sandy Hook	4/13/42	St. John River, N. B	5/20/42	576	37	15.6
Virginia:						
Little Creek	4/21/52	Hudson River, N. J	4/27/52	320	6	53.3
Little Creek	4/22/52	Hudson River, N. J	5/ 4/52	320	12	26.7
Little Creek	4/10/52	Neuse River, N. C	4/21/52	260	11	23.6

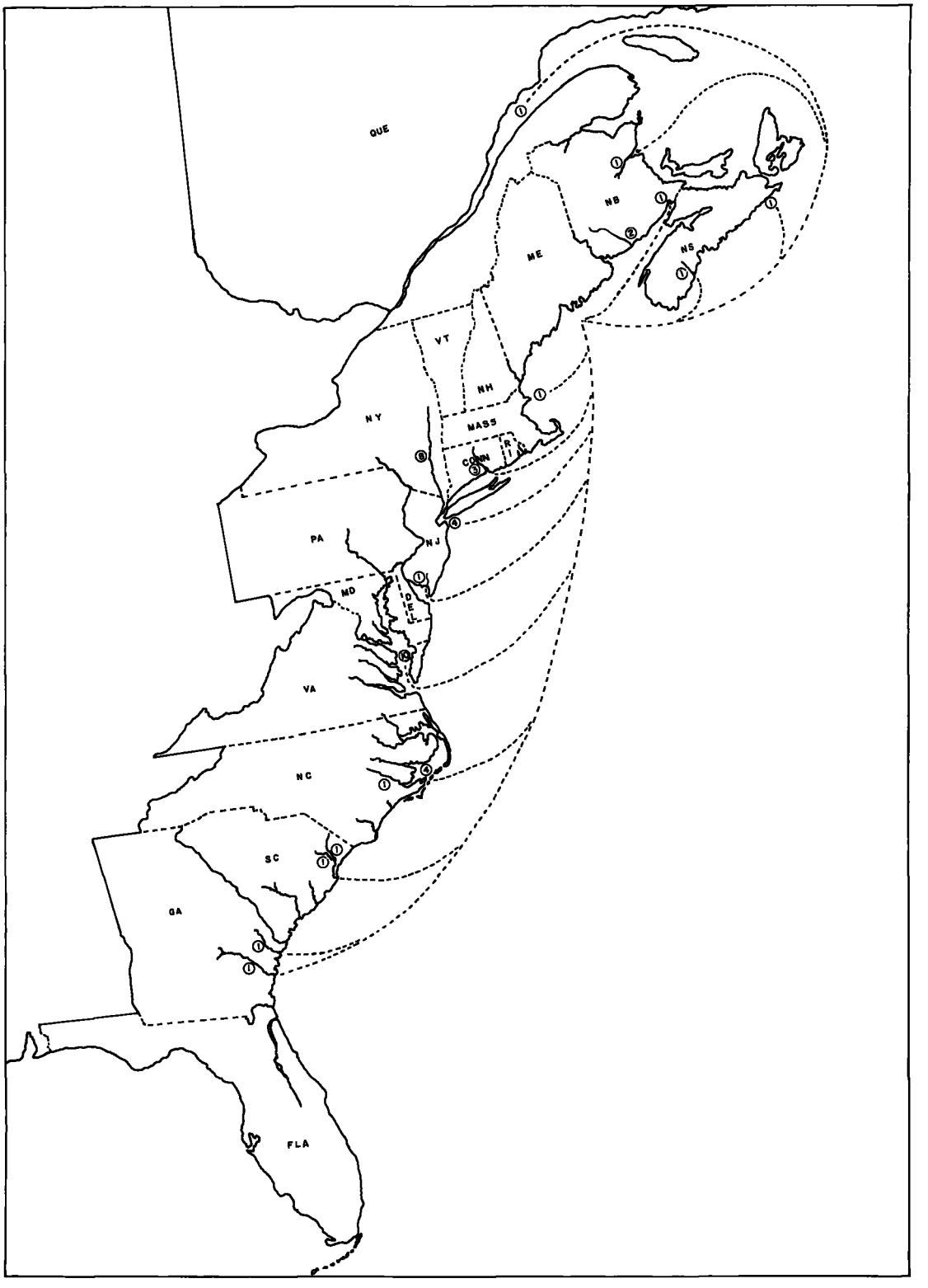

FIGURE 5.—Recoveries from the State of Georgia to the Province of Quebec of tags affixed in the Gulf of Maine during August and September.

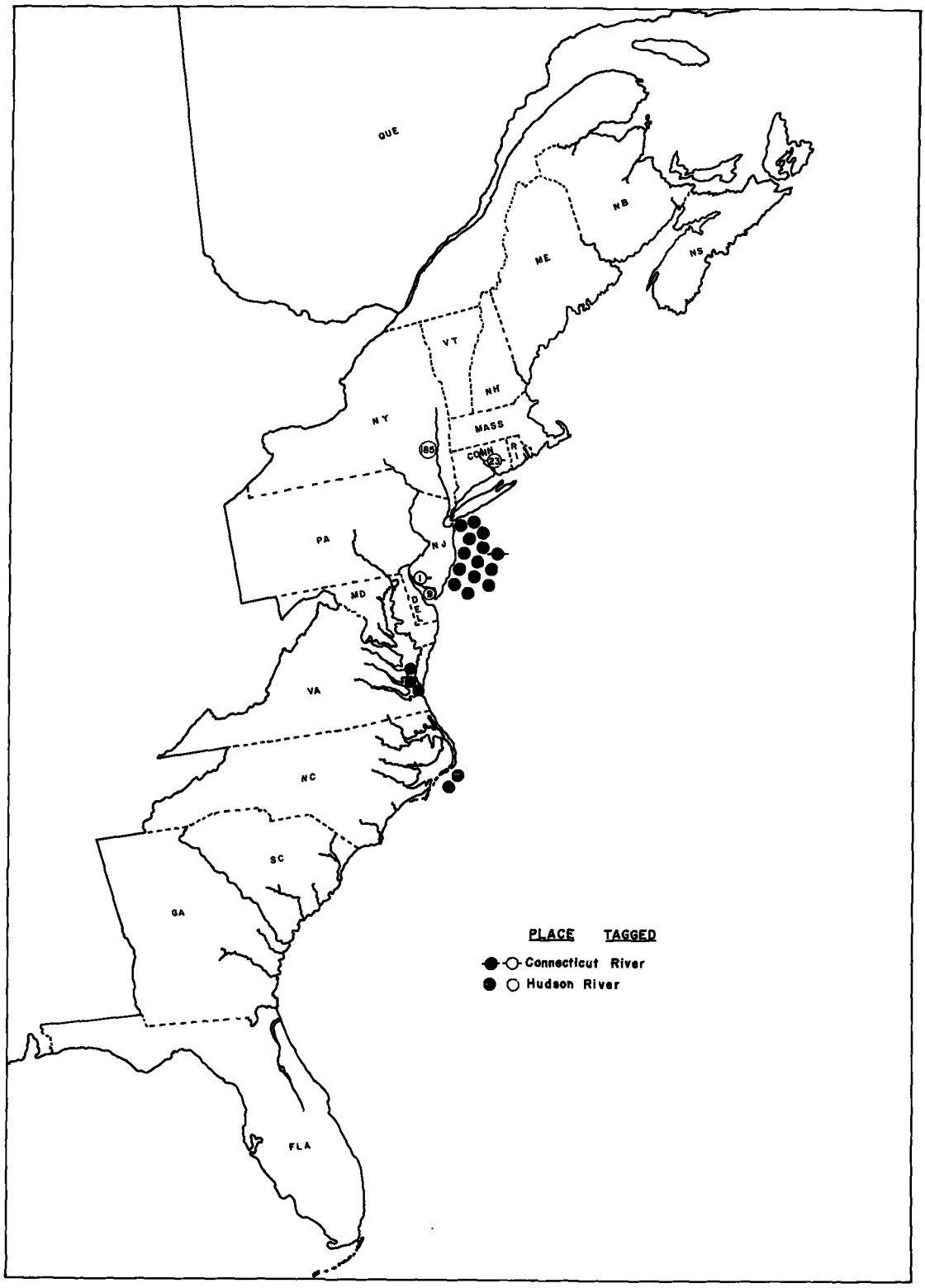

FIGURE 6.—Recoveries in the spring of subsequent years of tags affixed to shad on their spawning grounds in the Hudson and Connecticut Rivers.

to 53.3 miles. For reasons already given, however, these distances must be considered as the minimum for the individual fish listed.

OTHER EVIDENCE OF MIGRATION

The tag recoveries illustrated in figure 4 show that, after spawning, shad from Chesapeake Bay and the Hudson and Connecticut Rivers migrate to the Gulf of Maine, where they are caught during the summer and fall months. Since there is no reason to believe that untagged shad behave differently than tagged shad, the inference obtained is that untagged shad spawning in streams in Chesapeake Bay and the Hudson and Connecticut Rivers also migrate to the Gulf of Maine after spawning. That this is true is borne out by the large numbers of spent shad that have been reported in the Gulf of Maine since the early part of this century. These were believed to have come from Maine streams, as reported by Bigelow and Welsh (1925: pp. 115–116) who stated that:

> Large spent shad—presumably fish that have spawned in the Kennebec—are regularly caught in September and October about Mount Desert, where they have been the object of a considerable frozen-fish industry of late, as well as near the Isles of Shoals and off York Beach in August, while it has long been known that shad are present 40 to 50 miles at sea off the Maine coast throughout the autumn.

In recent years, shad runs in Maine streams have become almost nonexistent because of dam construction and pollution (Taylor 1951); the same is true of shad runs in the streams of Massachusetts. Yet, large numbers of shad are still found in the Gulf of Maine every summer. Usually, these are not fished extensively for food since they are spawned-out fish and normally bring a low price; but during World War II, when fish prices were generally high and demand was good, a large shad fishery developed. In 1946 over a million pounds were caught—mostly with purse seines (Taylor 1951).

Large shad catches are still made in the Gulf of Maine along with "scrap" fish by boats working out of Massachusetts ports during the summer. Some large catches of "scrap" fish are 100 percent shad, as reported in Massachusetts Fisheries Trends for July 1956 (U. S. Fish and Wildlife Service, 1956: p. 4), "Recent catches of large shad are reported by boats seining for menhaden. Two trips were landed that consisted of pure shad. . . . The two shad trips totaled about 120,000 pounds. . . ." It was reported that other trips brought in mixtures of shad and herring. During the summer of 1957 when menhaden were scarce, menhaden purse seiners turned to shad and landed over 2 million pounds of this species for processing into fish meal and oil.[2] These shad are in such abundance that undoubtedly most of them are from rivers other than those of Maine and Massachusetts, and therefore indicate a migration to this area during the summer months.

It has been shown (Walburg, 1956, 1957; Sykes 1956) that almost all shad spawning in North Carolina and all shad spawning south of North Carolina die after they spawn. This is evident in table 1—no tags were returned after the spawning season from the tags affixed to shad in the streams of these States. Therefore, recovery of Gulf of Maine-tagged shad in southern streams (fig. 5) indicates that these fish must have been tagged as immature shad which moved to the Gulf of Maine area during the summer months and then returned to southern rivers to spawn. This migration to the Gulf of Maine, along with that of immature shad from other Atlantic coast streams, accounts for the large number of immature shad found there each summer as reported as early as 1887 by Atkins (p. 684), who, writing about Maine fisheries, stated, "A more numerous class of immature individuals feed about the bays and in the mouths of the rivers during the summer, later than the ascent of the main body of breeders." Bigelow and Welsh (1925) reported that—

> Schools of small immature shad from a foot long and half a pound in weight up to 2 or 2½ pounds, not yet of breeding age . . . are reported evey year at Provincetown for a short period in June, are sometimes taken in the weirs at Beverly and Manchester in Massachusetts Bay in June, and are met with more or less commonly all summer off Cape Ann and thence eastward . . . .

Later, Bigelow and Schoeder (1953: p. 111) noted that "it seems established that most of the medium-sized shad and larger . . . are immigrants from the south, growing and fattening on the rich supply of plankton they find there, but returning to the rivers west and south of Cape Cod to

[2] In a letter dated Apr. 9, 1958, from Dwight L. Hoy, Commodity Industry Analyst, U. S. Fish and Wildlife Service, Gloucester, Mass.

spawn." Some direct evidence of this was available to Bigelow and Schoeder from preliminary tagging results, which are reported in this paper.

HOMING BEHAVIOR

Considerable evidence is available to show that shad do return to their native streams to spawn. Hollis (1948) released about a thousand juvenile shad, averaging 10 centimeters in length, at Edenton, N. C., in October 1941, after inserting small plastic belly tags into their body cavities. During the spawning migration, 3 to 5 years later, three tags were recovered within a radius of 10 miles from the tagging site. None was returned from any other area.

Later, in a cooperative experiment between the U. S. Fish and Wildlife Service and the Chesapeake Biological Laboratory, Solomons, Md., E. A. Hollis [3] and C. M. Coker [4] inserted 737 belly tags into fingerling shad on October 26, 27, and 28, 1950, and released the fish near the mouth of Mill Creek, which empties into the Patuxent River at Solomons, Md. Four of the tags were recovered 4 years later, three were recovered 5 years after tagging, and one was recovered 6 years after tagging. Three of the tags were returned from dealers and it was not possible to locate their place of capture. Three tags were returned from Chesapeake Bay where the tagged fish could have been on their way to the Patuxent River, and two tags were from Solomons Island. None was recovered from an area which would indicate that the shad might spawn in any place but its "home" stream.

The returns from these two experiments were small, but when the mortality between young and adult stages is taken into consideration and also the fact that small belly tags can easily be overlooked in the viscera of an adult fish, the returns are perhaps all that could be expected. While these experiments do not prove conclusively that shad return to their native stream to spawn, the tag returns, though few in number, suggest that they do.

Hammer (1942) made a study of the scales and body measurements of shad taken in Chesapeake Bay and its tributaries. He used measurements of the fresh-water zone of the scales to compute the juvenile body lengths attained at the termination of the young shads' stay in fresh water. These calculated lengths from various streams differed significantly, indicating that "mature Chesapeake shad return to spawn in the stream of their origin." Otherwise, as a result of intermixing, the calculated lengths would be similar. Other scale characteristics denoted the existence of populations peculiar to each river.

As previously noted, the shad which spawn in streams south of North Carolina die after spawning. No repeater shad were found in samples of scales taken from these rivers and less than 3 percent of the North Carolina shad were found to be repeater fish (LaPointe 1958). In contrast, repeater shad spawning in streams tributary to Chesapeake Bay make up to 27 percent of the population (Walburg and Sykes, 1957) and in the Hudson and Connecticut Rivers up to 50 percent (Moss 1946; Talbot 1954). This is good evidence that little if any mixing or straying of shad of the more northern populations into the populations spawning in southern streams occurs. Otherwise, repeater shad would be found in the southern stocks.

Further evidence that shad return to their home streams to spawn is found in data presented by Fredin (1954) and Talbot (1954). These workers reported, respectively, that 83 percent of the fluctuations in size of run in the Connecticut River and 85 percent in the Hudson River depend upon the spawning populations in previous years. In other words, each of the runs of shad to these rivers is self-perpetuating and fluctuates independently of shad runs in other streams. The Hudson River shad run has reached peaks of abundance twice in the past 50 years (Talbot 1956; unpublished data for 1956) while shad runs of neighboring streams such as those in the Connecticut River have fluctuated independently and in the Delaware River have been at a low level of production during the same period (Sykes and Lehman, 1957). Such variance among streams could exist only if the majority of the shad return to their home stream to spawn.

The only evidence available that might be construed as contradicting the home-stream theory so far as the American shad is concerned is found in the shad transported from the Atlantic coast to the Sacramento River in California and the Columbia River between Washington and Oregon.

[3] Now with Maryland Tidewater Fisheries.
[4] Now with Estacion Experimental Agricola, Puerto Rico.

Shad became established in these rivers and soon spread to other streams of the Pacific coast. In this case, however, the transplanted shad did not have their hereditary home stream available to them; hence, if these fish were seeking their home stream, straying might be expected to be a normal occurrence rather than the exception.

The available evidence, therefore, indicates that most Atlantic coast shad do return to their native streams to spawn, and it definitely indicates that shad, having once spawned in a stream, will return to that stream to spawn again if they survive natural and fishing mortalities.

DISCUSSION AND CONCLUSIONS

The recoveries of tagged shad indicate a definite migration pattern with few or no deviations. Occasionally, unmarked shad have been reported in areas that do not conform to the general pattern. For instance, each year in the Connecticut River a number of emaciated adult shad are found in the canal near Windsor Locks during the summer and fall months. It is believed that these fish are trapped in the canal, and remain there until they die or until, by chance, they are carried out into the river during a lockage.

Small numbers of adult shad are also caught each year on eel racks in the upper Delaware River during the summer and fall months (Sykes and Lehman, 1957). Others have been reported in the lower Hudson River during the fall or winter months and they have been reported in Chesapeake Bay almost all through the year. In every instance, however, these shad have been in small numbers and no tags have ever been recovered from them. It must be concluded that these cases are unusual and that the vast majority of the fish follow the migratory pattern shown by the tag returns and the corresponding abundance of shad, as reflected by catches, during this migration.

One factor that might be expected to obscure the recovery pattern of tags and, hence, lead to false conclusions regarding migrations, is the time of year that each type of fishing gear operates in each area of recovery. In other words, tag recoveries might have been made at certain times, only because certain fishing gear was operating at those times. This, however, does not appear to be the case. In Maine, tags were recovered in July through September from operators of purse seines, otter trawls, and gill nets. The purse seines operate from May to December, overlapping the period of shad catches and tag recoveries by at least 1 month before and after the shad catch season. Tags were recovered in Massachusetts from late June to the first week in November. In this State, purse seines operate from late June until October during the time most tags are returned. In both Maine and Massachusetts, otter trawls and gill nets are operated throughout the year but shad are taken in abundance only during August, September, and October,[5] the period in which the tagged shad were caught.

At Fire Island, New York, pound nets have been set as early as March and are in operation throughout the summer and fall until November. A few mature shad are taken here during late March, April, and May, most of which appear, according to tag recoveries, to be heading for the Connecticut River; and spawned-out shad are taken during June. Rarely have shad been caught at any other time of the year.

The pound nets along the New Jersey coast formerly were fished almost all year; some were removed in December or January. In recent years, they have usually been taken up from December through February. Shad are taken in abundance in this area only during the spring spawning run, and it is only at this time that tagged shad have been recovered, with the exception of the one tag taken during December, previously mentioned. In Chesapeake Bay [6] and the bays of North Carolina, pound nets are operated from January through April, and from September through November, but shad, both tagged and untagged, are caught only during the spring spawning run.

In all rivers supporting a spawning run, shad are abundant only during the spawning run and the majority of the shad fishermen set their nets only during this period. In most rivers, however, fishing gear is operated throughout the year for other species, and this would disclose the presence of shad if they were in the rivers in any numbers at a time other than during the regular shad

[5] In a letter dated Oct. 22, 1956, from Dwight L. Hoy, commodity industry analyst, U. S. Fish and Wildlife Service, Gloucester, Mass.

[6] In a letter dated Feb. 11, 1957, from William H. Massmann, Virginia Fisheries Laboratory, Gloucester Point, Va.

season. It appears, therefore, that shad are in abundance only at those places and times indicated by the tag returns and that the pattern of tag return is not the result of peculiarities in the operation of fishing gear.

Returns from shad tagged in the St. Lawrence River by Vladykov (1950) are of interest, since the migration pattern of these fish appears to agree with that indicated by our tagging data farther south. Vladykov found that after spawning shad left the St. Lawrence River during July and August and spent the balance of the summer and fall in the Gulf of Maine. He surmised that they spent the winter and early spring "between the Gulf of Maine and Nova Scotian Banks." However, as can be seen in figures 2 and 3, Canadian-spawned shad are caught as far south as Chesapeake Bay in the spring. In a later paper Vladykov (1957) reports that three shad tagged in the St. Lawrence River during the summer were recovered the following spring in the Middle Atlantic area—one near Old Point Comfort, Virginia; one off Bowers Beach, Delaware; and another off Sandy Hook Bay, New Jersey. It would appear that Canadian shad not only spend the summer months in the Gulf of Maine as do the more-southern spawning shad, but that they, too, spend the winter in the Middle Atlantic area.

We can now conclude from the evidence available that the majority of the Atlantic coast shad make regular migrations each year and return to their native streams to spawn. This pattern has been disclosed by the recovery of approximately 39 percent of the more than 17,000 shad tagged; by the presence at certain seasons of large numbers of immature and adult shad in areas where shad are not natively abundant, and conversely, by the absence of shad in other areas during certain times; and by studies of the scales of shad which have shown that there are separate races in each stream.

In studies of the American shad carried out over a period of 19 years, tag recoveries have revealed a consistent migration pattern, which can be summarized as follows: After spawning, adult shad in streams from Chesapeake Bay to the Connecticut River migrate northward and spend the summer and fall in the Gulf of Maine. Canadian shad migrate southward to the Gulf of Maine and also spend the summer and fall there. There is little evidence as to where shad spend the winter months; but it appears that they are scattered along the Middle Atlantic area, for beginning in January or February as the spawning season approaches, they move inshore and are taken in the commercial fisheries from North Carolina to Long Island. They then migrate either north or south to their native streams and spawn, repeating this cycle each year that they escape natural and fishing mortalities. The young shad leave their native streams in the fall, probably spend the winters in the Middle Atlantic area, migrate to the Gulf of Maine each summer along with the adults, and when mature return to their native streams to spawn. Those that spawn in streams south of Chesapeake Bay, and particularly south of North Carolina, die after spawning.

From these studies it appears that shad, like salmon, migrate long distances in the sea and return to their native streams to spawn. How or by what mechanism they are guided has not yet been satisfactorily determined.

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EFFECT OF NEW JERSEY-NEW YORK POUND-NET CATCHES ON SHAD RUNS OF HUDSON AND CONNECTICUT RIVERS

BY PAUL R. NICHOLS

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ABSTRACT

A shad-tagging study conducted off the New Jersey-New York coasts during the spring of 1956 indicated that the New Jersey-New York ocean pound-net shad catch was composed of 76 percent Hudson River shad and 13 percent Connecticut River shad. Since the majority of shad caught off the coasts of New Jersey and New York are native to the Hudson and Connecticut Rivers, large ocean catches in any one year could affect the size of runs available to these rivers. The New Jersey-New York coastal shad catch has no effect on the deviations that occur between calculated and predicted size of Hudson River and Connecticut River shad runs. It was found that the New Jersey-New York pound-net shad catch is dependent on the size of the Hudson River shad population.

EFFECT OF NEW JERSEY–NEW YORK POUND-NET CATCHES ON SHAD RUNS OF HUDSON AND CONNECTICUT RIVERS

By PAUL R. NICHOLS, *Fishery Research Biologist*
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From the early years of this century until 1950, the Atlantic coast commercial catch of American shad (*Alosa sapidissima*) declined from approximately 50 million pounds to 8 million pounds. As part of an investigation sponsored by the Atlantic States Marine Fisheries Commission to determine the causes for the decline in abundance of shad, the United States Fish and Wildlife Service conducted studies on the Hudson River (Talbot 1954) and Connecticut River (Fredin 1954) shad fisheries 1950 and 1951. These studies showed that, within the limits of the populations studied, the largest single factor influencing fluctuations in abundance in both rivers was the number of shad escaping the commercial fishery to spawn. Regression formulas were presented by which the size of each population could be predicted 1 year in advance. Deviations between predicted and actual population size were also given.

One factor which could affect the magnitude of these deviations is mortality (fishing and natural) occurring outside of the rivers. The studies on the Hudson and Connecticut Rivers and limited experiments by E. H. Hollis,[1] indicate that Hudson and Connecticut River shad are taken outside these rivers along the Atlantic coast from North Carolina to Maine, particularly along the coast of New Jersey and off Staten Island, N. Y. If the major part of the shad catch from the New Jersey–Staten Island coast is composed of shad native to the Hudson and Connecticut Rivers, then a large ocean catch in this area in any one year could possibly affect the size of the runs available to these rivers. The present study was conducted to determine the effect of the New Jersey–New York pound-net catch on the shad runs of the Hudson and Connecticut Rivers.

[1] Unpublished report, U. S. Fishery Laboratory, Beaufort, N. C.

NOTE.—Approved for publication, December 6, 1957. Fishery Bulletin 143.

An expression of appreciation is due the members of the staff of the U. S. Fishery Laboratory, Beaufort, N. C., who helped in the field work and reviewed this paper. The aid of the shad fishermen of the middle and north Atlantic areas is gratefully acknowledged. Without their cooperation and return of tags this study could not have been completed.

LIFE HISTORY

The shad, largest member of the herring family in the United States, is anadromous. It spends most of its life in the sea but ascends coastal rivers to spawn. Shad enter the rivers of the Atlantic coast progressively later from south to north, commencing as early as November in Florida and as late as May and June in Canadian rivers. Shad are prolific spawners, as shown by Lehman (1953). The annual fecundity of 22 female shad collected in the Hudson River in 1951 was found to range from 116,000 to 468,000 ova, and was directly proportional to the length, weight, and age of the fish. According to Leim (1924), the eggs hatch in 12 to 15 days at 52° F. (12° C.), in 6 to 8 days at 63° F. (17° C.), and the larvae are about 9 to 10 mm. long at the time of hatching. The larvae develop into their final form in 4 to 5 days at a water temperature of 63° F. The young shad remain in the rivers until fall when they migrate to sea. Upon reaching sexual maturity in 3 to 5 years they return to fresh water to spawn, and it is during this migration that shad are taken by fishermen.

NEW JERSEY-NEW YORK OCEAN POUND-NET SHAD FISHERY

Since 1896, the first year for which detailed information is available, pound nets have been the principal type of commercial gear used in taking shad along the New Jersey and New York

coasts. Fyke nets, floating traps, haul seines, gill nets, and weirs have accounted for small catches, but their take is relatively unimportant compared to the pound-net landings. Pound nets are operated along the New Jersey coast from Cape May to Raritan Bay and in New York from Staten Island to the eastern tip of Long Island. The majority of shad are taken between Beach Haven, N. J., and Staten Island, N. Y. Relatively large catches of shad were taken off Long Island between the years 1939 and 1946, but since 1946 catches in this area have been negligible.

Each year shad appear in large numbers along the New Jersey–Staten Island coast during the months of March, April, and May; however, the largest catches are usually made during April. Table 1 shows the pound-net catch of shad and number of pound nets fished in New Jersey and New York for most years from 1921 through 1956. From 1921 through 1926, the operating units of gear included floating trap nets and weirs which accounted for some of the landings; however, these gears took less than 5 percent of the total catch. In recent years the number of pound nets fished in these areas has decreased. In 1931, 632 pound nets were licensed in the States of New Jersey and New York, but by 1954 only 220 were licensed.

TABLE 1.—*Pound-net shad catch and number of pound nets licensed in New Jersey and New York, 1921–56*

[Statistics for 1921–38, from U. S. Bureau of Fisheries; for 1939–54, from U. S. Fish and Wildlife Service; for 1955–56, from preliminary data of U. S. Fish and Wildlife Service]

Year	Catch (in pounds)			Units of gear		
	New Jersey	New York	Total	New Jersey	New York	Total
1921	36,423	7,052	43,475	217	414	631
1926	63,830	10,059	73,889	198	422	620
1929	19,780	1,446	21,226	181	445	626
1931	56,228	13,060	69,288	186	446	632
1932	54,231	2,988	57,219	163	308	471
1933	63,109	15,758	78,867	153	301	454
1935	251,200	21,900	273,100	156	295	451
1937	1,145,600	38,700	1,184,300	191	136	327
1938	602,200	98,800	701,000	175	125	300
1939	445,100	145,100	590,200	194	106	300
1940	1,199,800	84,400	1,284,200	193	132	325
1942	2,605,400	258,900	2,864,300	171	74	245
1943	1,200,000	565,000	1,765,000	125	67	192
1944	1,838,200	446,100	2,284,300	129	60	189
1945	1,249,900	758,200	2,008,100	113	74	187
1946	[1] 499,877	296,500	796,377	[2]	103	.....
1947	337,700	291,100	628,800	127	141	268
1948	467,500	267,500	735,000	122	161	283
1949	300,700	139,200	439,900	77	153	230
1950	267,900	213,600	481,500	76	138	214
1951	156,500	48,400	204,900	88	144	232
1952	561,600	282,600	844,200	138	117	255
1953	78,400	25,500	103,900	110	94	204
1954	130,100	121,600	251,700	89	131	220
1955	288,800	111,554	400,354	51	[3]	.....
1956	226,544	122,685	351,229	48	[3]	.....

[1] From New Jersey Department of Fish and Game.
[2] Units of gear not determined.
[3] Not available.

Analysis of the catch data in table 1 shows that the New Jersey–New York pound-net shad catch was low from 1921 through 1933, followed by a tremendous increase from 1937 through 1945. From 1946 through 1956 the commercial catch again decreased and is now at a moderately low level. Part of this decrease in catch in recent years can probably be attributed to a decline in the amount of gear fished.

TAGGING STUDY, 1956

During the spring of 1956, shad were tagged from pound nets located off the coasts of New Jersey and Staten Island, N. Y., to determine the composition or population origin of the fish taken in these waters. Beach Haven, the southernmost point on the New Jersey coast where pound nets are fished for shad, was selected as the southern tagging site. Staten Island, where the largest pound-net catches of shad are taken, was selected as the northern tagging site. Point Pleasant, N. J., located about midway between Beach Haven and Staten Island, was selected as the third tagging location.

Shad were brailed from the pound net and held in washtubs on the fantail of the pound boat. Individual shad were removed from the tub, placed in a tagging cradle, tagged, and released. Fish were tagged with Petersen disk tags, consisting of two red plastic disks fastened directly under the dorsal fin by means of a nickel pin. Observations at the time the fish were returned to the ocean indicated that the shad suffered no apparent ill effects from the handling or tagging and that mortality from the tagging operation was probably small.

Shad were tagged throughout the shad fishing season from March 28 through May 23, so that as near as possible the entire run was proportionally sampled. During this period a total of 2,959 shad were tagged: 943 at Beach Haven, 962 at Point Pleasant, and 1,054 off Staten Island.

After the tagged fish were released, the success of the tagging study was largely dependent upon return of tags by commercial fishermen. About 1 week prior to the fishing season, biologists interviewed all commercial shad fishermen who fished the Hudson and Connecticut Rivers and off the New Jersey and New York coasts, and explained the tagging program. During the fishing season

each commercial fisherman was contacted weekly to pick up tags they had recovered and to pay them the 50-cent reward for each tag returned.

Recoveries from areas outside of the present study area were dependent on return of the tags by mail. Fortunately, commercial fishermen in those areas were familiar with shad-tagging programs because of previous studies that have been conducted at various places along the coast. This undoubtedly helped in the return of tags, but it is probable that returns were not as good in the outside areas as in the areas canvassed. However, since returns from areas outside the Hudson and Connecticut Rivers were relatively few, any error caused by unrecovered tags would be minor and hence would not significantly affect the results obtained in this study.

A total of 1,183 tags was returned during the 1956 fishing season: 108 were returned by mail and 1,075 were collected by biologists in the field. In addition to the 1,183 tags actually returned, 15 were reported lost or misplaced. No correction was made for lost or misplaced tags since they were few in number and the location at which they were affixed could not be determined.

A number of types of fishing gear were instrumental in effecting the recovery of the tags. In the Hudson River, gill nets are used almost exclusively for catching shad. The nets are operated as stake gill nets south of Bear Mountain Bridge at Peekskill, N. Y., and as drift gill nets north of this area. Drift gill nets are the major gear fished in the Connecticut River; however, a few stake nets and haul seines are also fished. Pound nets accounted for the majority of recoveries outside the rivers. Of all tags returned, stake gill nets accounted for 702 (59.3 percent), drift gill nets 332 (28.1 percent), pound nets 122 (10.3 percent), sport fishermen 6 (0.5 percent), haul seines 3 (0.3 percent), and miscellaneous gears 18 (1.5 percent). Less than 1 percent of the tags were returned with insufficient data. These were included in the category of miscellaneous-gear recoveries.

Recaptures of tagged shad during 1956 began with the opening of the fishing season along the New Jersey coast, continued through the spawning migrations into the rivers, and ended in the latter part of September, several months after the spawned-out fish had returned to the sea. Fish tagged at the three tagging sites were recaptured along the Atlantic coast from Chesapeake Bay to the Gulf of St. Lawrence, with the majority being taken in the Hudson and Connecticut Rivers. Of the recaptures, 951 were made in the Hudson River, 91 in the Connecticut River, 13 in Delaware Bay, 12 in Chesapeake Bay and its tributaries, 5 in Canadian waters, 6 off the New England coast, 1 off the New Jersey coast, and 104 in the Sandy Hook, Raritan, and Lower New York Bay areas (table 2). In this paper the latter area will henceforth be termed the "New York Bay area."

During the tagging study, tagged fish were available to all New Jersey and New York coastal pound nets. Eleven tagged fish were recaptured by pound nets in the Beach Haven and Point Pleasant areas and these were subsequently released. Pound-net operators in the New York Bay area kept recaptured tagged fish and claimed the tag reward. During the 1956 season (table 2), 104 tagged shad were recaptured in the New York Bay area from all tagging locations. To determine the percentage of the New Jersey–New York pound-net catch native to the Hudson and Connecticut Rivers, the number of tagged shad from each tagging location recaptured in the New York Bay area was subtracted from the total tagged at each site. Therefore, the corrected number of shad tagged at each location free to enter

TABLE 2.—*Tag returns from shad tagged off the New Jersey-New York coasts during the spring of 1956*

Area of recovery	From tagging station at—						Total tags returned	
	Beach Haven, N. J.		Point Pleasant, N. J.		Staten Island, N. Y.			
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Hudson River	247	81.2	317	79.1	387	81.0	951	80.4
Connecticut River	32	10.5	48	12.0	11	2.3	91	7.7
New York Bay	9	3.0	21	5.2	74	15.5	104	8.8
Other areas	16	5.3	15	3.7	6	1.2	37	3.1
Total	304		401		478		1,183	

TABLE 3.—*Tag returns from shad tagged off the New Jersey-New York coasts, excluding New York Bay, in 1956*

Area of recovery	From tagging station at—						Total tags returned	
	Beach Haven, N. J.		Point Pleasant, N. J.		Staten Island, N. Y.			
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Hudson River	247	83.7	317	83.4	387	95.8	951	88.1
Connecticut River	32	10.8	48	12.6	11	2.7	91	8.4
Other areas	16	5.4	15	3.9	6	1.5	37	3.4
Total	295		380		404		1,079	

the Hudson and Connecticut Rivers was as follows: Beach Haven—934; Point Pleasant—941; and Staten Island—980, or a total of 2,855.

Table 3 shows the number and percentage of tags returned, excluding New York Bay recaptures, from shad tagged during the 1956 study. A total of 1,079 tags were returned from the 2,855 tagged fish, which represents a 37.8-percent return. Of the tags returned, 951 (88.1 percent) were returned from the Hudson River, 91 (8.4 percent) were returned from the Connecticut River, and 37 (3.4 percent) were returned from other areas.

During the 1957 shad season, 144 of the shad tagged on the New Jersey coast in 1956 were recovered by fishermen from North Carolina to Canada. Of these recoveries, 82.1 percent were from the Hudson River, 8.9 percent were from the Connecticut River, and 9.0 percent were from other areas. Thus, 1956 and 1957 recoveries compare favorably.

In previous limited tagging studies at Belford, N. J., in 1940, 1943, and 1945, E. H. Hollis [2] found that 85.2 percent of the tag recoveries were made in the Hudson River, 5.4 percent in the Connecticut River, and 9.4 percent in other areas. Similar tagging experiments in Sandy Hook Bay, N. J., in 1936, 1938, 1942, 1944, and 1946, indicated that 75.0 percent of the tagged fish were recaptured in the Hudson River, 6.6 percent in the Connecticut River, and 18.4 percent in other areas. (E. H. Hollis.[2]) The results obtained from these tagging experiments are similar to those obtained in our 1956 study.

The number of recoveries and areas of recovery of fish tagged at the three stations are shown in figures 1, 2, and 3. The migration pattern of the tagged fish was similar in that shad tagged at all three areas were recaptured from Chesapeake Bay to New England and Canada, with the majority of the recaptures being made in the Hudson River. All recaptures of tagged fish south of Rhode Island were made before or during spawning (before June 30). Eleven recoveries were made north of this area; four of these were taken in Canadian rivers before June 30, presumably before spawning. Seven spawned-out fish were recaptured in August and September (6 in United States waters and 1 in Canadian waters), during the 1956 fishing season. Three of these were recaptured by otter trawl in 45 to 60 fathoms of water in the Ipswich Bay area off the coast of Massachusetts, one off Nantucket Island, Mass., two off the coast of Maine, and one off the coast of Nova Scotia, Canada. It is probable that some of these recaptures were shad native to the Hudson or Connecticut Rivers, since shad native to rivers from Chesapeake Bay to Canada spend the summer and fall months in this general area (Talbot and Sykes, 1958).

To obtain a reliable estimate of the proportion of the New Jersey–New York pound-net shad catch that is native to the Hudson and Connecticut Rivers, the fishing rates in these rivers must be known. The calculated fishing rate in the Hudson River in 1956 was 44 percent and in the Connecticut River 24 percent.[3] Nine hundred fifty-one tagged shad were recaptured in the Hudson River where the fishing rate was 44 percent. By simple proportion it was estimated that 2,161 tagged shad entered the Hudson River. Similarly, 91 tagged shad were recaptured in the Connecticut River where the fishing rate was 24 percent; therefore, it was estimated that 379 tagged shad entered the Connecticut River. Thus, from these figures and the corrected total number of tagged shad it was calculated that the New Jersey–New York pound-net catch in 1956 was

[2] Unpublished data, U. S. Fishery Laboratory, Beaufort, N. C.

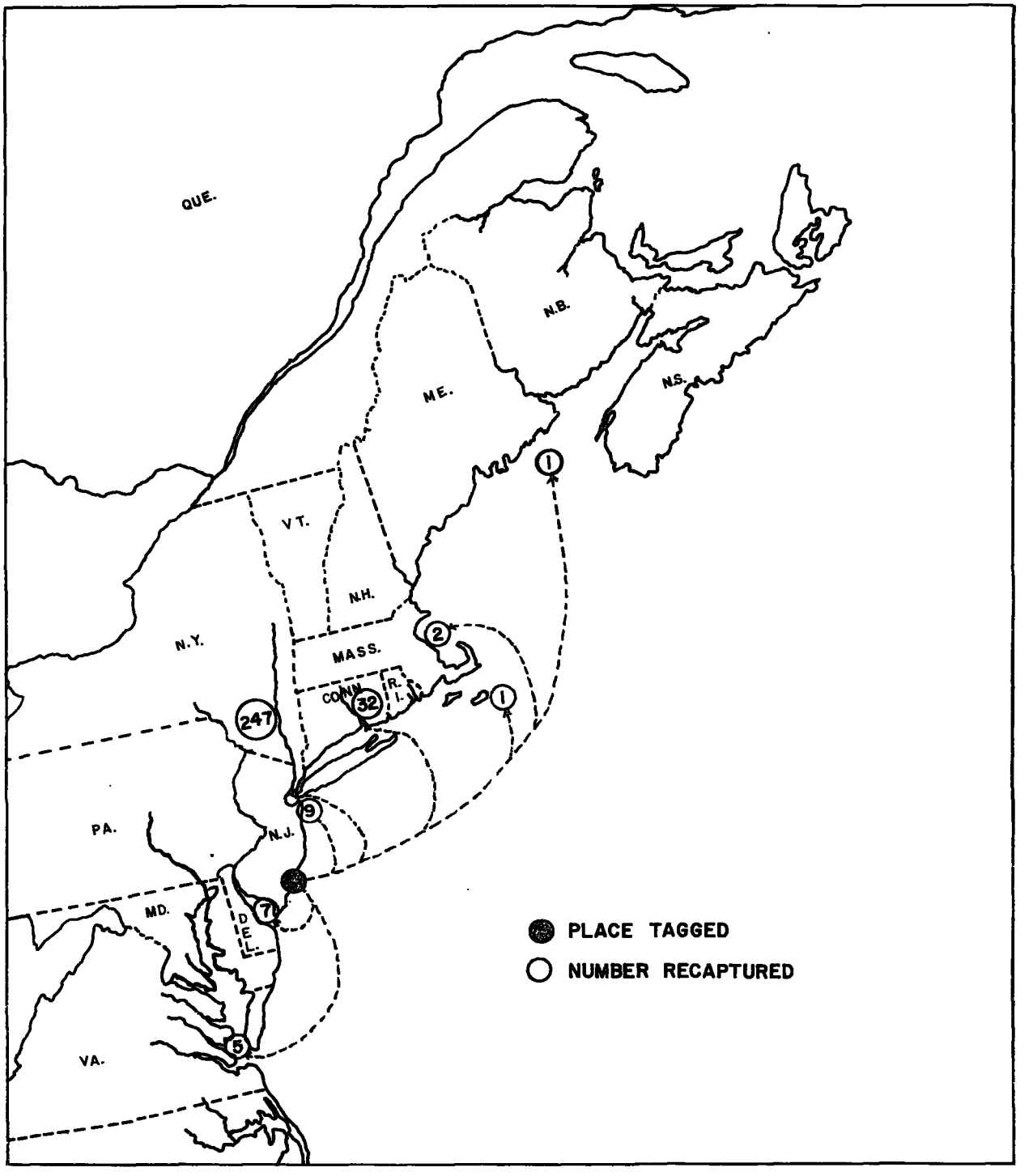

FIGURE 1.—Area and number of tag returns from shad tagged at Beach Haven, N. J., 1956.

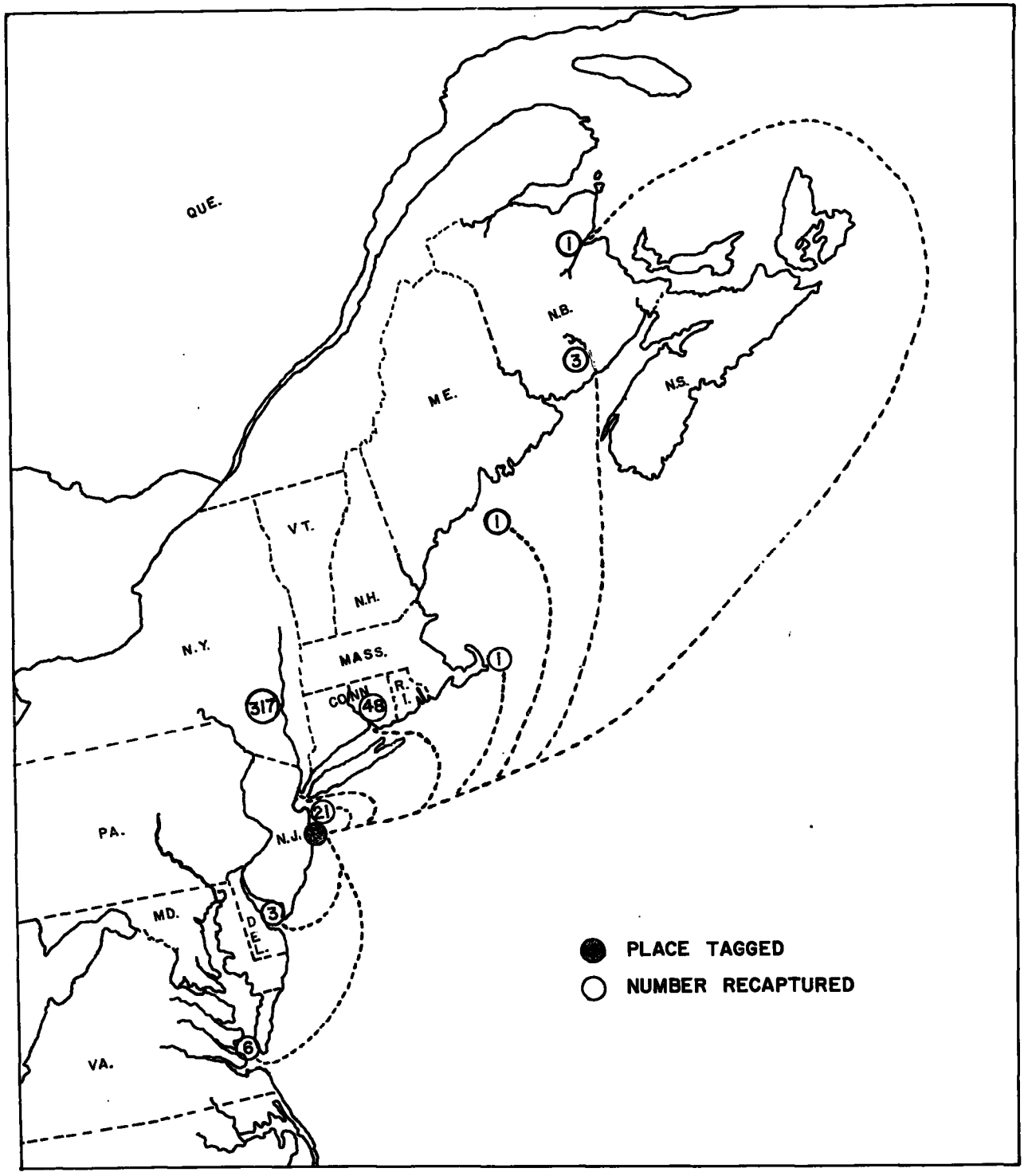

FIGURE 2.—Area and number of tag returns from shad tagged at Point Pleasant, N. J., 1956.

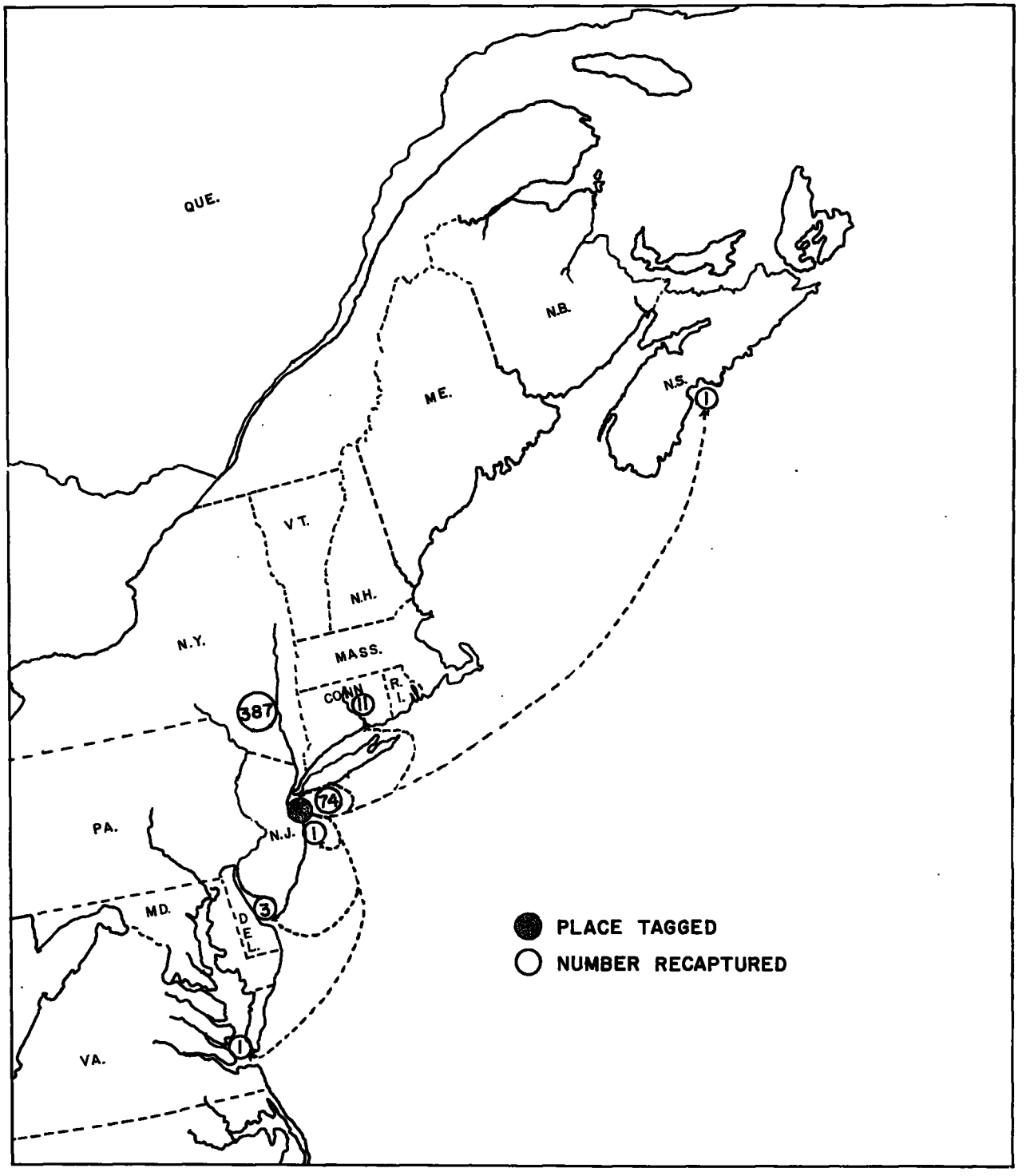

FIGURE 3.—Area and number of tag returns from shad tagged at Staten Island, N. Y., 1956.

composed of 76 percent Hudson River shad, 13 percent Connecticut River shad, and 11 percent shad from other areas.

The method outlined here assumes that the tagged fish are no more liable to capture than are the untagged. Previous studies in these rivers have shown that tagged shad are not significantly more vulnerable to capture than untagged shad, because of the size of the fish and the size of mesh fished. Analysis of the 1956 tagging results was not in disagreement with the earlier findings of other authors.

THE OCEAN POUND-NET FISHERY AND SHAD RUNS IN THE HUDSON AND CONNECTICUT RIVERS

The total populations of shad entering the Hudson and Connecticut Rivers as calculated from catch and effort data, and the predicted size of these populations based on escapements from the fishery in previous years, have been estimated for a number of years (Talbot 1954; Fredin 1954). These data are available for the Connecticut River from 1940 to 1956 [3] and for the Hudson River from 1921 to 1956,[3] and are shown in tables 4 and 5, together with the New Jersey–New York pound-net shad catch for most of these years. Also shown in the tables are the deviations between calculated and predicted shad runs in these rivers.

TABLE 4.—*Pound-net catch and calculated and predicted runs of shad, Connecticut River, 1940–56*

[In thousands of pounds; catch data from table 1. See text for source of Connecticut River data]

Year	New Jersey–New York catch	Population size [1]		
		Calculated	Predicted	Deviation [2]
1940	1,284	831	930	−99
1941		1,110	993	117
1942	2,864	1,008	1,113	−105
1943	1,765	1,068	1,029	39
1944	2,284	1,134	1,005	129
1945	2,008	927	1,059	−132
1946	796	1,098	960	138
1947	629	810	831	−21
1948	735	723	729	−6
1949	440	564	642	−78
1950	482	393	486	−93
1951	205	534	423	111
1952	844	747	465	282
1953	104	690	654	36
1954	252	573	657	−84
1955	400	519	669	−150
1956	351	669	702	−33

[1] Number of fish converted to pounds at ratio 1 fish=3.0 pounds.
[2] Calculated less predicted size of run.

[3] Data for years 1952 through 1956 are preliminary, U. S. Fishery Laboratory, Beaufort, N. C.

TABLE 5.—*Pound-net catch and calculated and predicted runs of shad, Hudson River, 1921–56*

[In thousands of pounds; catch data from table 1. See text for source of Hudson River data]

Year	New Jersey–New York catch	Population size		
		Calculated	Predicted	Deviation [1]
1921	43	349	73	276
1922		517	360	157
1923		446	505	−59
1924		334	524	−190
1925		440	305	135
1926	74	908	671	237
1927		884	1,380	−496
1928		634	1,067	−433
1929	21	500	858	−358
1930		442	1,252	−810
1931	69	1,006	974	32
1932	57	1,294	1,620	−326
1933	79	997	1,878	−881
1934		925	1,152	−227
1935	273	2,008	1,720	288
1936		3,796	3,292	504
1937	1,184	4,249	3,523	726
1938	701	3,253	3,578	−325
1939	590	4,437	2,996	1,441
1940	1,284	4,521	4,537	−16
1941		4,552	4,916	−364
1942	2,864	4,634	3,640	994
1943	1,765	4,484	4,522	−38
1944	2,284	5,473	4,533	940
1945	2,008	5,480	4,290	1,190
1946	796	4,167	5,664	−1,497
1947	629	2,588	3,230	−642
1948	735	3,225	2,509	716
1949	440	2,471	3,962	−1,221
1950	482	1,398	2,175	−777
1951	205	1,639	1,075	564
1952	844	2,321	2,435	−114
1953	104	2,200	3,048	−848
1954	252	2,752	2,671	81
1955	400	3,058	4,042	−984
1956	351	4,106	5,117	−1,011

[1] Calculated less predicted size of run.

Since a large proportion (76 percent) of the New Jersey–New York pound-net shad catch was composed of shad native to the Hudson River, a linear regression analysis was run between the calculated size of each year's Hudson River run and the shad catch in this area for the same years (table 5). The regression value obtained (r=0.81) was significant at the 1-percent level. Therefore, it can be inferred that the New Jersey–New York pound-net shad catch was dependent on the size of the Hudson River shad population. In other words, when the shad run bound for the Hudson River has been large the New Jersey–New York pound-net shad catch also has usually been large. Since a comparatively few Connecticut River shad were taken in this area (13 percent), fluctuations in the size of that population would not be expected to have any great influence on the New Jersey–New York pound-net shad landings.

The proportion of Hudson to Connecticut River shad taken by the ocean pound-net fishery in 1956 was 6 to 1 (76 percent Hudson River to 13 percent Connecticut). This was approximately the ratio

of the calculated size of the Hudson and Connecticut River shad populations in the same year (4,106,000 pounds to 669,000 pounds). Therefore, approximately the same percentage (6) of each population was taken by the ocean pound-net fishery in 1956.

The deviations that occur between calculated and predicted size of shad runs represent changes in the population of each river not accounted for by escapements (Fredin 1954). Both Talbot (1954) and Fredin indicated that catches of Hudson and Connecticut River shad made outside of the rivers may have an effect on the deviations between predicted and calculated population size. Since all but a small percentage of the New Jersey–New York pound-net shad catch is native to the Hudson and Connecticut Rivers, yearly fluctuations in these catches could possibly cause the deviations between calculated and predicted populations entering the two rivers.

To test this hypothesis, a linear regression analysis was calculated between the New Jersey–New York pound-net catch and these deviations in each river. For the Connecticut River (table 4) the relationship was nonsignificant ($r=-0.05$). For the Hudson River (table 5), a significant (5-percent level) but positive relation was found between these factors ($r=0.47$). This indicates that, in general, when the calculated Hudson River run is larger than the predicted run (deviation would have plus value) the New Jersey–New York pound-net shad catch is large. Likewise, when the calculated Hudson River run is less than the predicted run (deviation would have minus value) the New Jersey–New York pound-net shad catch is small. Therefore, the New Jersey–New York pound-net shad catch had no apparent effect on the deviations that occur between the calculated and predicted sizes of Hudson or Connecticut River shad runs.

In addition to the New York–New Jersey pound-net catches, large ocean catches of shad are made in the Gulf of Maine area by purse seiners working out of New England ports during the summer months. Some large catches of "scrap" fish were reported by the U. S. Fish and Wildlife Service (1956) to be 100-percent shad:

> Recent catches of large shad were reported by boats seining for menhaden. Two trips were landed that consisted of pure shad * * *. The two trips totaled about 120,000 pounds.

It was further reported that other landings at fish-meal plants consisted of a mixture of shad and herring. Undoubtedly, some of these fish were Hudson and Connecticut River shad, since after spawning adult shad native to rivers from Chesapeake Bay to Connecticut migrate northward and spend the summer and fall months in the Gulf of Maine (Talbot and Sykes, 1958). This extraneous fishing mortality may have an important influence on the deviations that occur between the calculated and the predicted sizes of Hudson and Connecticut River shad runs.

SUMMARY AND CONCLUSIONS

During the 1956 shad fishing season, 2,855 shad were tagged from pound nets located off the coasts of New Jersey and New York to determine the population composition or origin of the shad taken in these waters. Of the total number of fish tagged, 951 shad were recaptured in the Hudson River and 91 were recaptured in the Connecticut River. In 1956, the estimated fishing rate in the Hudson River was 44 percent and in the Connecticut River 24 percent. Based on the number of shad recaptured and the fishing rates in each river it was estimated that the New Jersey–New York pound-net shad catch in 1956 was composed of 76 percent Hudson River shad and 13 percent Connecticut River shad.

The total population of shad entering the Hudson and Connecticut Rivers calculated from catch and effort data and the predicted population size of shad entering the rivers based on escapements from the fishery in previous years have been computed for a number of years. A linear regression analysis calculated between the size of the Hudson River shad run and the New Jersey–New York pound-net shad catch indicates that the pound-net catch is dependent upon the size of the Hudson River shad population ($r=0.81$). Fluctuations in the size of the Connecticut River shad population would not be expected to have any great influence on the pound-net landings, since only 13 percent of the landings are composed of shad native to this river.

Since all but a small percentage of the New Jersey–New York pound-net shad catch is native

to the Hudson and Connecticut Rivers, yearly fluctuations in these catches could have some influence on the deviation that occur between calculated and predicted sizes of the runs entering each river. Linear regression analysis showed a significant but positive relation between the New Jersey–New York pound-net shad catch and the deviations in the Hudson River. In other words, when the calculated population size was larger than expected the pound-net shad catch was also high. When the calculated population size was smaller than expected, the pound-net catch was low. For the Connecticut River, the relationship was nonsignificant. Therefore, the New Jersey–New York pound-net shad catch has no apparent effect on the deviations that occur between the calculated and the predicted size of Hudson or Connecticut River shad runs.

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LARVAL DEVELOPMENT, GROWTH, AND SPAWNING OF STRIPED MULLET (*MUGIL CEPHALUS*) ALONG THE SOUTH ATLANTIC COAST OF THE UNITED STATES

By WILLIAM W. ANDERSON

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ABSTRACT

The larval and juvenile development of the striped mullet (*Mugil cephalus*) is described and illustrated from about 4 mm. to 116 mm. standard length.

Striped mullet appear to spawn along the south Atlantic coast of the United States from lower Florida to North Carolina over a broad area extending from about the 20-fathom line into the Gulf Stream. The data indicate that spawning occurs from October to February, but is confined largely to the period of November to January, with the peak in December.

Young striped mullet apparently remain at sea until they are from 18 to 28 mm. long (mostly 20 to 25 mm.), at which time they move in to the coast. In Georgia these young appear as early as November on the outer beaches but apparently do not go into the marshy estuarine waters until January.

Growth of young striped mullet in Georgia is estimated. They grow slowly during the colder winter months, but with the warming of the waters in spring growth speeds up. From about March to October the size increase is about 17 mm. a month. Mullet from the earliest spawning (October) reach a length of about 160 mm. standard length by the end of their first year. Growth of mullet as estimated by various workers along the south Atlantic and Gulf coasts of the United States is summarized.

Development of teeth on the tongues of young mullet and loss in the adult are described and illustrated.

LARVAL DEVELOPMENT, GROWTH, AND SPAWNING OF STRIPED MULLET (*MUGIL CEPHALUS*) ALONG THE SOUTH ATLANTIC COAST OF THE UNITED STATES

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BUREAU OF COMMERCIAL FISHERIES

The striped mullet (*Mugil cephalus* Linnaeus) is one of the most important food fishes of the Southern United States. It is of greatest importance in Florida, where about 28 to 30 million pounds are taken annually. Fisheries of considerable value exist in several other States—North Carolina, South Carolina, Alabama, and Mississippi. Fishing is done mainly with gill nets, trammel nets, beach seines, and stop nets.

The species has a very wide distribution. Hildebrand and Schroeder (1928, p. 196) give the habitat as, "Warm waters of both hemispheres; on the Atlantic coast of America from Cape Cod to Brazil."

That the early development of this important and common shore fish in the Southern United States has remained a mystery for many years is difficult to believe, but is true. Jacot (1920, p. 222), working with the species in North Carolina, stated, "Thus nothing is known of the spawning grounds of this species and therefore of its eggs or larvae, the earliest stage known being the already well developed young * * *." Jacot's smallest specimens were about 23 mm. total length. Higgins (1928, p. 625), who worked largely in North Carolina, said, "The larval stages of development of the mullet are unknown, but juvenile fish appear in the sounds about Beaufort in early February, when they are from 18 to 25 millimeters in length." Kilby (1949, p. 7), working with striped mullet in Florida, said, "In view of its commercial value and the universally admitted desirability of its conservation and perpetuation as a natural resource of the state, it might be assumed that the life history of the mullet is well known. Such an assumption, however, would be in error, because little has been published on the young, and specimens less than 16 mm. in standard length are apparently unknown." Broadhead (1953, p. 9), working with *M. cephalus* in northwest Florida, stated, "Nothing is known of the egg and larval development and the young fish are first encountered in shallow water, at which time they are about one inch long."

During a biological, chemical, and oceanographic survey of waters off the south Atlantic coast of the United States with the Service's MV. *Theodore N. Gill*, larval specimens of striped mullet, ranging in standard length from about 4 mm. to 30 mm., were obtained in the plankton and dip-net collections—providing a basis for contributing to a better understanding of the life history of one more economically important fish of the region.

This paper describes and illustrates the early larval development of striped mullet; gives occurrence of larval stages in the open ocean; discusses movement of the larvae from open ocean to inshore areas and their development and growth to juvenile size in the inshore areas; and discusses period and location of spawning.

MATERIAL

General information concerning striped mullet larvae taken in plankton tows and by dip net during cruises of the MV. *Theodore N. Gill* is presented in tables 1 and 2; locations of capture are illustrated in figure 1. (Cruise 1, February 10 to March 10, 1953; cruise 2, April 16 to May 15, 1953; cruise 3, July 15 to August 16, 1953; cruise 4, October 1 to November 14, 1953; cruise 5, January 20 to February 25, 1954; cruise 6, April 14 to April 29, 1954; cruise 7, June 9 to July 13, 1954; cruise 8, August 27 to October 1, 1954; and cruise 9, November 3 to December 12, 1954.)

Occurrence of young striped mullet in the seine collections of two areas in Georgia (open ocean beach and salt marsh) with respect to date, approximate abundance, and size range is presented in tables 3 and 4.

NOTE.—Approved for publication, October 25, 1957. Fishery Bulletin 144.

TABLE 1.—*Larvae of the striped mullet* (Mugil cephalus) *taken in plankton tows on* Theodore N. Gill *cruises 5 and 9, in 1954*

[No larvae were taken on the other 7 cruises]

Station number	Date	Position		Number of larvae (standard length)			
		North latitude	West longitude	3–5 mm.	5.1–7 mm.	7.1–10 mm.	10.1–20 mm.
Cruise 5:							
2–3	Jan. 30	27°02′	79°52′	1	1		
3	do	27°00′	80°03′	2			
3–4	do	27°10′	80°04′	1			
4	do	27°20′	80°03′	14	2		
10	Feb. 1	28°19′	80°12′		2		
14	Feb. 2	29°00′	80°10′		3		
50–49	Feb. 15	32°00′	78°16′	1			
63	Feb. 21	33°15′	76°22′				1
71	Feb. 22	34°03′	76°15′			1	
Cruise 9:							
51	Dec. 4	32°20′	77°35′	1			
52	do	32°35′	77°47′	2			
59	Dec. 5	33°22′	77°37′	1			
60	do	33°08′	77°20′	1			
70	Dec. 8	34°18′	76°31′	1			
71	do	34°03′	76°15′		1		

TABLE 2.—*Larvae of the striped mullet* (Mugil cephalus) *taken in dip nets on* Theodore N. Gill *cruises 1 and 5, 1953–54*

[No larvae were taken on the other 7 cruises]

Station number	Date	Position		Number of larvae (standard length)			
		North latitude	West longitude	10.1–15 mm.	15.1–20 mm.	20.1–25 mm.	25.1–31 mm.
Cruise 1:	*1953*						
Cape Canaveral	Feb. 19	28°26′	80°32′			1	
35	Feb. 26	31°20′	80°52′			1	
73	Mar. 6	34°09′	75°22′			5	3
Cruise 5:	*1954*						
Standard Station	Jan. 24	26°20′	76°44′			1	1
Office of Naval Research	Jan. 27	25°30′	76°30′				1
Do	Jan. 28	25°30′	76°30′	1			
4	Jan. 30	27°20′	80°03′			1	
5	do	27°40′	80°03′			1	
6	Jan. 31	27°40′	79°41′			2	
15	Feb. 2	28°59′	79°48′			7	2
20	Feb. 4	29°39′	80°45′			4	
37	Feb. 10	31°38′	80°17′		1	21	
38	do	31°36′	79°51′		1	57	
49	Feb. 15	32°11′	78°26′	1			
75	Feb. 22	34°39′	75°53′			6	
76	do	34°53′	76°09′		3		2

TABLE 3.—*Occurrence of young striped mullet* (Mugil cephalus) *in seine collections on St. Simons Beach, Ga., by date, approximate abundance, and size range*

[Size—standard length]

Date	Number	Approximate size range (mm.)	Date	Number	Approximate size range (mm.)
Jan. 4, 1956	34	22 to 26.	June 11, 1956	2	46 and 62.
Jan. 15, 1954	Many	20 to 25.	June 22, 1955	1	108.
Jan. 16, 1956	14	20 to 26.	July 21, 1953	1	107.
	4	96 to 195.	July 24, 1956	7	79 to 116.
Jan. 28, 1954	Many	19 to 24.	Aug. 5, 1955	2	104 and 127.
Jan. 30, 1956	Many	18 to 27.	Aug. 8, 1956	1	131.
	3	111 to 154.	Aug. 24, 1956	2	79 and 91.
Feb. 12, 1954	Many	20 to 28.	Sept. 9, 1956	2	75 and 85.
Feb. 15, 1956	Many	18 to 28.	Sept. 27, 1956	1	165.
	1	150.	Oct. 5, 1955	5	151 to 157.
Feb. 29, 1956	Many	18 to 29.	Nov. 3, 1955	1	160.
Mar. 11, 1954	10	21 to 22.	Nov. 16, 1955	1	150.
Mar. 11, 1955	17	20 to 25.	Nov. 19, 1954	4	18 to 19.
Mar. 25, 1955	1	20.	Nov. 20, 1956	4	118 to 143.
Mar. 29, 1954	9	19 to 24.	Dec. 2, 1955	Many	114 to 171.
Mar. 29, 1956	43	19 to 35.	Dec. 8, 1953	5	20 to 21.
Apr. 13, 1956	Many	19 to 40.	Dec. 18, 1956	17	100 to 218.
May 14, 1956	1	164.	Dec. 19, 1955	33	19 to 22.
May 28, 1956	1	53.		2	102 and 111.

Mrs. Fanny Lee Phillips kindly loaned me a collection of small striped mullet she obtained at Miami, Fla.: Crandon Park, January 21, 1957, 7 specimens about 8 to 12 mm. standard length; Crandon Beach, January 22, 1957, 5 specimens about 8 to 11 mm.; Crandon Park Beach, January 27, 1957, 5 specimens about 12 to 15 mm.; and Crandon Park Beach, January 28, 1957, 4 specimens about 14 to 18 mm.

METHODS

The manner of conducting plankton tows, dip netting, and all other procedures used aboard the MV. *Theodore N. Gill* are discussed in Anderson, Gehringer, and Cohen (1956).

Seine collections in Georgia on the open ocean beach on St. Simons Island and in the marshy

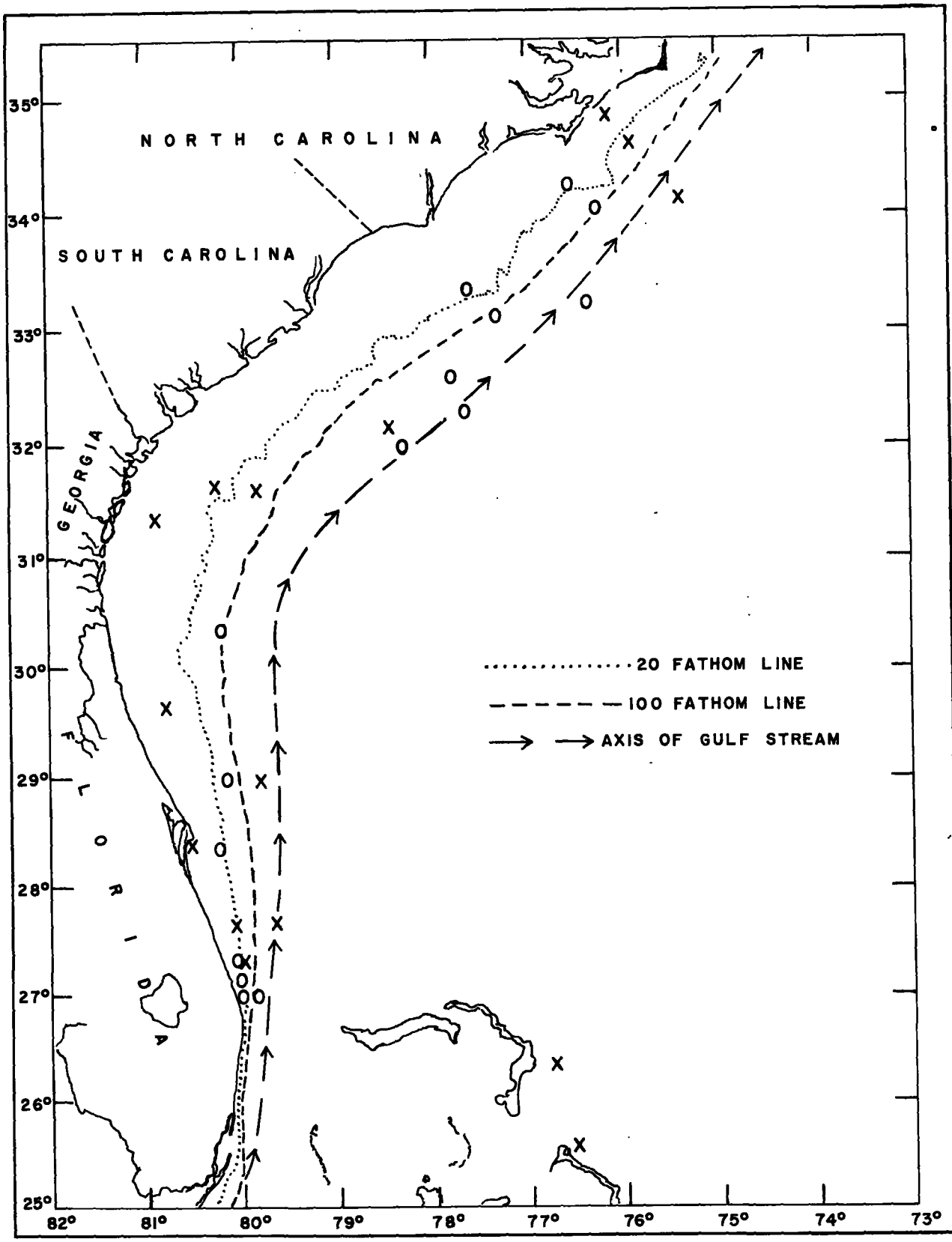

FIGURE 1.—Locations of capture of striped mullet larvae in plankton tows (circles), and by dip nets (X). (See tables 1 and 2 for occurrence data.)

TABLE 4.—*Occurrence of young striped mullet* (Mugil cephalus) *in seine collections in Sapelo Marsh, Ga., by date, approximate abundance, and size range*

[Size—standard length]

Date	Number	Approximate size range (mm.)	Date	Number	Approximate size range (mm.)
Jan. 4, 1956	16	22 to 28.	Apr. 27, 1956	Many	21 to 43.
Jan. 15, 1954	Many	19 to 29.		1	154.
Jan. 16, 1956	1	22.	May 4, 1954	1	56.
Jan. 28, 1954	Many	20 to 28.	May 6, 1953	Many	37 to 62.
Jan. 30, 1956	Many	19 to 23.	May 18, 1954	7	58 to 72.
Feb. 12, 1954	Many	19 to 29.	May 20, 1953	3	50 to 64.
Feb 15, 1956	Many	22 to 28.	May 24, 1955	15	39 to 62.
	2	128 and 141.	May 28, 1956	47	30 to 53.
Feb. 29, 1956	12	20 to 25.	June 9, 1955	1	48.
Mar. 11, 1954	Many	24 to 37.	June 11, 1956	29	39 to 54.
Mar. 11, 1955	Many	24 to 34.	June 18, 1953	1	63.
Mar. 15, 1956	Many	22 to 32.	June 26, 1956	10	35 to 54.
	3	92 to 118.	July 8, 1955	1	60.
Mar. 24, 1953	Many	24 to 40.	July 10, 1956	7	43 to 65.
Mar. 25, 1955	Many	24 to 34.	July 24, 1956	13	47 to 61.
Mar. 29, 1954	Many	22 to 40.	Aug. 8, 1956	2	59 and 69.
Mar. 29, 1956	Many	19 to 34.	Sept. 19, 1955	2	60 and 80.
Apr. 8, 1955	Many	20 to 40.	Oct. 14, 1955	1	97.
Apr. 13, 1956	Many	22 to 38.	Oct. 23, 1956	2	80 and 91.
Apr. 16, 1954	Many	20 to 52.	Nov. 3, 1955	2	114 and 143.
	3	118 to 130.	Nov. 16, 1955	1	125.
Apr. 22, 1953	Many	26 to 56.	Dec. 2, 1955	1	145.
Apr. 25, 1955	Many	30 to 50.			

estuarine area behind Sapelo Island were maintained on a biweekly basis from 1953 to 1956.

Measurements of larvae up to about 30 mm. standard length were made with a stereoscopic microscope and a micrometer eyepiece; larger specimens were measured with calipers.

Descriptions are based on preserved material unless stated otherwise.

In discussions of body proportions, only standard lengths (in small specimens from the tip of the snout to tip of the urostyle) were used; in other discussions, the larvae up to a total length of about 7 mm. are referred to in total lengths (in small specimens from tip of snout to tip of finfold or caudal fin), and above 7 mm. in standard length.

The curves portraying rates of growth of body parts and changes in certain body proportions were constructed from original measurements.

The method of presenting larval development is the same as that used for silver mullet, *Mugil curema* Cuvier and Valenciennes (Anderson 1957a). This generally follows Ahlstrom and Ball (1954) in discussing sequences of fin formation, body proportions, and pigmentation.

OCCURRENCE OF LARVAL AND JUVENILE FORMS

All available data indicate that most young striped mullet remain at sea (over a broad area from North Carolina to southern Florida) until they are from about 18 to 28 mm. long (but largely 20 to 25 mm.), at which time they move into the coast. They have apparently all moved inshore by early spring, as none were dip netted after early March (table 2).

In Georgia, these young appear on the outer beaches as early as November (earliest date recorded was November 19, table 3), but apparently do not go into the marshy estuarine waters until January. They are abundant along the beaches and in the marshy areas during January, February, March, and April; are apparently absent from the outer beaches during May and June, but abundant in the marsh areas during these months, indicating the population of young to be largely in the estuarine areas by May (tables 3 and 4).

During the summer and fall months these young of less than a year of age appear to scatter out so that they are never taken in abundance.

DEVELOPMENT FROM LARVAL TO JUVENILE STAGES

The smallest larva available was 4.0 mm. total length (3.9 mm. standard length). A developmental series from this larval size to a juvenile size of about 116 mm. is figured and described.

DEVELOPMENT OF FINS

Caudal

When fully developed, the caudal fin has 14 principal rays of which 12 are branched. There are usually about 15 secondary rays of which 7 are dorsal and 8 ventral.

At 4.0 mm. total length (fig. 2) the caudal shows evidence of development by a deep constriction of the finfold and a thickening ventral to the urostyle with initial development of about 7 rays. By 5.4 mm. (fig. 3) the fin has rounded, increased in size, and there is a distinct caudal peduncle, although the finfold is still evident; the urostyle has flexed upward and the 14 principal rays, plus

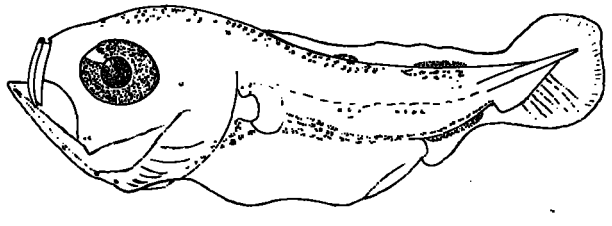

FIGURE 2.—Larva, 4.0 mm. total length.

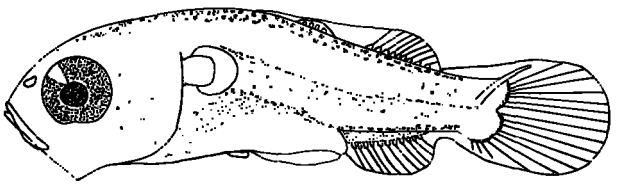

FIGURE 3.—Larva, 5.4 mm. total length.

about 3 ventral secondary rays, are visible. At about 6.7 mm. (fig. 4) some finfold remains, the fin has further increased in size, the caudal peduncle has changed form, the urostyle has reached its maximum flexion, and two dorsal secondary rays have developed. By 6.2 mm. standard length (7.9 mm. total length) the fin has lost the finfold and has about 4 each of dorsal and ventral secondary rays (fig. 5). A full complement of rays, 14 principal and 15 secondary, is present on the 9.7-mm. standard length specimen (fig. 6). By 12.1 mm. (fig. 7) forking of the fin has begun and the middle six of the principal rays are branched. Twelve rays are branched by 19.8 mm. (fig. 8) and the fin has reached final shape by 116 mm. (figs. 9 to 11). Only main forking of the 12 branched principal rays is shown in figures 10 and 11.

The caudal skeleton of a 25-mm. specimen is illustrated in figure 12. It is almost identical to the caudal structure given for *M. curema* by Hollister (1937, pp. 271–274).

Dorsals

A normal complement of rays consists of 4 spines in the first dorsal, and 1 spine and 8 soft-rays in the second dorsal.

Development of the dorsal fins is evident at 4.0 mm. total length by a thickening at the position of the bases (fig. 2), although the ray bases cannot be distinguished; the dorsal finfold is prominent and continuous with the caudal finfold. By 5.4 mm. (fig. 3) the 4 ray bases of the first dorsal are evident, the ray bases and 9 rays of the second dorsal (full complement) are well developed, and the finfold has become reduced and changed in shape. At 6.7 mm. (fig. 4) the 4 spines of the first dorsal are well developed and the rays of the second dorsal have increased in length; the finfold is still visible. The finfold has disappeared by 6.2 mm. standard length (7.9 mm. total length), and both spines and rays have increased in length (fig. 5). Branching has occurred in the last ray of the second dorsal by 9.7 mm. (fig. 6), in the last 2 rays at 12.1 mm. (fig. 7), in the last 7 rays at 19.8 mm., and barely in the first soft-ray at 26.9 mm. Development of

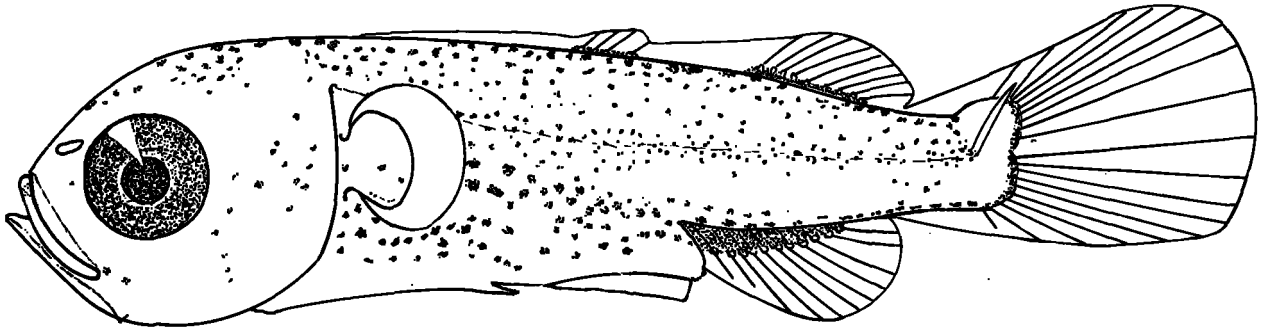

FIGURE 4.—Larva, 6.7 mm. total length.

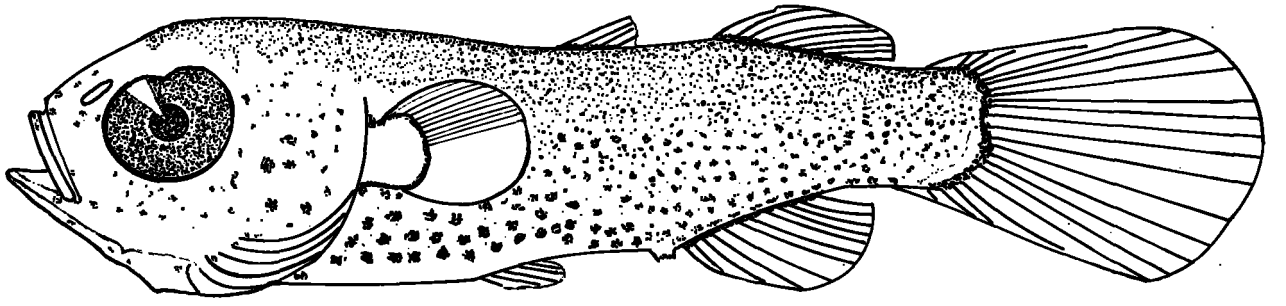

FIGURE 5.—Larva, 6.2 mm. standard length (7.9 mm. total length).

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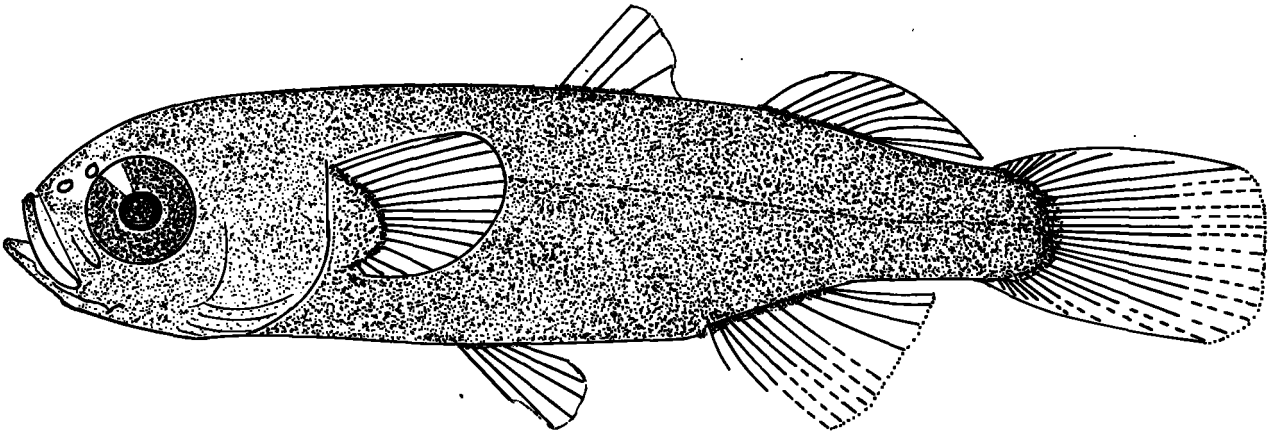

FIGURE 6.—Larva, 9.7 mm. standard length.

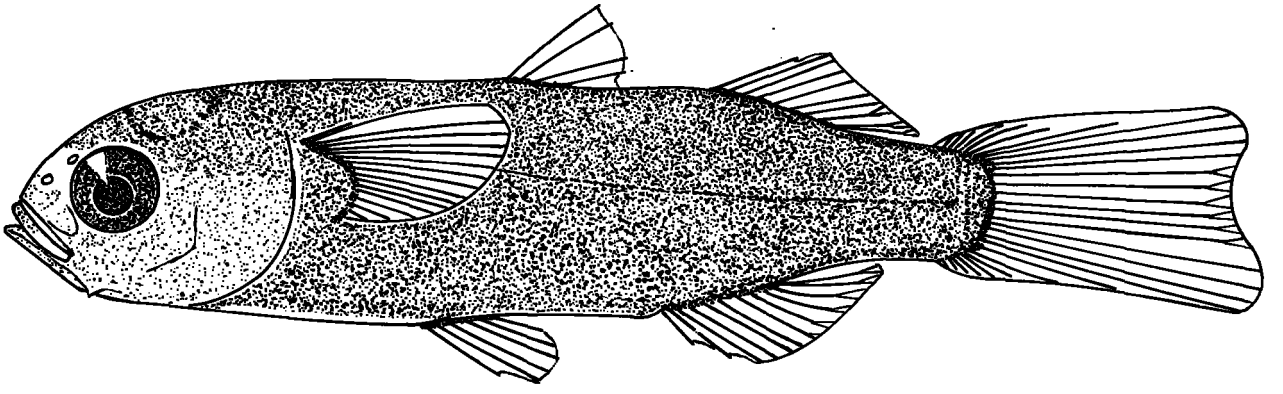

FIGURE 7.—Larva, 12.1 mm. standard length.

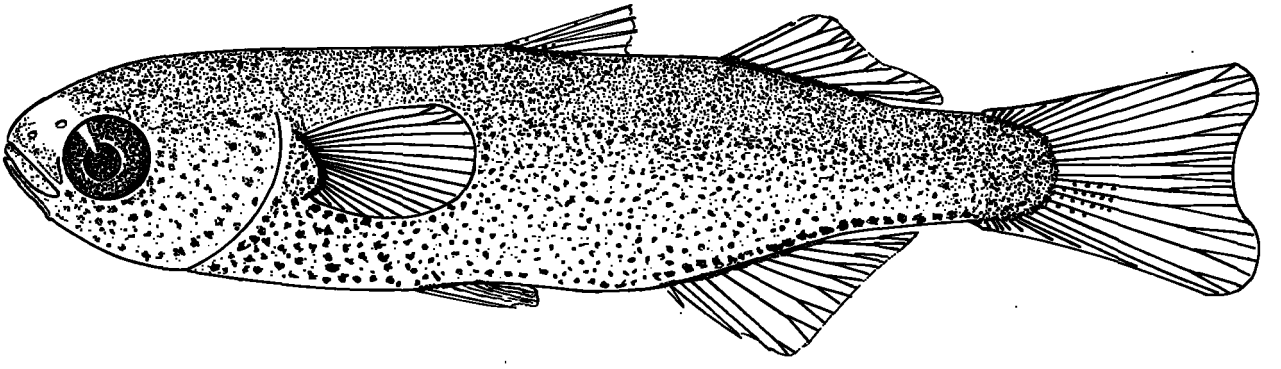

FIGURE 8.—Larva, 19.8 mm. standard length.

the dorsal fins to final shape is illustrated in figs. 8 to 11.

Anal

Juvenile and adult striped mullet have 3 spines and 8 branched soft-rays in the anal fin. Larval striped mullet have 2 spines and 9 soft-rays, the third spine forming from the first soft-ray when the young are between about 35 and 45 mm. standard length. I class the specimens as juveniles when this third anal ray has fused into a spine.

The developing anal base is visible at 4.0 mm. total length (fig. 2), although no ray bases have formed. By 5.4 mm. (fig. 3) the full complement of anal rays (11) has developed. Branching has occurred in the last ray at 6.2 mm. standard length (7.9 mm. total length), in the last 5 rays at 12.1

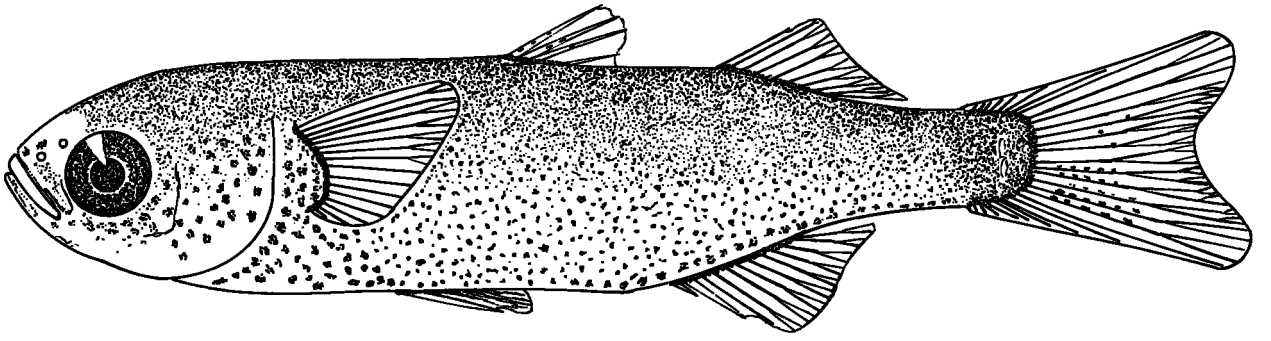

FIGURE 9.—Larva, 26.9 mm. standard length.

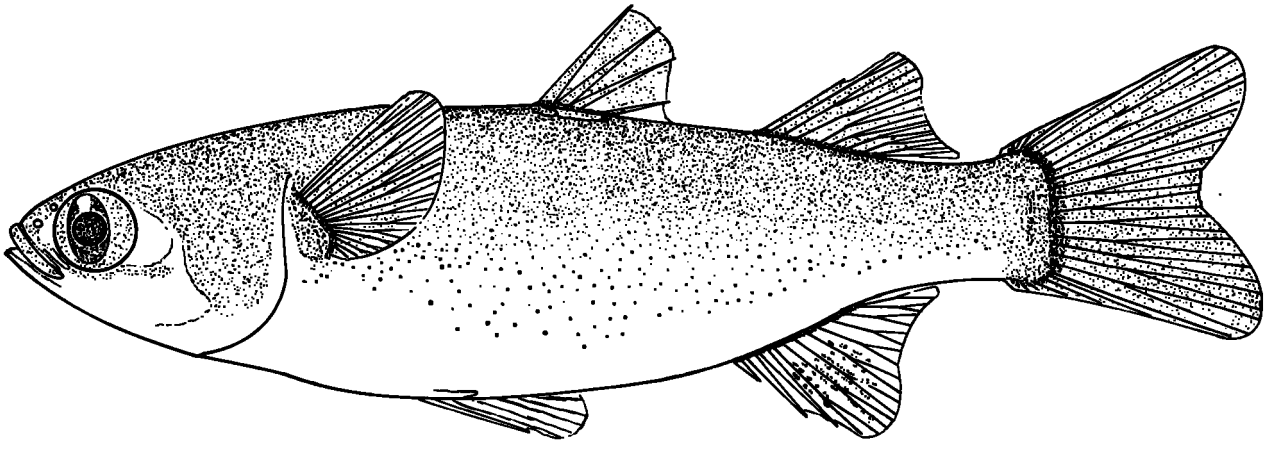

FIGURE 10.—Juvenile, 55 mm. standard length.

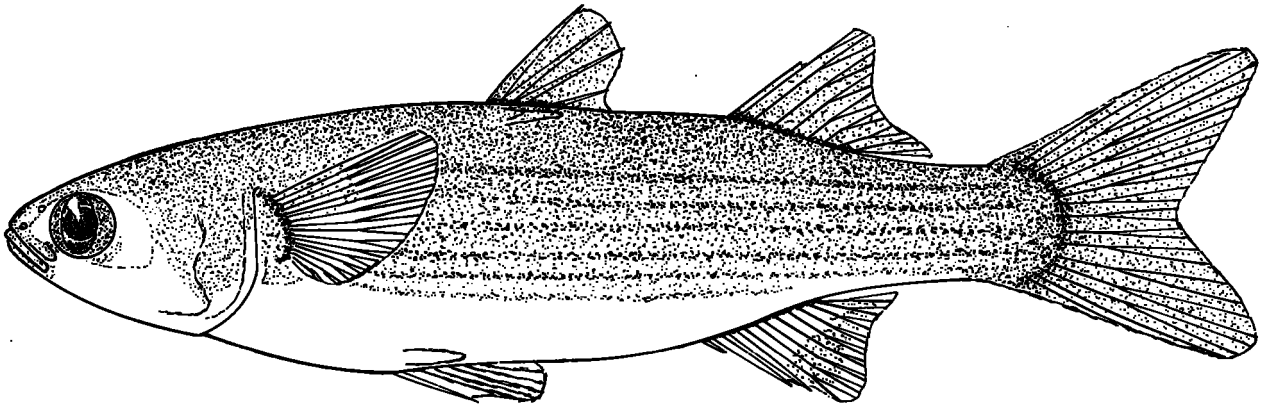

FIGURE 11.—Juvenile, 116 mm. standard length.

mm., and in the last 8 rays by 19.8 mm. (figs. 5 to 8). The finfold is lost between 6.7 and 7.9 mm. total length (figs. 4 to 5). Final fin shape is reached in juveniles between 55 mm. and 116 mm. (figs. 10 and 11).

Pectorals

The pectoral fin is evident at 4.0 mm. total length as a fleshy, rayless structure. No rays are discernible at 6.7 mm. total length but at 6.2 mm. standard length (7.9 mm. total length) 9 or 10 rays have developed in the upper part of the fin (figs. 4 and 5). The full complement of rays (16 or 17—rarely 15 or 18) is present in the 9.7-mm. specimen (fig. 6). Branching of the rays and development of this fin to final shape are demonstrated in figures 8 to 11.

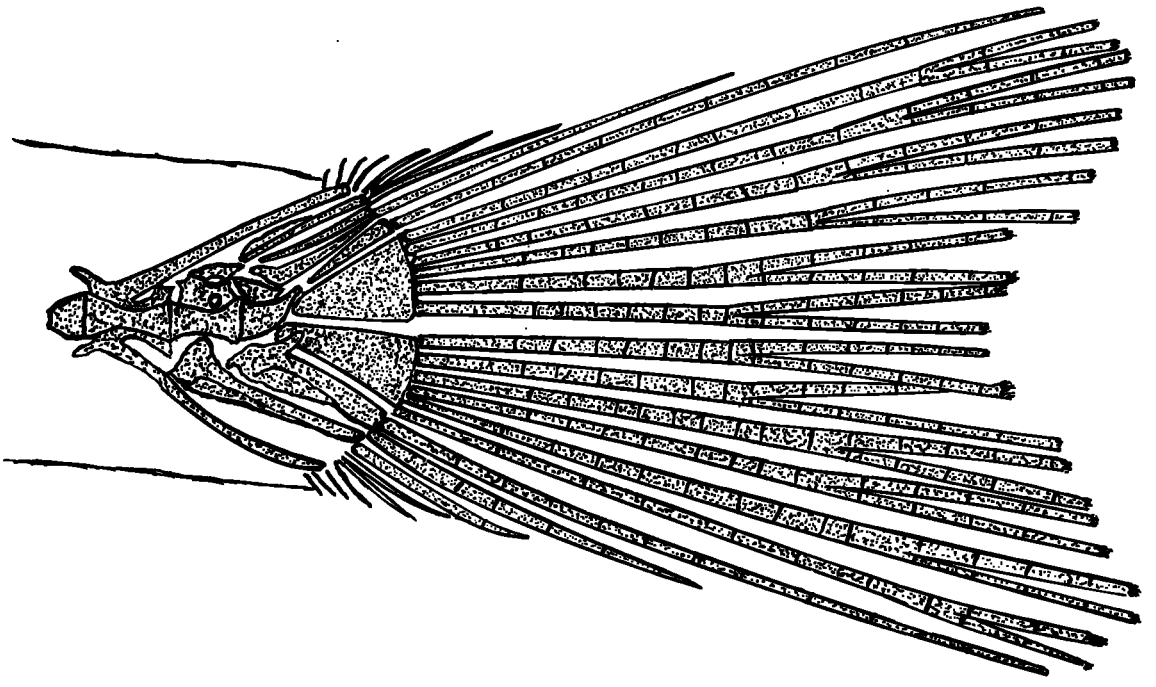

FIGURE 12.—Caudal skeleton of a 25-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

Ventrals

Ventral-fin buds are not present at 4.0 mm. total length but have formed by 5.4 mm. (figs. 2 and 3). Rays are present at 6.2 mm. standard length (7.9 mm. total length) and the full complement of 6 rays is present at 9.7 mm. (figs. 5 and 6).

PIGMENTATION

At about 4.0 mm. total length (fig. 2) pigment spots occur dorsally from the head through the position of the second dorsal fin, on the ventral aspect of the body from the anus to the developing caudal peduncle and along the dorsal surface of the body cavity from the pectoral fin to the anus, scattered along the midline of the body, and scattered sparsely on the sides of the head.

In the sea-stage larvae, from about 5 to 27 mm., development of pigment on the body and head is a process of spreading and intensifying as illustrated in figures 3 to 9. One of the striking characteristics is the large, less-numerous melanophores on the ventral aspect of the body as compared with the smaller, more numerous ones of the dorsal aspect. In some specimens, as in figures 6 and 7, the more typical pigmentation described gives way to pigmentation so dense as to make the specimens almost black.

In juveniles of about 55 mm. (fig. 10) the larger melanophores have disappeared and the fish have a peppered appearance with numerous small pigment spots on the dorsal aspect which thin rapidly toward the belly—pigment is absent on the lower sides of the head and body. Between this size and about 116 mm. the typical "striped" pigmentation develops (fig. 11).

At 12.1 mm. (fig. 7) there is no pigmentation in any of the fins, but at 19.8 and 26.9 mm. there are a few pigment spots in the first dorsal fin and a patch on the caudal fin (figs. 8 and 9). By 55 mm.—and remaining essentially the same at 116 mm.—pigment has developed in the second dorsal, anal, and pectoral fins, and has intensified as illustrated in figures 10 and 11.

Young striped mullet go through what has been termed a "silvery" stage. Kilby's (1949, p. 15) description is better than most accounts in the literature:

> Living individuals are of a brilliant silver ventrally and laterally and show no pattern on the sides. Dorsolaterally the silver becomes progressively duller until the color reaches a dusky tan on the dorsal surfaces of the head and body. All surfaces are irridescent and show flashes of pale, whitish blue as the light strikes the fish from different angles.

His smallest specimens were 16 mm. standard length. He also states that the silvery coloration fades rapidly when the specimens are preserved in formalin and becomes dull and dusky within a few days. Jacot (1920, p. 205) found this "silvery" stage in specimens 23 mm. (his smallest) to about 32 mm. total length, but found it difficult to distinguish those from 30 to 35 mm. as silvery or dusky, because the two colors merged at this size.

BODY PROPORTIONS

The relations of distances from snout to insertions of the first dorsal fin, second dorsal fin, and anal fin, to standard length show less variation than the other characters studied. There is an initial rapid rate of increase up to about 6 mm., a slowing down between about 6 mm. and 25 to 30 mm., a slight upward shift in the regression lines at about 25 to 30 mm., and then rather uniform development to about 200 mm. These relationships are illustrated in figures 13 and 14.

The relations of head length, eye diameter, and body depth at pectoral to standard length are illustrated in figures 14 and 15. The same general pattern of development occurred as in relations of distances from snout to insertions of fins to standard length—an initial rapid rate of increase to about 6 mm., a slowing down between 6 mm. and 25 to 30 mm., an upward shift in the regression lines at about 25 to 30 mm. (30 to 40 mm. for eye diameter), followed by a rather uniform rate of development to about 200 mm.—but the variations were greater. I found a similar pattern of development in the silver mullet, *M. curema* (Anderson 1957a).

MISCELLANEOUS STRUCTURES

Scales

These structures begin to develop when the larvae are between 8 and 10 mm. standard length, and are well developed and evident over the body and head in specimens 12 to 14 mm. Jacot (1920) gave a detailed account of scale characters and development in young from about 23 mm. total length (about 19 mm. standard length) up to adults.

Preorbital

The preorbital bone becomes evident in specimens between 8 and 10 mm. standard length, but there are no serrations at this stage—serrations become evident in specimens between 15 and 19 mm. I found a range of from 7 to 13 serrations on the preorbital bones of larvae between about 19 and 30 mm. Anderson (1957b) illustrates the preorbital, maxillary, and premaxillary bones of a 30-mm. specimen of *M. cephalus* in comparison with those of *M. curema* and *Agonostomus monticola* (Bancroft). Jacot (1920, p. 205) said of *M. cephalus*—

> The *preorbital* in the juvenile stage has some 10 or 12 points, teeth or serrations, of fair size. As the fish grows these points become more and more numerous, less slender and less distinct. In older fish they become blunt and stocky until in a large individual (502 mm.) there were 53 teeth on the margin, crowded so as to place about 4 to a millimeter.

Teeth

The best description of adult teeth characters for the genus *Mugil* is given by Schultz (1946, p. 389)—

> the teeth in the lower lip are setiform or ciliform, partly embedded or conspicuous; teeth in upper lip similar. The outer row of teeth in both lips is usually more prominent, with simple tips, and if inner rows occur these are either bifid or trifid, at least on adults (apparently the teeth in certain species of this genus become bifid or even trifid in large adults); * * *

He also stated—

> In this genus I find that in small specimens of certain species the teeth have simple tips, but later the inner teeth have bifid tips and in the largest adults some possess trifid tips. The teeth of the outer row usually have simple tips, but in some large specimens these are bifid too.

I found no evidence of developing teeth in a series of striped mullet larvae ranging between 12 and 15 mm. In a 17.5-mm. specimen, I found a single row of 8 to 10 small, simple-tipped teeth barely protruding from each half of the upper lip—none in the lower lip. In cleared and stained specimens of about 19.5 mm., I found from 15 to 20 simple-tipped teeth in a single row in each half of the upper lip—none in the lower lip. A cleared and stained 25-mm. specimen had about 23 to 24 simple-tipped teeth in a single row in each half of the upper lip (these teeth were beginning to curve inward at the tips), and a single row of about 15 simple-tipped teeth in each half of the lower lip.

Cleared and stained mouthparts of a 52-mm. specimen revealed the upper lip had a double row of teeth—the outer row having much larger teeth, which curved inward at the tips much in resemblance of a leaf rake. There were about 42 to 44 simple-tipped teeth to each side of the lip in the

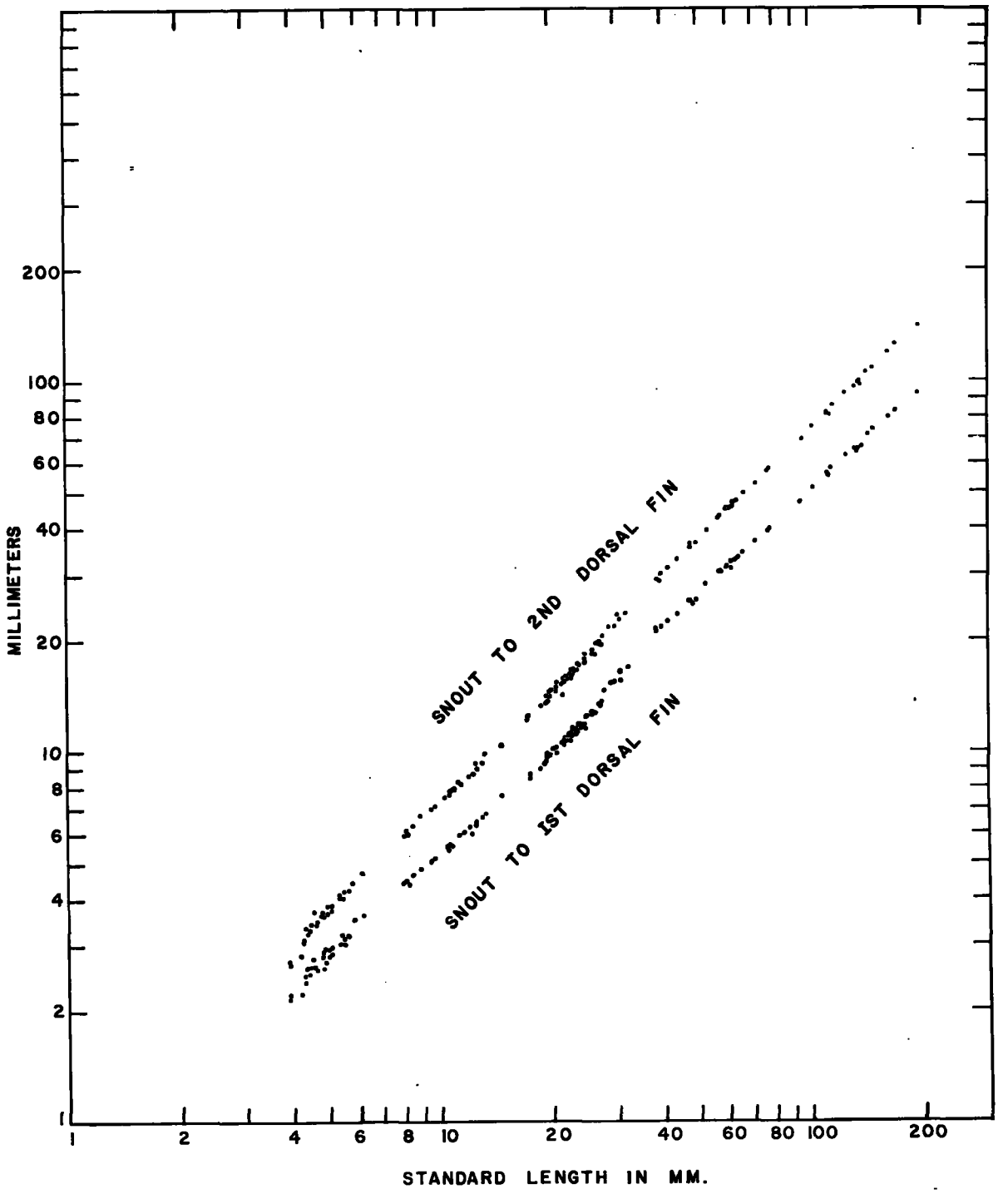

FIGURE 13.—Relation of the distances from snout to insertions of first and second dorsal fins to standard length. (Specimens smaller than 7 mm. were from plankton tows in open ocean; some specimens about 8 to 18/19 mm. were taken near Miami, Fla. (see Material, p. 502), and some were dip netted in open ocean; specimens 15 to 28 mm. were dip netted in open ocean; and those 29 to about 200 mm. were seined from marsh and beach areas in Georgia.)

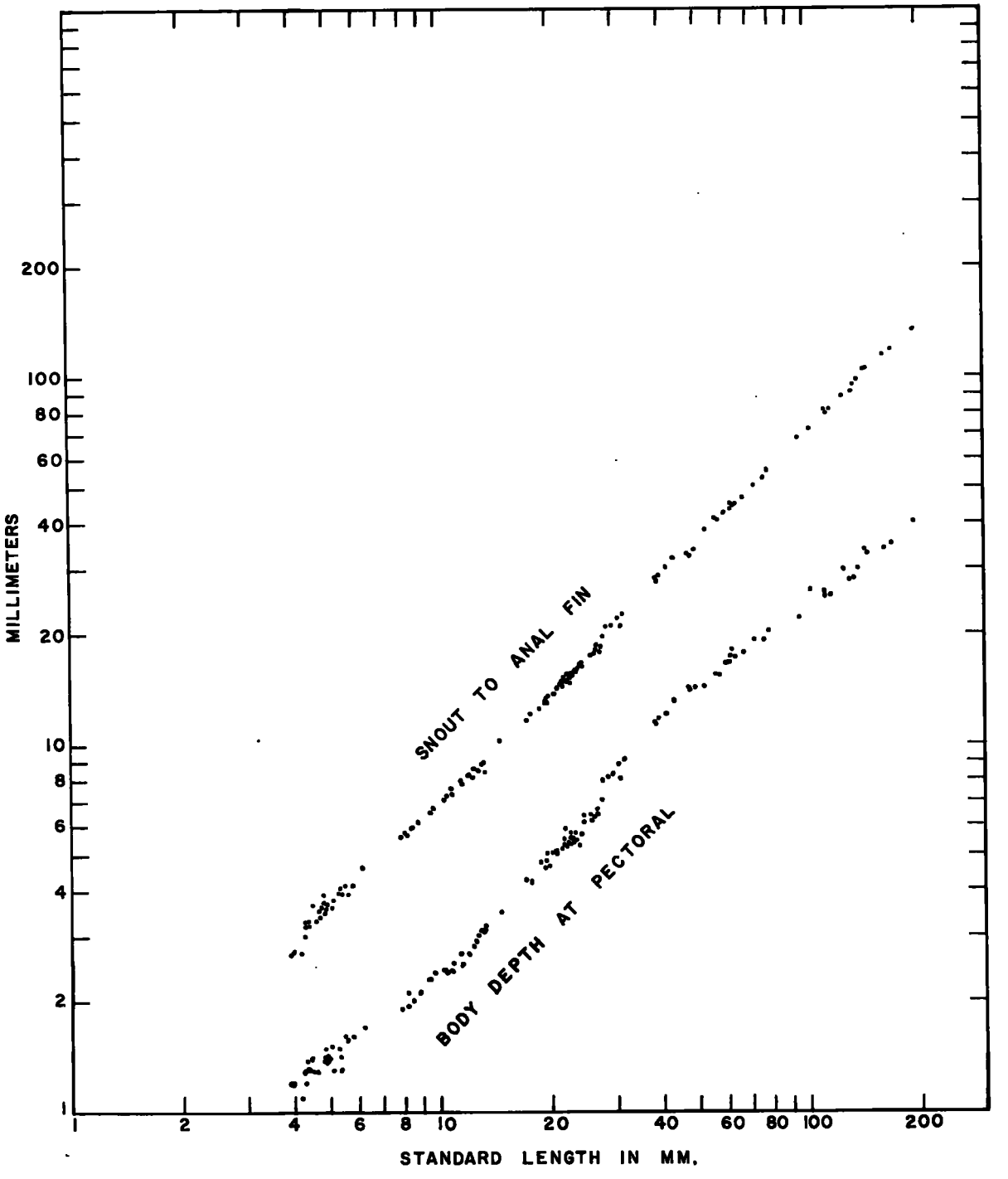

FIGURE 14.—Relation of the distance from snout to insertion of anal fin and of body depth at pectoral to standard length.

outer row, and about 33 to 35 inward pointing, bifid-tipped teeth to each side in the inner row. The lower lip had about 45 to 48 simple-tipped teeth in a single row to each half of the lip.

In the cleared and stained mouthparts of a 105-mm. specimen, there were about 62 to 64 teeth with simple tips to each half of the upper lip in the outer row. The inner set of teeth of the

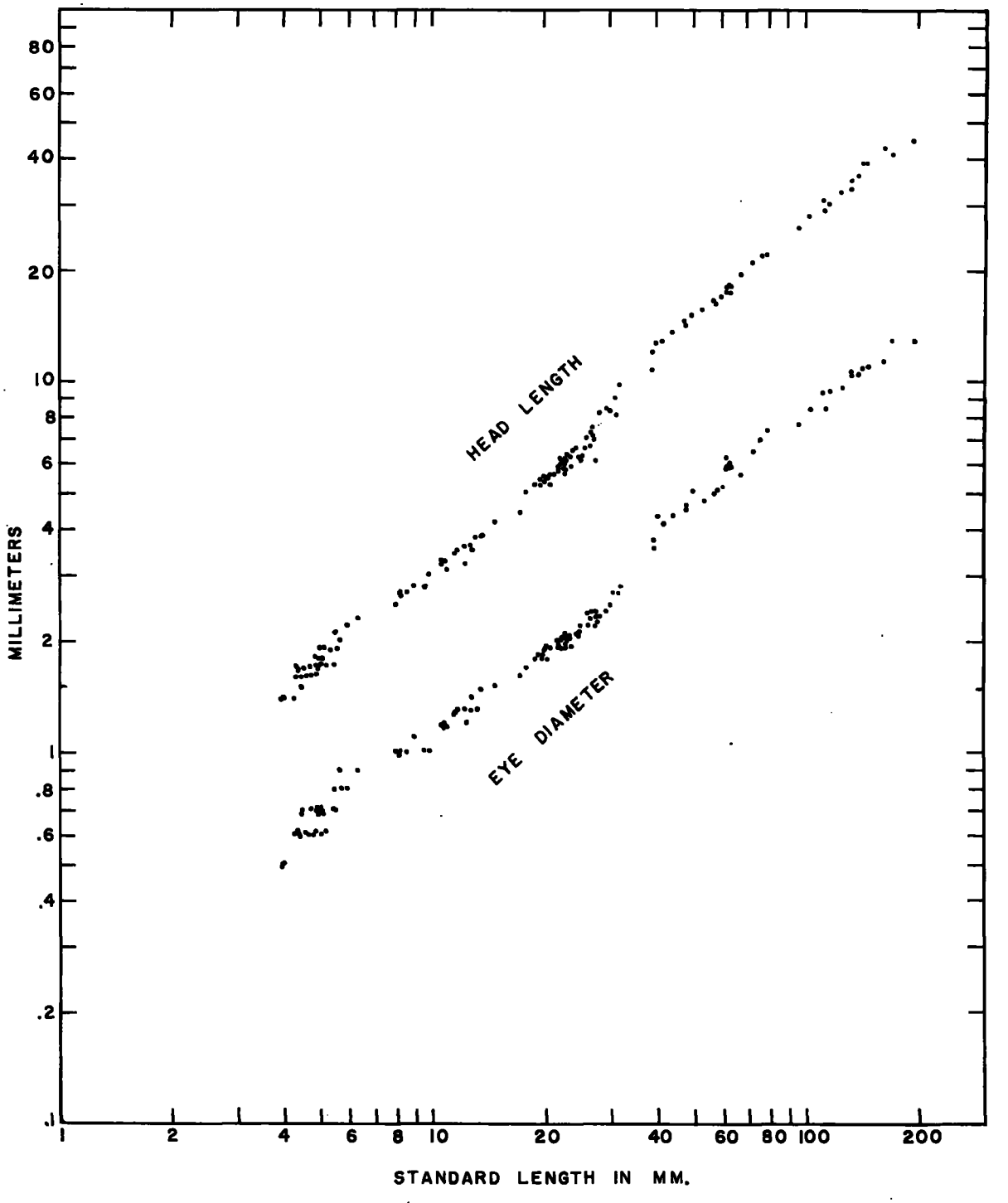

FIGURE 15.—Relation of head length and of eye diameter to standard length.

upper lip was no longer in a single series, but rather was "brushlike" in arrangement with 2 to 4 close-set rows—there were about 130 to 150 teeth to each half of the lip, all with bifid tips and curving inward. There were two rows of teeth in a single series in the lower lip—those of the outer row much the larger. In the outer row, there were 80 to 85 teeth to each half of the lip, all with simple

upcurved tips; and in the inner row from 50 to 55 to each half of the lip, all with bifid tips.

Schultz (1946, p. 389) indicated that in the genus *Mugil*, teeth are probably not present on the vomer, palatines, and tongue. Examinations of cleared and stained material of *M. cephalus* verified the absence of teeth on the vomer and palatines.

The tongue presents a peculiar picture of development of teeth in the larval and juvenile stages and of their loss in the adult stage. In a 19-mm. standard length specimen, about 16 small, simple-tipped teeth were arranged around the edges of the tongue (fig. 16). Development of the teeth and bony structures supporting them in specimens of 29, 59, and 117 mm. standard length is illustrated in figures 17 to 19. The tongue from a 390-mm. adult had no teeth on the outer surface, but when the outer covering of the tongue was removed the bony structures (without teeth) shown in figure 20 were found embedded in the tongue. It would appear that with age the teeth and supporting structures are overgrown, with the teeth and at least part of the bony structures being absorbed.

The cleared and stained tongues from 60-mm. and 122-mm. specimens of *M. curema* had no teeth or bony structures.

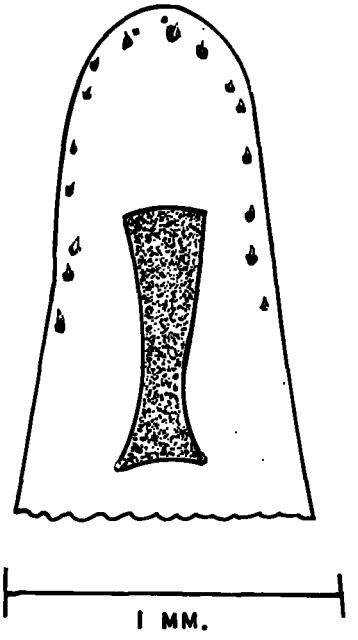

FIGURE 16.—Teeth on the tongue of a 19-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

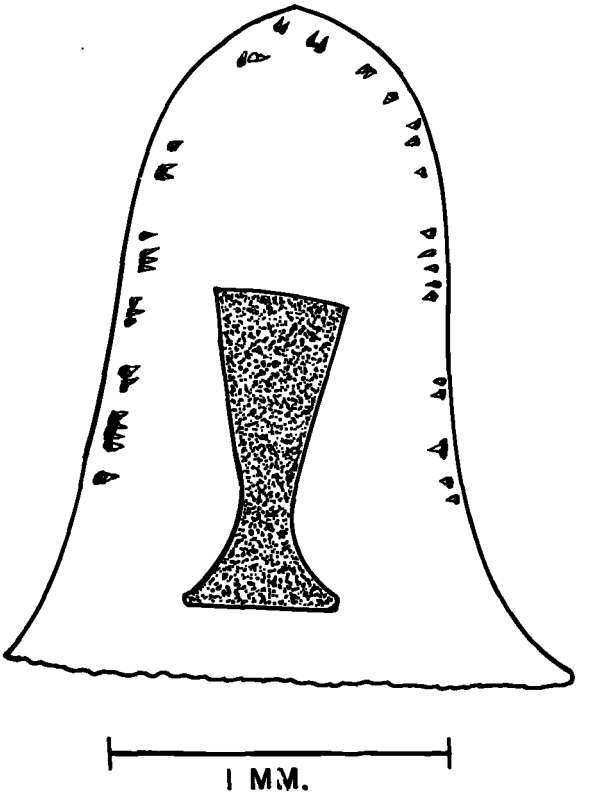

FIGURE 17.—Teeth on the tongue of a 29-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

Adipose eyelid

This structure is not evident in specimens under 30 mm., but appears to begin development at sizes between 30 and 40 mm. By about 50 mm. it is well developed and covers much of the eye (fig. 10). A detailed account of this structure is given by Jacot (1920, pp. 205–206).

Nostrils

The nostril is single and oval in shape at 5.4 mm. total length, the opening becomes gradually longer and slenderer up to 6.2 mm. standard length, and the nostril is double with well-separated openings at 9.7 mm. (figs. 3 to 6).

Gill rakers

Adults have been reported to have as many as 83 gill rakers on the lower limb of the first arch (Fowler 1936, p. 585). The number of gill rakers increases with age or size, as I found the following counts of gill rakers on the lower limb of the first arch in a series of larval and juvenile specimens: 15 in a 19-mm. standard length fish; 22 in a 29-

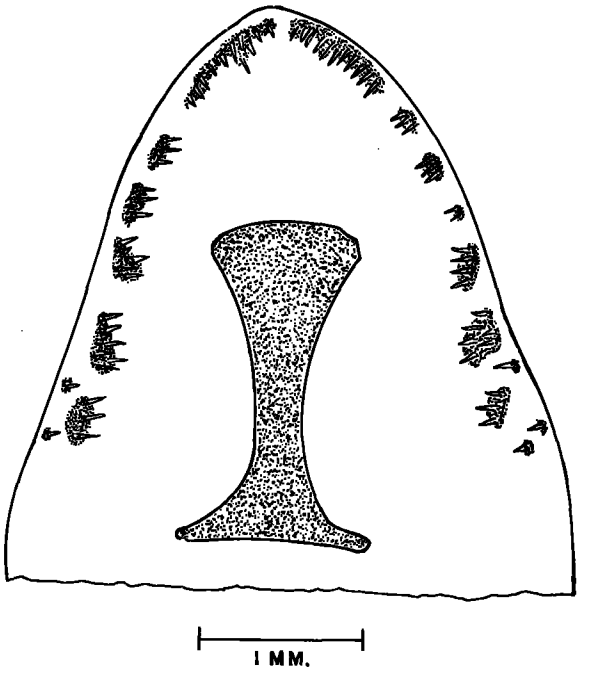

FIGURE 18.—Teeth on the tongue of a 59-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

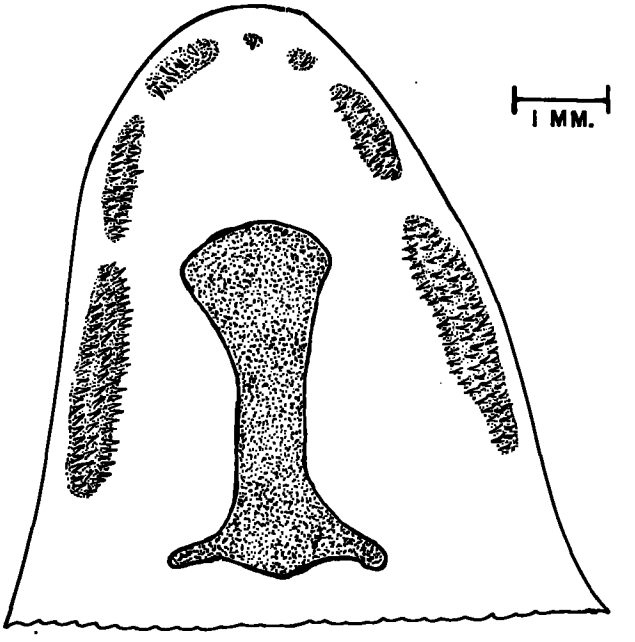

FIGURE 19.—Teeth on the tongue of a 117-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

mm. specimen; 32 in a 59-mm. specimen; and 48 in a 117-mm. specimen.

GROWTH

Two investigators have estimated the growth of striped mullet along the south Atlantic coast of the United States.

Jacot (1920, p. 220), working largely in North Carolina, said, "The arrival of the jumping mullet in April marks the beginning of its second season on our Atlantic coast; its age ranges from 14 to 17 months and its size from 120 to 200 mm. (5 to 8 inches)." Converted to standard lengths these fish would be 95 to 160 mm. In his summary (p. 227), Jacot said the fish have reached a foot or more (300+ mm. total length or 235 mm. standard length) by the second fall (October and November), and are 2 years old and mature.

Higgins (1928, pp. 528–529), also working in North Carolina, stated—

> Juvenile mullet of 22 millimeters body length appear at Beaufort by the middle of January. They become more abundant during February, March, and April, but there is little growth until the middle of April, when the water temperature reaches about 20° C. In May the rate of growth increases rapidly and continues, at an average of approximately 2 centimeters per month, through October.

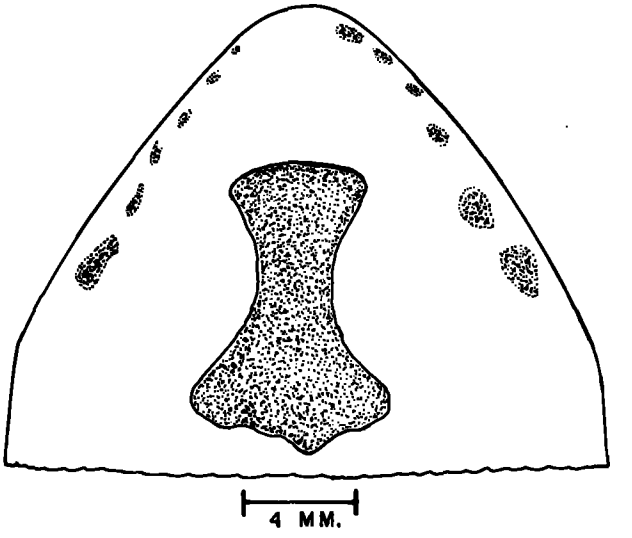

FIGURE 20.—Bony structures in the tongue of a 390-mm. specimen. (Camera Lucida drawing from cleared and stained material.)

He also said,

> The yearling stock that appears at Beaufort in the middle of January as individuals less than 1 inch long and attains a total length of about 7 inches by October seldom is taken.

(Seven inches=177 mm. total length or about 140 mm. standard length.) Higgins also indicated

(p. 626) that in the sounds during the winter and spring months he found a size group of mullet which ranged from 110 to 180 or 190 mm. body length (approximates standard length).

For Georgia, I estimated the growth of striped mullet from the seine material. The first recruits appeared along Georgia beaches in November when about 18 or 19 mm. standard length (fig. 21). By January, the largest of these recruits were about 29 mm., indicating a growth of only 5 mm. a month. No growth was evident during the coldest winter months, but between February and March the growth was about 10 mm.—this coincides with warming of the waters along the Georgia coast (Anderson 1957a). From March to October, increase in size progresses at a rate of about 17 mm. a month. From these data it appears that striped mullet in Georgia from the earliest spawning (October; see Spawning, p. 518) reach a length of about 160 mm. standard length by the end of their first year. Those spawned later in the season, and hence being several months younger, reach a size of 90 to 100 mm. by winter (fig. 21).

During the winter and early spring (November to April), it is evident that at least two year classes of striped mullet are represented in the seine collections (fig. 21). The older group, which ranges in size from about 95 to 160 mm., represents fish late in their first year to early in their second year of life (a similar situation was reported for North Carolina by both Higgins and Jacot). Applying the growth rate of 17 mm. a month, it seems quite probable that the smallest of these would reach a size of about 200 mm. by late fall or at approximately 2 years of age (Jacot estimated 300+ mm. total length or about 235 mm. by the second fall and 2 years old). We captured only a few of these larger mullet.

Kilby (1949, p. 19), from work on the west coast of Florida said,

> Assuming that the larger specimens collected in succeeding months represent the larger specimens of preceding months, it appears that a given specimen of 18 mm. in October may reach approximately 27 mm. by late November, 35 mm. by the latter half of January, 54 mm. by mid-March, and 65 mm. by mid-April.

This growth is comparable to the rate of increase I have found for the species in Georgia, but indicates a more steady rate of growth not interrupted by a period of no growth during midwinter.

Gunter (1945, p. 51), from work in lower Texas, indicates that the young striped mullet appear on Texas beaches as early as November at a size of 24 to 25 mm. total length (about 20 mm. standard length) and that the largest of these reach a size of about 108 mm. total length (about 87 mm. standard length) by June. This rate of growth is identical to that which I find for the species in Georgia. However, Gunter indicates the largest specimens of this group to be 148 mm. total length (about 117 mm. standard length) in November at about 1 year of age. This growth rate from June to November is much lower than the rate I found for Georgia and Higgins found for North Carolina. I believe, as Gunter himself suggested, that some of his mullet in these later months were *M. curema*—this would more nearly fit the size range that might be expected at this time of year for *M. curema* (Anderson 1957a).

In summary, it appears that the growth rates of striped mullet as indicated by these studies in widely separated sections of the south Atlantic and Gulf coasts of the United States are quite comparable, except that in North Carolina a more extended winter season delays growth for a longer period in the spring. Figure 22 is a diagrammatic presentation of the growth rates, for the first year only, as presented by various workers from North Carolina to Texas.

SPAWNING

Suggestions as to time and place of spawning for the striped mullet along the south Atlantic and Gulf coasts of the United States have been made by several investigators. Before presenting my own findings, a summary of these previous observations is desirable.

Jacot (1920), from work in North Carolina, said that spawning occurs from September to December with peak spawning in October and November. He indicated with reference to place of spawning (p. 222) that "they move slowly down the coast *en masse* both outside and inside the Banks, spawning as necessity demands."

Higgins (1928, p. 625), also working in North Carolina, said—

> At present no spawning fish have been observed, nor have the eggs been taken in tow nets, but it is believed that proper means will reveal the presence of eggs in the open sea. As the fish with evidently mature eggs are taken on their seaward migration at this time of year, spawning

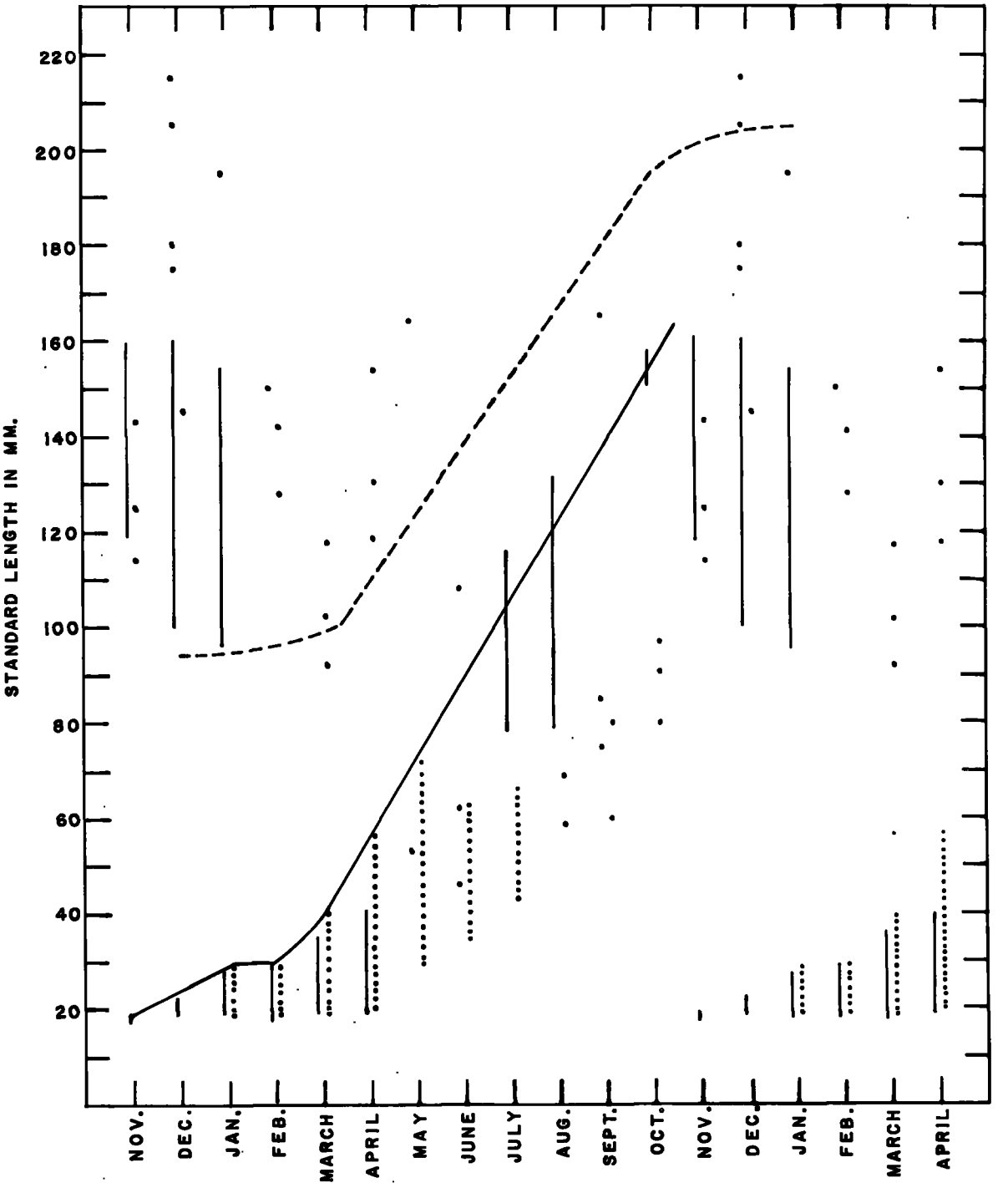

FIGURE 21.—Monthly size ranges of striped mullet, *M. cephalus*, seined from two locations in Georgia: St. Simons Beach (vertical solid line) and Sapelo Marsh (vertical dotted line). Data cover period of March 1953 to December 1956. Size ranges given represent the smallest to largest specimens taken during any given month in this period. Isolated specimens are indicated by large black dots (see tables 3 and 4 for occurrence data). The growth curves are discussed in text.

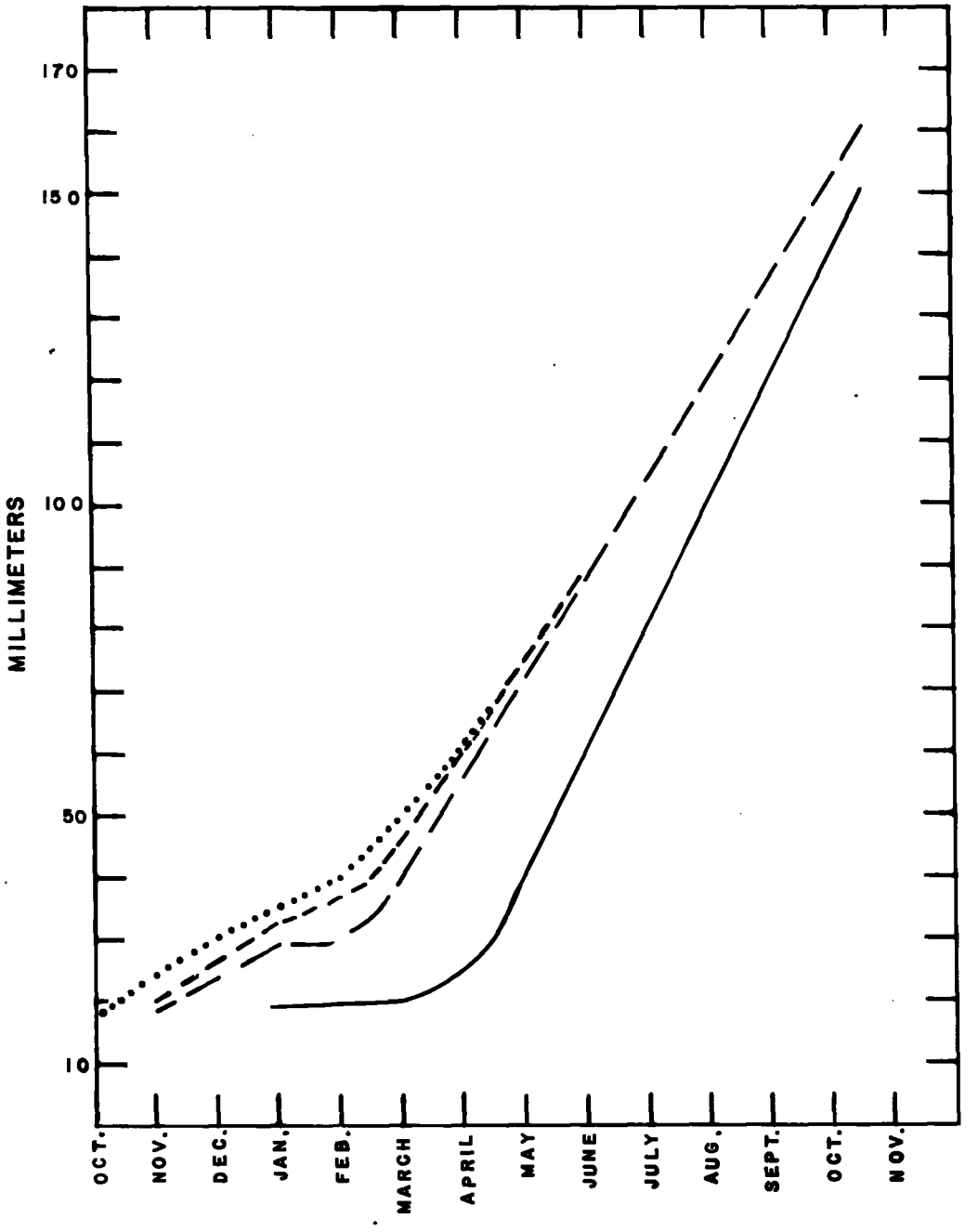

FIGURE 22.—Growth of striped mullet during first year of life as estimated by several workers; Higgins for North Carolina (solid line); Anderson for Georgia (long dashes; present paper); Gunter for Texas (short dashes); and Kilby for west coast of Florida (dotted line).

may be said to occur during November and December; and it is likely that the spawning season is of limited duration, as the eggs are of approximately the same development throughout the ovaries of the fish, and as the young appear the following spring in very uniform size groups.

Taylor et al. (1951, p. 115) indicated that adult striped mullet in North Carolina "school up" in the fall (October and November) and move to the inlets. Of these he said,

> These fish carry spawn, indicating that this is a spawning migration. The fish move out of the inlets in November and December, usually on a northerly wind (according to old-timers) and spawn in the ocean. Spawning is believed to occur in the vicinity of the inlets because

within 2 or 3 weeks, young mullet are found entering the inlets.

Gunter (1945, p. 51) said of striped mullet in Texas—

> In summary, the large mullet go to the Gulf in the fall and congregate near the passes on the outside beaches. Spawning takes place there and extends from late October to early January, with the peak probably falling in late November and early December.

Broadhead (1953, p. 21), from work in northwest Florida, said—

> No observations of the spawning of mullet have been made in northwest Florida. However, indirect evidence indicates that the fish spawn offshore, probably from 5 to 20 miles, in the Gulf of Mexico.

He indicated (p. 6) that this spawning occurs in the late fall and is about completed by early December.

Kilby (1955, p. 213), from work along Florida's west coast, said—

> In summary, the breeding season is long, extending from October through May at Cedar Key and from December through July at Bayport.

In summary, these workers, excepting Kilby, have indicated a late-fall to winter spawning period (October to January limits—peak November to December), and most indicate that spawning occurs at sea, ranging from close to shore to some 20 miles at sea.

My observations on time and place of spawning along the south Atlantic coast of the United States are based on three sets of data: Larvae taken in plankton tows from the MV. *Theodore N. Gill* operations (table 1); larvae from dip-net collections of the *Gill* cruises (table 2); and occurrence of young on the Georgia coast as indicated by seine collections in beach and marsh habitats (tables 3 and 4).

Figure 1 illustrates the locations of capture of larvae from plankton and dip-net operations.

Information from plankton tows alone (table 1) shows a spawning season extending from late November or early December into February. Assuming a period of 3 to 4 weeks for larvae to attain a size of about 20 mm., the dip-net data (table 2) likewise indicate a spawning season of December into February. Under the same assumption, data from Georgia seine collections (tables 3 and 4) show that spawning occurs as early as October, with November 19 the earliest date larvae about 20 mm. were taken; but these small larvae were not taken in abundance until January, indicating a peak spawning beginning in December. From these data, the spawning season of striped mullet along the south Atlantic coast of the United States is indicated as October to February, but it is confined largely to a period of November to January with the peak in December.

My evidence is that striped mullet spawn offshore from lower Florida to North Carolina over a broad area extending from about the 20-fathom line into the Gulf Stream. Figure 1 illustrates that larvae taken in plankton tows were over this area, whereas none were taken near shore except in lower Florida where the Continental Shelf is narrow and the Gulf Stream close to shore. I found silver mullet to spawn in this same offshore habitat (Anderson 1957a).

There is only one authentic record of observations of spawning activities of striped mullet, and this is further evidence of offshore spawning. Arnold and Thompson (1958) report observing a school of mullet spawning in the Gulf of Mexico over the Continental Slope in depths from 500 to 900 fathoms about 40 to 50 miles southeast of the Mississippi River Delta.

In contrast with spawning of the silver mullet, which begins in early spring when water temperatures are rising over the Continental Shelf (Anderson 1957a), the striped mullet spawn during late fall or winter, when water temperatures are falling.

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