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U. S. DEPARTMENT OF COMMERCE

DANIEL C. ROPER, Secretary

BULLETIN

OF THE

UNITED STATES BUREAU OF FISHERIES

VOL. XLVIII

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CONTENTS

Page

PRELIMINARY REPORT ON THE LIFE HISTORY OF THE COMMON SHRIMP, *Penaeus setiferus* (LINN.). By F. W. Weymouth, Milton J. Lindner and W. W. Anderson. (Bulletin No. 14, issued Sept. 29, 1933.) 1–26

THE HOMING INSTINCT AND AGE AT MATURITY OF PINK SALMON (*Oncorhynchus gorbuscha*). By Frederick A. Davidson. (Bulletin No. 15, issued Aug. 26, 1934.) 27–39

REPRODUCTION AND DEVELOPMENT OF WHITINGS OR KINGFISHES, DRUMS, SPOT, CROAKER, AND WEAKFISHES OR SEA TROUTS, FAMILY SCIAENIDAE, OF THE ATLANTIC COAST OF THE UNITED STATES. By Samuel F. Hildebrand and Louella E. Cable. (Bulletin No. 16, issued Sept. 19, 1934.) 41–117

RACES OF HERRING, *Clupea pallasii*, IN SOUTHEASTERN ALASKA. By George A. Rounsefell and Edwin H. Dahlgren. (Bulletin No. 17, issued May 23, 1935.) 119–141

EFFECTS OF CRUDE OIL POLLUTION ON OYSTERS IN LOUISIANA WATERS. By Paul S. Galtsoff, Herbert F. Prytherch, Robert O. Smith, and Vera Koehring. (Bulletin No. 18, issued Nov. 29, 1935.) 143–210

AGE AND GROWTH OF THE CISCO, *Leucichthys artedi*, (LE SUEUR), IN THE LAKES OF THE NORTHEASTERN HIGHLANDS, WISCONSIN. By Ralph Hile. (Bulletin No. 19, issued Feb. 27, 1936.) 211–317

SUPPLEMENTAL NOTES ON THE FISHES OF THE GULF OF MAINE. By Henry B. Bigelow and William C. Schroeder. (Bulletin No. 20, issued Nov. 17, 1936.) 319–343

ADAPTATION OF THE FEEDING MECHANISM OF THE OYSTER, *Ostrea gigas*, TO CHANGES IN SALINITY. By A. E. Hopkins. (Bulletin No. 21, issued Dec. 15, 1936.) 345–364

DETECTION AND MEASUREMENT OF STREAM POLLUTION. By M. M. Ellis. (Bulletin No. 22, issued Apr. 7, 1937.) 365–437

EXPERIMENTAL OBSERVATIONS ON SPAWNING, LARVAL DEVELOPMENT, AND SETTING IN THE OLYMPIA OYSTER, *Ostrea lurida*. By A. E. Hopkins. (Bulletin No. 23, issued Oct. 19, 1937.) 439–503

FURTHER NOTES ON THE DEVELOPMENT AND LIFE HISTORY OF SOME TELEOSTS AT BEAUFORT, N. C. By Samuel F. Hildebrand and Louella E. Cable. (Bulletin No. 24, issued Mar. 15, 1938.) 505–642

THE MIGRATIONS OF PINK SALMON (*Oncorhynchus gorbuscha*) IN THE CLARENCE AND SUMNER STRAITS REGIONS OF SOUTHEASTERN ALASKA. By Frederick A. Davidson and Leroy S. Christey. (Bulletin No. 25, issued May 17, 1938.) 643–666

THE GEOGRAPHIC DISTRIBUTION AND ENVIRONMENTAL LIMITATIONS OF THE PACIFIC SALMON (genus *Oncorhynchus*). By Frederick A. Davidson and Samuel J. Hutchinson. (Bulletin No. 26, issued June 11, 1938.) 667–692

THE SALMON AND SALMON FISHERIES OF SWIFTSURE BANK, PUGET SOUND, AND THE FRASER RIVER. By George A. Rounsefell and George B. Kelez. (Bulletin No. 27, issued Oct. 17, 1938.) 693–823

THE LIFE HISTORY OF THE STRIPED BASS, OR ROCKFISH, *Roccus saxatilis* (WALBAUM). By John C. Pearson. (Bulletin No. 28, issued Oct. 26, 1938.) 825–851

ERRATA

Page 164, line 4 should read "of an automatic siphon arrangement similar to that shown in figure 4, received an"
Page 174, first 2 lines should be deleted.
Page 177, last line should read "duration of test."
Page 232, last line of second paragraph should read "(pp. 237–249)."
Page 588, line 8 should read "of the eye as in the adult."

U.S. DEPARTMENT OF COMMERCE
Daniel C. Roper, Secretary
BUREAU OF FISHERIES
Frank T. Bell, Commissioner

PRELIMINARY REPORT ON THE LIFE HISTORY OF THE COMMON SHRIMP *PENAEUS SETIFERUS* (LINN.)

By F. W. WEYMOUTH, MILTON J. LINDNER
and W. W. ANDERSON

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 14

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1933

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PRELIMINARY REPORT ON THE LIFE HISTORY OF THE COMMON SHRIMP *PENAEUS SETIFERUS* (LINN.)

By F. W. WEYMOUTH, PH.D., MILTON J. LINDNER, and W. W. ANDERSON, *United States Bureau of Fisheries*

CONTENTS

	Page
Introduction	1
Production and value of shrimp	2
Previous work on life history	6
Life history	8
Nature of data	8
Interpretation of data	9
Recognition of age groups	9
Spawning	11
Sex-ratio	14
Larvae	15
Life history—Continued	Page
Interpretation—Continued	
Young	15
Growth	18
Fate of adults	19
Habits	21
Depletion and protection	22
Summary	23
Bibliography	25

INTRODUCTION

The present report is concerned with the salient features of the life history of the common or so-called "lake shrimp" (*Penaeus setiferus*) of the South Atlantic and Gulf coasts and the bearing of these facts on the problems of the shrimp industry. The information has been obtained in the carrying out of a program of cooperative shrimp investigation in which the Bureau of Fisheries has been supported by the States of Louisiana, Georgia, and Texas. The loyalty and industry of the staff and of our associates have made possible the substantial results here recorded and the members deserve the particularized credit for which our space is too limited.[1]

Although the study is far from complete, it seems best to place the information obtained on record, in part because it is the most complete life history available for any species of shrimp and in part to give the purposes and needs of the investigational program.

A brief statement will first be given of the extent and importance of the shrimp fishery in the United States, and next the state of knowledge at the beginning of the present work; then the life history of *Penaeus setiferus* will be outlined very briefly, after which the evidence from which these facts were drawn will be given in such detail as is now possible (this will constitute the great bulk of the paper); and finally, the bearing of this information upon the problems of depletion and protection will be discussed briefly.

[1] The staff of the shrimp investigations includes F. W. Weymouth, Milton J. Lindner, and Gordon Gunter with headquarters in New Orleans, La., W. W. Anderson at Brunswick, Ga., J. S. Gutsell at Beaufort, N.C., and Kenneth H. Mosher at Aransas Pass, Tex. J. N. Gowanloch and Forrest Durand, of the Bureau of Research and Statistics of the Louisiana Department of Conservation, have been so closely associated in the cooperative program as scarcely to be differentiated from the staff members. We gladly acknowledge the aid of Dr. Waldo Schmitt, U.S. National Museum, in the identification of material; and of Dr. R. Von Ihering, of the Instituto Biologico, for information concerning the shrimp fishery of Sao Paulo, Brazil. We are also greatly indebted to many men in the shrimp industry, in particular to the late John Dymond, Jr., former president of the Southern Canners Exchange; R. R. Rice, of Aransas Pass, Tex., and Senator Jules Fisher, of New Orleans, La., who have aided in the collection of data and have placed at our disposal their records for statistical analysis. Approved for publication, Mar. 22, 1933.

PRODUCTION AND VALUE OF SHRIMP

The shrimp fishery of the United States produced a total of 113,263,000 pounds in 1929 and 92,327,000 pounds in 1930, ranking in each year ninth in volume among all the fisheries. The value to the fishermen of the shrimp taken in 1929 was $4,575,000; this placed the fishery fifth in value. It was exceeded only by the salmon, oyster, haddock, and halibut. In 1930, due to a decline in price and in catch, the value was $3,134,000, so that it fell to tenth rank.

As may be seen from table 1, more than 95 percent of the shrimp taken were from the South Atlantic and Gulf States, slightly over 40 percent coming from Louisiana alone. Here occur the following species: *Penaeus setiferus, Penaeus brasiliensis, Macrobrachium* sp., *Xiphopenaeus kroyeri, Trachypenaeus constrictus*

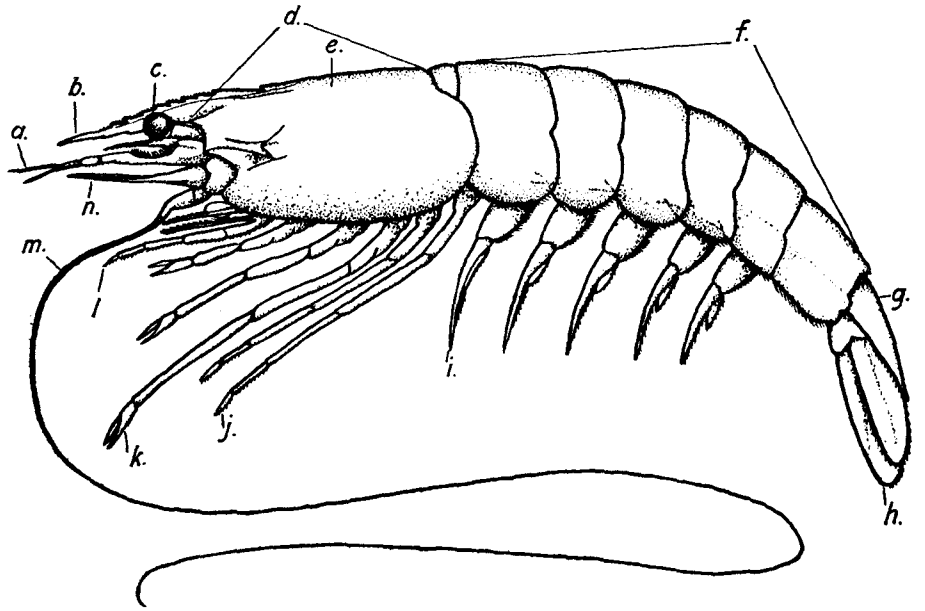

FIGURE 1.—Side view of the common shrimp (*Penaeus setiferus*) with some of the more conspicuous structures labeled; *a*, antennule; *b*, rostrum or "spine"; *c*, eye; *d*, cephalothorax or "head"; *e*, carapace or "head shell"; *f*, abdomen or "tail"; *g*, telson or "tail spine"; *h*, uropod or "tail fin"; *i*, first pleopod or "swimming leg"; *j*, fifth pereiopod or "walking leg"; *k*, chela or "pincer" of third periopod; *l*, third maxilliped; *m*, antenna or "whisker"; *n*, antennal scale or acicle.

and *Sicyonia* sp. They may be distinguished as follows: *Macrobrachium* is easily recognized from its presence in fresh or slightly brackish water. Only the first two pair of walking legs have pincers, the first being relatively very large. It supports a distinct river fishery of small volume not here considered. All of the other species belong to the *Penaeidae* and agree in having the first three pairs of walking legs, instead of only two, armed with pincers, a family character. These shrimp are characteristically salt-water forms, although they may be found in brackish bays at certain times of year. The two species of *Penaeus* may be told from *Trachypenaeus* and *Xiphopenaeus* by the fact that the rostrum is armed with spines both above and below. *P. setiferus* differs but little from *P. brasiliensis*. The most easily recognized distinguishing characteristic is to be found in the groove on either side of the rostrum. In *P. setiferus* these grooves, conspicuous along the side of the rostrum, become shallow as they reach the carapace and are soon lost. In *P. brasiliensis*, however, the grooves continue to the back margin of the carapace. (See figs. 3 and 4.)

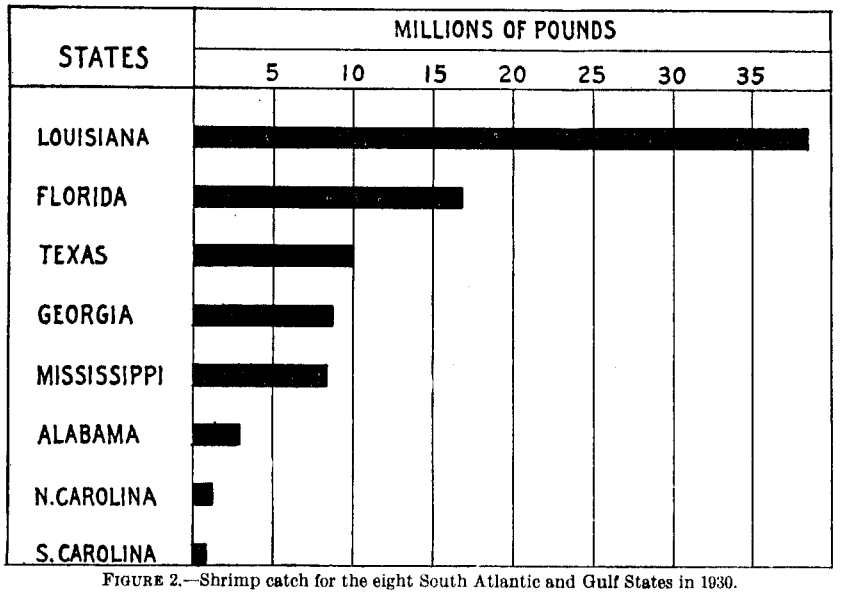

FIGURE 2.—Shrimp catch for the eight South Atlantic and Gulf States in 1930.

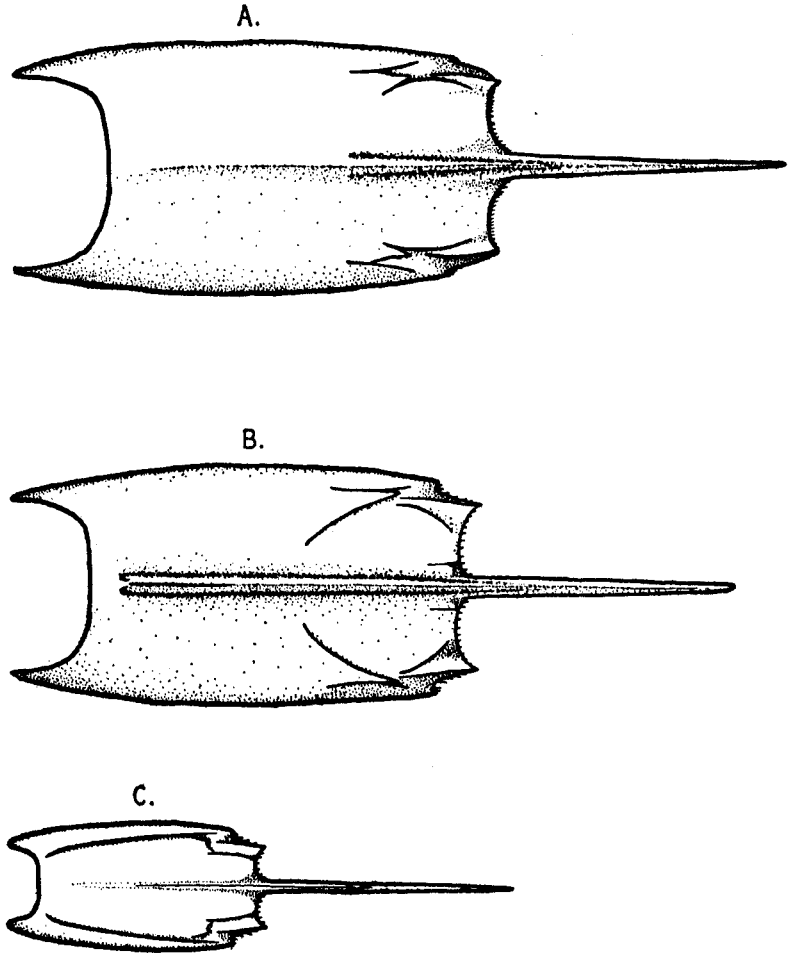

FIGURE 3.—Dorsal view of the carapaces of *A*, the common shrimp (*Penaeus setiferus*); *B*, the grooved shrimp (*P. brasiliensis*); and *C*, the sea bob (*Xiphopenaeus kroyeri*) showing the presence of rostral grooves in the grooved shrimp and their absence in the common shrimp and the sea bob.

TABLE 1.—*Shrimp taken in the United States in 1930 according to districts* [1]

Section	Catch		Value	
	Pounds	*Percent*	*Dollars*	*Percent*
South Atlantic and Gulf States	88,117,000	95.43	2,995,000	95.56
Pacific Coast States	2,785,000	3.02	49,000	1.56
Alaska	932,000	1.01	42,000	1.34
Middle Atlantic States	341,000	.37	29,000	.93
Mississippi River	147,000	.16	15,000	.48
New England States	5,000	.01	4,000	.13
Total	92,327,000	100.00	3,134,000	100.00

[1] No catch was reported in the Chesapeake Bay States or in the States bordering on the Great Lakes.

Trachypenaeus shows a family resemblance to *Penaeus* but is much smaller and the rostrum, although armed with 7 to 9 spines above, is smooth below. *Xiphopenaeus* differs from all the other penaeids in having a rostrum as long or longer than the carapace and the fourth and fifth pairs of walking legs much elongated and slender. These four long legs, together with the two antennae or "feelers" projecting beyond the "head" gave rise to the term "six barb" among the French fishermen. This has been corrupted to "sea bobs", and it is by this name that they are generally known. *Sicyonia* is an uncommon small form readily distinguished by the very short rostrum and the crest which continues from the rostrum down the middle of the body.

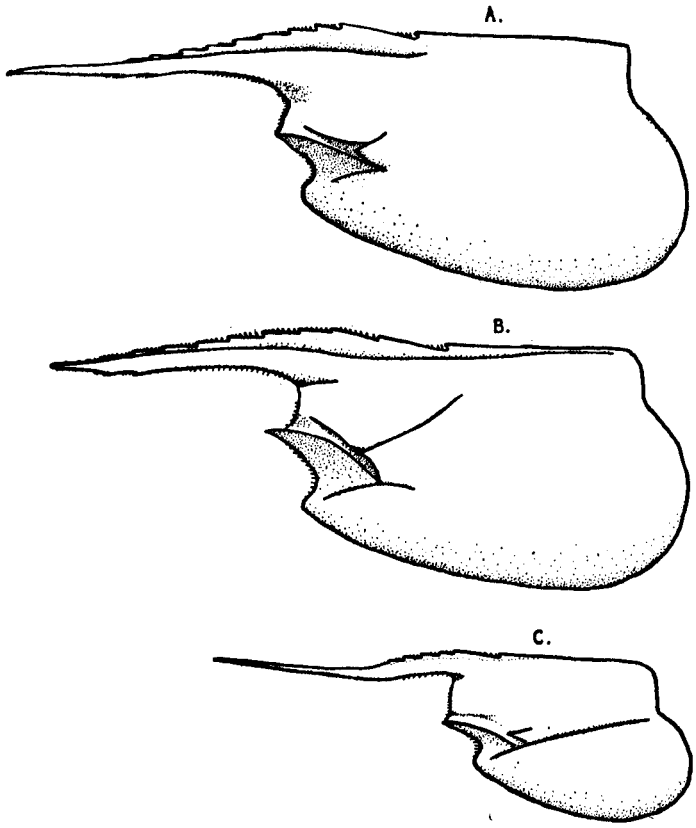

FIGURE 4.—Lateral view of the carapaces of *A*, the common shrimp; *B*, the grooved shrimp; and *C*, the sea bob. In both the common shrimp and the grooved shrimp teeth appear on both the upper and lower surfaces of the rostrum, while in the sea bob they are absent from the lower surface.

Of the penaeids, *Sicyonia* and *Trachypenaeus* are incidental only and of no economic importance. *Xiphopenaeus* may contribute 2 or 3 percent to the catch. It is too small to be used in canning but finds its way into the fresh markets and drying platforms. *P. brasiliensis* may at times be abundant but forms less than 5 percent of the total. The single species *Penaeus setiferus* accounted for about 90 percent of all the shrimp taken in the United States, or 100 of the 113 million pounds caught in 1929.

TABLE 2.—*Shrimp taken in the South Atlantic and Gulf States for 1929 and 1930, arranged by States*

	1929				1930			
	Catch		Value		Catch		Value	
	Pounds	*Percent*	*Dollars*	*Percent*	*Pounds*	*Percent*	*Dollars*	*Percent*
Louisiana	49,455,982	45.56	2,025,336	45.66	38,664,487	43.88	1,159,626	38.71
Florida	18,618,564	17.15	879,192	19.82	16,848,576	19.12	635,506	21.22
Mississippi	13,101,450	12.07	421,491	9.50	8,489,050	9.63	318,871	10.65
Georgia	12,377,619	11.40	581,015	13.10	8,852,712	10.05	334,576	11.17
Texas	9,415,317	8.67	327,008	7.37	10,189,318	11.56	377,016	12.59
Alabama	4,396,400	4.05	154,139	3.48	2,982,200	3.38	97,219	3.25
North Carolina	897,495	.83	30,560	.69	1,298,610	1.47	40,752	1.36
South Carolina	287,711	.27	16,625	.37	792,733	.90	31,814	1.06
Total	108,550,538	100.00	4,435,366	99.99	88,117,686	99.99	2,995,380	100.00

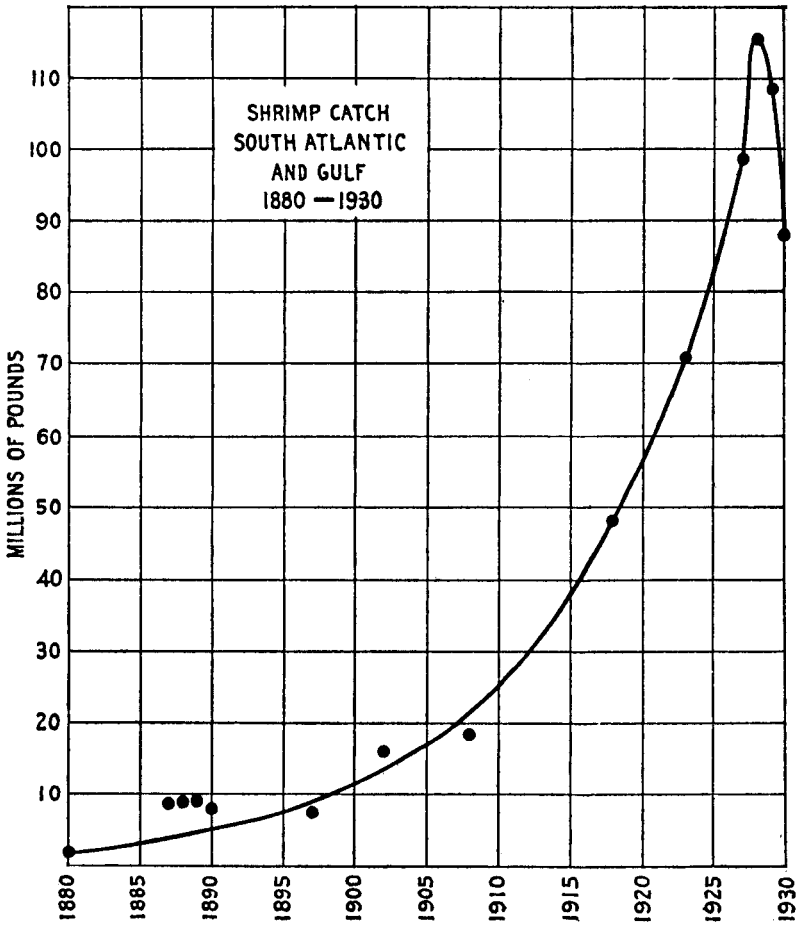

FIGURE 5.—Shrimp catch for the South Atlantic and Gulf States from 1880 to 1930.

Another phase deserves emphasis. While the shrimp ranks high among the fisheries of the United States, it is preeminent among those of the South Atlantic and Gulf States. Here among eight coastal States it ranks first in value, being followed by the oyster and the mullet; and second in volume, being exceeded only by the menhaden, which, however, ranks only fourth or fifth in value. In volume the shrimp is followed by the oyster and the mullet.

A fishery of this magnitude, the most important in the South, giving employment to thousands of fishermen and factory operatives, deserves careful attention if it is to be maintained in this valuable state. The rapid expansion of the fishery during the past 40 years, throughout which time it has doubled in volume every 8 or 9 years, has suggested caution, and recently the men in the industry have taken the initiative in asking for investigation, fearing, apparently, that some of the fluctuations in the catch were the forerunners of serious depletion. The prime requisites for successful handling of the problems of the shrimp, as of other fishery resources not adapted to cultivation, are information as to the abundance and knowledge of the life history. The first is needed to tell when protection is required and the second to guide such protection into intelligent and effective channels.

Unfortunately data for even the roughest analysis of abundance is lacking. State and Federal data give only the total catch and except for the last year or so no indication of the effort that produced the catch. Some private records alone serve to show the boat catches by which the effort could be analyzed, but these records are too scattered and cover too short a time to solve the problem. The outlook in this direction is, however, now more hopeful, for in Louisiana, a law, originally drafted with the assistance of members of our staff, in the future will give figures from which depletion may be detected as it appears. In consequence of these conditions we are unable to present in this report any data on the important question of abundance.

On the other hand, we must have an adequate knowledge of the life history and habits of the shrimp in order that, should depletion become apparent, intelligent protective measures may be applied at once. The only purpose of this preliminary report is to make available what information has been obtained against the time when it may be necessary to frame protective measures. Data on many points are far from conclusive but still may be useful for legislative action; the paper must be considered solely as such a progress report in spite of the fact that the data at hand establish a more complete life history than has hitherto been available for any shrimp of economic importance.

PREVIOUS WORK ON LIFE HISTORY

At the time the present investigation was started the information available concerning the American penaeids, and especially *Penaeus setiferus*, other than that in purely systematic papers was very meager. Fritz Müller in 1863 had reported from Brazil the occurrence of a nauplius larva presumably belonging to the genus *Penaeus*. In 1883 Brooks obtained penaeid larvae at Beaufort, N.C., and was able to trace the main stages of the larval history. He assumed them to be the young of *Penaeus brasiliensis*, but neither he nor Müller established the specific characters for the larvae. This work was solely morphological, interest being centered in the occurrence of the primitive nauplius larvae previously found only in lower crustacea.

In this connection it may be well to point out a peculiarity of the *Penaeidae* which has made study of the life history difficult. Unlike the majority of the higher Crustacea, the female penaeid does not carry the developing eggs attached to the abdominal legs. In consequence, although eggs of the other shrimp and crabs, as for example *Crago vulgaris* of the North Sea, may readily be obtained for study, no one has ever reported a fertilized egg of *Penaeus*. The mature ovarian egg is very small, measuring from one fourth to one third of a millimeter in diameter, and the unique larval history of *Penaeus* is related to this fact. The minute larvae hatching as nauplii pass through 6 or 8 distinct stages, in contrast to the condensed development of most deca-

pods in which the eggs, well supplied with stored yolk, hatch into larvae corresponding to stages occurring late in the larval history of *Penaeus*.

No further work was done until more than 20 years later at the Gulf Biologic Station, Cameron, La. In 1908 Spaulding and Guilbeau and in 1910 Gates reported on the shrimp. Facilities were not available at the Gulf Biologic Station for an intensive study of the shrimp; consequently these preliminary papers contain only brief observational notes on the behavior and a few scattered length measurements. Spaulding, whose observations were the most extensive, reports that larval shrimp, less than one half inch in length, were obtained in Calcasieu Pass in August and September. These were similar in form to the adult, but a series of larval stages was not obtained nor was identification of the species possible. No females with developed ovaries were taken, but from a study of the males and the time of appearance of the larvae he concludes that there is a single breeding season extending from the first of May to the last of July. He thought it possible that the eggs were laid in the Gulf but presents no direct evidence. The size at maturity is not established.

In 1918 the Louisiana Department of Conservation began a more intensive study of the shrimp. This work was done by Percy Viosca and published partly under his name (1920) and partly under that of Tulian, who was then commissioner (1920, 1923, 1926). Viosca's findings are more extensive than his predecessor's but it is to be regretted that none of the data upon which his conclusions were based is given in any of the publications. As a result it is impossible to evaluate his interpretations of the life history. He states that *Penaeus setiferus* spawns in the Gulf, chiefly on the evidence that sexually mature shimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1¼ inches is reached. "By May reasonable numbers of baby shrimp appear in the shallow waters near the coast line and a large proportion gradually migrate into brackish water, all growing rapidly throughout the summer."

This is all the information toward a life history of *Penaeus setiferus* available in 1930.

The following is a bald summary of the life history as determined by the present work.

The eggs are laid from March or April to August or September in the outside waters of the ocean or Gulf. The post-larval young beginning at a length of 7 mm are found in bays, creeks, bayous, and lakes in warm, shallow, brackish water with mud bottoms. The young grow rapidly and with increasing size gradually migrate to deeper water of greater salinity.

During July at an average length of about 90 mm they enter the commercial catch, appearing first in the bays, creeks, and other "inside" waters and later outside.

They continue in the fishery, furnishing all of the fall catch, with its peak in October, until the following spring and summer, when they spawn and disappear at the age of 1 year. By late fall they have reached a length of about 120 mm, which they maintain during the winter. Resuming growth in the spring, they show a rapid and striking differentiation in the size of the sexes and spawn at lengths of 130 to 170 mm for the males and 135 to 190 mm for the females. Their fate is unknown, but their complete disappearance from the commercial catch is undoubted.

The breeding season is characterized by (1) a development of the gonads; (2) a rapid differentiation in size between the sexes; (3) a difference in the behavior of the

sexes, so that the proportion of sexes, uniform during the winter, shows wide fluctuation. Far more mature shrimp of both sexes are found outside than inside.

The shrimp is most abundant in shallow coastal waters near river mouths or deltas. It is omnivorous, feeding on a variety of animals and plants.

LIFE HISTORY

NATURE OF DATA

First in importance are the length frequencies obtained by measuring shrimp taken by the standard commercial gear, the otter trawl. All of the shrimp measured in Texas were samples from the catch of fishermen; the same is true of part of the data from Louisiana. The remainder of the shrimp were obtained with standard gear from boats operated by members of the staff in Louisiana, Georgia, and North Carolina. This experimental fishing differs from the commercial fishing solely in the localities fished. The fishermen obviously cannot afford to fish in localities yielding small catches, while in the experimental fishing these localities give information fully as valuable as those where many shrimp are taken. Of these length-frequency series the most important are those for *Penaeus setiferus*, although similar but far less complete data are available for *Penaeus brasiliensis*, *Xiphopenaeus kroyeri*, and *Trachypenaeus constrictus*. The series from Georgia is, because started earlier and unmarred by breaks, the most valuable.

The total length measured from the tip of the rostrum to the tip of the telson has been used as the standard measurement. This measurement was chosen over other linear measurements such as carapace length and over weight and volume after a study of the variability of measurements obtained in various ways. Weight and volume are subject to great variation because of the adhering water on a body as irregular in shape as the shrimp. These measurements consume much time and require apparatus not easily used aboard small boats. In obtaining the total length the shrimp is placed, ventral surface down, on the scale of a special measuring board with the rostrum in contact with a fixed block. The measurement is read and recorded to the nearest millimeter. For plotting and analysis the measurements are first tabulated, then grouped into 5-mm classes in such a way that the mid-point always falls on a 3 or an 8. For example, all shrimp measuring from 131 to 135 mm (both figures inclusive) are grouped together in a class interval with a mid-point of 133 mm and so plotted in a frequency polygon. Similarly, all from 136 to 140 mm are grouped with a mid-value of 138.

Measurements other than total length have been made for special purposes and in smaller numbers; most notable are those for racial studies now in progress.

The measurements from the four localities, covering, in the case of Georgia, over 2 years, now number more than 150,000 and therefore represent an adequate basis for statistical treatment. (See table 3.)

TABLE 3.—*Shrimp (Penaeus setiferus) measured during semimonthly periods in the three major regions of investigation*

Period	Georgia		Louisiana		Texas		Period	Georgia		Louisiana		Texas	
	Males	Females	Males	Females	Males	Females		Males	Females	Males	Females	Males	Females
1931							1932						
Feb. 1	547	638					Jan. 1	456	528	328	317	178	222
Feb. 2	1,024	1,111					Jan. 2	476	561			172	228
Mar. 1	476	563					Feb. 1	301	343			777	823
Mar. 2	559	627					Feb. 2	275	338			193	207
Apr. 1	819	830					Mar. 1	507	514	485	607	291	309
Apr. 2	732	821					Mar. 2	457	526	361	378	186	214
May 1	1,222	1,314					Apr. 1	1,260	1,322	272	265	420	480
May 2	1,012	1,287	155	139	495	536	Apr. 2	1,348	1,592	126	82	101	99
June 1	604	1,010			575	525	May 1	125	212	326	285	118	282
June 2	81	411	37	50	311	289	May 2	662	931	233	248	393	407
July 1	453	411			494	506	June 1	349	596	73	49	177	223
July 2	427	373	530	476	69	131	June 2	314	688	248	290	101	99
Aug. 1	918	521	969	788	222	178	July 1	373	356	237	270	314	286
Aug. 2	1,730	1,398	964	889	433	367	July 2	963	683	255	287	306	294
Sept. 1	1,551	1,467	1,996	2,004	315	310	Aug. 1	1,017	704	217	204	792	608
Sept. 2	1,552	1,720	1,972	2,028	488	512							
Oct. 1	664	752	1,151	1,308	598	602	Total	28,110	30,401	14,936	15,244	10,751	11,305
Oct. 2	1,320	1,389	1,339	1,261	588	612							
Nov. 1	632	679	1,994	2,206	394	406							
Nov. 2	1,158	1,323	319	362	463	537							
Dec. 1	1,737	1,862	349	451	439	561							
Dec. 2					348	452							
Subtotal	19,227	20,507	11,775	11,962	6,232	6,524							

Beside length measurements, all observers have recorded the conditions of the gonads, permitting these specimens to be classified not only by length but also by stage of sexual maturity.

The field examination has been by naked eye, but in addition all the observers have made microscopic examination of part of the specimens and preserved material for future study as a check on the field classification.

Smaller shrimp than those taken by the commercial gear have been seined or taken by small beam trawls or "try nets" with bobbinet casings. These shrimp, ranging from 7 to 20 mm, have been measured under the low power of the microscope with an eyepiece micrometer.

Of a different nature is the material obtained by plankton nets. The study of the larval stages thus obtained is not yet complete.

INTERPRETATION OF DATA

RECOGNITION OF AGE GROUPS

The interpretation of the length-frequency data from Georgia upon which, as our most complete series, most of our knowledge of the life history is based, may conveniently begin with those for July 1931. Here there is a well-marked bimodality of the curve due to the presence of two completely separated groups differing markedly in size. This is plainly shown in figure 6, in which the smaller group with a mode at about 95 mm extends from 65 to 125 for both males and females, while the larger group, centered about 153 mm for the males and 175 for the females, extends for the males from 140 to 170 mm and for the females from 150 to 190 mm. There is thus a gap of 20 mm between the two groups. At no other time of the year can two completely separated groups be found. Examination of the other records show an essentially similar condition during July in Louisiana and during August in Texas.

Let us first trace these groups backward to see whence they come. In the case of the larger group this is easily done. Neglecting minor changes of size, this group can be traced back through the spring and winter to the previous year, where we may leave them for the present. (See fig. 10.)

The smaller group is less easily followed. They are not present in the commercial catch in the earlier months. An extensive search for this group of young has been carried on by seining in shallow water, representing many degrees of salinity,

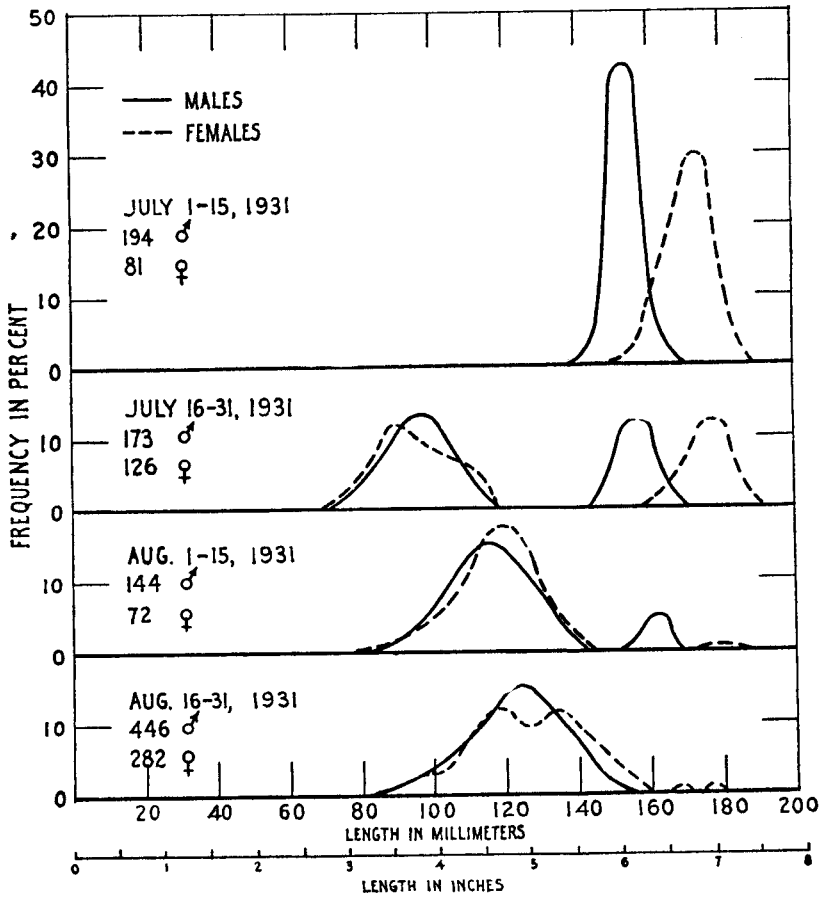

FIGURE 6.—Half-month frequency distributions of the common shrimp from the outside waters of Georgia, July 1 to August 31, 1931, showing the first appearance of the young shrimp of the year and the disappearance of the mature shrimp from the commercial catch.

from ocean beaches to creeks and lakes far inland. Many localities yielded nothing. So far no young have been found on ocean or Gulf beaches either in Georgia, Louisiana, or Texas. In the marshes near the grass small shrimp were taken but proved to be young and adult palaemonids. Finally, in the summer of 1931, the young were found in the slightly brackish waters of Dover Creek at Lampadozier, Ga., 10 or 12 miles from the sea. Here the young from 7 or 8 to 40 mm have been systematically collected during the proper seasons.

In Louisiana during 1932 the young have been obtained under a variety of conditions ranging from the slightly brackish waters of Bayou Rigaud in lower Barataria Bay to the almost fresh waters of Little Lake. The latter is more than 20 miles

distant from the Gulf in a direct line and much farther by the winding bayous and canals through which the shrimp would have to pass if, as seems probable, they were spawned at sea. Also during 1932 these young shrimp have been found in similar localities near Beaufort, N.C., and Aransas Pass, Tex., consequently records are now on hand for these young from the four States in which the investigations are in progress. The habitat of the post-larval young up to about 50 mm seems to be on the inside and appears to be characterized by shallow water, muddy bottoms, high temperature, and moderate to very low salinity. A more detailed study of the physical characteristics of the localities in which young shrimp are found is in prog-

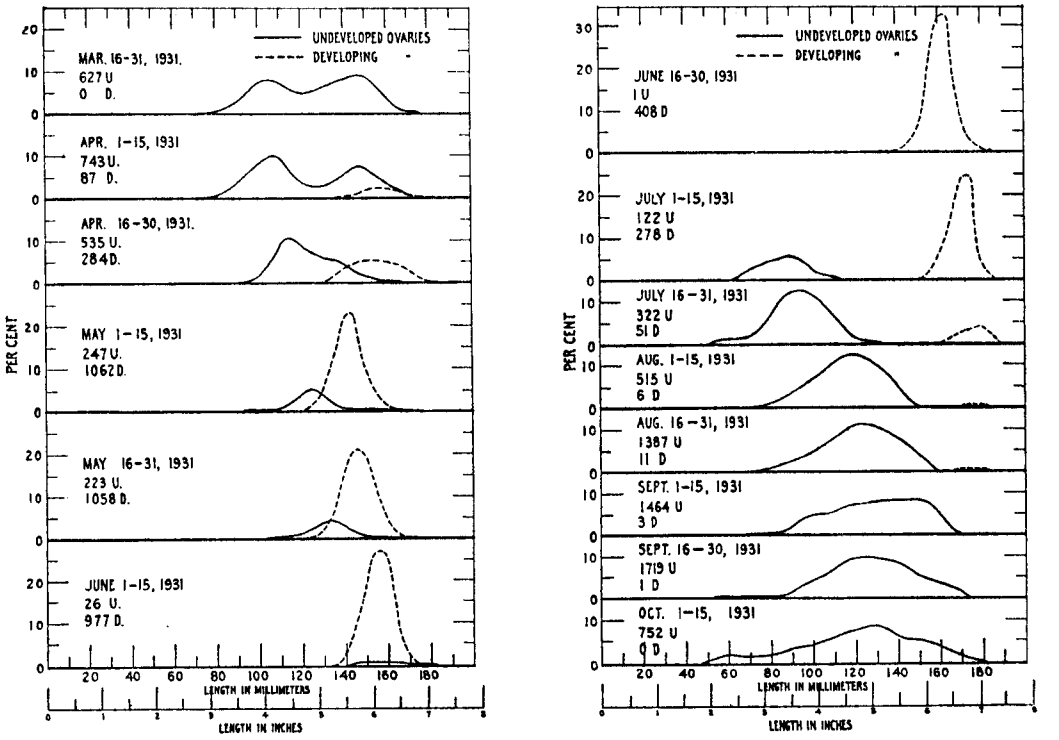

FIGURE 7.—Frequency distributions of the immature and maturing females of the common shrimp in Georgia waters during the spawning season of 1931. Solid lines represent distribution of female shrimp with ovaries composed exclusively of undeveloped eggs and broken lines indicate distribution of shrimp with maturing eggs.

ress. These bayous, creeks, and lake margins are also nursery grounds for many species of fish, the larvae and young of which are taken while seining for the young shrimp. While *Crago*, the shrimp of the North Sea, differs in many respects from *Penaeus*, the young also make their early growth far from the sea (Ehrenbaum 1890).

SPAWNING

What is the origin of these very young, apparently just emerged from the larval state, some of which can be found from April through September? We naturally turn to the larger group which we have said was present at this time. If we classify the large shrimp by the observed state of the gonad, we have the following picture. In Georgia, in 1931 from the middle of April to the end of July, some degree of maturity was observable in the ovaries. The members of the small group appearing in July were without exception immature. Some scattering representatives of the

larger mature group were found in August and even September, but the score of individuals taken are in striking contrast with the hundreds obtained in earlier months.

Although we have distinguished four or five stages of ovary development in our records, it is difficult to separate these sharply or to determine how long each lasts. Judging from the appearance of the ripest stages that we have recognized and of the young, some shrimp are spawning within 2 or 3 weeks from the date on which ovary development is first noticed. We may say, therefore, that in Georgia in 1931 the larger group was spawning from the last of April to the middle of August and that the young entering the commercial catch in July came from the earlier spawners among these large shrimp. The intervening time had been spent by the young probably in the smaller and more brackish creeks in feeding and growing.

Having thus established the previous history and relations of the two groups found in the commercial catch of July, we may profitably complete the presentation of all the data on breeding and spawning that we have obtained. Like Ehrenbaum in his work on *Crago vulgaris*, we must confess to serious gaps in this phase of the life history.

The *Penaeidae* as a group are characterized by marked sexual dimorphism, including certain elaborate and well-marked secondary sexual characters associated with sperm transfer.

In *Penaeus setiferus*, in contrast to the crabs, the female is much larger than the male. Thus, in Georgia, in June 1931, males and females of a comparable degree of maturity averaged 144.5 and 156.5 mm, respectively, the females thus exceeding the males by 8.31 percent. There are other differences in general form; according to Alcock (1906) the rostrum of the female is proportionally larger, a persistent juvenile character.

The most interesting differences for the question that we are now considering are those of the secondary sexual characters. In *Penaeus* the males produce spermatophores, often of considerable complexity. The inner ramus of the first pair of pleopods is modified, forming a structure called the petasma or andricum. By means of the petasma the spermatophore is presumably transferred to the female, although the process as far as we know has never been observed. In *Penaeus setiferus* the endopodite of the second pair of pleopods is also modified to some extent and probably also plays a part in the transference of the spermatophore.

In most species the female has on the ventral surface of the thorax between the bases of the last pair of pereiopods a structure of plates partially enclosing a space into which the spermatophore is placed. This thelycum varies greatly in complexity, in some species (*Penaeus brasiliensis* and *Xiphopenaeus kroyeri*) being well formed, in others less developed.

In *Penaeus setiferus* the thelycum is vestigial in character and does not function as a secondary sexual organ. The spermatophore is attached, by a gluelike secretion of the male, to the ventral surface of the female between the bases of the third and fourth pereiopods. Two winglike processes on the anterior end of the attached spermatophore fit securely into the grooves between the third and fourth pereiopods and form an inverted funnel into which the "glue" flows, fastening the spermatophore to the female.

The spermatophore so attached is quite easily dislodged. This may, to a certain extent, explain why in *Penaeus setiferus* spermatophore-bearing females are much less abundant in the catches than are similar females of *Penaeus brasiliensis* and

Xiphopenaeus kroyeri. In fact, only 20 such females have been obtained from the thousands of shrimp examined. Considering only females handled during those months in which spermatophores have been found, we have the relations shown in table 4.

TABLE 4.—*Penaeus setiferus spermatophore records April to August 1931 and April to July 1932*

State	Females examined	Spermatophores found	Percent
Georgia	11,015	3	0.027
Louisiana	3,561	7	.20
Texas	3,911	10	.26

All these 20 spermatophore-bearing females were in the ripest of the stages distinguished by examination of the ovary. Their lengths, which range from 141 to 186 mm with a mean at 166.3, agree well with the lengths of females showing the last stages of maturity.

The period in which these females are found is from April to August, inclusive, which covers almost the entire season during which the ovaries appear ripe. All were taken in fairly deep water, either in open sounds or the sea or Gulf, in localities where the salinity is the highest found in the range of the shrimp for this season of the year.

The next question is as to the time during which the male is capable of furnishing spermatophores. The spermatophores when formed are easily recognized in, or expressed from, the lower end of the vasa deferentia of the male, and records of their presence or absence are at hand for part of our series of length-frequency data. In 1932 in Louisiana maturing males were first present in the latter part of March, thus appearing slightly in advance of maturing females. They usually appear slightly earlier and last as late in the season as mature females. We may conclude, therefore, that during the period that females are capable of spawning, breeding males are also present.

To summarize: Ripe females are common during April, May, June, July, and present but scarce in August and September (Georgia, 1931). Spermatophore-bearing females have been obtained from April to August (these must be within a few hours of spawning). Mature males are present throughout this period. Young in the first post-larval stages are found from at least late April to August. We feel justified in assuming, on the basis of these data, that in 1931 spawning occurred during April, May, June, July, and to a reduced extent in August and September, even without having as yet observed spawning or having obtained fertilized eggs. Of course, the dates of spawning will vary from season to season.

It may next be inquired, Where are the shrimp spawning grounds? On this important question our evidence is again indirect, consisting of four types of data—the relative distribution of males and females, the relative distribution of the various stages of maturity, the distribution of that stage of maturity represented by the spermatophore-bearing females, and the distribution of larvae.

The plankton material containing penaeid larvae has not yet been analyzed and therefore cannot throw light on the location of the spawning grounds.

As stated, all spermatophore-bearing females have been obtained in fairly deep water of high salinity. Since we have good reason to think that the spermatophores

are soon dislodged and the eggs must be laid and fertilized before this happens, we may infer that spawning occurs in these localities.

There remains to consider the distribution of the sexes and the stages of their maturity. As the simplest we shall first consider the distribution of the stages of sexual maturity. If the numbers of immature and maturing males or females from different localities are compared, the greater proportion of maturing individuals will be found in outside waters. (See fig. 8.) This is more marked with the later stages of maturity. Thus, in Georgia, in 1932, an intermediate stage of ovary development was over twice as common in outside waters as in the creeks, while the last stage of ovary development recognized was six and one half times as common. As will be recalled, the spermatophore-bearing females, which represent the last stage of maturity, were all found in the Gulf or ocean with a single exception taken in an exposed sound. A satisfactory analysis of these data will require the inclusion of figures from another breeding season and must be presented at a later date. The present data can be interpreted in but one way—that by far the greater proportion of spawning takes place in the Gulf or ocean and that only a slight amount, if any, occurs on the inside. The spawning seems to be correlated with high salinity.

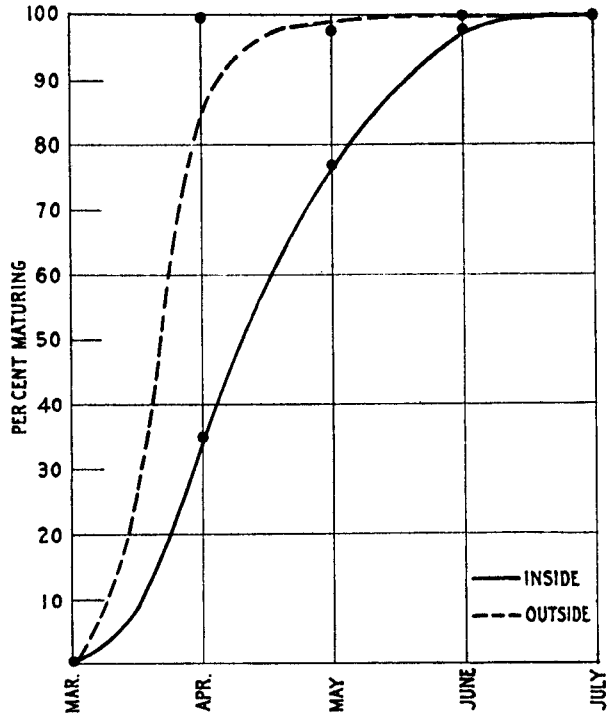

FIGURE 8.—Percent of maturing females in the inside and outside waters of Georgia from March to July 1931.

SEX RATIO

A comparison of the proportion of the two sexes in the catch at different times of year and in different localities shows fluctuations associated with spawning. Since additional data will be required for a satisfactory analysis of these fluctuations, only brief mention of the facts will here be made. As may be seen from figure 9, in Georgia from February 1931 to July 1932 there is a well-marked annual cycle. During the winter (from the last half of September 1931 to the last half of April 1932, inclusive) the proportion is constant, the females constituting slightly over 52 percent of the 25,601 shrimp measured. During the similar part of the preceding year the females furnished essentially the same proportion of the 11,283 shrimp. In contrast, the period from the last half of May to the first half of September 1931, inclusive, and again from the first half of May to the first half of August 1932 (where, at this time, our record ends) there are sudden and remarkable fluctuations of the proportion, the females rising above 80 percent and falling nearly to 30.

This period covers the time during which the adults mature, spawn, and disappear. A few weeks after spawning begins and when about half the females are maturing the

fluctuations begin and only end with disappearance of the adults from the fishing. The rise in proportion of the females succeeded by a fall appear to be the result of differential behavior of males and females associated with spawning. We have found no indication of a sex reversal in *Penaeus* such as has been claimed by Berkeley for *Pandalus*.

Further data is being collected on this interesting question.

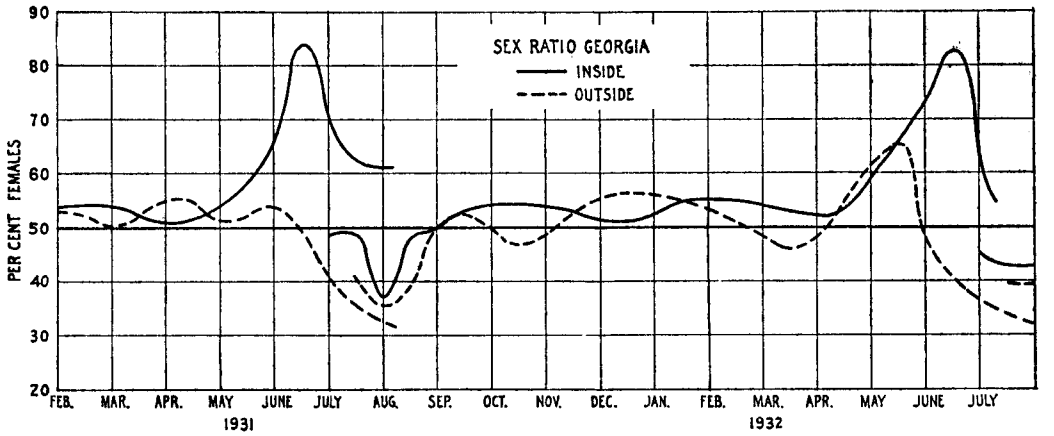

FIGURE 9.—Percent of females appearing in catches from inside and outside waters of Georgia from February 1, 1931, to August 15, 1932, during which period 58,521 shrimp were measured and examined.

LARVAE

The study of the larvae of *Penaeus* by Müller (1863, 1864), Brooks (1883), and Kishinouye (1900b) have shown the main features of the unusual larval history beginning with the nauplius, not found elsewhere among the higher crustacea. There are a large number of stages (6 to 8) including nauplius, metanauplius, protozoea, zoea, metazoea, and mysis. In no case has the species of the larvae been known with certainty, and in consequence there exists no data for the identification of the larvae. This is a serious lack where 4 species of penaeids appear in the commercial catch and 15 or 20 have been recorded, the larvae of which may be encountered. Other facts indispensable to this phase of the life history, such as the duration of the stages and their behavior, are also lacking.

The extensive plankton collections of the investigation have not yet been studied in detail, and although larvae are present we are as yet unable to give a satisfactory summary of their distribution.

YOUNG

From the distribution of the mature adults, spawning must take place predominantly, if not exclusively, in outside waters of high salinity. What little is known of the distribution of the larvae does not conflict with this. The distribution of the postlarval young is, however, different. These forms, essentially similar to the adult except in size, the smallest that we have obtained measuring 7 mm in length, give up the swimming habitat of the larvae and seek the bottom, thus resembling the adult in habits as in form. The young, as has been stated, are found on muddy bottoms in shallow water of high temperature and low salinity exclusively in bays or inside waters and often far from the ocean or Gulf. The upper limit of size of the young in

this habitat is not sharply defined; some shrimp as large as 100 mm have been encountered, but the majority are below 40 mm.

We have no data on the growth in this earliest stage, but they first appeared in the Georgia commercial catch at an average size of 90 mm (70 to 105) in July 1931, and again in July 1932, 2 or 3 months after the beginning of spawning. The reactions that lead the larvae from the outside more saline waters to the brackish muddy-bottom waters favored by the young, or lead the young back to the waters of higher salinity where they first enter the commercial catch, have not been studied, although they must hold the key to an understanding of one of the most interesting phases of the shrimp life history.

To compare with this picture just given of the spawning, larvae and young of *Penaeus setiferus*, we may review the findings of Ehrenbaum (1890) on *Crangon* (*Crago*), Mortensen (1897) on *Palaemon*, and Kishinouye (1900a), Spaulding (1908), Gates (1910), and Viosca (1920, Tulian 1920, 1923, and 1926) on *Penaeus*. Ehrenbaum found that in the North Sea the ovigerous females of *Crago* and the small free swimming larvae are found only in the strongly salt water of the flats and about the offshore islands of the North Sea. Only very exceptionally are larvae or ovigerous females taken in the brackish waters of the estuaries.

In sharp contrast, the young, measuring 5 to 10 mm, are found in great numbers from spring to late summer in the Dollart and Jade Rivers, far upstream in brackish water. From the percentage of ovigerous females found at different seasons, Ehrenbaum concluded that there were two spawning seasons and that hatching occurred primarily in July and to a less extent in March. No additional support for the double spawning season has been presented by the later writers.

In *Palaemon fabricii*, studied by Mortensen, the females spawn in deep water in May, the eggs hatching chiefly in June. As in *Crago* the larvae are pelagic and never appear in the brackish water of fjords or creeks. After a pelagic life of 3 to 5 weeks, the first young appear early in July. The young are found in the rapidly growing vegetation of the shallow water of little creeks and fjords. The larger females are said to lay a second batch of eggs shortly after the hatching of the first. In neither of these species has fertilization been observed.

It will be seen that the distribution of the ripest females, the larvae, and the young in both these species agree with what we have observed in *Penaeus*.

The data of Kishinouye (1900a) are of more interest because they deal with various Japanese species of *Penaeus* closely related to the forms we are studying. Unfortunately, the basis of his statements are not given in the English summary of his paper. He gives tables for sexual maturity in five species. The period of May to September, inclusive, contains all these mature seasons, although most are individually shorter than this. In three species the males are said to be sexually mature throughout the year. The eggs ripen in spring and spawning takes place in summer and autumn. Kishinouye describes the spermatophores in several species. Eggs are said to be discharged from time to time as they ripen. He mentions finding the larvae in shallower water than that in which the spawning shrimp live but does not specifically describe the habitat of the young.

The breeding season given by Kishinouye agrees in general with our findings. It is not true of the male of *Penaeus setiferus* that mature individuals are present at all times of the year, as he claims for certain species. We are very much inclined to doubt that in *Penaeus setiferus* spawning takes place from time to time as the eggs ripen; it is more likely that all the eggs are spawned at one time.

Only those findings of Spaulding, Gates, and Viosca relating to the spawning and young will be given here. Spaulding thought that the breeding began about the middle of June and that spawning took place "in the deeper water of the larger bays or even in the Gulf." He interpreted his data as showing either a long breeding season during the summer or two breeding seasons a year. Two years later (1910) Gates reported that there was only one breeding season and that "this extends from, approximately, the first of May to the last of July." Our investigations show that the period given by Gates covers the most intensive portion of the spawning season and that the entire season may be longer by a month or two on either end. Contrary to Gates' assertion that "the smaller the shrimp the earlier it spawns", we find that the larger shrimp mature first, consequently they also probably spawn first (fig. 7).

Viosca states that *Penaeus setiferus* spawns in the Gulf, chiefly on the evidence that sexually mature shrimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1¼ inches is reached. "By May, reasonable numbers of baby shrimp appear in the shallow waters near the coast line and a large proportion gradually migrate into brackish waters, all growing rapidly throughout the summer."

That the sexually mature shrimp are more abundant in the Gulf than in the inside waters agrees with our experience, but that no mature are taken in the bays is too sweeping a statement. Although always strikingly less abundant, especially in the more mature stages, we have records of many shrimp in advanced stages of ovary development from the inside waters both of Louisiana and of Georgia.

Viosca was led, apparently, to infer that the larvae live in the plankton up to a length of 1¼ inches by his inability to obtain smaller young. The largest larvae found by Müller were 4.5 mm long, the smallest post-larval young about 5 mm. We have obtained young as small as 7 mm. Obviously the larvae do not reach a length of 1¼ inches (31.75 mm). Either this size was inferred but not actually seen, or, if seen, some other crustacean was mistaken for *Penaeus*. We have been unable to find young of this size on the outside, either in the plankton, the trawl material, or on the ocean beaches, although we have obtained them in inside waters in all four States in which we have worked.

Although a gradual inward migration of young such as pictured by Viosca would be a reasonable process, the presence of many young of 7 mm and up in the creeks, bayous, and lakes, and their complete absence on ocean beaches show that the larvae often pass directly to shallow brackish waters. Like Viosca we have found that the larger young of 20 to 50 mm move, in general, seaward through the summer and fall, so that there is always a gradient of decreasing size from the waters of greater salinity toward fresh water.

Owing to the extended spawning season, the advent of the young into the commercial catch is followed week by week by new contingents which move into the fishing zone and become large enough to be taken by the trawls. As a result, the lower limit of size in the commercial catch is approximately constant through the summer and into the fall, as might be expected, since the limit is set by the selective action of gear and the movements of the young and not by growth. It may be affected, however, in a minor way by changes in temperature or by changes in the fishing areas which are not always strictly comparable from month to month.

GROWTH

Because of the fact that young are constantly being added to the population sampled by the fishing, it is extremely difficult to approximate the growth. As the earliest spawned shrimp continually increase in length, and small of a relatively uniform size are constantly appearing, the range of sizes, of course, increases; consequently the growth is not represented by the mean or modal lengths, which each month are based on a new assortment of ages. It is clear that the increase of the means is much slower than the growth of shrimp of any particular age.

The advancing upper size limit of the entire group should measure the growth of the older shrimp but is difficult in practice to determine. No statistical measure exists which will be comparable for all these types of compound frequency curves. In discussing the series of length frequencies, we have used the mode, or most abundant size as determined by inspection, for the average, and for the upper and lower limits a point where the ordinate has fallen to 1 percent of the total number of measurements. Admittedly inaccurate, this may serve, however, as a first approximation for the purposes of the present discussion.

The length-frequency data obtained with a standard trawl in the ordinary fishing grounds is ill adapted to show growth. For the present, therefore, only the most general features will be sketched and a more detailed analysis postponed to a future time when another season's records are available.

The average size of the young at the time of appearance in July 1931 was about 90 mm, with a range from 70 to 105. (See fig. 10.) At this time there is no significant difference in size between the sexes; in fact a clear differentiation does not occur until the following April. Through July and August growth is rapid; and by the 1st of September the most common size is about 130 mm, while the largest exceed 160 mm. The lower limit rises slightly and remains at approximately 80 mm until the first of the following year. We may consider that with the present gear about 70 mm is the minimum size entering the commercial catch to any extent.

During September, October, and November the average length fluctuates between 120 and 130 mm. During this period the females seem slightly the larger. This is the time of the fall maximum of abundance and the peak of the average commercial catch. From a value of 130 mm early in November the average size falls slightly, reaching a low point of about 120 mm near the first of the year. The difference in size between the sexes also disappears. This corresponds in a general way with the low period of the commercial catch.

Obviously these decreases of average size must result from behavior, which is differential with regard to size—the large and the small shrimp must frequent different localities or react differently in other ways. It is suggestive that the winter decrease of size is accompanied by a very marked decrease of abundance. During the low temperatures of the winter, movements or habits of the shrimp are changed in such a way as to remove the majority of them from the field of the commercial fishery on the Georgia coast.

Following the first of the year (1932) the lower limit begins slowly to rise and by the 1st of April has increased from 80 to 100 mm. It is apparent that by January the last shrimp spawned in the preceding summer have entered the commercial catch and that the increase of the lower limit now reflects the growth. This seems the more probable, since the average advances at the same rate from 120 to 140 mm during this time.

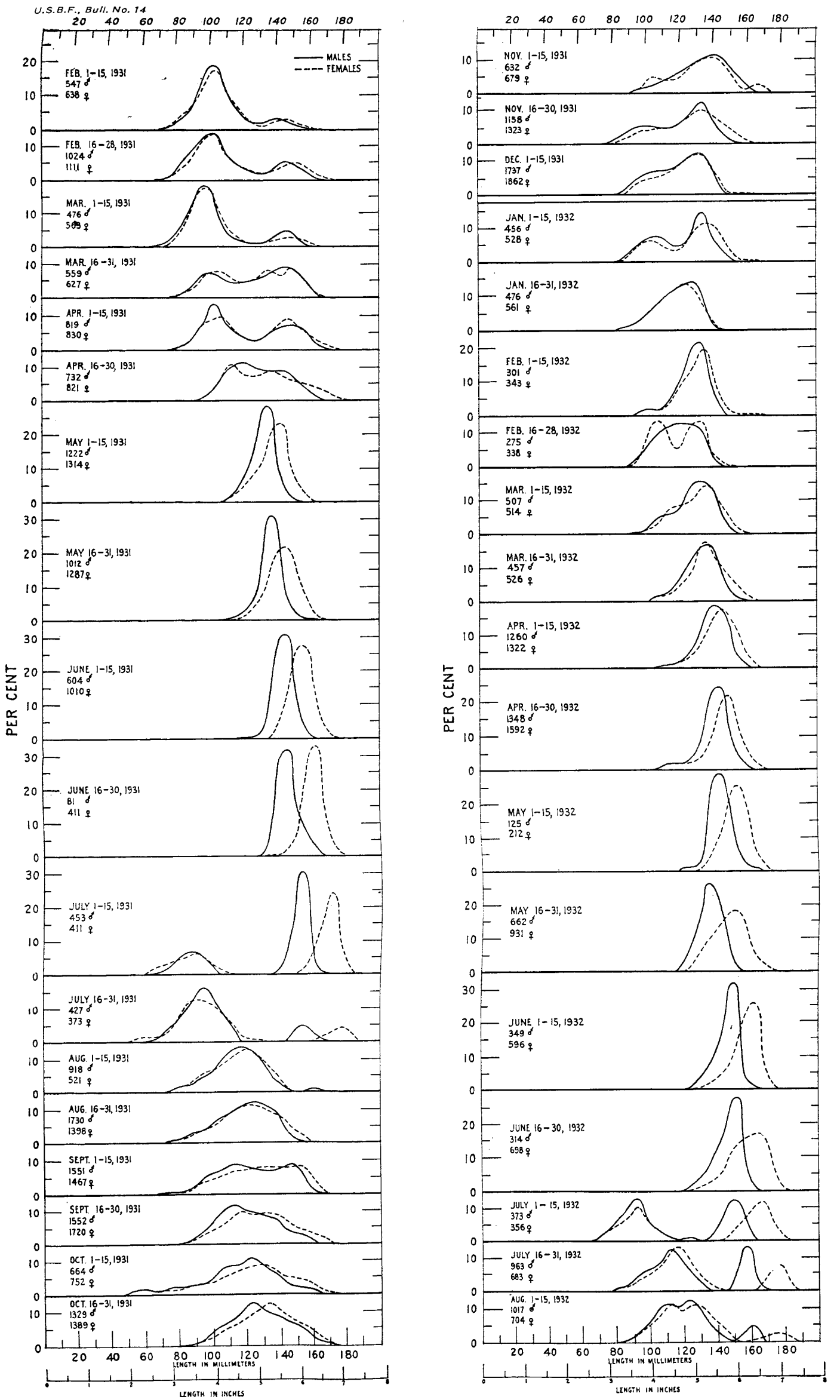

FIGURE 10.—Frequency distribution of the population of common shrimp in half-month periods for Georgia from February 1, 1931, to August 15, 1932. These curves represent the measurements of 58,521 shrimp. With but few variations the distributions for Louisiana and Texas follow those for Georgia very closely.

During the following months of April, May, June, and July 1932, accompanying a steady increase of water temperature from 56° F. in March to 86 in July there is a remarkable exhibition of growth. This is manifested in three ways. The steady ensuing growth is differential, being more strongly expressed in the females than the males; there is a surprising reduction of the size range; and the sex products mature rapidly.

As will be recalled, this period coincides with the time during which mature shrimp are taken. These first appear among the largest; but soon the smallest have exceeded the minimum size for sexual maturity, maturing becomes general, and by the 1st of July no immature of any size can be found in this group of shrimp.

The progress of growth is very interesting. During the spring, in each sex a distribution of wide range without a sharp mode is converted into a compact group with little variation of size and a well-marked mode. This may be caused by either or both of two processes—first, the more rapid growth of the smaller and younger members; second, the disappearance of the larger individuals that have spawned. Whatever the process, its orderly progress is striking. In fact, a frequency distribution from May or June may readily be identified by its characteristic shape.

Although up to April there has been no significant difference in size between the sexes as evidenced from the frequency curves (except for the short period in the fall of 1931 already noted), the growth of the females, beside producing a characteristically compact and homogenous group of this sex, rapidly outstrips that of the males until in June, as previously stated, the sexes differ in length by 8 percent, the males averaging 144 and the females 156 mm. By this time the range has been so reduced that the ninth decil of the males (the largest males remaining after the upper 10 percent have been cut off) is below the average of the females and the first decil of the females is above the average length of the males.

FATE OF ADULTS

A question of great interest and importance both from the theoretical and the practical standpoint is the fate of the larger group present in July. The smaller group of shrimp, traced into earlier months, was found to have been spawned by the larger, and the larger to have overwintered from young of the previous spring or summer. Traced onward from July the smaller group persists through the winter and spawns the following spring and summer. Does the group of larger shrimp also survive the winter and take part in a second spawning?

Again our evidence is indirect but impressive. We shall consider the length frequency and sexual maturity data in the light of the abundance of the shrimp. No accurate measure of the abundance of the shrimp in the waters of Georgia at different seasons is available. An approximation, however, is furnished by the number of shrimp taken in experimental trawling. By these useful, although imperfect, data let us follow the abundance of the group of small shrimp from the time of their entrance into the commercial catch until their disappearance. The numbers increase rapidly, being constantly augmented by new young of later and later hatchings. The maximum of abundance is reached in the fall, usually September or October, agreeing in time with the fall peak of the commercial catch. (See fig. 11.) Although the fall peak of the total catch tends to be overemphasized by the intensity of the fishing at this season and in general economic factors prevent a complete correspondence, nevertheless the fall catch rests on a period of marked abundance of shrimp. From

this peak the abundance declines and reaches a low point in late winter and early spring, coinciding with the low point of the catch which falls in February, March, or April.

The numbers obtained by experimental trawling then again increase, reaching a second peak in April or May at the time of the spring catch of large, mature shrimp so prized by the canners. The crest is more prominent and earlier than the spring catch would suggest.

From this peak of abundance there is a rapid and steady decline. In the first half of July, when the young of the year make their first appearance in the commercial catch, the two groups are approximately equal in abundance. By the latter part of the month the abundance of the group of larger shrimp has already fallen

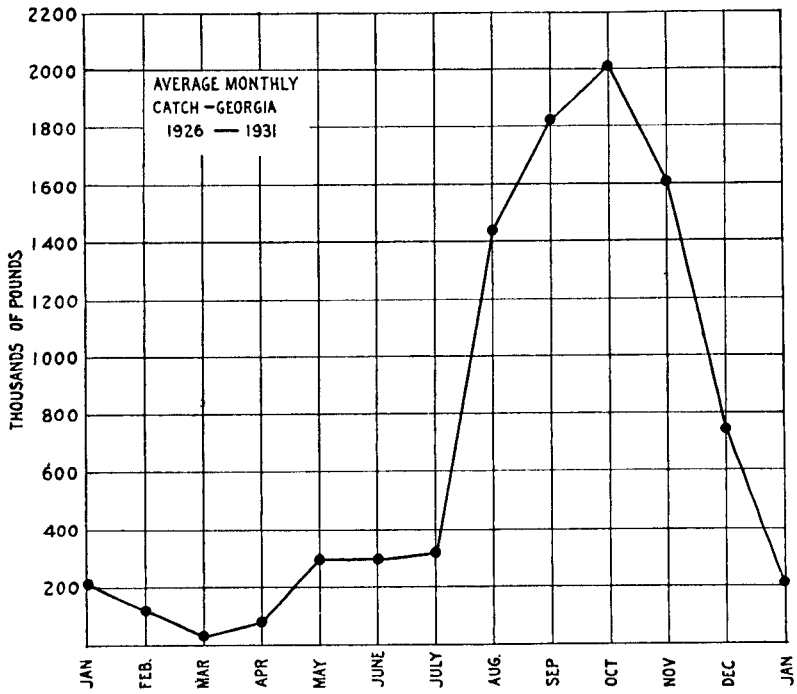

FIGURE 11.—Average monthly shrimp catch in Georgia from 1926 to 1931, inclusive. The average monthly polygons for Louisiana and Texas follow the Georgia polygon very closely.

below that of the growing young. The group of large shrimp can be more or less clearly recognized in August by their greater length, but the rapid growth of the young (see fig. 10) soon brings about an overlap, so that size alone will not suffice to identify them. The group of large shrimp are at this time sexually mature, and by this criterion a few may be found in September, but the number is very small—two or three out of hundreds. A careful study of the size frequency curves and those of sexual maturity fail to disclose further trace of them, and we are forced to conclude that they disappear from the fishery in Georgia. We have also been unable to find spent individuals such as should be present after the spawning season if the adults remained within the range of the fishery. Among the thousands of immature shrimp no undoubtedly spent female has been found, although some males examined may possibly belong to this category; the number of these, however, is small.

Kishinouye (1900a) believes that certain species of *Penaeus* die after spawning while others live through a second year. He does not indicate the basis of this belief.

Without evidence, it is idle to speculate whether the process of spawning is fatal to the shrimp—whether, like the salmon, they are weakened and soon succumb to enemies and disease or whether they retire to some new and as yet undiscovered habitat. All we know is that they play no further part in the fishery. The shrimp is therefore an "annual", being spawned in the spring or summer, spawning at the same season of the following year, and then passing out of the fishery. Since it is probable that those spawned early furnish the early spawners of the next year, the life span is very close to 1 year. This is the condition in Georgia. Whether or not in Louisiana and Texas the life span will prove to be the same is not yet settled, but the data so far available give no evidence of an essentially different life history.

It should again be emphasized that the above account refers only to *P. setiferus*. How many of these findings may apply to *P. brasiliensis*, *Xiphopenaeus kroyeri*, and *Trachypenaeus constrictus* remains to be determined. A consideration of these forms has been deferred because of their lesser importance and because data on these less common species has accumulated far more slowly.

HABITS

Observation of the shrimp under natural conditions is so difficult that only the most obvious habits can be thus determined. Systematic observations in aquaria have not yet been carried out. In spite of the paucity of direct observation it may be well to assemble what general knowledge is available. As already stated, *Penaeus setiferus*, like other penaeids, is a shrimp of subtropical littoral waters. The range of temperature under which we have taken it is 9° to 31° C. (48° to 88° F.). In the colder waters of the North Sea in Europe or of Alaska no penaeids are taken, the fishery depending rather on pandalids or cragonids. As with the Indian species observed by Alcock, *P. setiferus* appears to favor the deltas of large rivers like the Mississippi, although it is not confined to such localities. For example, shrimp are taken in large numbers off Cape Canaveral, Fla., in a region where there are no large streams. Perhaps the relation to rivers rests on the fact that, as we have seen, the young for part of their development frequent brackish or almost fresh water.

It appears to be more common on muddy than on sandy bottoms, but it must be remembered that mud is more common than sand in the neighborhood of large deltas.

Like other shrimp, *Penaeus setiferus* swims in two ways. Usually it swims forward by means of the pleopods or abdominal legs. When moving rapidly it swims or rather leaps backward by flexing the powerful muscular abdomen and sweeping the large tail fin under the body. In this way it may leap out of the water like a fish or out of an uncovered aquarium.

Although the shrimp spend most of their time on the bottom, there are a few well-authenticated cases where a school has been seen swimming near the surface. At times they bury themselves in the mud.

No systematic examination of the stomach contents has been carried out, but a few observations indicate that it is a voracious and well-nigh omnivorous feeder. This is supported by the observation of Viosca (Tulian 1920), and of Alcock (1906) and Kishinouye (1900a) on other species. Worms, crustacea (not excluding shrimp of the

same species), small mollusks, and plant debris are all eaten. Often it appears to eat the mud or sand for the organic matter which it contains. The presence of considerable amounts of mud or sand in the intestine appears to be the rule. In aquaria, fish or other shrimp are readily and successfully attacked and eaten.

Convincing evidence is at hand that the behavior of the shrimp is influenced by temperature and salinity, but as yet no observations have been made on its reactions to these stimuli or to others such as light, hydrogen-ion concentration, and oxygen tension. Early work on these important features of the shrimp's behavior occupies a prominent place in the program of the cooperative investigation.

DEPLETION AND PROTECTION

The shrimp investigation was initiated by the Federal and State Governments to supply the biological information necessary to guide analysis of the state of the fishery and to permit the framing of effective protective legislation when such is needed. It is not possible here to discuss in detail the bearing of the facts presented in this report upon the questions of depletion and protection; the intention is to do this in a subsequent publication. Here we may only indicate the lines which such a discussion must take.

First, it should be emphasized that depletion can only be detected by a careful analysis of the abundance of shrimp and that knowledge of abundance requires adequate statistical data. Existing catch statistics are inadequate, since they do not show the effort by which the indicated total catches were obtained. In addition we must know the amount of gear and number of men, or the individual boat catches must be recorded for analysis. Improvements in the method of gathering statistics have recently been made by Louisiana, and it is to be hoped that all of the eight South Atlantic and Gulf States will so modify their regulations covering the reporting of fish taken as to make possible the future analysis of abundance.

Fortunately it is not necessary to take an alarmist attitude, as we have obtained no evidence of serious depletion. At the same time common prudence should make impossible a complacent inaction until depletion is easy to see and hard to remedy. While there is yet time a concentrated effort should be made to institute the collection of statistics which may be used effectively in the immediate future.

In the absence of evidence of serious depletion at the present time we are unwilling to urge increased stringency of existing regulatory measures. We shall therefore merely suggest the bearing of the facts of the life history of the shrimp on the problems of protection and indicate the types of restriction which may be employed when analysis of the catch statistics indicates that additional protection is needed.

The outstanding features of the life history of the shrimp which may affect the question of its resistance to overfishing are: (1) Its short life span of 1 year, (2) its extended breeding season of about 5 months, (3) the very large number of eggs produced, and (4) its extensive habitat in the littoral waters of the South Atlantic and Gulf.

The shrimp's life span of 1 year, shorter than that of any other important economic animal, is clearly an unfavorable factor. The shrimp fishery must obviously lack the stability shown, for example, by the halibut fishery, where animals from 7 to 20 years of age appear in the catch and the entire failure of the young of any particular year would not seriously reduce the total. When the pressure of over-

fishing begins to be felt the shrimp will show sudden and violent fluctuations probably disastrous to the fishery.

Its extended breeding season of at least 4½ months, longer than that of the majority of animals of economic importance, and the large number of eggs produced are factors very favorable to the shrimp, since they render almost impossible the failure of an entire breeding season.

The South Atlantic and Gulf coasts, cut by a multitude of tidal rivers and bayous, furnish an unequaled extent of shallow, littoral waters of all degrees of salinity in which the shrimp flourishes. This extensive favorable habitat and the wide range extending from Massachusetts south to Brazil is an obviously advantageous condition. Without it, the multitude of shrimp would not have developed in this region. But while it may furnish a breeding reserve in places not readily fished, it affords no complete protection. The shrimp seems to be confined wholly to a narrow coastal strip favorable for fishing, since, as we have seen, *Penaeus setiferus* appears to be absent from deeper water. Certain of the creeks and bayous in which the young are found are unsuitable for fishing; but since these young all move to the larger bays or to outside waters during the winter, at some time all shrimp on our coast must run the gauntlet of trawls and seines. The number that escape depends wholly on the intensity of the fishery.

It is clear that under natural conditions the favorable factors were so far in the ascendancy as to produce an amazing abundance of shrimp. Even the great numbers taken by man have not sufficed to produce an alarming depletion. We must look forward, however, to a time when the increasingly intense fishery will turn the balance against the shrimp. Then the catch, maintained by constantly increasing effort, will begin to show great variations from year to year, some of them ruinous to fishermen and canners.

When additional protection becomes necessary it may take one or more of four lines—limitation of sizes taken, closure of certain seasons, closure of certain areas, and regulation of gear. All of these have been tried; the regulation of gear and the closure of certain areas, as, for example, nursery grounds and inside waters furnishing a preponderance of young, and certain seasons promise the most satisfactory results. Experiments now in progress will, it is hoped, indicate how gear may advantageously be modified.

SUMMARY

The present paper contains the results so far attained in certain phases of a cooperative program of study of the shrimp initiated by the United States Bureau of Fisheries and participated in by the States of Louisiana, Georgia, and Texas.

The shrimp supports the most valuable fishery in the South. Little has been known of its abundance, life history, and habits, consequently it warrants an investigation of some magnitude.

The importance of the shrimp fishery may be seen from the fact that in the United States in 1929, 113,263,000 pounds were caught, the value of which to the fishermen was $4,575,000. Of this, 95 percent was produced by the eight South Atlantic and Gulf States, Louisiana alone contributing 43 percent. In the South the shrimp exceeds the combined value of the two fisheries next below it.

Otter trawls operated from gas-driven boats take about 90 percent of the shrimp, the remaining 10 percent being caught by seines and cast nets.

Of the six species of shrimp caught in the South the common shrimp (*Penaeus setiferus*) is the most valuable. This species comprises about 95 percent of the catch in the South Atlantic and Gulf States, or about 90 percent of the entire amount of shrimp taken in the United States.

P. setiferus spawns from March or April to August or September apparently in the outside waters.

The post-larval young, measuring from 7 or 8 mm up, are first encountered in bays, bayous, and "lakes", sometimes far inland, but not on ocean or Gulf beaches. Their habitat is warm, shallow, brackish waters with muddy bottoms.

The young grow rapidly, and as they grow they seek deeper waters of greater salinity. During July, at an average size of about 90 mm, they enter the commercial catch, first on the inside, later outside. They continue in the fishery until the following spring and summer, when they spawn and disappear at the age of 1 year. During this time they grow to a length of about 120 mm; remain at this size through the winter, resume growth in the spring; and, after a rapid differentiation of the size of the sexes, spawn at length about 130 to 170 mm for the males and 135 to 190 mm for the females. Their fate is unknown, but that they disappear from the commercial catch following spawning is undoubted.

During the breeding season in the inside waters of Georgia there is a much greater proportion of females than males, while in the outside waters there is a greater proportion of males.

In Georgia at the beginning of the breeding season there is evident a differential behavior of the males and females; a differential growth rate between the sexes, with the females outstripping the males; and a change in the length frequency groupings from a wide to a very narrow range.

The common shrimp is most abundant in the coastal waters near river mouths or delta regions. It is omnivorous in its feeding habits. At present the shrimp fishery does not appear to show serious depletion, consequently increased stringency of existing laws is not imperative.

In the life history of the shrimp there are two factors favoring depletion—the short life span and exposure to fishing at all times. On the other hand, there are two factors opposing depletion—the extended breeding season and the large number of eggs produced. The most recent and at present one of the most decisive factors of the environment is the fishing of man. To date the favoring factors have maintained a vast shrimp population. With a more and more intensive fishery, the unfavorable factors must at some time become the more powerful. Because of the short life of the common shrimp, depletion, when it appears, will probably run a disastrously rapid course; consequently vigilance in safeguarding the industry is necessary. Against this time, methods of protection must be carefully planned.

There are four types of regulation applicable to the shrimp fishery; namely, closed seasons, closed areas, size limits, and restriction of gear. The fishery records of the various States are entirely inadequate to permit an analysis of abundance. For the safety of the shrimp industries it is imperative that this lack of catch records should speedily be remedied. It is recommended that all States collect on a standard form uniform records of the daily catch of each fisherman; certain of the States are now working on this problem. It is only by such records that any accurate indication of threatened depletion may be detected.

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U.S. DEPARTMENT OF COMMERCE
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THE HOMING INSTINCT AND AGE AT MATURITY OF PINK SALMON

(ONCORHYNCHUS GORBUSCHA)

By FREDERICK A. DAVIDSON

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 15

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1934

For sale by the Superintendent of Documents, Washington, D.C. - - - - - - - - - - - - - - Price 5 cents

THE HOMING INSTINCT AND AGE AT MATURITY OF THE PINK SALMON (*ONCORHYNCHUS GORBUSCHA*)[1]

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CONTENTS

	Page
Introduction	27
Marking pink salmon fry	28
Interpretation of results from marking experiments	29
Homing instinct	29
Age of pink salmon at maturity	34
Pink salmon marking experiment in British Columbia	36
Summary	38
Literature cited	39

INTRODUCTION

The pink salmon, *Oncorhynchus gorbuscha* (Walbaum), like the other species of Pacific salmon spend part of their life cycle in the sea and part in the rivers and creeks where they spawn and die. In southeastern Alaska, the pink salmon begin their spawning migration from the sea in the latter part of June and continue until late in September. Although the salmon migrate into the streams during the early summer months spawning does not begin until the second or third week in August. In March and April of the following year, the fry which have developed in size to a little over an inch in length (see fig. 1) and weigh less than 0.008 of a pound, emerge from their nests in the gravel and migrate directly to the sea. During their sojourn in the sea the fry develop into adult salmon weighing from 3 to 8 pounds and upon reaching maturity return to the streams to spawn.

The population of mature pink salmon that returns to spawn in any stream varies in size from year to year. This is due not only to the influence of changes in the natural elements of the habitats (stream and ocean) in which the population develops but likewise, and to a far greater extent, to the changes in the intensity of the commercial fishery that is imposed upon it during its migration from the sea. In view of this fact the Bureau of Fisheries is endeavoring to regulate the intensity of the commercial salmon fishery in Alaska so as to provide for an adequate run of pink salmon in every stream each season.[2] In order to secure an accurate count of the number of mature pink salmon migrating each season into each of several important salmon streams in southeastern Alaska, the Bureau has constructed weirs (see fig. 7) through which the salmon are counted on their way to the spawning grounds.

[1] Bulletin No. 15. Approved for publication, Feb. 21, 1934.

[2] On June 6, 1924, Congress approved an act which provided that not less than 50 percent of all the adult salmon returning to any stream should be permitted to ascend the stream to spawn.

The operation of these weirs each season is providing records of the size of the pink-salmon runs in each of the several streams on successive years. Hence it is possible, by means of these records, to make a study of the returns in numbers of adults resulting from the spawning of pink-salmon populations of varying size in an individual stream. However, in making such a study it is essential to know the extent to which the pink-salmon fry, after reaching maturity, return to spawn in the streams from whence they came and likewise the age at which they mature and return to spawn.

In life history studies of other species of Pacific salmon[3] it has been shown that their homing instinct and age at maturity can be determined by marking the fry (removing two of their fins) as they leave a particular stream and then examining the subsequent runs of mature salmon for individuals bearing the marks. In this way the extent to which the adult salmon return to spawn in their parent stream and likewise the age at which they return may be readily determined. Two experiments of this type have been carried on with pink-salmon fry, one at the Federal hatchery on the Duckabush River in the State of Washington and one in Snake Creek at Olive Cove, Alaska.

MARKING PINK-SALMON FRY

The marking experiment at the Duckabush River hatchery was carried on in the spring of 1930 and is the first known attempt to mark pink-salmon fry at the time they normally migrate from the streams. The fry in this experiment, as well as in the Snake Creek marking experiment, were marked by the removal of both their dorsal and adipose fins. This double mark was used because mature salmon are quite frequently found with one fin missing due to natural causes.[4] Furthermore it is not only necessary to remove 2 fins but likewise 2 fins that are widely separated on the body. In this way, the chances are remote of finding a mature salmon with an identical mark which is due to natural causes.

The 36,000 fry that were marked in this experiment were taken from the hatchery tanks where they had previously hatched under artificial conditions. The dorsal and adipose fins were removed by clipping them close to the backs of the fry with a pair of straight-bladed finger-nail clippers. The two fry pictured in figure 1 show the appearance of normal and marked individuals. Owing to the small size of the fry it was necessary to select apparatus that would facilitate their marking and minimize their mortality during the marking operation. The apparatus shown in figure 2 was found to give satisfactory results.

The shock due to the operation in removing the fins from the fry did not appreciably affect their mortality. In fact, the mortality of the fry during confinement in the tanks was practically the same in both the unmarked and marked stocks. Under normal conditions when there was an abundant supply of fresh water in the tanks the mortality during a 24-hour period did not exceed 2 percent of the total numbers in either of the stocks. However, if the supply of fresh water was reduced, the mortality would, in extreme cases, mount to 25 percent of their total number within a few hours.

The marking experiment in Snake Creek at Olive Cove, Alaska, was carried on in the spring of 1931. The 50,000 fry that were marked in the experiment were

[3] See the following references: Gilbert (1913) for coho salmon, Rich and Holmes (1928) for chinook salmon, Snyder (1921 to 1924) for chinook salmon,and Foerster (1929) for sockeye salmon.

[4] See page 37 for a discussion of the errors resulting from the use of only single fin marks in salmon marking experiments.

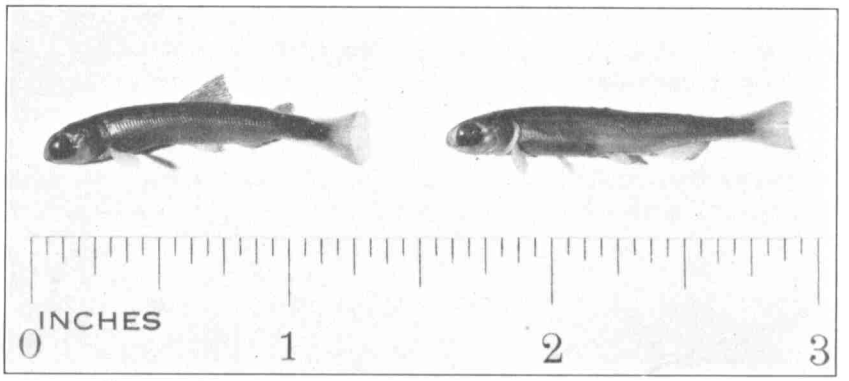

FIGURE 1.—Normal and marked pink-salmon fry at time of seaward migration.

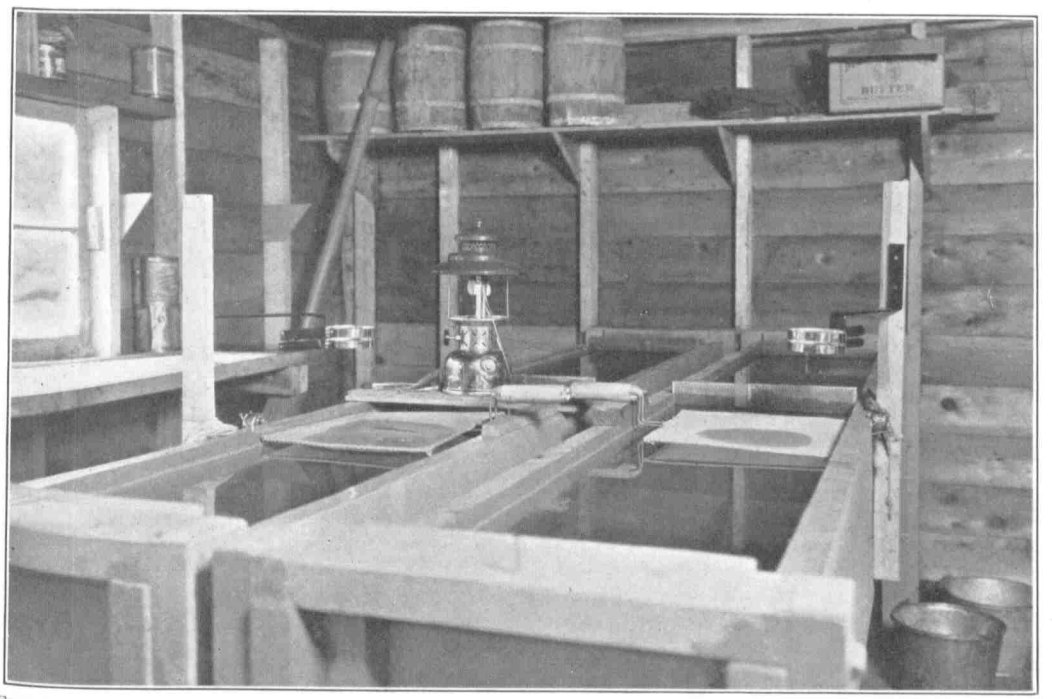

FIGURE 2.—Apparatus used in marking pink-salmon fry. Operator stands in front of shallow square net that rests on sides of tank just at surface of water. The small amount of water in the center of the net is sufficient to maintain fry in a semiasphyxiated state when they are placed there preparatory to marking. The two reading lenses, 4 inches in diameter, suspended above near side of net more than double image of a fry when it is held under them while being marked. The gas lamp beside net provides a direct light for operator and incidently radiates heat upon the hand that is used to catch the fry and hold them while being marked. Tanks are supplied with running water from stream. In order to keep an accurate account of number of fry marked the tally counter mounted on side of tank near frame that supports the reading lenses, is tripped every time operator marks a fry. Upper compartment of each tank is used to provide temporary storage for unmarked fry. After marking, fry are released in lower compartments where they are held from 12 to 24 hours before liberation in stream.

caught in the stream during their seaward migration from the spawning grounds where they had hatched under natural conditions. The fry were caught with a small screen wire trap net (see fig. 6) that was anchored in the middle of the stream where the current was the swiftest. Although thousands of fry were caught in the trap, not one was caught during the day, the fry migrating only at night. Many trips were made to the spawning grounds throughout the period the fry were migrating, but invariably no pink-salmon fry could be found during the daytime, either in the stream or in the pools along the sides of the stream. With the aid of a lantern they could be found in the stream any time during the night, but at dawn they disappeared, and those that did not reach the bay hid under the rocks or in the gravel.

The actual marking of the fry did not involve any difficulties for the method of marking had been worked out at Duckabush the year before. The only change in the routine from that used at Duckabush was that the marking was done at night so that the fry could be liberated at the time they normally migrated.

INTERPRETATION OF RESULTS FROM MARKING EXPERIMENTS

HOMING INSTINCT

The 36,000 pink-salmon fry that were marked at the Duckabush River hatchery in the spring of 1930 came from the spawn of 1929. Working upon the supposition that the pink salmon mature at 2 years of age,[5] the 1931 run of mature salmon in the Duckabush River was examined for individuals bearing the marks. In order to determine the extent to which the Duckabush River pink salmon returned to their parent stream to spawn, the 1931 runs in all the streams along the south shore of the Strait of Juan de Fuca, east of Port Angeles (see fig. 3) were likewise examined for individuals bearing the marks.

The hatchery operations on the Duckabush River made it possible to examine each one of the 3,800 mature pink salmon that composed the 1931 run. This was done at the time they were removed from the river and put in a retaining pond where they were held until fully mature and ready to spawn. The runs in the other streams along the canal and the south shore of the strait were examined by frequent observations of the schools of salmon as they migrated into the shallow waters on the spawning grounds. Where possible the salmon were collected in the shallow areas by means of a large net and carefully examined for individuals bearing the marks. The hatchery attendants at the State hatchery on the Dungeness River examined the 40,000 pink salmon in that stream that were spawned artificially. The observation of the schools of salmon on the spawning grounds began in the latter part of August and continued until late in September.

Out of the 3,800 pink salmon examined in the Duckabush River 5 females and 3 males were found bearing distinct adipose and dorsal scars. One female bearing both a dorsal and adipose scar was observed in the Hamma Hamma River in which approximately 1,500 pink salmon were spawning. One male bearing both a dorsal and adipose scar was found dead along the banks of the Dosewallips River in which approximately 5,000 pink salmon were spawning.[6] The dorsal scars on most of the marked

[5] Gilbert (1913) from a study of the markings on the scales of pink salmon taken in various localities came to the conclusion that the pink salmon invariably mature at 2 years of age. Furthermore, since the runs of pink salmon in the Duckabush River and neighboring streams occur only on alternate years, the pink salmon in these streams must either mature at 2 or 4 years of age. A further discussion of Gilbert's work is given in this paper under the section "Age at maturity of pink salmon."

[6] The Hamma Hamma, Duckabush, and Dosewallips Rivers are the only streams on Hood Canal in which pink salmon spawn in any numbers. The pink-salmon runs in these streams usually occur at the same time during the season.

salmon were roughened by the partial regeneration of a few spines. A marked salmon of this type is shown in figure 4. Only a few of the dorsal scars were perfectly smooth, showing no signs of regeneration, as seen on the marked salmon in figure 5. The adi-

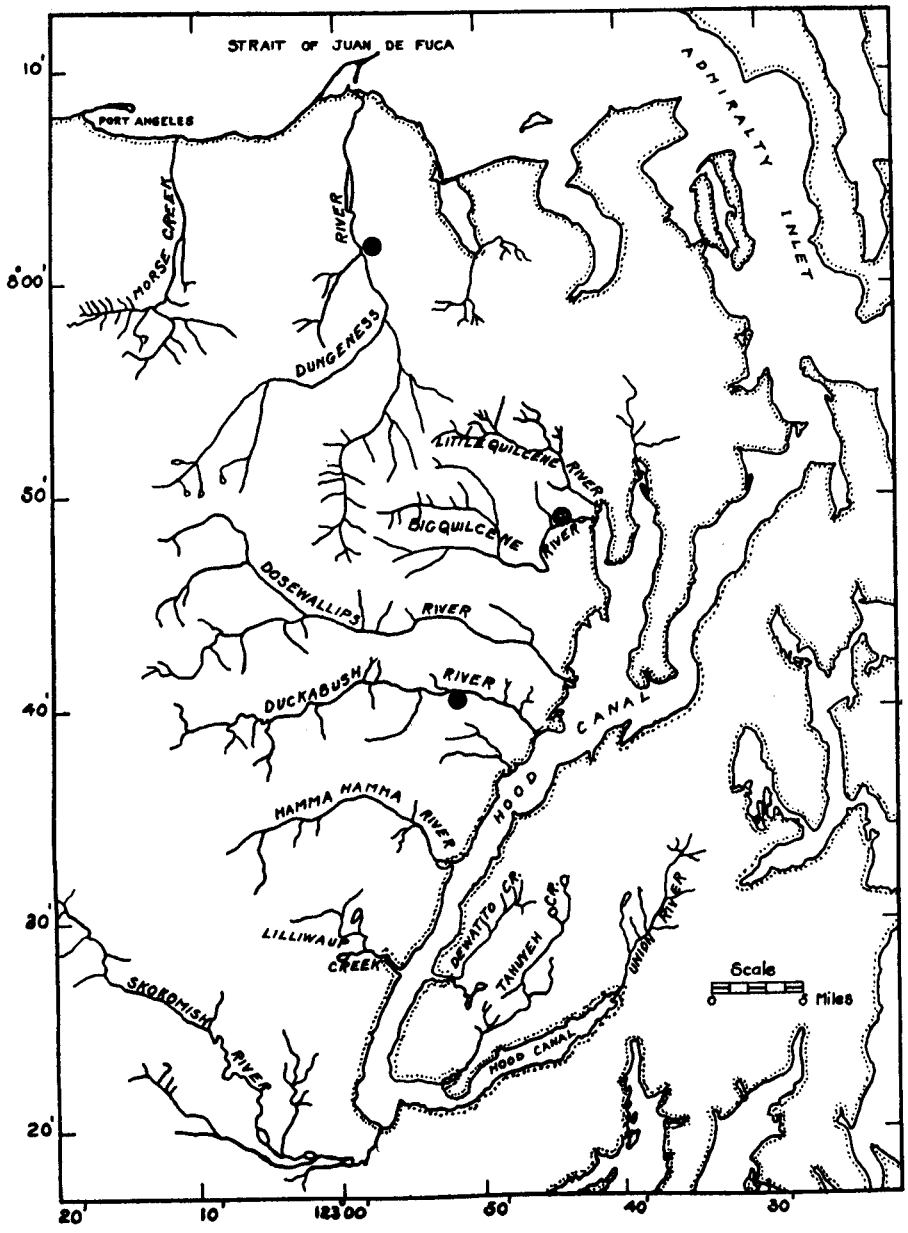

FIGURE 3.—Hood Canal and the south shore of the Strait of Juan de Fuca, Wash. The large dots mark the location of fish hatcheries. The pink salmon spawn only in the Hamma Hamma, Duckabush, Dosewallips, and Dungeness Rivers, and Morse Creek.

pose scars, with a few exceptions, were perfectly smooth and showed no signs of regeneration.

A number of pink salmon with only adipose fin scars were also recovered in the streams during the survey in the fall of 1931. Thirteen were found in the Duckabush

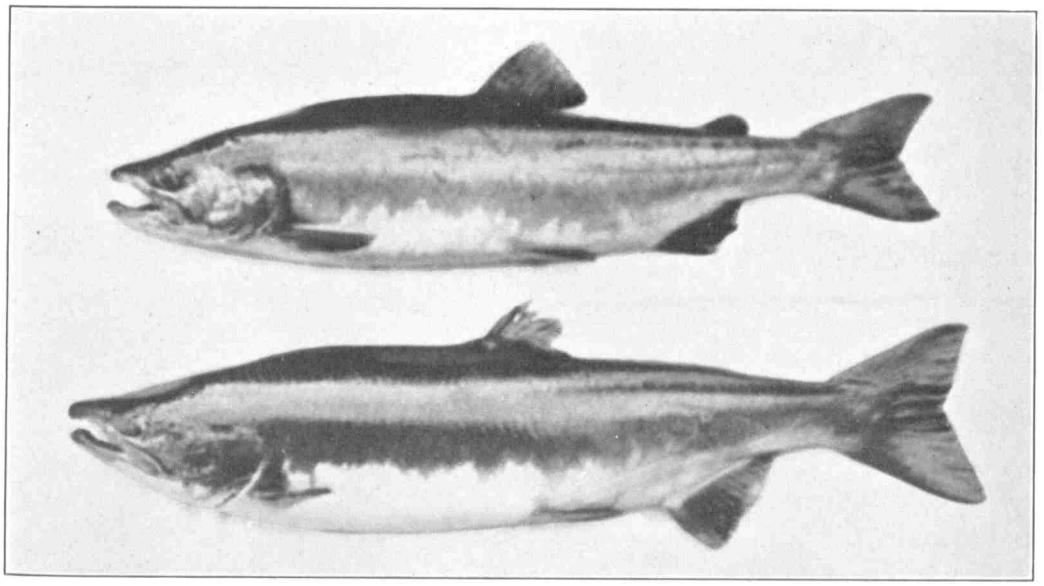

FIGURE 4.—Normal (upper) and marked (lower) adult pink salmon. The dorsal fin on the marked individual has partially regenerated.

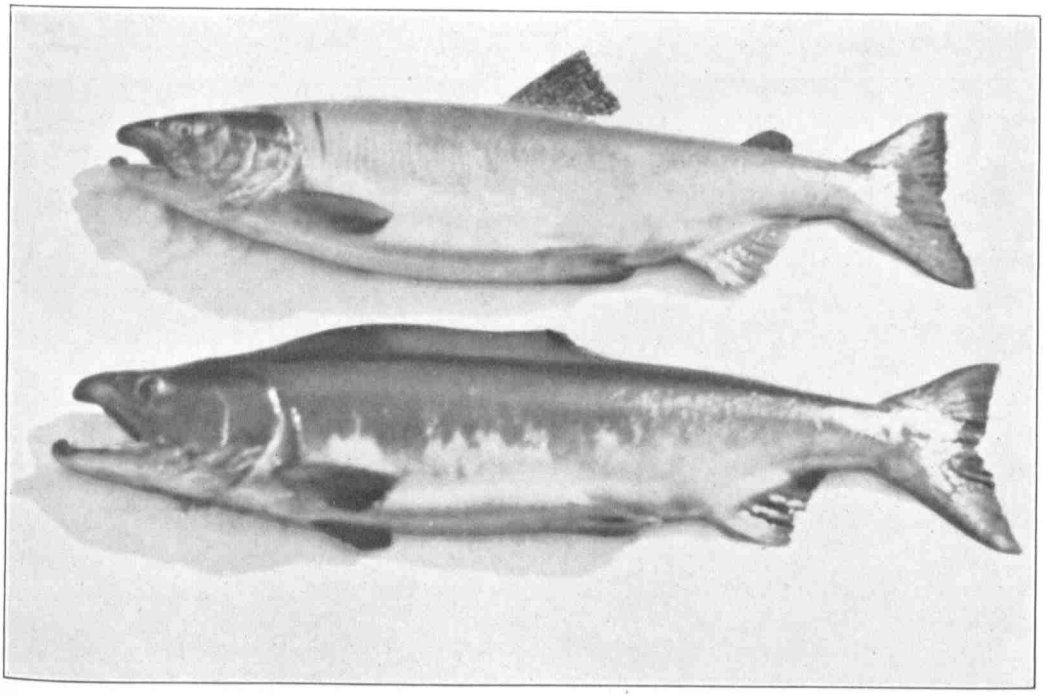

FIGURE 5.—Normal (upper) and marked (lower) adult pink salmon. Neither the dorsal nor adipose fin on the marked individual show signs of regeneration.

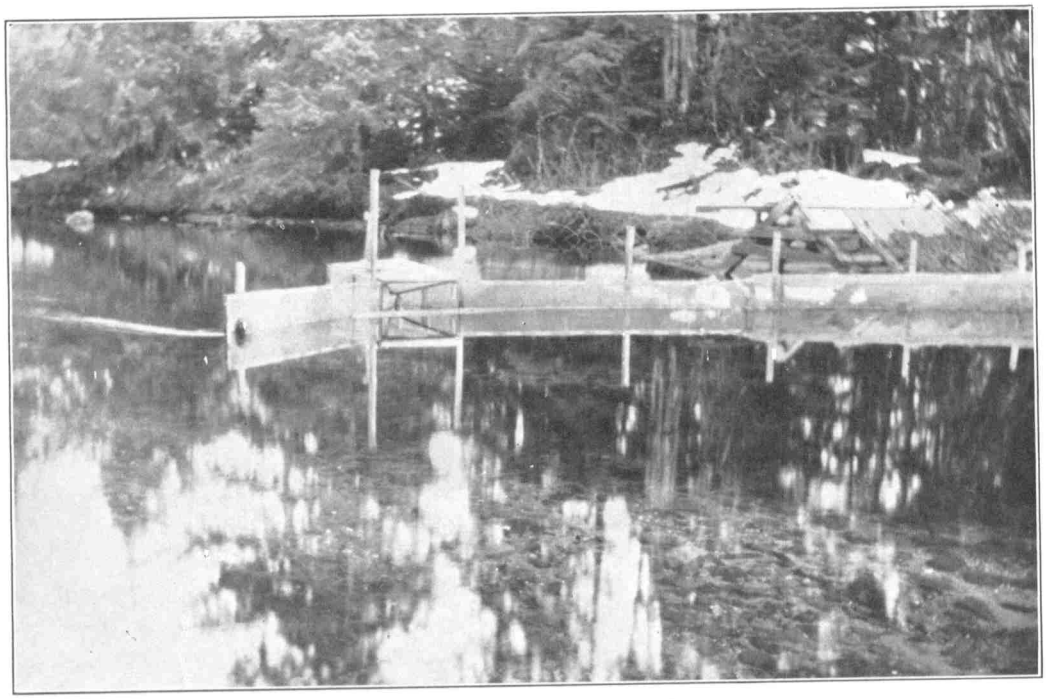

FIGURE 6.—Screen-wire trap and net used in catching the pink-salmon fry in Snake Creek.

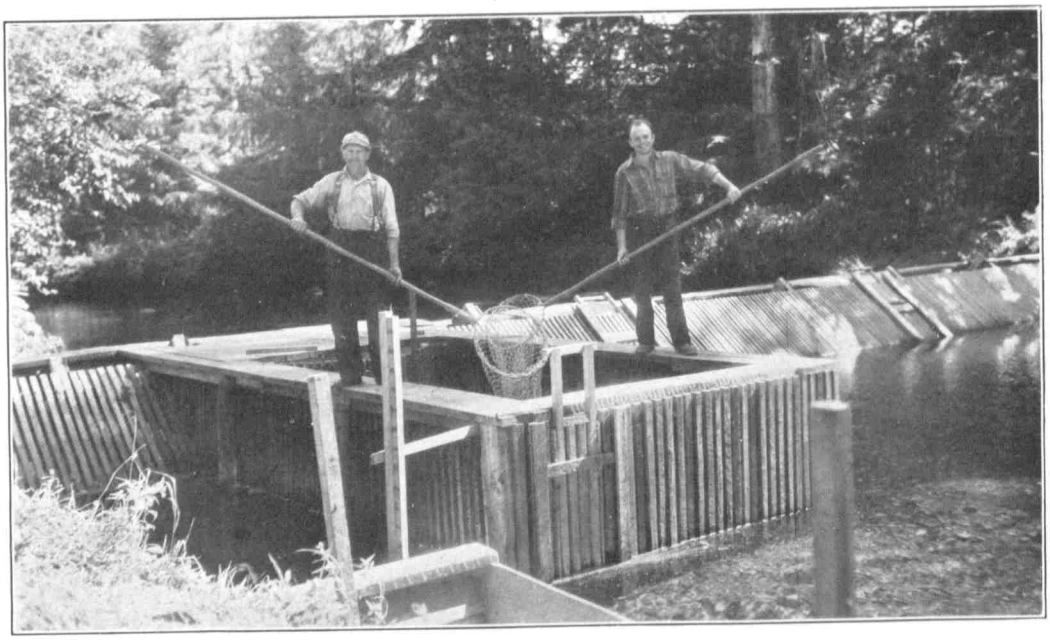

FIGURE 7.—Fish trap built in weir at Snake Creek. The large dip nets held by the operators were used to lift the salmon out of the trap. The sliding gate in the weir just to the right of the trap was opened when the salmon were counted through the weir.

River, 1 in the Dosewallips River, 3 in the Dungeness River, and 1 in Morse Creek. In a controlled experiment wherein 500 fry were kept for a number of months after being marked it was found that their dorsal fins had a greater tendency to regenerate than did their adipose fins. It may be that some of the 13 salmon with only adipose scars that were found in the Duckabush River were marked individuals whose dorsal fins had regenerated. However, owing to the frequent occurrence of salmon whose adipose fins are missing due to natural causes,[7] it is exceedingly illogical as well as hazardous to consider any of the individuals with only adipose scars as marked salmon whose dorsal fins regenerated. Especially is this true of the 3 pink salmon with only adipose scars that were found in the Dungeness River, for out of the 40,000 pink salmon that were examined in that stream when they were spawned artificially not one was found with both its dorsal and adipose fins missing.

The 50,000 pink-salmon fry, marked in Snake Creek at Olive Cove, Alaska, in the spring of 1931, hatched from the eggs spawned in the stream in the fall of 1930. Since marked pink salmon returned to the Duckabush River at 2 years of age, it was believed that they would likewise return to Snake Creek at 2 years of age. Hence the run of mature pink salmon in Snake Creek and the runs in the neighboring streams were examined during the summer of 1932 for individuals bearing both dorsal and adipose fin scars.

The runs of pink salmon in Snake Creek are usually rather large, ranging between 50,000 to 100,000, so that it was impractical to try to catch and observe each fish in the run. By making use of the counting weir that is operated in the creek it was possible to devise a method whereby a large portion of the individuals composing the run could be examined. An enclosure or trap was built above the weir, as shown in figure 7, into which the salmon could pass through a V-shaped opening in the weir. The opening into the enclosure was never blocked so that the salmon could pass through it at all times. The salmon that were trapped in the enclosure were removed by means of large dip nets, examined for missing fins, and then thrown into the stream above the weir so that they could continue on their way to the spawning grounds. At times during the day the salmon collected in such large numbers in the stream that it was necessary to open the gates of the weir (see fig. 7) and count them as they passed through on their way up stream. An accurate account was kept each day of the number of pink salmon lifted from the trap and the number counted through the weir. Although only a portion of the entire run of pink salmon in the stream was examined for marked individuals as it passed through the trap, it was possible, as will be shown later, to calculate the number of marked individuals in the entire run. The 1932 run of pink salmon in Anan Creek, a neighboring stream (see fig. 8), was examined for marked individuals in a similar manner by the operation of a trap that was built in its weir.

In addition to the examination of the 1932 pink-salmon runs in Snake Creek and Anan Creek a survey, similar to that made in the streams along Hood Canal in 1931, was made of the other pink-salmon streams in the vicinity of Olive Cove.

An examination of the 1932 run at Olive Cove shows that out of a total of 7,944 pink salmon lifted out of the trap, 23 (10 males and 13 females) had both dorsal and adipose fin scars, 5 had only dorsal fin scars, and 10 had only adipose fin scars. Although the marked individuals (those with dorsal and adipose fin scars) are the

[7] In both marking experiments it was not uncommon to find a fry whose adipose fin had never developed. By marking the fry under the reading lenses it was not difficult to determine the presence or absence of the fins.

only individuals that can be considered as returns, it is interesting to note that the dorsal scars on the 5 salmon having only these scars were identical to the dorsal scars on the 23 marked salmon. It is not at all unlikely that these 5 individuals resulted from the fry whose adipose fins were missed when they were marked. Regardless of this close resemblance, these 5 individuals cannot be considered as returns, for by so doing, the 10 salmon with only adipose scars would likewise have to be considered as returns. This as previously pointed out [8] would be a hazardous thing to do.

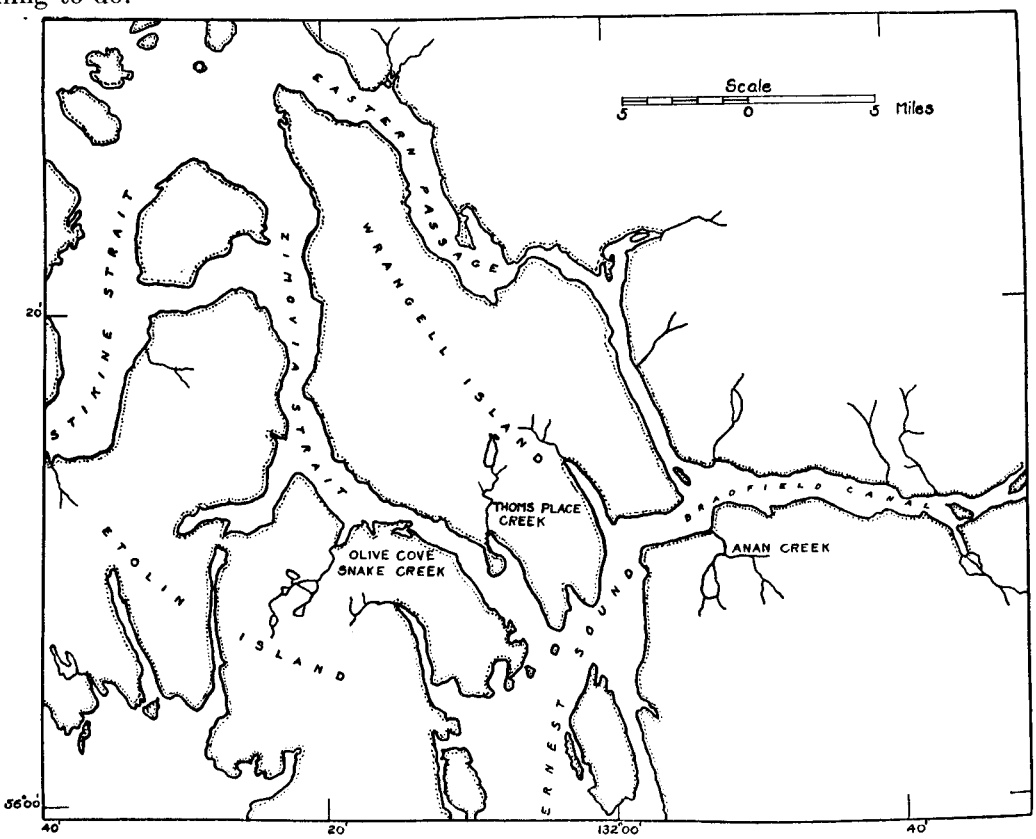

FIGURE 8.—Snake Creek at Olive Cove, Alaska, and vicinity. All of the streams shown on the map support a large population of pink salmon each season.

The method used in calculating the number of marked salmon in the entire run of pink salmon in Snake Creek in the summer of 1932 is given in the following equation: [9]

$$23+\left(10{,}640\times\frac{23}{7{,}944}\right)=54$$

where 23 equals the number of marked salmon found in the trap, 10,640 equals the total number of salmon counted through the gates in the weir, 7,944 equals the

[8] See discussion on page 29.

[9] This equation is based upon the assumption that there was the same proportion of marked salmon in the numbers counted through the weir as in the numbers lifted out of the trap. There is no reason to believe that the trap was selective in regard to the marked salmon; i. e., that more of the marked salmon in the run passed through the trap than through the gates in the weir. On days when the water in the creek was low and the visibility good, marked salmon were observed passing through the gates in the weir. During these times a total of 9 marked salmon were seen passing through the gates.

total number of salmon lifted out of the trap, and 54 equals the number of marked salmon in the entire run of pink salmon.

Out of the 132,351 pink salmon that composed the 1932 run at Anan Creek, 13,965 were examined as they were lifted out of the trap. Two individuals bearing fin scars were found among the salmon caught in the trap, one had only a dorsal fin scar and the other had only an adipose fin scar. No marked salmon were either caught in the trap or observed in the stream. Although the salmon with only the dorsal fin scar might have originated from a fry whose adipose fin was missed when marked, the absence of any marked individuals (those with both dorsal and adipose fin scars) in the salmon caught in the trap makes it rather improbable that this individual was a Snake Creek salmon.

The stream located nearest to Snake Creek in which pink salmon spawn in large numbers is Thoms Place Creek, approximately 10 miles south of Olive Cove and on the opposite side of Zimovia Strait. This stream was visited a number of times during the summer when the pink salmon were migrating into Snake Creek. During these visits only a few pink salmon were seen in the stream and none of these was marked. Toward the last of August when the run in Snake Creek was practically completed, a large run of pink salmon migrated into Thoms Place Creek. A survey of this stream was again made at this time, but no marked pink salmon were observed in the run.

A survey was made of the streams along Eastern Passage, the streams in Bradfield Canal other than Anan Creek, and the streams along the shores of Stikine Strait. Owing to the unusual lateness of the pink-salmon runs throughout the whole district it was not until late in August that the pink salmon collected in the shallower regions of the streams where they could be observed. About 200,000 pink salmon in all were observed as they swam about in the shallow waters of the streams. No individuals with both their dorsal and adipose fins missing were found in any of the streams that were visited.

In view of the returns from these marking experiments, it is conceivable that the extent to which the pink salmon return to their parent streams to spawn may be dependent upon the proximity of other pink-salmon streams in the vicinity. That is to say, the pink salmon composing the runs in streams that are more or less isolated from other pink-salmon streams may show very little or no tendency towards straying whereas the pink salmon in streams flowing into bays and in close proximity to other pink-salmon streams may stray more or less into the neighboring streams. The straying of the marked Duckabush River pink salmon into the Hamma Hamma and Dosewallips Rivers may be due to the close proximity of these streams to the Duckabush River. The Dosewallips River is located 4 miles north of the Duckabush River and the Hamma Hamma River is located 9 miles south of the Duckabush River.

The apparent lack of straying of the Snake Creek marked pink salmon might well be due to its isolation from the other large pink salmon streams in the district. Although Thoms Place Creek is only 10 miles south of Olive Cove, the main run of pink salmon in this stream is usually much later than the run in Snake Creek. No marked individuals were found either among the pink salmon in this stream during the early part of the summer or in the large run that occurred late in August. The other pink-salmon streams in the district are all located more than 20 miles distant from Olive Cove. Anan Creek, in which a weir trap was operated in a manner similar to the operation of the trap in Snake Creek, is 25 miles distant from Olive Cove. The

run of pink salmon in Anan Creek also appears at practically the same time during the season as the run in Snake Creek. If the Snake Creek marked salmon strayed any distance from their parent stream in perceptible numbers, it is highly probable that they would have been picked up by the trap in the Anan Creek weir. However no marked pink salmon were either found in the trap or observed in the stream. This, together with lack of recovery of marked pink salmon in any of the other more distant streams in the vicinity, makes it rather improbable that the Snake Creek pink salmon strayed in perceptible numbers from their parent stream.

AGE OF PINK SALMON AT MATURITY

The scales of the pink salmon like the scales of the other species of Pacific salmon, tend to grow at a rate proportional to the growth of the fish. This is accomplished by the deposition of new material around the border of the scale. Delicate ridges appear on the surface of the scale at intervals during its growth which form concentric rings separated by spaces of varying width. (See fig. 9.) The variation in the width of the spaces between the rings may be attributed to a corresponding variation in the rate of growth of the fish. That is during the spring and summer when the fish grows rapidly the rings on the scale are widely separated whereas during the fall and winter when growth is greatly retarded the rings are crowded together. In this way the surface of the scale is marked by bands of widely spaced rings followed by bands of closely spaced rings. Since the wide band of rings is formed in the spring and summer and the narrow band in the fall and winter, the two together represent a year's growth.

C. H. Gilbert (1913) in his paper "Age at maturity of the Pacific coast salmon" pointed out that the pink salmon all mature at 2 years of age as judged by the age reading of the growth rings on their scales. He described the pink-salmon scale as having three definite bands of growth rings. A central band of widely spaced rings of the sea type [10] followed by a band of closely set rings, which is in turn followed by another band of widely spaced rings. The first two bands of rings represent the growth of the fish during the first spring and summer in the sea and the first and only winter in the sea. The second band of widely spaced rings represents the growth of the fish during the second spring and summer in the sea. Since the second summer's growth band is never followed by a winter band of rings, Gilbert came to the conclusion that the pink salmon always mature at the close of the second year of their life.

Owing to the rapid growth the pink salmon must make, during their 16 or 17 months' sojourn in the sea, in order to mature at 2 years of age, some doubt has been expressed in regard to their age at maturity as determined from the bands of growth rings on their scales. In view of this fact a study was made of the scales on the marked pink salmon that were known to return to the Duckabush River and to Snake Creek at 2 years of age. The scale pictured in figure 9 is from a marked salmon that returned to Snake Creek and the scale pictured in figure 10 is from a marked salmon that returned to the Duckabush River. These scales were chosen because they are representative of the scales of the other marked pink salmon found in these streams.

The growth rings on the scale in figure 9 may be divided into the three characteristic bands described by Gilbert (1913). The first band of widely spaced rings, i. e., those laid down in the life of the salmon during its first spring and summer in the sea,

[10] Since the pink salmon fry in most cases leave the streams before their scales have appeared, the only rings that are formed in their scales are those that form during their life in the sea.

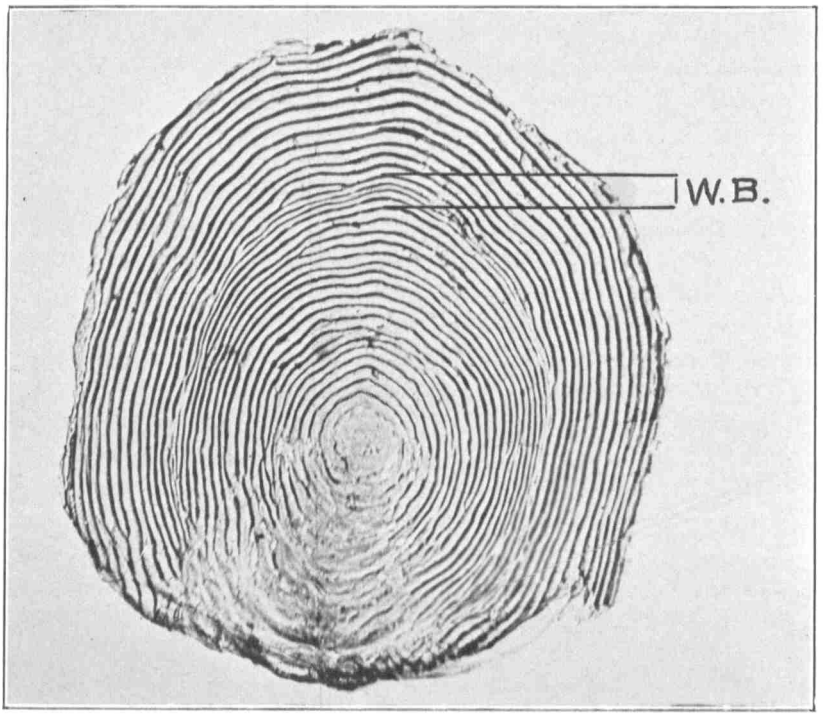

FIGURE 9.—The scale of a marked pink salmon recovered in the 1932 run of pink salmon in Snake Creek at Olive Cove, Alaska. The letters "W.B." indicate the winter band of growth rings.

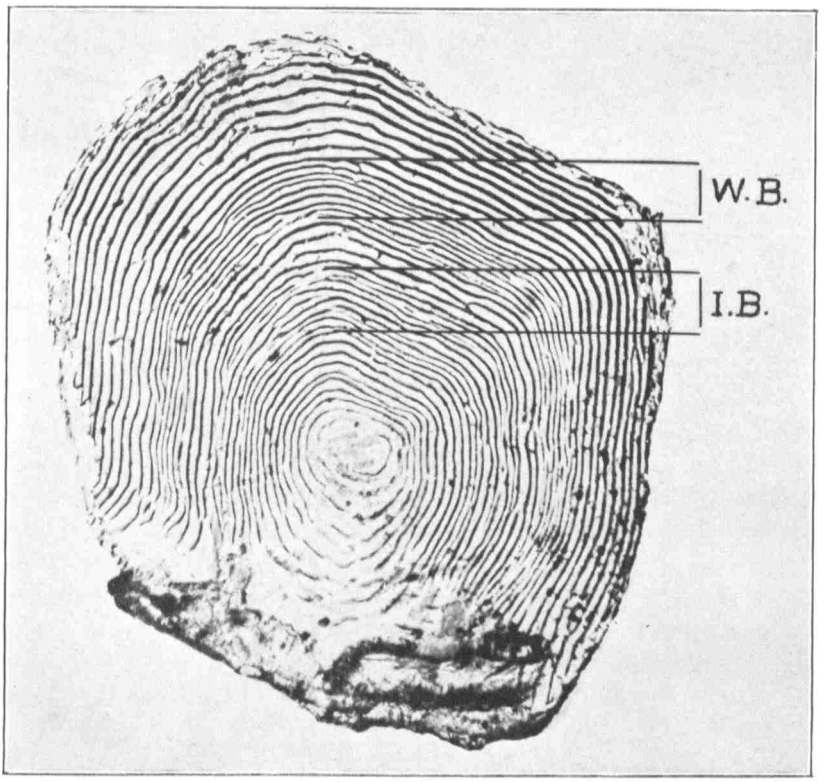

FIGURE 10.—The scale of a marked pink salmon recovered in the 1931 run of salmon in the Duckabush River, Wash. The letters "W.B." indicate the winter band of growth rings and the letters "I.B." indicate the incidental band of growth rings.

occupies the central area of the scale. This band is terminated at its outer border by a narrow band of closely set growth rings or the winter band (*W.B.*). The second band of widely spaced growth rings, i. e., those laid down in the life of the salmon during its second spring and summer in the sea, immediately follows the winter band (*W.B.*) and terminates at the margin of the scale.

The growth rings on the Duckabush River pink-salmon scale shown in figure 10 likewise may be divided into the three characteristic bands. The first band of widely spaced growth rings is, however, not very distinct since the rings near its center are in such close proximity that they form a rather definite incidental band of closely spaced rings (*I.B.*). The winter band of closely spaced growth rings (*W.B.*) and the succeeding second band of widely spaced growth rings are on the other hand very distinct and well marked around the circumference of the scale. This incidental band of closely spaced rings (*I.B.*) that occurred in the life of the salmon during its first spring and summer in the sea is no doubt due to a temporary retardation in its rate of growth. The occurrence of such aberrations on the scales of the Pacific salmon was recognized by Gilbert (1913, p. 5), who says:

> Thus it comes that the surface of the scale is mapped out in a definite succession of areas, a band of widely spaced rings always followed by a band of closely crowded rings, the two together constituting a single year's growth. That irregularities occur will not be denied, and this is natural, inasmuch as growth may be checked by causes other than the purely seasonal one.

Had not the scale in figure 10 been known to have come from a pink salmon that matured at 2 years of age, it would still be illogical to assume the incidental band of closely spaced rings (*I.B.*) to be a true winter band. Such an assumption would mean that the salmon bearing this scale spent 3 summers and 2 winters in the sea and matured at 3 years of age. This, however, would be impossible since the pink salmon runs in the streams on Hood Canal and along the Strait of Juan de Fuca occur only on alternate years. Hence the salmon composing these runs must mature at 2 or some multiple of 2 years of age.

Since the pink-salmon runs in the Duckabush River occur only on the odd years, it is impossible for any of the pink salmon in this stream to mature at 3 years of age. In order to check the possibility of any of the pink salmon in this stream maturing at 4 years of age, the run in this stream was examined for individuals bearing the marks in the summer of 1933. No marked salmon were found in the 1933 run and every fish was examined carefully at the time it was spawned artificially by the hatcherymen.

The runs of pink salmon in Snake Creek occur every year, hence the 1933 run in Snake Creek was examined in order to check the possibility of the pink salmon in this stream maturing at 3 years of age. The salmon run in this stream was examined in the same way that it was examined during the summer of 1932. No marked pink salmon was found in the 1933 run. There was, however, a number of pink salmon with deformed and missing adipose fins found in this run, which is further evidence that pink salmon with missing adipose fins due to natural causes are not infrequently found in the runs.

There is still other evidence which indicates that the pink salmon mature at 2 years of age. In 1913 and 1915 large shipments of eyed pink-salmon eggs were sent from the Pacific coast to the fish hatcheries in the New England States. These eggs were hatched artificially and in the spring of 1914 and the spring of 1916 the fry were liberated in a number of streams along the coast. In the summer and fall

of 1915 a large number of mature pink salmon returned to the streams in which the fry were liberated. A number of ripe eggs were removed from some of the females and after fertilizing them they were taken to the hatchery where they later developed into normal fry. In the summer and fall of 1917 another large run of pink salmon appeared in the streams in which the fry were liberated. Some of these salmon were sent to Dr. C. H. Gilbert who, after examining their scales, claimed that they had retained their original habit of migrating directly to the sea upon leaving their nests in the gravel and returning to the rivers to spawn and die at 2 years of age.[11]

The scales of the pink salmon that have appeared in Snake Creek and in other streams in southeastern Alaska on different years have been examined and all show bands of growth rings similar to those on the scale in figure 9. The scales of the unmarked as well as those of the marked salmon that appeared in the 1931 run in the Duckabush River were also similar to the scale shown in figure 10. In fact all the evidence thus far collected indicates that the pink salmon mature at 2 years of age and until contradictory evidence is found it may be assumed with relative certainty that they mature consistently at the close of their second year of life.

PINK SALMON MARKING EXPERIMENT IN BRITISH COLUMBIA

In the spring of 1931 Dr. A. L. Pritchard, of the Canadian Pacific Biological Station, working at McClinton Creek in Massett Inlet, British Columbia, marked 185,000 pink-salmon fry by the removal of only their adipose fins. The returns from this marking experiment are reported in table 1.[12] In discussing the significance of these returns Pritchard (1932, p. 10) makes the following statements:

> The return of 95 marked fish (52 percent of the recoveries) to McClinton Creek definitely establishes that there is a tendency on the part of the pink salmon of this locality to return to its native spawning area and that maturity is reached at the end of 2 years.
>
> It is not unlikely that the 22 fish taken in Massett Inlet and 16 in Naden Harbour and Otard Bay would have ultimately appeared in McClinton Creek had they not been caught by the commercial nets, in which case the return to McClinton Creek would have been 73 percent of the recoveries.
>
> The capture in other localities of 50 fish lacking the adipose fin (27 percent of the recoveries) is evidently indicative of a certain degree of wandering. Although not a single fin abnormality was discovered among 310,000 pink-salmon fry handled at McClinton Creek and the Tlell River, reports from other areas indicate the possibility that such abnormalities may exist to a very small extent. It is felt, however, that the indications shown by the large returns from some of the outlying districts should not be considered insignificant.

According to these statements Pritchard is apparently of the opinion that little hazard was involved by the use of only the adipose-fin mark for the future indentification of the salmon, and that all of the salmon reported in table 1 were originally McClinton Creek fry.

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[11] For a detailed discussion of the results from this transplantation of the pink salmon on the Atlantic coast see Reports of the Commissioner of Fisheries, 1916 and 1917, pp. 30 and 75, respectively.

[12] See A. L. Pritchard (1932) for data on recoveries of the adipose-marked salmon in the various localities as given in this table.

TABLE 1.—*Returns from the pink-salmon marking experiment at McClinton Creek, British Columbia*

[As reported by A. L. Pritchard (1932)]

Locality of recovery	Number of recoveries [1]	Approximate distance from McClinton Creek	Locality of recovery	Number of recoveries [1]	Approximate distance from McClinton Creek
		English miles			*English miles*
Alaska:			Southern British Columbia, Johnstone Strait	24	400
Karluk Beach [2]	8	1,000	Queen Charlotte Islands area:		
Snake Creek, Olive Cove [3]	10	180	Naden Harbour	14	40
Anan Creek [3]	1	180	Otard Bay	2	110
Northern British Columbia (exclusive of Queen Charlotte Islands):			Massett Inlet	22	10
Wales Island	1	120	McClinton Creek	95	0
Naas River area	1	140			
Skeena River	4	130			
Chatham Sound	1	110			

[1] Pritchard assumed that pink salmon with only adipose fin scars recovered in the summer and fall of 1932 originated from the McClinton Creek marking experiment.
[2] The data from Karluk Beach were reported by J. T. Barnaby of the U.S. Bureau of Fisheries.
[3] The data from Snake Creek at Olive Cove and Anan Creek were reported by F. A. Davidson of the U.S. Bureau of Fisheries.

One of the causes of error in the earliest marking experiments was the use of single fin marks for the future indentification of the salmon. Rich and Holmes (1928, p. 217) in reviewing these experiments make the following statements:

> The greatest cause of error in the earlier experiments was the failure of the investigators to realize that salmon occasionally lose one or more of their fins in other ways, and that as a result, if only one fin is removed experimentally, the mark may be duplicated accidently. For example, Hubbard removed the adipose fin from chinook fingerlings at the Clackamas hatchery in Oregon in 1895. The reported returns from this marking are so greatly opposed to the known facts of the life history and growth of chinook salmon that they are obviously in error, and there can be no question that they included fish not marked by Hubbard.

That the adipose fins of pink salmon are likewise missing due to natural causes was pointed out by the author in discussing the returns from the Duckabush River marking experiment. (See pp. 29–31 of text.)

In reporting the 10 pink salmon with only adipose fin scars from Snake Creek in Olive Cove, Pritchard failed to mention the fact that 50,000 pink-salmon fry were marked in this stream at the same time the fry were marked in McClinton Creek. Since the fry in Snake Creek were marked by the removal of both their dorsal and adipose fins, these 10 salmon were probably native to Snake Creek and consisted of salmon whose adipose fins were naturally missing or marked salmon whose dorsal fins had regenerated. (See discussion on p. 31 of the text.) The 8 pink salmon with only adipose fin scars reported by Barnaby from Karluk Beach were found during a 2-day examination of approximately 45,000 pink salmon composing part of the run into the Karluk River. Had Barnaby examined the entire run of 3,500,000 pink salmon in the Karluk River it is conceivably possible that, if the above proportion prevailed, he would have found in the neighborhood of 600 pink salmon with deformed or missing adipose fins. This together with the great distance that separates these 2 streams makes it highly improbable that these 8 pink salmon were of McClinton Creek origin. Furthermore if all the pink salmon with only adipose fin scars recovered in the Alaskan streams were of McClinton Creek origin, then it is conceivably possible that pink salmon with both dorsal and adipose fin scars, those of Snake Creek origin, should likewise have been found in the British Columbia streams. However no pink salmon bearing both dorsal and adipose fin scars were reported from Canadian waters.

In view of the returns from the Duckabush River and Snake Creek marking experiments, it is doubtful if the adult pink salmon often stray into streams other than those in the close proximity of their parent stream. The Dungeness River is approximately 60 miles distant from the Duckabush River, and in the examination of the 40,000 pink salmon at the Dungeness hatchery no salmon were found that could be considered as originating in the Duckabush River. Anan Creek is approximately 25 miles from Snake Creek in Olive Cove and during the examination of the 13,965 trap-caught salmon at Anan no pink salmon were found that could be said to have originated in Snake Creek. In fact no pink salmon were found in any of the streams in the vicinity of Olive Cove that could be said to have come from the Snake Creek marked fry.

It is not improbable that the 22 adipose marked pink salmon picked up by the commercial fishermen in Massett Inlet were of McClinton Creek origin. However for Pritchard to assume that all the salmon with adipose fin scars recovered in the other localities were likewise of McClinton Creek origin is to make an assumption too broad to remain within the realm of probability.

SUMMARY

In the spring of 1930, 36,000 pink-salmon fry were marked at the Duckabush River hatchery, Washington, by the removal of both their dorsal and adipose fins. These fry were hatched artificially from the spawn of 1929. In the summer and fall of 1931, 3,800 pink salmon returned to the Duckabush River, 8 of which were found to have both their dorsal and adipose fins missing. The Dosewallips River is located 4 miles north of the Duckabush River, and the Hamma Hamma River is located 9 miles south of the Duckabush River. One pink salmon with both its dorsal and adipose fins missing was found in each of these streams. Since the pink-salmon run in these streams occurs only on alternate years no run appeared in the summer and fall of 1932.

In the spring of 1931, 50,000 pink-salmon fry were marked in Snake Creek at Olive Cove, Alaska, by the removal of their dorsal and adipose fins. These fry hatched in the stream under natural conditions and came from the spawn of 1930. In the summer and fall of 1932, 18,584 pink salmon returned to Snake Creek, 54 of which had both their dorsal and adipose fins missing. The nearest pink-salmon stream in the vicinity of Snake Creek is Thoms Place, a small stream about 10 miles south of Snake Creek. The pink-salmon run in this stream, however, does not occur until the run in Snake Creek is practically completed. The other pink-salmon streams in the vicinity are all more than 20 miles distant from Snake Creek. No pink salmon with both their dorsal and adipose fins missing were found in any of the streams in the vicinity.

In view of the returns from these marking experiments is conceivable that the extent to which the pink salmon return to their parent streams to spawn may be dependent upon the proximity of other pink-salmon streams in the vicinity. That is to say, that the pink salmon composing the runs in streams that are more or less isolated from other pink-salmon streams may show very little or no tendency toward straying, whereas the pink salmon in streams flowing into bays and in close proximity to other pink-salmon streams may stray more or less into the neighboring streams.

The marked pink salmon that have thus far returned from these marking experiments have all returned at 2 years of age. Their age at maturity, as determined by

the number of bands of growth rings on their scales, was in every case consistent with the age at which they actually matured and returned to spawn. The scales of the pink salmon that have appeared in Snake Creek and in other streams in southeastern Alaska on different years have been examined and all show bands of growth rings on their scales similar to those on the scales of the marked Snake Creek salmon. The scales of the unmarked pink salmon that appeared in the 1931 run in the Duckabush River were likewise similar to the scales of the marked salmon that were recovered in the run.

Additional evidence in regard to the age at which the pink salmon mature is found in the original establishment of pink-salmon runs in a number of streams in the New England States. Large shipments of eyed pink-salmon eggs were sent to the hatcheries in the New England States in 1913 and 1915. The fry that developed from these eggs in the spring of 1914 and the spring of 1916 were liberated in a number of streams along the coast. In the summer and fall of 1915 a substantial run of adult pink salmon returned to the streams in which the fry were liberated. A similar run of pink salmon occurred in the summer and fall of 1917. Dr. C. H. Gilbert, an authority on the Pacific salmon, examined some of the scales taken from the adult pink salmon in these streams in 1917 and claimed that, in spite of their new environment, the pink salmon retained their original habit of returning to the rivers to spawn and die at 2 years of age.

All of the evidence thus far collected indicates that the pink salmon mature at 2 years of age and until contradictory evidence is found, it may be assumed with relative certainty that they consistently mature at the close of their second year of life.

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U.S. DEPARTMENT OF COMMERCE
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BUREAU OF FISHERIES
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Reproduction and Development of Whitings or Kingfishes Drums, Spot, Croaker, and Weakfishes or Sea Trouts Family Sciaenidae, of the Atlantic Coast of the United States

By SAMUEL F. HILDEBRAND and LOUELLA E. CABLE

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 16

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1934

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REPRODUCTION AND DEVELOPMENT OF WHITINGS OR KINGFISHES, DRUMS, SPOT, CROAKER, AND WEAKFISHES OR SEA TROUTS, FAMILY SCIAENIDAE, OF THE ATLANTIC COAST OF THE UNITED STATES[1]

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CONTENTS

	Page
Introduction	41
Artificial keys to the eggs and young as far as known	42
The whitings or kingfishes (*Menticirrhus americanus*, *M. saxatilis* and *M. littoralis*)	51
Characters of the adults	52
Key to the species	52
Menticirrhus americanus (Linnaeus)	53
Spawning	53
Descriptions of the young	54
Distribution of the young	62
Growth	62
Menticirrhus saxatilis (Block and Schneider)	64
Spawning	65
Description of the eggs and young	65
Distribution of the young	70
Growth	70
Menticirrhus littoralis (Holbrook)	70
Spawning	71
Descriptions of the young	71
Distribution of the young	75
Growth	75
Star drum (*Stellifer lanceolatus* (Holbrook))	75
Spawning	76
Descriptions of the young	76
Distribution of the young	83
Growth	83
Banded drum (*Larimus fasciatus* Holbrook)	84
Spawning	84
Descriptions of the young	85
Distribution of the young	91
Growth	91
The weakfishes or sea trouts (*Cynoscion nebulosus*, *C. regalis*, and *C. nothus*)	91
Key to the species	91
Cynoscion nebulosus (Cuvier and Valenciennes). Spotted trout; speckled trout; spotted weakfish	92
Spawning	93
Descriptions of the young	94
Distribution of the young	101
Growth	102
Cynoscion regalis (Bloch and Schneider). Gray trout; gray weakfish	102
Spawning	103
Descriptions of the eggs and young	104
Distribution of the young	107
Growth	108
Cynoscion nothus (Holbrook). Bastard trout	110
Spawning	111
Descriptions of the young	112
Distribution of the young	115
Growth	116
Bibliography	116

INTRODUCTION

The account of the Sciaenidae that follows is based mostly on specimens collected on the coast of North Carolina. However, some specimens from the coast of New Jersey, from Chesapeake Bay, and from the coast of Texas have also been studied. In the preparation of the keys to the eggs and young, specimens were used as far as

[1] Bulletin no. 16. Approved for publication, Apr. 3, 1934.

available, and the last six papers listed in the bibliography were drawn upon freely. The keys form a sort of summary of the present state of knowledge of the characters of the eggs and young of the Sciaenidae of the Atlantic coast of North America. It is hoped that they will prove useful in the further study of the eggs and the young of this family of large fishes, most of the members of which are of much economic importance.

It is evident from the present treatise that considerable gaps remain to be filled to make known fully the embryology and larval development of the Sciaenidae, though quite a number of stages in the development of several species, heretofore unknown, are described and figured. It has been particularly difficult to identify the eggs; and female fish, ripe enough for stripping, have been taken seldom. In a few instances the eggs were secured by confining nearly ripe females in tanks. However, this procedure was successful only if the females were ripe enough to spawn the first or second night after capture. If not, the fish retained the eggs. It was shown by Hildebrand and Cable (1930, p. 418) that spots (*Leiostomus xanthurus*), though containing advanced roe, retained it for several months after capture, that is, long after the spawning season had ended. The principal hope of securing the eggs for certain identification, therefore, lies in the capture of fully, or almost fully, ripe fish.

The illustrations accompanying this report, unless otherwise stated, were prepared by the junior author, who also made many of the preliminary identifications and assisted in various ways in the study of the specimens. The senior author is responsible for the final identifications and the composition of the report.

ARTIFICIAL KEYS TO THE EGGS AND YOUNG SO FAR AS KNOWN

The following series of keys are entirely artificial, that is, they are designed to identify the fish rather than to show the natural relationship. The eggs of only three species of Sciaenidae from the Atlantic coast of the United States are known to date. A key by which the eggs of these three species may be identified is offered. The other keys are intended to identify the young of various sizes. The "Key to the newly hatched young" is based on live specimens hatched in the laboratory. It is limited, therefore, to the three species for which the eggs are known. All the other keys are based on preserved specimens. The length of the newly hatched young given in some instances exceeds that of the specimens treated in the next key, notwithstanding that the "smaller" specimens (1.7 to 1.8 millimeters long) were older fish, as shown by their development. The apparent decrease in length no doubt is caused by shrinkage in the preservatives. Some of the species included in the keys for the larger size groups are missing in those for the smaller fish, because the smaller stages are not yet known.

The size groups chosen for the keys are thought to be close enough together to make it possible to identify specimens of intermediate lengths. Specimens of lengths intermediate of those on which the keys are based should be identified by the key covering a range nearest their size. For example, specimens 11 millimeters long could be identified most readily by using the key for specimens 8 to 10 millimeters long, whereas specimens 14 millimeters long should be identified by using the key prepared for specimens 15 to 20 millimeters in length. Specimens exactly half way between two groups, in general, should be identifiable as readily by the key for the smaller specimens as by the one for the larger ones.

No key is offered for specimens more than 35 millimeters long because it is believed that such specimens have sufficient adult characters developed to be identified by keys prepared from adult fish, such as appear in various taxonomic treatises.

More complete descriptions of the eggs and young than are contained in the keys presented occur in the following works. For descriptions of the eggs and newly hatched young of *Menticirrhus saxatilis* see Welsh and Breder (1924). For accounts of the egg and larval development of *Bairdiella chrysura* consult Kuntz (1914) and Hildebrand and Cable (1930). For descriptions of young *Sciaenops ocellatus* and *Pogonias cromis* refer to Pearson (1929). For accounts of the development of the eggs and the young of *Cynoscion regalis* see Welsh and Breder (1923) and Pearson.[2] And for descriptions of young *Leiostomus xanthurus* and *Micropogon undulatus* refer to Hildebrand and Cable (1930). Accounts of the other species included in the keys are contained in the present paper.

KEY TO THE EGGS[3]

[Sciaenid eggs so far as known are pelagic and spherical in form]

a. Eggs generally with only 1 oil globule, rarely with more than 2.

b. Range in diameter 0.66 to 0.77 millimeter, average 0.69; yolk with only a few pigment spots (dark green in color) in advanced state of development, none in younger stages; embryo and oil globule in advanced stages with somewhat scattered dark dots. *Bairdiella chrysura*

bb. Range in diameter probably about 0.8 to 0.92 millimeter, average 0.84; yolk profusely dotted (with dark green granules) in advanced state of development, some dots appearing during the cleavage stages; embryo and oil globule profusely spotted. *Cynoscion regalis*

aa. Eggs generally with more than 1 oil globule, often with 3 or 4, sometimes with as many as 13 to 18, reduced to 1 in advanced embryonic stages. Range in diameter 0.76 to 0.92 millimeter, average about 0.83. Yolk without pigment spots, the embryo with rather prominent scattered grayish dots. *Menticirrhus saxatilis*

KEY TO NEWLY HATCHED YOUNG[4]

a. Length at hatching 1.5 to 1.8 millimeters, average about 1.6; vent nearer end of snout than tip of tail (notochord) by a distance equal to almost twice the diameter of eye. Caudal portion of body with a congregation of dark green chromatophores forming a suggestion of a cross bar at midcaudal length. *Bairdiella chrysura*

aa. Length at hatching 1.75 to 2.0 millimeters, average about 1.9; vent less than an eye's diameter nearer end of snout than tip of tail (notochord). Caudal portion of body with two cross bars composed of dark green chromatophores, one at about midcaudal length and the other one (less distinct) about midway between the vent and the first mentioned bar. *Cynoscion regalis*

aaa. Length at hatching 2.0 to 2.25 millimeters; vent about an eye's diameter nearer end of snout than tip of tail (notochord); caudal portion of body with 3 equally spaced black and golden bars, the first one being situated immediately behind the vent. *Menticirrhus saxatilis*

KEY TO SPECIMENS 1.7 TO 1.8 MILLIMETERS LONG

a. Caudal portion of body long and slender, much longer than rest of body; distance from end of snout to vent about 2.75 times in length to tip of tail (without finfold); depth immediately behind vent notably less than diameter of eye.

[1] Unpublished manuscript in the files of the Bureau of Fisheries entitled "Seasonal Distribution and Abundance of Pelagic Marine Fish Eggs and Young Fishes at the entrance to Chesapeake Bay, Va."

[3] The key is based on live eggs.

[4] The key is based on live larvae. Keys to all other young are founded on preserved specimens.

b. Head and body rather deep, greatest depth about 4.0 in length to tip of tail (notochord); mouth well developed, very strongly oblique, the gape anteriorly well above middle of eye. Color plain or with a row of minute dark chromatophores along ventral outline of the tail, none in advance of vent, sometimes with one dark chromatophore on middle of side above vent, occasionally a few on the head ..... *Leiostomus xanthurus*

bb; Head and body more slender, greatest depth about 4.5 in length to tip of tail (notochord); mouth less perfectly developed, the gape anteriorly at about middle of eye; the imperfectly developed maxillary apparently reaching only slightly past anterior margin of eye. Ventral outline of the trunk as well as the tail with distinct, well separated black chromatophores, also a few definite ones on the head, none on side of the trunk and tail. *Cynoscion regalis*

aa. Caudal portion of body proportionately shorter and deeper; distance from snout to vent about 2.2 to 2.5 times in length to tip of tail (without finfold); depth immediately behind vent equal to or greater than diameter of eye.

c. Head and trunk rather short and deep, the greatest depth about 3.1 times in length without caudal finfold; preanal distance 2.1 to 2.4 times, and postanal distance without finfold 1.75 to 1.9 times; depth immediately behind vent about equal to diameter of eye. Ventral outline of chest and abdomen with dark markings, with a large prominent spot just in advance of vent; anterior half to two-thirds of ventral outline of tail with a close-set series of dark dots; base of primitive pectoral pale ..... *Cynoscion nebulosus*

cc. Head and trunk very short and deep, the greatest depth about 2.6 times in length without caudal finfold; preanal distance 2.25 times; and postanal distance without finfold 1.88 times in length; depth immediately behind vent notably greater than diameter of eye. Caudal portion of body with an almost continuous dark longitudinal line along middle of side, and another one on the ventral outline; no prominent dark spot in advance of vent; base of primitive pectoral pale ..... *Menticirrhus americanus*

ccc. Head and trunk rather short and deep, the greatest depth about 3.1 times in length without caudal finfold; preanal distance 2.4 times and postanal distance without finfold 1.6 times; depth immediately behind vent about equal to diameter of eye. Median line of abdomen with a small black spot just before vent, generally with an elongated black spot on ventral outline at about midcaudal length, sometimes with several small dark spots; inner surface of base of primitive pectoral black ..... *Stellifer lanceolatus*

cccc. Head and trunk moderately long and deep, greatest depth 3.1 to 3.4 in length without caudal finfold; preanal distance 1.9 to 2.0 times and postanal distance 1.9 to 2.2 times; depth immediately behind vent somewhat greater than diameter of eye. Ventral outline of tail generally with a row of black spots; a black spot at angle of opercle; fresh specimens with a black vertical band at shoulder, which generally fades in preservative; inside of base of primitive pectoral pale ..... *Bairdiella chrysura*

KEY TO SPECIMENS 2.5 TO 3.0 MILLIMETERS LONG

a. Caudal portion of body long, slender, generally longer (much longer in *Cynscion regalis* and *Leiostomus xanthurus*) than rest of body; distance from snout to vent about 2.0 to 2.5 times in total length (without caudal finfold).

b. An abrupt and pronounced break present in contour at vent; caudal portion of body very slender; depth immediately behind vent less than 1.5 times diameter of eye; distance from tip of snout to vent about 2.2 to 2.6 in total length without caudal finfold.

c. Caudal portion of body moderately slender, depth immediately behind vent about 1.1 times the diameter of eye; mouth almost vertical; the gape anteriorly near level of upper margin of eye; a few dark chromatophores on chest or abdomen; an elongate one posterior to hind-gut at its juncture with the tail; a series of widely spaced chromatophores along the ventral outline of the tail; no black lateral stripe or spots present ..... *Leiostomus xanthurus*

cc. Caudal portion of body very slender, depth immediately behind vent about equal to diameter of eye; mouth moderately oblique; the gape anteriorly at or below middle of eye; ventral outline of chest and abdomen generally with a few chromatophores, a prominent one just in advance of vent; ventral outline of tail with well separated dark chromatophores, one at about midcaudal length enlarged and usually with long radiating lines; no black lateral stripe or spots present ..... *Cynoscion regalis*

bb. The break in contour at vent less pronounced; caudal portion of body proportionately deeper; depth immediately behind vent about 1.7 to 1.85 times diameter of eye; distance from tip of snout to vent about 2.0 in total length without caudal finfold; mouth strongly oblique, the gape anteriorly generally above middle of eye; ventral outline of trunk and tail with very small dark chromatophores, none on side or back---*Micropogon undulatus*

aa. Caudal portion of body shorter, about equal to or shorter (without finfold) than rest of body; distance from snout to vent about 1.75 to 1.9 in total length (without caudal finfold).

d. Caudal portion of body anteriorly with a black lateral stripe, continuous or composed of more or less separated elongated spots; ventral outline behind vent with close-set black chromatophores, often forming a nearly continuous line.

e. Body moderately deep, the greatest depth about 2.6 in total length without caudal finfold; vent situated almost exactly at midbody length; depth immediately behind vent about 1.25 times diameter of eye; mouth moderately oblique, the gape anteriorly being somewhat below middle of eye; black lateral stripe on anterior half to two-thirds of tail composed of somewhat disconnected dashes; no black on the dorsal outline.

Cynoscion nebulosus

ee. Body very deep, the greatest depth about 2.4 times in total length without caudal finfold; vent situated well in advance of midbody length; depth immediately behind vent about 1.5 times diameter of eye; mouth strongly oblique, the gape anteriorly being about on a level with upper margin of eye; black lateral stripe on anterior half to two-thirds of tail continuous; dorsal outline of anterior part of tail with an almost continuous black line----------*Menticirrhus americanus*

dd. Caudal portion of body without a black lateral stripe; ventral outline behind vent with a few to a series of several well-separated black chromatophores.

f. Inner surface of base of primitive pectoral black; no black cross bar at shoulder, nor a black spot at lower angle of opercle; an elongate black spot on ventral surface at about midcaudal length.

g. Body quite deep and robust, greatest depth 2.3 to 2.5 in total length without caudal finfold; mouth large, very broad, rather strongly oblique, the gape anteriorly being about on a level with the middle of the eye; maxillary reaching almost to middle of eye; preopercle with a few spines--------*Stellifer lanceolatus*

gg. Body more slender, the greatest depth 2.8 to 3.2 in total length without caudal finfold; mouth somewhat smaller, narrower, rather less strongly oblique, the gape anteriorly being about on level with lower margin of pupil; maxillary reaching about to anterior margin of pupil; preopercle without evident spines.

Larimus fasciatus

ff. Inner surface of base of pectoral not black; a broad black cross bar at shoulder (at least in fresh specimens), and a black spot at lower angle of opercle; ventral surface of tail with a series of dark dots, none of them especially enlarged; body quite slender, the greatest depth 2.8 to 3.0 in the total length without the caudal finfold.

Bairdiella chrysura

KEY TO SPECIMENS 3.5 TO 4.0 MILLIMETERS LONG

[Caudal fin generally more or less developed, and the notochord is bent upward posteriorly]

a. Body moderately slender, the greatest depth more than 3 (about 3.3 to 3.8) times in length to end of notochord.

b. Body without a black longitudinal stripe on side; mouth strongly oblique, the gape anteriorly above middle of eye; vent near midbody length, the distance from snout to vent being contained 2.0 to 2.1 times in length to end of notochord.

c. Body abruptly more slender posterior to vent; greatest depth of body 3.3 to 3.4, and the greatest depth behind vent 6.2 to 7.5 in length to end of notochord; eye large, equal to length of snout, its diameter 1.35 to 1.4 in greatest depth behind vent.

Leiostomus xanthurus

cc. Body proportionately deeper behind vent; greatest depth of body 3.4 to 3.8, and the greatest depth behind vent 4.8 to 5.6 in length to end of notochord; eye smaller, shorter than snout, 1.9 to 2.2 in greatest depth behind vent-----*Micropogon undulatus*

bb. Body with a black longitudinal stripe on side; ventral outline of tail with a rather close-set series of dark spots, none of the spots especially enlarged; mouth less strongly oblique, the gape anteriorly about on level with middle of eye; vent situated behind midbody length, the distance from snout to vent being contained 1.75 to 1.8 times in length to end of notochord; body moderately elongate, the greatest depth 3.4 to 3.6 in length to end of notochord ..... *Cynoscion nebulosus*

aa. Body deeper, the greatest depth generally less than 3 (about 2.2 to 3.0) times in the length to the end of the notochord.

d. Inside of base of primitive pectoral pale, never black; body moderately elongate; greatest depth generally more than 2.5 (about 2.6 to 3.0) times in length to end of notochord; vent at or near midbody length, the distance from snout to vent being contained about 1.75 to 2.0 times in the length to end of notochord.

e. Body without a dark longitudinal stripe on side; ventral outline without a continuous stripe, with or without a series of dark spots; vent almost at midbody length, the distance from snout to vent being contained about 1.9 to 2.0 times in the length to end of notochord.

f. No black cross bar at shoulder; ventral outline of tail with a series of well-separated black spots, one of the spots at about midcaudal length enlarged, generally with branching lines; chest and abdomen with a few large branching chromatophores; greatest depth 2.7 to 3.0 in length to end of notochord ..... *Cynoscion regalis*

ff. Shoulder region with a broad ill-defined black cross bar (at least in fresh specimens); ventral outline of tail with several indefinite dark spots, also two on the back, none with branching lines; greatest depth about 2.6 in length to end of notochord. *Bairdiella chrysura*

ee. Body with a dark longitudinal stripe on the side, one along the ventral outline of the tail and another one on the back; vent somewhat behind midbody length, the distance from snout to vent being contained about 1.75 times in the length to end of notochord; greatest depth about 2.7 in length to end of notochord ..... *Menticirrhus americanus*

dd. Inside of base of primitive pectoral black; body quite deep; greatest depth generally less than 2.5 (about 2.2 to 2.5) times in length to end of notochord; vent notably behind midbody length, the distance from the snout to vent being contained about 1.5 to 1.7 times in the length to the end of the notochord.

g. Body robust anteriorly; a large vacant space between brain and cranium; preopercle with spines; mouth moderately oblique, the gape anteriorly not much above lower margin of eye; maxillary reaching about to pupil ..... *Stellifer lanceolatus*

gg. Body more compressed anteriorly; no vacant space between brain and cranium; no preopercular spines; mouth strongly oblique, the gape anteriorly on level with middle of eye; maxillary reaching under middle of eye ..... *Larimus fasciatus*

KEY TO SPECIMENS 5 TO 6 MILLIMETERS LONG

[The vertical fins, and sometimes the pectoral fins, are sufficiently developed to permit the enumeration of at least the soft rays]

a. Anal fin long, with II, 9 to 13 rays. (Spines not always developed.)

b. Body moderately deep, the greatest depth about 2.7 to 3.0 in length to base of caudal fin; mouth strongly oblique, the gape anteriorly only slightly below upper margin of eye; anal with 11 or 12 soft rays; body without dark stripes or bars; a prominent black chromatophore present below posterior half of base of anal ..... *Cynoscion regalis*

bb. Body rather deep, greatest depth about 3.1 in length to base of caudal fin; mouth rather strongly oblique, the gape anteriorly about on level with middle of eye; anal with 12 or 13 soft rays; body without dark stripes or bars; ventral outline behind vent with a series of small dark spots of about uniform size ..... *Leiostomus xanthurus*

bbb. Body quite deep, greatest depth 2.6 to 2.8 in length to base of caudal fin; mouth moderately oblique, the gape anteriorly usually on level with lower margin of pupil; anal with 9 or 10 soft rays; a broad black ill-defined bar across chest and extending to shoulder; ventral outline behind vent with a single prominent black chromatophore situated below last anal rays ..... *Bairdiella chrysura*

aa. Anal fin shorter, with I or II, 6 to 8 rays. (Spines not always developed.)

c. Body moderately slender, the greatest depth more than 2.2 times in the length to base of caudal; vent at or near midbody length, never more than an eye's diameter in advance of or behind the midpoint between tip of snout and base of caudal.

d. Anal fin with only 1 spine and 7, rarely 8, soft rays; body rather deep, compressed, depth about 2.75 in length to base of caudal; mouth moderately oblique, the gape wholly below level of lower margin of eye; caudal portions of body usually with a dark stripe along middle of side and another along ventral edge, these sometimes faint or broken up into spots ..... *Menticirrhus americanus*

dd. Anal fin with 2 spines; body without stripes, or at most with an indication of a stripe along middle of side of caudal portion, the color of the stripe when present being subsurface.

e. Eye small, shorter than snout, the diameter also less than depth of caudal peduncle.

f. Mouth strongly oblique, the gape anteriorly about on level with middle of eye; maxillary reaching to or slightly past anterior margin of eye; anal with 8 soft rays; color plain, consisting principally of dark chromatophores along ventral outline, none on head or side ..... *Micropogon undulatus*

ff. Mouth slightly oblique, the gape anteriorly about on level with lower margin of eye; maxillary reaching about under middle of eye; anal with 6 or 7 soft rays (sometimes insufficiently developed to be enumerated accurately); color consisting principally of dark chromatophores on head, along sides and along ventral outline behind vent ..... *Pogonias cromis*

ee. Eye larger, equal to or longer than snout, the diameter also equal to or greater than depth of caudal peduncle; anal fin with II, 8 rays.

g. Body moderately slender, depth 3.3 to 3.5 in length to base of caudal; vent somewhat nearer base of caudal than tip of snout; distance from snout to vent 1.6 to 1.85 in length to base of caudal; a broken dark band on middle of side under second dorsal sometimes present, the color being subsurface; a large black chromatophore with branching lines present below base of posterior anal rays and generally another one on upper part of side, somewhat in advance of origin of second dorsal ..... *Sciaenops ocellatus*

gg. Body rather deep, greatest depth 2.6 to 2.8 in length to base of caudal; vent generally nearer tip of snout than base of caudal; distance from snout to vent 2.0 to 2.3 in length to base of caudal; no dark lateral band; a few dark points on chest and abdomen; a slight dark spot at origin of anal generally present and another definite one at end of anal; a slight shoulder spot present ..... *Stellifer lanceolatus*

cc. Body very deep, depth about 2.15 times in length to base of caudal; vent notably more than an eye's diameter nearer base of caudal than tip of snout; distance from snout to vent 1.4 times in length to base of caudal; mouth strongly oblique; the gape anteriorly somewhat above middle of eye; anal with II, 6 to 8 rays; inside of base of pectorals black. *Larimus fasciatus*

KEY TO SPECIMENS 8 TO 10 MILLIMETERS LONG

[All the fins are developed and an accurate enumeration of the rays is now possible]

a. Anal fin with a single weak spine and 7 or 8 soft rays; body wholly or largely covered with large black chromatophores; no dark band on snout in front of eye; base of pectoral fins not black.

b. Body moderately compressed and fairly deep, greatest depth 3.6 to 3.8 in length to base of caudal fin; pupil of eye almost perfectly round; caudal fin nearly symmetrical, long and pointed; anal fin usually with I, 7 (rarely 8) rays; spinous dorsal often partly black; ventrals colorless ..... *Menticirrhus americanus*

bb. Body strongly compressed and deep; depth 2.8 to 3.0 in length to base of caudal; pupil of eye elliptical, that is, vertically elongate; caudal fin asymmetrical, more or less rounded, never sharply pointed, the longest rays in lower half of fin; anal fin usually with I, 8 (rarely 9) rays; spinous dorsal and ventrals usually wholly black ..... *Menticirrhus saxatilis*

bbb. Body somewhat compressed, rather broad and low; depth 3.6 to 4.0 in length to base of caudal; pupil of eye elliptical, that is, vertically elongate; caudal fin asymmetrical, more or less rounded, never sharply pointed, the longest rays in lower half of fin; anal fin with I, 7 rays; fins all colorless ..... *Menticirrhus littoralis*

aa. Anal fin with 2 spines, usually rather strong, and 6 to 13 soft rays; body generally with few or no black chromatophores on sides and back, largely unspotted.

c. Dorsal fin with X to XII–I, 20 to 22 rays (the spines sometimes not all developed).

d. Body quite deep, depth 2.6 to 2.75 in length to base of caudal; an abrupt decrease in depth posterior to vent; vent more than an eye's diameter in advance of anal; mouth strongly oblique, the gape anteriorly only a little below middle of eye; anal fin with II, 8 rays; caudal fin long, pointed; an elongate black spot or line in advance of upper anterior angle of gill opening; no black chromatophores at origin of first dorsal. *Stellifer lanceolatus*

dd. Body moderately deep, depth about 2.5 in length to base of caudal; no abrupt decrease in depth posterior to vent; vent not more than an eye's diameter in advance of origin of anal; anal fin with II, 9 or 10 rays; caudal fin round; no black spot or line in advance of upper anterior angle of gill opening; some black chromatophores on upper part of side near origin of first dorsal ---------- *Bairdiella chrysura*

ddd. Body somewhat more slender, depth about 3.0 in length to base of caudal; no abrupt decrease in depth posterior to vent; vent less than an eye's diameter in advance of origin of anal; mouth rather strongly oblique, the gape anteriorly about on level with lower margin of pupil; anal fin with II, 6 or 7 rays; no black spot or line in advance of upper anterior angle of gill opening; upper surface of head and sides variously dotted with black chromatophores ---------- *Pogonias cromis*

cc. Dorsal fin with X or XI–I, 23 to 34 rays (the spines not always developed).

e. Dorsal and anal fins long, the former with 30 to 34, and the latter with 12 or 13 soft rays; mouth moderately oblique, the gape anteriorly slightly above level of lower margin of eye; maxillary reachings almost to middle of eye; caudal fin rather short, slightly rounded or straight; a few dark chromatophores present along ventral outline only ---------- *Leiostomus xanthurus*

ee. Dorsal and anal fins shorter, the former with 23 to 29 rays, and the latter with 6 to 12 rays (rarely with 13 in *Cynoscion regalis*).

f. Body very deep, strongly compressed, depth about 1.9 in length to base of caudal; mouth rather strongly oblique, the gape anteriorly a little above lower margin of eye; anal fin short with II, 6 rays; caudal fin rather long pointed; sides with large branching chromatophores, variable in number among specimens, partly at least arranged in longitudinal series; lower half of pectorals and ventrals black. *Larimus fasciatus*

ff. Body more slender, the depth more than 2.5 times in length to base of caudal; anal fin longer, with more than 7 soft rays; basal half of pectorals and ventrals not black.

g. Anal generally with 8 or 9 soft rays (*Cynoscion nothus* rarely with 10 rays).

h. Second dorsal moderately short, with 23 to 25 soft rays; eye large, about as long as snout, its diameter nearly equal to least depth of caudal peduncle; a broken lateral stripe present posteriorly, the color subsurface; body variously marked above and below with black chromatophores; a large branching chromatophore at base of posterior anal rays, and usually another prominent one on upper part of side, somewhat in advance of second dorsal ---------- *Sciaenops ocellatus*

hh. Second dorsal rather long, with 28 or 29 soft-rays; eye small, shorter than snout, its diameter shorter than least depth of caudal peduncle; ventral surface with small black chromatophores; sides and back plain without black markings ---------- *Micropogon undulatus*

hhh. Second dorsal moderately long, generally with 25 to 27 rays (sometimes 24 to 28); eye rather small, somewhat shorter than snout, its diameter notably shorter than least depth of caudal peduncle; body moderately deep; depth 3.0 to 3.25 in length to base of caudal; vent far in advance of origin of anal, the distance notably longer than diameter of eye; black lateral band wanting; 2 elongate dusky spots at base of anal, 1 at anterior rays and another at the posterior ones --- *Cynoscion nothus*

gg. Anal generally with 10 to 12 soft rays (*Cynoscion regalis* sometimes with 13).

i. Body moderately deep; depth 2.95 to 3.0 in length to base of caudal; vent more than an eye's diameter in advance of origin of anal; snout

moderately blunt; lower jaw scarcely projecting; no black lateral stripe, sides generally with groups of black chromatophores; a large black branching chromatophore below base of last anal rays--*Cynoscion regalis*

ii. Body more elongate; depth 3.6 to 4.0 in length to base of caudal; vent less than an eye's diameter in advance of origin of anal; snout pointed; lower jaw projecting prominently; a black lateral stripe present on posterior part of body; a black band in front of eye, sometimes extending through eye to opercle; no prominent black chromatophores at base of anal----------*Cynoscion nebulosus*

KEY TO SPECIMENS 15 TO 20 MILLIMETERS LONG

[Scales usually are developed at this range in size and sometimes the body is fully covered at a length of 20 millimeters]

a. Anal fin with a single weak spine and 7 to 9 soft rays; mouth more or less inferior, nearly horizontal; lower jaw with a rather prominent knob at tip (which develops into a short thick barbel as the fish grows).

b. Body moderately deep, greatest depth 3.6 to 3.8 in length to base of caudal; pupil almost perfectly round; caudal fin long and pointed, the longest rays being longer than head; anal with I, 7 (rarely 8) rays; spinous dorsal and ventrals with black chromatophores, not wholly black----------*Menticirrhus americanus*

bb. Body deeper, greatest depth 3.25 to 3.4 in length to base of caudal; pupil elliptical; caudal fin broadly pointed, the longest rays in lower half of fin, notably shorter than head; anal with I, 8 (rarely 9) rays; spinous dorsal and ventrals black. *Menticirrhus saxatilis*

bbb. Body quite elongate, greatest depth 3.75 to 4.2 in length to base of caudal; pupil elliptical; caudal fin asymmetrically rounded, the longest rays in lower half of fin, shorter than head; anal with I, 7 rays; spinous dorsal and ventrals not pigmented. *Menticirrhus littoralis*

aa. Anal fin with 2 rather strong spines and 6 to 13 soft rays; lower jaw without a knob at tip.

c. Snout more or less pointed; lower jaw projecting prominently; anal with II, 9 to 13 rays (rarely II, 8 in *Cynoscion nothus*).

d. Anal usually with 9, occasionally with 8 or 10, soft rays; body rather deep, the greatest depth 3.2 to 3.6 in length to base of caudal; caudal fin evidently very long and pointed, the longest rays longer than head; chromatophores small, forming indefinite blotches, blotches on back and in lateral line if present separate, not forming cross bars----------*Cynoscion nothus*

dd. Anal usually with 11 or 12, occasionally with 13, soft rays; body rather deep as in *C. nothus*; caudal fin rather long and pointed, the longest rays about equal to length of head; chromatophores large, forming rather distinct blotches, those on back and in lateral line connected, forming more or less definite cross bars on anterior part of body----------*Cynoscion regalis*

ddd. Anal with 10 or 11 soft rays; body slender, the greatest depth 3.9 to 4.1 in length to base of caudal; caudal fin short, broadly pointed, the longest rays notably shorter than head; chromatophores very small, arranged so as to form an indefinite lateral band and another band along base of dorsal and generally extending forward on head; no blotches or cross bars present----------*Cynoscion nebulosus*

cc. Snout not pointed, usually short and blunt; lower jaw not projecting (except in *Larimus fasciatus*) equal to or more usually shorter than upper jaw; anal with II, 6 to 8 rays, exclusive of *Leiostomus xanthurus* which has II, 12 or 13.

e. Anal long, with 12 or 13 soft rays; second dorsal with 30 to 34 soft rays; body moderately deep, the greatest depth about 3.4 to 3.8 in length to base of caudal; margin of caudal fin distinctly concave----------*Leiostomus xanthurus*

ee. Anal shorter, with 6 to 10 soft rays; second dorsal shorter, with 19 to 29 soft rays; margin of caudal rounded or pointed.

f. Second dorsal with 19 to 22 soft rays; first dorsal with 10, 11, or 12 spines.

g. First dorsal with 11 or 12 spines; anal with 8 to 10 soft rays.

h. Head broad, spongy; eye small, shorter than the snout; interorbital notably broader than eye; anal with 8 soft rays; caudal fin long, pointed----------*Stellifer lanceolatus*

hh. Head narrow, compressed, not spongy; eye larger, fully as long as snout, about as wide as interorbital; anal with 9 or 10 soft rays; caudal fin rather short, the margin round ..... *Bairdella chrysura*

gg. First dorsal with 10 spines; anal with 6 or 7 soft rays; head deep, compressed; mouth inferior; a series of short barbels generally visible on lower jaw; dark cross bars present ..... *Pogonias cromis*

ff. Second dorsal with 23 to 29 soft rays; first dorsal with 10 spines only.

i. Body very deep, compressed, the depth 2.4 in length to base of caudal; mouth strongly oblique, the gape anteriorly above lower margin of eye; second dorsal with 24 to 27 soft rays; anal with 6 to 8 soft rays; caudal fin long, pointed; body with very large chromatophores, forming an indefinite band on anterior part of body; pectorals and ventrals largely black; spinous dorsal with big black spots ..... *Larimus fasciatus*

ii. Body more elongate, the depth being contained more than three times in length to base of caudal; mouth only slightly oblique, the gape wholly below the eye; caudal fin more or less rounded, not long and pointed.

j. Second dorsal with 28 or 29 soft rays; caudal fin long, pointed, as long as head; a row of short, slender barbels visible on chin in some specimens. *Micropogon undulatus*

jj. Second dorsal with 23 to 25 soft rays; caudal fin short, angulate, shorter than head; no barbels on chin ..... *Sciaenops ocellatus*

KEY TO SPECIMENS 30 TO 35 MILLIMETERS LONG

[At this size the body generally is fully pigmented and frequently the color pattern of the adult is present]

a. Anal fin with a single weak spine and 7 to 9 soft rays; mouth notably inferior, nearly or quite horizontal, the conical snout usually projecting beyond it; lower jaw with a very short thick barbel at tip.

b. Ventral fins small, shorter than pectorals, not reaching beyond tips of pectorals; scales on chest not much smaller than on rest of body; sides with dark blotches or more usually with black bands.

c. Body slender, greatest depth 3.8 to 4 in length to base of caudal; pupil round; anal rays typically 7, rarely 8; caudal fin long and pointed, the longest rays fully as long as head; sides with dark blotches, usually forming indefinite cross bars, not forming a V on the side under spinous dorsal ..... *Menticirrhus americanus*

cc. Body deeper, greatest depth 3.5 to 3.65 in length to base of caudal; pupil eliptical; anal rays typically 8, sometimes 9; caudal fin not long and pointed, angulate, the longest rays shorter than the head; sides usually with black cross bars, the second and third nearly or quite meeting on middle of side, forming a V under spinous dorsal. *Menticirrhus saxatilis*

bb. Ventral fins large, longer than pectorals and reaching far beyond them; scales on chest notably reduced in size; body slender, greatest depth 4.05 to 4.3 in length to base of caudal; pupil eliptical; anal rays typically 7; caudal fin short, the lower lobe longest, notably shorter than head; sides with a few black dots, no large blotches or bars, color mostly silvery ..... *Menticirrhus littoralis*

aa. Anal fin with 2 rather strong spines; mouth superior, terminal, or only slightly inferior, the snout not projecting prominently; lower jaw with or without barbels, numerous if present.

d. Snout pointed; lower jaw projecting prominently; barbels wanting; upper jaw anteriorly with enlarged canines, curved backward; body elongate, greatest depth 3.2 to 4.2 in length to base of caudal; anal with 9 to 13 soft rays (rarely only 8 in *Cynoscion nothus*).

e. Body rather deep, greatest depth 3.2 to 3.6 in length to base of caudal; snout only moderately pointed; mouth oblique, the gape anteriorly somewhat above lower margin of eye; lower jaw projecting moderately; caudal fin long, pointed, the longest rays longer than head; sides usually with dark blotches or dark bars, no longitudinal black bands present.

f. Anal fin usually with 9, occasionally with 8 or 10 soft rays; sides generally with dark blotches in two series, one along the back and the other on the middle of the side ..... *Cynoscion nothus*

ff. Anal fin usually with 11 or 12, occasionally with 13, rays; sides with more or less definite dark cross bars ..... *Cynoscion regalis*

ee. Body more slender, greatest depth 3.95 to 4.2 in length to base of caudal; snout sharply pointed; mouth less oblique, the gape anteriorly below eye; lower jaw projecting strongly; caudal fin not very long nor sharply pointed, the longest rays shorter than head; anal fin with 10 or 11 rays; side and back each with a black longitudinal band, no blotches or cross bars present ..... *Cynoscion nebulosus*

dd. Snout not pointed; lower jaw equal to or shorter than the upper, projecting slightly in *Larimus fasciatus;* no enlarged canine teeth in upper jaw; body sometimes deep, sometimes elongate; anal with 6 to 8 soft rays, exclusive of *Leiostomus xanthurus* which has 12 or 13.

g. Anal long, with 12 or 13 soft rays; second dorsal with 30 to 34 soft rays; body moderately deep, greatest depth about 3.3 times in length to base of caudal; margin of caudal fin distinctly concave ..... *Leiostomus xanthurus*

gg. Anal shorter, with 6 to 10 soft rays; second dorsal shorter, with 19 to 29 soft rays; margin of caudal round or pointed, not concave.

h. Second dorsal with 19 to 22 soft rays; first dorsal with 10, 11, or 12 spines.

i. Body deep, compressed, depth 2.5 to 2.65 in length; head narrow, compressed; mouth horizontal, inferior; lower jaw distinctly shorter than the upper one, with numerous small barbels; anal with 6 or 7 soft rays; body with about 5 black cross bars ..... *Pogonias cromis*

ii. Body not quite as deep, depth about 2.9 to 3.1 in length to base of caudal; mouth somewhat oblique, terminal, the jaws of about equal length; no barbels on lower jaw; anal with 8 to 10 soft rays; no cross bars on body.

j. Head, narrow, compressed; interorbital not broader than large eye; skull hard, not spongy; anal with 9 or 10 soft rays; caudal fin round, not long; no dark blotches on back ..... *Bairdiella chrysura*

jj. Head broad, scarcely compressed; interorbital about two times as wide as the small eye; skull soft, spongy, cavernous; anal with 8 soft rays; caudal fin long and pointed; back with a series of black blotches. *Stellifer lanceolatus*

hh. Second dorsal with 23 to 29 soft rays; first dorsal with 10 spines only.

k. Body deep, compressed, greatest depth 2.6 to 2.8 in length to base of caudal; mouth strongly oblique, the lower jaw projecting somewhat; anal with 6 to 8 soft rays; caudal fin long and pointed; body with a broad cross bar under spinous dorsal and 4 or 5 narrower ones behind it ..... *Larimnus fasciatus*

kk. Body elongate, the depth about 3.3 to 3.6 in length to base of caudal; mouth horizontal, inferior, lower jaw included; anal with 8 soft rays; no cross bars on body.

l. Second dorsal with 28 to 29 soft rays; a row of short slender barbels usually visible on lower jaw; caudal fin long and pointed, the longest rays equal to length of head; body with small dark spots on sides and back. *Micropogon undulatus*

ll. Second dorsal with 23 to 25 soft rays; barbels wanting; caudal fin short, only slightly angulate, the longest rays notably shorter than head; body with dark spots placed as in *M. undulatus*, but larger and more distinct. *Sciaenops ocellatus*

THE WHITINGS OR KINGFISHES (Menticirrhus americanus, M. saxatilis and M. littoralis)

Three species of whiting, namely, *Meticirrhus americanus*, *M. saxatilis*, and *M. littoralis*, occur on the coast of North Carolina. The species resemble each other so closely that the fishermen generally fail to distinguish them, and they are not separated in the market. The most widely used common names, in books at least, are whiting and king whiting. Other local names are kingfish, roundhead, sea mullet, and sea mink. The fish are known at Beaufort as "sea mullet", and much less commonly as "sea mink." Since the species are not separated in the market, the relative abundance of each cannot be ascertained from commercial records. It is

known from personal observation, however, that *americanus* is by far the most numerous and commercially the most important species in the vicinity of Beaufort. The other two are about equally common, but not abundant.

The whitings are choice food fishes and generally command a good price. One or more species is common enough to enter into the commercial catches along the coast all the way from Massachusetts to Texas. The States having the largest catches in 1929 are the following: [5] New Jersey, 52,408 pounds; Virginia, 54,650; North Carolina, 387,168; South Carolina, 100,754; Georgia 51,500; Florida, 664,943; and Louisiana, 41,829 pounds.

It is evident from the foregoing records that the whitings are important food fishes over a wide range of the eastern and southern shores of the United States. The writers are pleased, therefore, to offer some new information in regard to the life histories of these useful fishes.

No young under 9 or 10 millimeters in length have been recognized either as *saxatilis* or *littoralis*. Since the local species of the genus are readily distinguishable at the size mentioned, as pointed out in the descriptions of the young, it is improbable that the smaller specimens (unless it be the very smallest ones) consist of more than one species, and all seem referable to *americanus*.

The three local species apparently all spawn simultaneously at Beaufort, the reproductive period occurring in the spring and early summer. A rapid rate of growth is indicated during the first several months of life. The habitat of the smaller young, ranging from about 10 to 60 millimeters in length, appears to be identical in *saxatilis* and *littoralis*, as these fish were taken only in the surf along the outer shores of the "banks", while *americanus* occurs further off shore and also in the inside protected waters. The adults of *americanus* and *saxatilis* are found both in the inside and outside waters, while *littoralis* evidently is confined almost entirely to the outside open waters.

CHARACTERS OF THE ADULTS

The body is long and rather low in the three species under consideration. The back is notably narrower than the abdomen, and much more strongly curved than the ventral outline. The head is low, and the conical snout projects well beyond the horizontal mouth. A short, thick barbel is present at the chin. The number of vertebrae is about the same in each species. In one specimen of each species counted, *americanus* and *littoralis* each had 10 body and 15 caudal vertebrae, and *saxatilis* had 10 body and 16 caudal vertebrae. The pupil of the eye is large and nearly or quite round in *americanus* at all ages, while it is smaller and vertically quite elongate in the young of about 6 inches and less in length of *saxatilis* and *littoralis*. In large preserved specimens of the last-mentioned species the pupil does not always appear elongate. Dorsal with 10 or 11 spines; anal with 1 weak spine. The chief diagnostic characters of the adults are included in the following key.

KEY TO THE SPECIES

a. Scales on chest not especially smaller than on sides; pectoral fins long, reaching to or past tips of the ventrals.

b. Sides plain or with obscure bars, not forming a V; anal usually with 7 soft rays; none of the dorsal spines especially produced, and none reaching far, if at all, beyond origin of second dorsal; scales 86 to 90, counting vertical series above lateral line ..... *americanus*

[5] The statistics are taken from the "Fisheries Industries of the United States in 1930", by R. H. Fiedler. Appendix II, Report, U.S. Commissioner of Fisheries, 1931 (1932), pp. 109–552, 23 figs. Washington. The fish are listed under "king whiting" or "king fish."

bb. Sides usually with black bars, the one on the nape and the one below the spinous dorsal meeting on the side forming a V; anal usually with 8 soft rays; the longest dorsal spine produced, reaching far past origin of second dorsal; scales 91 to 96, counting vertical series above lateral line ..... *saxatilis*

aa. Scales on chest much smaller than on sides; pectoral fins short, failing conspicuously to reach tips of ventrals; dorsal spines short, none of them produced; anal usually with 7 soft rays; scales 70 to 75, counting vertical series above lateral line; coloration normally plain silvery ..... *littoralis*

MENTICIRRHUS AMERICANUS (Linnaeus)

Menticirrhus americanus ranges from New York to Texas and apparently is commercially the most important species of the genus from Chesapeake Bay southward. The maximum weight reported is 2½ pounds. However, the average weigh probably does not exceed a half pound per fish. This species is taken throughout the year in the vicinity of Beaufort. It becomes quite scarce, however, during the winter and especially during cold spells. It is most numerous in the spring when large catches are made with "sink nets",[6] operated chiefly from Beaufort Inlet to Cape Lookout. During comparatively recent years, since the otter trawl has come into use locally, it is taken in the deeper waters with that gear also. In the inside waters it is taken chiefly with drag nets or seines. It takes the hook now and then, but it scarcely holds a place at Beaufort as a sport or game fish.

SPAWNING

Fish with well-developed roe have been seen at Beaufort from time to time from April to June. However, mature eggs of this species have not been secured. It is evident from the capture of two larvae 4.0 and 5.5 millimeters long in the tow on April 23 and 26 (1927) that spawning, some years at least, commences as early as April. The capture of young under 10 millimeters, and some under 5.0 millimeters in length during each succeeding month until about the middle of September shows almost certainly that the spawning season at Beaufort extends from April through August and possibly into the early part of September. (See table 1.) The principal spawning period, judging mainly from the abundance of the larvae in the tow, seems to extend from the latter part of June through July and August. Fish with large roe were seen most commonly during May and June.

Spawning in the vicinity of Beaufort probably occurs chiefly along the outside shores of the "banks", although it seems probable that some spawning may take place also within the inside waters. While the eggs if taken (in the tow) were not recognized, it is known that adult fish are common along the outer shores of the banks during the spawning season, where they no doubt congregate to carry out reproductive activities. Furthermore, 15 of the 18 young, 5.0 millimeters and under in length in the collection were caught along the outside shores. The larger young, up to 20 millimeters in length, of which many were taken, too, were much more numerous there than in the inside waters. It seems highly probable, therefore, that spawning in the vicinity of Beaufort takes place chiefly in the ocean along the shores of the "banks."

Welsh and Breder (1923, p. 187) suggest that this species may have two spawning seasons. No evidence of more than one spawning period was secured at Beaufort. (See table 1.) However, the spawning season, as pointed out in a preceding para-

[6] Sink nets are gill nets, weighted and sunk to the bottom (hence sink nets) in several fathoms of water.

graph, evidently is a long one. Therefore, the range in the size of the young of any one season is very great. The range in length in September, for example, according to examples measured extends from 2.75 to 156 millimeters. (See table 2.) Specimens of early and late spawnings, without intermediate ones, might readily lead to the conclusion that they represented the product of two distinct spawning periods. It is possible that the authors mentioned might have been misled because of insufficient material, that is, by the absence of specimens in their collections from the entire spawning period.

Spawning evidently takes place about simultaneously in Chesapeake Bay and Beaufort, as Hildebrand and Schroeder (1928, p. 293) report the observation of ripe fish from Cape Charles, Va., in May and other ripe ones in the Norfolk (Va.) market in June. These writers, also, report the capture in Chesapeake Bay of "young, three fourths inch or more in length, early in the summer." Welsh and Breder (1923, p. 186), working at Atlantic City, N.J., on the other hand, had found no ripe fish and no spent ones there as late as August (1920), although many females with well-developed but hard, row were seen. Nor do these investigators report the capture of young in that locality. Therefore, it would seem that the fish spawn much later in New Jersey than in North Carolina.

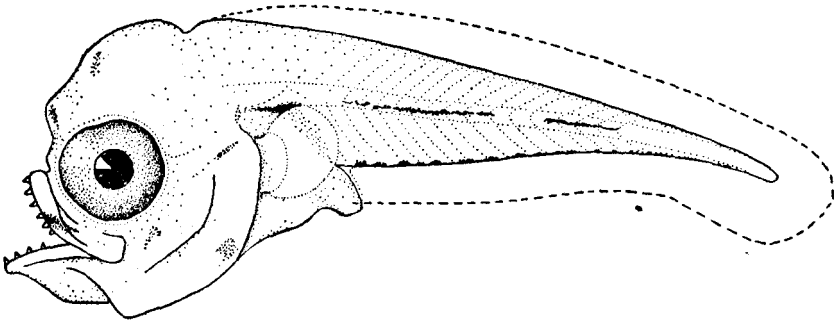

FIGURE 1.—*Menticirrhus americanus*. From a specimen 1.7 millimeters long.

DESCRIPTIONS OF THE YOUNG

Specimen 1.7 millimeters long.—The head and body are rather robust, somewhat compressed, greatest depth only a little less than length of body to vent. The tail is moderately slender, it tapers gradually and ends in a sharp point as usual in recently hatched teleosts. Myomeres are too indistinct to be definitely enumerated, about 16 evident. The mouth is very strongly oblique and moderately large, and prominent teeth are present on the jaws. The eye is prominent, being fully half as long as the head, and it has a round pupil. The vent is situated somewhat in advance of midbody length. The vertical finfold, in the only specimen of this size at hand, is largely torn away, being present, however, around the tip of the tail. The distal portion of the notochord is straight and in line with the axis of the body. The color is mostly pale, with dark markings (specks) around the mouth, along most of the ventral outline and along the middle of the tail. These markings are close enough together to form a longitudinal dark line along the ventral outline of the tail and another one along the middle line of the anterior portion of the tail. These dark lines are quite characteristic and are an aid in identifying the very small larvae with larger ones in which the dark lines are more strongly emphasized (fig. 1).

The specimen described, which was taken in the tow, has been compared with preserved specimens of newly hatched larvae of *saxatilis*. The latter were hatched by the late William W. Welsh from eggs stripped from fish taken at Atlantic City, N.J., on July 27, 1920. The larvae (preserved in formalin) although quite as long as the specimen described, evidently are much younger, as shown by the state of development. The resemblance is not striking, as the specimen of *americanus* is much deeper anteriorly, and the mouth, jaws, and teeth are much further advanced in development. The specimens of *saxatilis* retain no color markings. It is evident, however, from the description and illustrations by Welsh and Breder (1923, pp. 190–193) that rather definite markings were present when the larvae were alive. A slight resemblance is evident in the markings of the most advanced stage figured by Welsh and Breder of *saxatilis* and the 1.7 millimeter specimen of *americanus* already described. This resemblance consists chiefly in a series of dark dots along the ventral outline of the tail. The pupil of the eye is round in the specimens at hand of both species, although in larger examples (10.0 millimeters and upward in length) of *saxatilis* the pupil is vertically elongate, whereas it is always nearly or quite round in *americanus*.

The comparison of the small fry at hand of *americanus* and *saxatilis*, because of the comparatively great difference in age, even though they are of about equal length, does not aid greatly in determining the likenesses and differences that exist between the early larval stages of the two species. Since no newly hatched larvae of *americanus* have been secured, no young of *saxatilis* under 10.0 millimeters (exclusive of the newly hatched fry), and none of *littoralis* less than 9.0 millimeters in length, the study of the relationship of the smaller fry of the local species of the genus must await the collection of specimens of the proper sizes and ages.

Specimens 2.9 millimeters long.—The body is very deep, somewhat compressed, with an abruptly more slender and rapidly tapering tail which ends in a sharp point. A very sharp break in the ventral outline occurs at the vent, where the depth diminishes abruptly. The greatest depth of the body is only slightly less than the length of the body to the vent. Myomeres are mostly indistinct, about 23 evident. The mouth is somewhat less oblique than in the smaller specimen described in the foregoing paragraph, the margin of the upper jaw being about on the same level as the upper margin of the eye, and the gape reaches nearly to the pupil. The teeth in the jaws apparently are much smaller than in the smaller specimen described in the preceding section. The vent is situated notably nearer the tip of the tail (notochord) than the tip of the snout. The vertical finfold remains continuous, with slight indications of rays at the distal part of the tail. Pectoral finfolds are rather prominent, but the ventrals are not evident. The general color is pale, with faint ill-defined dark spots about the mouth and along the ventral outline of the abdomen. Two prominent longitudinal black stripes are situated on the anterior two thirds of the tail, one follows the middle line and the other the ventral outline. Several minute dark dots forming an indefinite line are present also on the dorsal outline of the anterior part of the tail (fig. 2).

The very deep body, with the abruptly more slender tail and the two evident black stripes on the caudal portion of the body are the chief recognition marks at this size. These characters also identify smaller specimens, as shown in the description of a 1.7 millimeter fish, but they are much more prominent and pronounced in somewhat larger specimens.

Specimens 3.8 millimeters long.—The body is deep and compressed, and the tail has become proportionately much deeper and less sharply tapering since a length of about 2.9 millimeters was attained. The break in the ventral contour described in smaller fish remains, but is less pronounced. The greatest depth is now equal to only about two-thirds the length of the body to the vent. The mouth, although still strongly oblique, has become somewhat lower, the gape anteriorly being only slightly above the lower margin of the eye, and the maxillary (which is now well developed) reaches a little beyond the middle of eye. The pupil is nearly or quite round, as in smaller specimens, and the vent remains situated nearer the tip of the notochord than the tip of the snout. The bases of the soft dorsal and anal fins are evident and indications of rays are present. The notochord has become curved upward, and below it the caudal fin is partly developed with rather definite rays. The pectoral fins are short and broad, with indications of rays, and the ventral fins are not evident. The color has changed little since a length of 2.9 millimeters was attained. The dark markings about the mouth, along the ventral outline of the abdomen, and on the tail remain virtually as described in the smaller fish, except that the dark markings on the dorsal outline of the tail are a little more prominent and form a somewhat more defi-

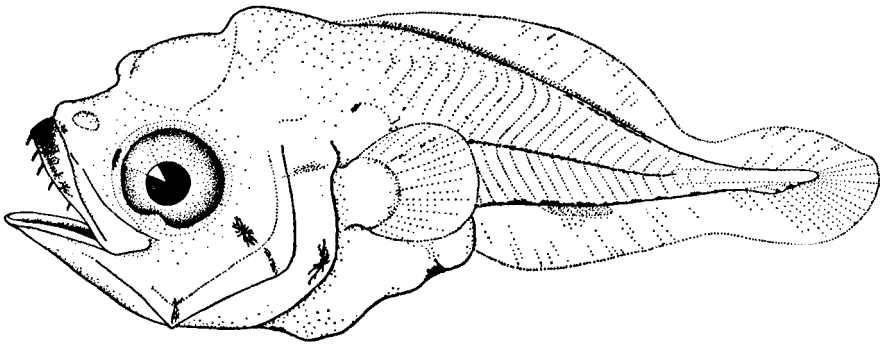

FIGURE 2.—*Menticirrhus americanus*. From a specimen 2.9 millimeters long.

nite stripe. Several indefinite dark markings now are present on middle of side, extending from the eye to opposite the vent (fig. 3).

The principal recognition marks are the same at this size as in 2.9 millimeter specimens previously described. The chief changes have taken place in the development of the tail, which has become much deeper posteriorly, the mouth is less strongly oblique, and some of the fins are becoming differentiated.

Specimens about 5.8 millimeters long.—The fish is much more shapely than it was when smaller. Yet, the body is quite unlike that of the adult, as it is deep and compressed. The break in the ventral outline, behind the vent, pronounced in smaller fish, is no longer prominent, and the caudal portion of the body has become proportionately much deeper. The greatest depth of the body is now scarcely equal to two-thirds of the preanal length and is contained about 2.75 times in the total length to the base of the caudal fin. Myomeres are indistinct anteriorly and again posteriorly, about 25 evident. The mouth remains moderately oblique, and the lower jaw is a little shorter than the upper. The gape is wholly below the level of the lower margin of the eye and the maxillary reaches nearly opposite the anterior margin of the eye. The vent is situated a little nearer the tip of the snout than the end of the caudal fin. Considerable advancement in the development of the fins has been made since a length of 3.8 millimeters was attained, most of the soft rays being fairly well

differentiated in the second dorsal and the anal, and a fairly accurate count of the anal rays may be made, the number being 7 or 8. The caudal fin is better developed than the dorsal and anal; it is round in outline and the longest rays are about equal to the depth of the body just posterior to the vent. The pectorals apparently have made little advancement and the ventral fins are not evident. The dark longitudinal stripes on the caudal portion of the body, described in smaller fish, generally are not evident. The stripes, having broken up into large chromatophores, remain in rather definite rows in some specimens, but are more scattered in others. In still other

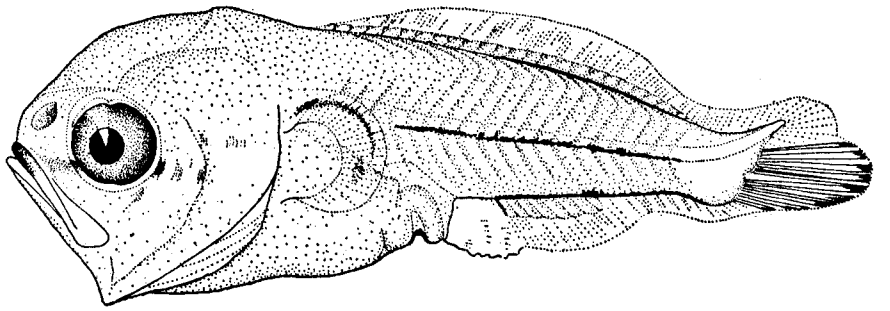

FIGURE 3.—*Menticirrhus americanus*. From a specimen 3.8 millimeters long.

specimens of this size, and even larger ones, the stripe along the lateral line, however, remains well defined. Considerable variation in color, that is, with respect to the number, intensity, and arrangement of the spots present, is evident. The distal portion of the tail remains pale and almost transparent (fig. 4).

The chief recognition marks at this size are the deep compressed body, the large oblique mouth, the short anal fin, and the rather large, dark markings on the caudal portion of the body. However, these markings are faint in some specimens, as shown in the foregoing description, while they are large and well defined in others.

Specimens 8 millimeters long.—The body is proportionately more slender than in specimens 5.8 millimeters long and the head is much broader. The rest of the body,

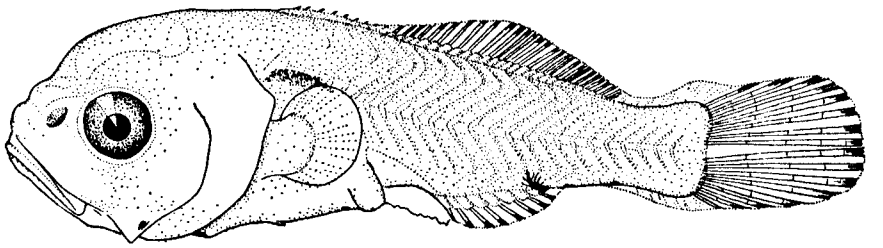

FIGURE 4.—*Menticirrhus americanus*. From a specimen 5.8 millimeters long.

however, remains quite strongly compressed. The greatest depth is contained about 3.0 times in the total length to the base of the caudal fin. The mouth is only slightly oblique, the lower jaw is a little shorter than the upper, and the maxillary reaches nearly to the posterior margin of the eye. Considerable advancement in the development of the fins has been made. The spinous dorsal is evident now, and the ventral fins are rather long and prominent. The pectoral fins have increased greatly in length and reach the vent. The caudal fin has become produced and pointed, the longest rays being nearly as long as the head. The middle portion of the body is largely spotted with dark chromatophores of various sizes, which are present also on

the head and nape. Dusky color is present around the mouth and across the middle of the mandible. The distal portion of the tail remains pale and more or less transparent, the upward curved notochord within it being plainly visible under the microscope with transmitted light. Slight dark color has appeared on the anal and on the margin of the spinous dorsal (fig. 5).

The fish at this size bears about the same recognition marks as in somewhat smaller specimens. However, the head is less strongly compressed, the mouth is less oblique, the spinous dorsal and ventral fins are now developed, the caudal fin has be-

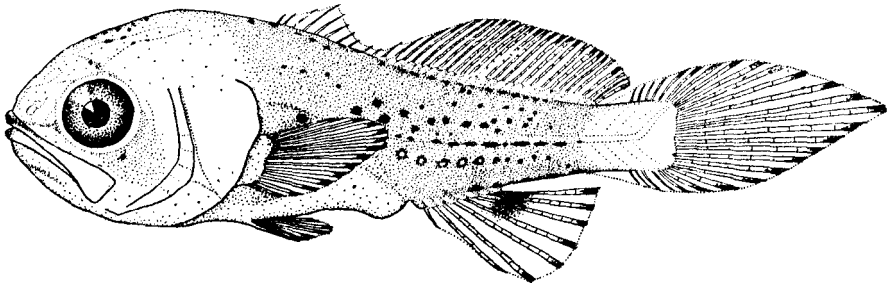

FIGURE 5.—*Menticirrhus americanus*. From a specimen 8 millimeters long.

come somewhat produced and pointed, and the dark markings on the body have increased greatly in number and cover a larger area.

Specimens 10 millimeters long.—The body is moderately deep, compressed, the greatest depth being contained about 3.6 to 3.8 times in the length to base of caudal fin. The head is moderately compressed, and its length is greater than depth of body, being contained about 2.75 to 3.1 in length to base of caudal. The interorbital is strongly convex; the eye is only a little longer than the snout, and it has a rather large, perfectly round pupil. The mouth is moderately oblique, the upper lip anteriorly being slightly below the level of the lower margin of the eye; the maxillary reaches nearly to posterior margin of eye; and the upper jaw projects beyond the lower

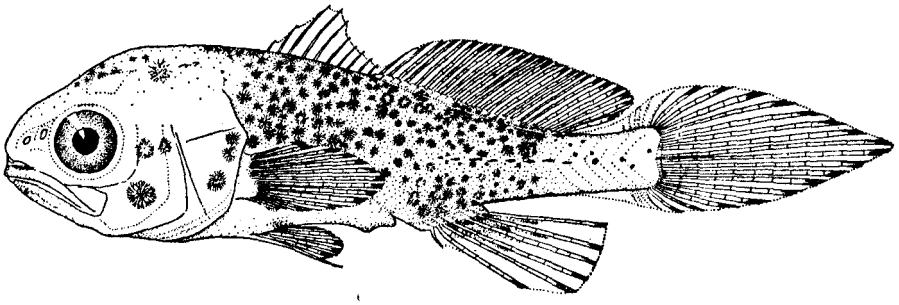

FIGURE 6.—*Menticirrhus americanus*. From a specimen 11 millimeters long.

one. The fins are all well developed, and the rays may be enumerated accurately. The longest dorsal spines reach only slightly past the origin of the second dorsal when deflexed; the caudal fin is nearly symmetrical and quite pointed; and the ventral and pectoral fins are long, generally coterminal, reaching nearly or quite to the vent. The fish has dark chromatophores almost everywhere, except on its ventral surface. They are most numerous on the side from opercular margin to end of base of anal, and few on the head and caudal peduncle. The spinous dorsal and the anal fin generally are partly black; the caudal fin has at most a few dark points on the base, and the other fins are without color (fig. 6).

The present species, at a length of 10 millimeters, is intermediate of the other local species of the genus in the shape of the body, that is, the body is deeper and more strongly compressed (especially the head) anteriorly than in *littoralis*, and less so than in *saxatilis*. It also has a larger and an almost perfectly round disk-shaped pupil, whereas the pupil is vertically elongate and somewhat eliptical in *littoralis* and *saxatilis*. (The shape of the pupil often becomes somewhat distorted during preservation and, therefore, the difference in shape is not always as plainly evident in preserved specimens as in fresh material.) The caudal fin is quite long and pointed and nearly symmetrical in *americanus*. In the other species this fin is quite broadly and asymmetrically rounded, the longest rays being in the lower half of the fin. In *americanus* the spinous dorsal often is partly black, while the ventral fins are colorless, or at most with only a few dark points. In *saxatilis* the spinous dorsal and the ventral fins are wholly black, whereas in *littoralis* these fins are colorless.

Specimens 13 to 15 millimeters long.—The body has become less strongly compressed since a length of 10 millimeters was reached and has become deeper in the region of the vent, causing a notably less pronounced tapering in the depth from the head to the vent. The length and greatest depth of the body, however, remains proportionately about the same as in the 10-millimeter fish. The head is less compressed; the mouth is more nearly horizontal, and the snout now projects slightly beyond the upper jaw. The caudal fin has become proportionately longer and more strongly pointed. No other changes in the fins that appear to be worthy of note are evident. The color has changed little. The general tendency is toward fewer large branching chormatophores and more numerous small dark points. The spinous dorsal and the anal are at least partly black; the second dorsal, the pectorals, and the caudal are unmarked, or the caudal at most may have a few dark markings on the base; and the ventral fins may have only a few dark dots or be solidly black at the base.

The fish obviously has made fair headway toward the adult form in the shape of the head, the body, and the mouth. This species at the size just described differs from *littoralis* about as in the smaller fish previously described, that is, the body is deeper, the pupil is round, the caudal is longer and more pointed, the spinous dorsal is at least partly black, the soft dorsal is unmarked, and the ventral fins have at least some dark points if not partly black. No specimens of *saxatilis* between 11 and 17 millimeters in length are at hand. Therefore, the exact differences between specimens of *americanus* and *saxatilis* of this size cannot be stated at this time.

Specimens 18 to 20 millimeters long.—The body has continued to grow rather more elongate and rounder. The head remains somewhat deeper than wide, however, and the greatest depth (which occurred at the posterior part of the head in smaller specimens, now falls under the spinous dorsal) is contained 3.6 to 3.8 times in the length to the base of the caudal fin. The mouth is nearly horizontal and inferior, and the conical projecting snout is only a little shorter than the eye. A slight knob has appeared at the tip of the lower jaw, which is the beginning of the development of the characteristic mandibular barbel of the adults of the genus. Scalation is nearly complete (although not shown in the illustration). The caudal fin remains long and pointed. The longest rays now definitely occur in the lower half of the fin, and are somewhat longer than the head. Pigmentation has progressed rather rapidly. While variation is evident among specimens, most usually the entire body is spotted with black or dark brown. The spinous dorsal and the anal fins are largely black, as in smaller fish; the ventral fins bear dark spots; and generally two dark blotches have appeared on the base of the caudal fin (fig. 7).

Considerable headway toward acquiring the shape and form of the adult has been made, and the conical projecting snout and the rudimentary mandibular barbel at once identify the fish as a Menticirrhus. The shape of the body in the present species remains intermediate of the other local species of the genus, that is, the body is slightly deeper than in *littoralis*, but not as deep as in *saxatilis*. The pupil, of course, remains round, whereas it is definitely elliptical in the other two species. The tail is longer and more strongly pointed, the longest rays being longer than the head, whereas in *littoralis* and *saxatilis* the longest rays are shorter than the head.

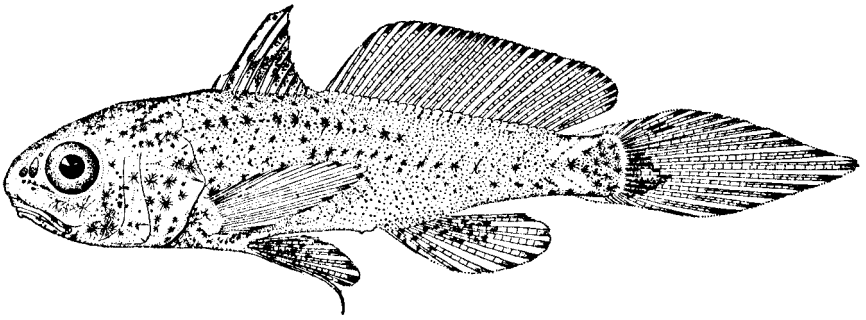

FIGURE 7.—*Menticirrhus americanus*. From a specimen 20 millimeters long.

Specimens 30 to 35 millimeters long.—The body has become somewhat rounder anteriorly since a length of 18 to 20 millimeters was attained, and the greatest depth now is contained in the length to the base of the caudal fin 3.8 to 4 times, which are proportions prevailing in the adult. The mouth is inferior and horizontal, and the snout projects rather prominently, as in the adult. The mandibular barbel is very short, a mere knob, and scalation is complete. None of the dorsal spine are produced and the longest ones reach to the origin of the second fin when deflexed. The caudal fin is long and pointed, the longest rays being slightly below the middle of the fin and

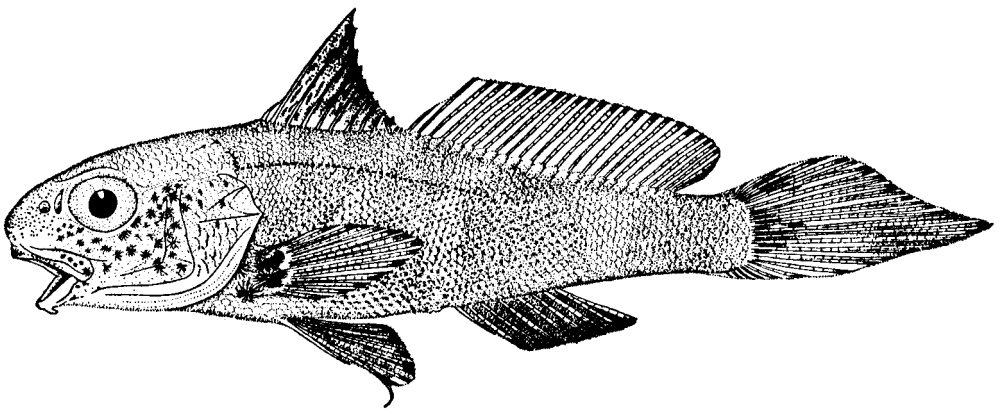

FIGURE 8.—*Menticirrhus americanus*. From a specimen 30 millimeters long.

quite as long as the head. The pectoral fins are long and reach almost to the tips of the ventrals, or nearly to the vent. The body is fully pigmented, some specimens being much darker than others. The lower parts generally are silvery and the upper parts brownish. The ground colors are overlaid with irregular dark specks or spots, which follow the rows of scales more or less definitely. Some specimens have dark blotches and others bear suggestions of dark cross bars. The spinous dorsal is largely

black. A large black spot generally is present on the base of the caudal, preceded by a pale crossline, the rest of the fin being plain translucent. The anal and ventral fins usually are dusky to black, and the pectoral fins generally are plain translucent, or sometimes with dusky points (fig. 8).

The round pupil and the long pointed tail remain as dominant characters in distinguishing the present species from the other two local species of the genus. The long pectorals and the large scales (which are not notably reduced on the chest) also aid in distinguishing the present species from *littoralis*, while it differs further from *saxalitis* in the more elongate body.

Specimens 50 to 60 millimeters long.—The fish has acquired virtually the shape of the adult, the body being only a little more strongly compressed anteriorly. The proportions of the depth to the length are the same as in fish 30 to 35 millimeters long, and these proportions also occur in the adults. The snout is more sharply conical, projects beyond the mouth more prominently than in smaller fish, and is now fully as long as the eye. The mandibular barbel is developed and is about half as long as the pupil. No important changes have taken place in the development of the

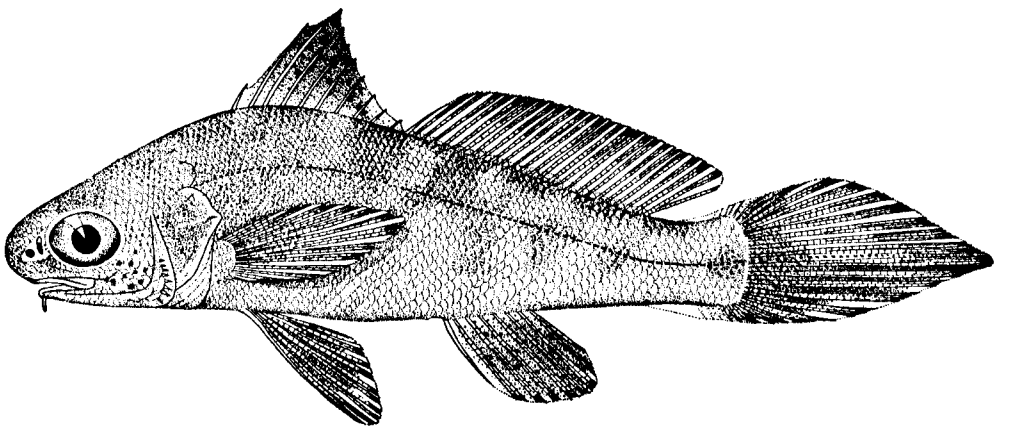

FIGURE 9.—*Menticirrhus americanus*. From a specimen 59 millimeters long.

fins. The spines in the first dorsal are somewhat shorter, and the lower lobe of the caudal remains notably more pointed and proportionately longer, than in the adult. The color remains about as in 35-millimeter fish. Some specimens retain indefinite dark blotches on the sides, and others have more or less definite oblique bars. In the majority of specimens at hand the base of the caudal is dusky, and this color extends on the lower lobe of the fin. The anal and ventrals are in part white, as in the adult (fig. 9.)

Specimens 50 to 60 millimeters long are enough like the adult to be recognized readily. Specimens of this size differ more strongly from full-grown fish in the shape of the caudal fin than in any other one character, and this member does not acquire the adult shape, namely, a slightly concave upper lobe and a moderately short, rather sharply rounded lower lobe, until the fish reach a length of about 100 millimeters. At a length of 50 to 60 millimeters the spinous dorsal has become quite pointed, though none of the rays are especially produced, nor do any of them reach far beyond the origin of the second dorsal. The fish may be distinguished from the other species of the genus at this size by about the same characters which identify the adults, namely, the rather small scales (86 to 90 vertical series above the lateral line), which are not

reduced on the chest; the short anal, which typically has only 7 rays; the long pectorals, which reach nearly or quite to the tips of the ventrals; and by the presence of obscure bars and blotches on the sides and back. The large roundish pupil remains conspicuous and readily distinguishes this species from the other local forms.

DISTRIBUTION OF THE YOUNG

It has been shown elsewhere (p. 53) that the young under 20 millimeters in length were taken more abundantly off Beaufort Inlet than in the inside waters. The larger ones, however, were caught equally as often and in equally large numbers within the harbor and adjacent waters as off the inlet. This species was not taken in the surf along the outer shores of the "banks", which apparently is a favorite habitat of the young of the other local species of the genus. It seems evident, furthermore, that the young, like the adults, are chiefly bottom dwelling. Larvae under 10 millimeters in length appeared in the surface tow only 3 times, whereas in about an equal number of hauls on the bottom they were taken 22 times. Individuals over 10 millimeters in length were not taken at the surface with the gear used, namely, 1-meter tow nets, and only a few exceeding a length of 10 millimeters were taken with this apparatus on the bottom.

The failure to capture the larger young with meter tow nets on the bottom where they certainly were present, as shown by large catches made with an especially constructed otter trawl, no doubt was caused by their ability either to avoid the meter nets or to escape from them. It is unfortunate that no satisfactory net for catching fish, except small larvae, at the surface has become available. Since the surface of the waters could not be properly sampled for young of about 10 millimeters and upward in length, it cannot be stated definitely that these larger young do not occur there. However, according to the data secured (which may not be entirely reliable, as already shown) the habitat of the young is almost identical with that of the adult; that is, fish of nearly all ages inhabit both inside and off-shore waters and apparently are almost wholly bottom dwelling.

GROWTH

While the measurements secured are not numerous, it is believed, nevertheless, that they show in a general way the growth of the young during the first several months of life. All the measurements made, both of young and adults, are tabulated by months in 5-millimeter groups in table 1. It is evident from this table that the young of the 0-class are readily distinguishable from the older fish until about the end of September. In October and November this class is less clearly distinct. During the winter months, that is, from December to March, an insufficient number of fish was taken to give reliable data. In table 2 the range in size of the 0-class and the arithmetical average of the specimens measure are shown for each month. The upper extreme may not be quite accurate for the fall months. However, the few larger specimens that may have been wrongly assigned to either year class would not affect the average length greatly.

It is evident from the tables presented that the range in size of the 0-class is very great toward the end of the summer and in the fall. In September, for example, when spawning probably has just ended, the range in length of the specimens of the 0-class measured extends from 2.5 to 156 millimeters. In November the difference in size of the specimens of this same class (if the data were correctly interpreted) is

even greater, as the range extends from 15 to 209 millimeters. This large range in size, no doubt, is caused in part by a difference in the rate of growth; more particularly, however, to the very long spawning season, which apparently extends from April through August.

TABLE 1.—*Length frequencies of 1,779 Menticirrhus americanus*

[Measurements to nearest millimeter; in 5-millimeter groups]

Total length	April	May	June	July	August	September	October	November	December	January	February	March
0–4												
5–9	1	2	9	5		3						
10–14	1	1	6	132	6	10						
15–19			11	32	14	1						
20–24			2	2	5	3		1				
25–29				5	4	3	1					
30–34				7	13	15	2	3				
35–39				9	35	8	4	1				
40–44				9	37	2	3	7				
45–49				15	41	4	7	7				
50–54				12	22	1	16	5				
55–59				18	29	4	15	7				
60–64				16	20	8	20	13				
65–69				14	26	12	16	11	1			
70–74				4	24	22	8	9				
75–79				14	16	20	8	9				
80–84				10	20	15	10	4				
85–89				11	39	10	5	10				
90–94				6	7	9	2	3				
95–99				2	16	2	2	8	1			
100–104				2	7	9	3	5				
105–109				1	7	6		3	2			
110–114					4	3	2	1	1	3		
115–119					5	3		2		3		
120–124					1	1	1	5	3	2		
125–129					3	2		3	2	6	1	
130–134		1	2		2		2	9	3	1		
135–139		1	2			2		5	2	4		
140–144			3					6	1	3		
145–149			9				1	10	2	3		
150–154			14		1	1	1	5	1			
155–159			13		1	2	1	13	7	2		
160–164			16		1	2	1	12	3	2		
165–169	2		15				2	17	3			
170–174	1		21				2	8	6	1		
175–179	1		13					17	8			
180–184			9				2	30		1	2	
185–189	1		5			1	1	22	1			
190–194	1		5			2		13	2		1	
195–199	2		4			2	2	20		1		1
200–204		1	2		1			10				4
205–209			2					8				1
210–214					1		1	5				
215–219				2			1	1			1	1
220–224					2			2				
225–229		1	1		2	1		1			1	1
230–234		1			1	2	1	5				3
235–239				1	1		2	1				2
240–244	1				3	2	2	1				3
245–249				1	1		2	2				
250–254	1					1		1				5
255–259	1			1	1	1	1	2	1		1	1
260–264	1	1			1	1		2				1
265–269	1	1			1	4		1				2
270–274					1			1				
275–279							1					
280–284				1		4	2	2		1		1
285–289							1		1			1
290–294		1										
295–299							1	2			1	
300–304											1	
305–309							1		1			
310–314	1											
315–319												
320–324												
325–329												
330–334												
335–339												
340–344								1			1	
345–349										1		

The average rate of growth as shown by the tables, is quite regular and rapid during the first several months of life. The data are not sufficient to show how it progressed during the winter nor the second summer. However, since the average length during November of various samples taken over a period of several years, consisting of a total of 327 fish, is 135.01 millimeters (5⅜ inches) with an apparent maximum length of 209 millimeters (8⅛ inches), it seems evident that some of the earliest and fastest growing individuals of this year class reach a marketable size, and probably maturity, during their second summer. Others may require a year longer.

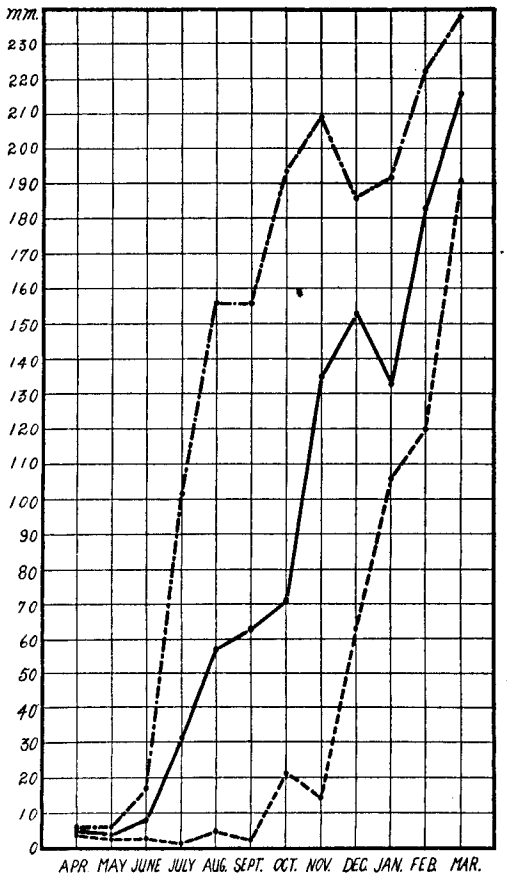

FIGURE 10.—Growth of *Menticirrhus americanus* during first year or so of life. Solid line, average size; dot and dash line, maximum size; broken line, minimum size. (Graph based on table 2.)

Welsh and Breder (1923, p. 188) produce limited data which they believed tended to show that the fish reached a length of only 140 to 240 millimeters (5½ to 9½ inches) at Fernandina, Fla., by the second winter, the modal length being around 170 millimeters (6¾ inches). In New Jersey the rate of growth was thought to be a little slower, as individuals apparently in their second winter averaged only about 160 millimeters (6¼ inches) in length. The authors conclude that maturity is reached in about 3 years. We agree that some individuals no doubt require 3 years to reach a marketable size and maturity. However, it seems certain, as already shown, that at Beaufort not an inconsiderable number becomes mature and marketable before an age of 3 years is attained.

TABLE 2.—*Monthly summaries of length measurements of 1,519 Menticirrhus americanus during their first year of life (based on table 1)*

Month	Fish measured	Smallest millimeter	Largest millimeter	Average millimeter	Month	Fish measured	Smallest millimeter	Largest millimeter	Average millimeter
April	2	4	5.5	4.75	October	140	21	194	71.2
May	3	2.75	6	3.91	November	328	15	209	135.01
June	28	3	17	8.0	December	49	63	[1] 186	153.2
July	326	1.7	102	31.42	January	32	106	[1] 192	[1] 133.28
August	406	5	156	57.48	February	6	120	223	183.33
September	183	2.5	156	63.05	March	16	191	237	216.6

[1] The apparent decrease in length, of course, shows that the larger individuals of the year class either were not present or not properly represented.

MENTICIRRHUS SAXATILIS (Bloch and Schneider)

The range of *Menticirrhus saxatilis* extends from Maine to Florida. Therefore, its range overlaps considerably that of *americanus* and also to a lesser extent that of *littoralis*. However, it ranges farther northward and apparently not as far southward as the other local species. In Chesapeake Bay and southward *saxatilis* is less numer-

ous than *americanus*, but northward (the northern limit of the range of *americanus* being New York) it is more numerous. This species occurs in the vicinity of Beaufort, generally in small numbers, virtually throughout the year. It is taken both in the sounds and estuaries and along the outer shores of the "banks." Its local commercial value, however, is rather small. It is reported to reach a maximum weight of 3 pounds, but it probably does not average over a half a pound in the markets of North Carolina. It is caught in the same way as, and often in company with, *americanus*.

SPAWNING

Ripe fish were not obtained at Beaufort. It is possible, however, to determine the time and place of spawning in a general way from the collection of a rather small number of young fish. The smallest young of this species obtained were 10 millimeters long, and were caught on June 20 (1932). On this same date a total of 29 specimens, ranging from 10 to 62 millimeters in length, was caught. Two days later 2 specimens 91 and 93 millimeters long were taken. These specimens no doubt belong to the same year class and are the product of the current year's spawning. During July, of several years, 14 specimens, ranging more or less gradually from 20 to 116 millimeters in length, besides some larger ones, which quite certainly are older fish, were secured. During August, 5 young, ranging from 70 to 95 millimeters in length, were taken. Fish 91 to 93 millimeters long quite probably are a few months old, while specimens only 10 millimeters long may be only a few weeks old. The specimens collected in June, supported in a measure by those taken in July and August, appear to show that spawning begins not later than April and that it extends through May. Additional data quite probably would show that spawning extends over an even longer period of time.

The smaller specimens, 70 millimeters and less in length, were all taken in the surf on the outer shores of the "banks." The larger ones were taken there in part also and in part in the estuary of Newport River. The presence of the small fish on the outer shores of the banks suggests that spawning may take place near there, as it quite surely does in the other local species of the genus.

Spawning takes place about the same time in Chesapeake Bay as at Beaufort, beginning probably a little later, for Hildebrand and Schroeder (1928, p. 291) report the capture of fish 16 millimeters long in Chesapeake Bay late in June. These investigators also report the collection of specimens ranging from 35 to 154 millimeters in length late in September and others in October 50 to 185 millimeters long, all of which they believe to belong to the 0-class.

Welsh and Breder (1923, p. 190) state that spawning (presumably at Atlantic City, N.J., where they carried on investigations) commences in June and continues until August, and reaches its maximum in late June or early July. They took ripe fish in July which were stripped, and the eggs were incubated and hatched in the laboratory. The same authors report spawning early in June at Woods Hole, Mass. The information available, then, indicates that spawning begins a month or two later in New Jersey and Massachusetts than it does at Beaufort, and that it probably ends correspondingly later.

DESCRIPTIONS OF THE EGGS AND YOUNG

The egg and its development.—The following account of the egg and its development is based on the description given by Welsh and Breder (1923, p. 190, figs. 46–49). The eggs are spherical, 0.76 to 0.92 millimeter in diameter, and lighter than sea water.

They are almost colorless, having only a slight yellowish tinge, and they contain from 1 to 18 oil globules. If only one globule is present it is larger than if several are present. During the development of the egg the oil globules become amalgamated until only one remains at hatching. The incubation period has a duration of 46 to 50 hours in water temperatures of 68° to 70° F. Segmentation and development proceeded as in Bairdiella (Kuntz, 1914). About 18 hours after fertilization grayish chromatophores appeared on the dorso-lateral aspects of the embryo and on the surface of the oil globule. Six hours later the chromatophores had become black on the oil globule, and the embryo was dotted with black. Some black chromatophores were scattered also over the yolk near the embryo.

Newly hatched young.—The following account of the newly hatched young is based on descriptions and figures by Welsh and Breder (1923, pp. 190–193, figs. 50–53). The fry are 2.0 to 2.5 millimeters long at hatching, and they float in an inverted position. The head is slightly deflected, the vent is notably in advance of midbody length, and the oil globule lies in the posterior part of the yolk sac. Pigmentation consists of three vertical bands, each consisting of black and dull gold chromatophores, the first one being above the vent and two posterior to it. A patch of chromatophores of the same colors lies in the dorsal finfold anteriorly, and similar ones are scattered over the yolk sac.

None of the larvae lived over 7 days. They lost the gold pigment by the second day and all markings had become less conspicuous. By this time the pectoral fins had become plainly visible. On the fourth day only traces of dark bands remained, and a row of black chromatophores had appeared along the ventral surface posterior to the vent. The blotch in the dorsal finfold remained conspicuous, the eye had become pigmented, the pectoral fins had become dotted with black and gold chromatophores, and the abdomen had a golden tinge. The yolk sac was almost completely absorbed, and the mouth was open. On the fifth day the larvae, when at rest, floated with the head downward. With the unaided eye the fry appeared dark brown anterior to the vent, and the tail was transparent. On the sixth day the eye had a steel-blue luster, and no trace of rudimentary fins was evident. On the seventh day, shortly before the longest survivors died, a few of the fry had attained a length of 2.8 millimeters. Therefore, very little growth had been gained.

The larvae described by Welsh and Breder were preserved, in part, and were compared by us with the smallest fry of *americanus* taken at Beaufort. Although specimens of the last-mentioned species, quite as small as the larvae described in the preceding paragraphs, were taken at Beaufort, the resemblance is very remote, as stated elsewhere (p. 55), which apparently is caused partly by a difference in age and partly by the differences of the two species.

The account of the development of this species must remain incomplete for the present, as the stages between the newly hatched young and specimens 10 millimeters in length have not been secured.

Specimens 10 millimeters long.—The body is rather deep, compressed, the greatest depth being contained about 2.8 to 2.9 in length to the base of caudal fin. The head is quite narrow, compressed, and its length is equal to or a little longer than the greatest depth of the body. The interorbital is convex. The eye is longer than the snout, and it has a very small vertically slightly elongate pupil. The mouth is large and moderately oblique, the upper lip anteriorly being nearly on a level with the lower margin of the pupil. The maxillary reaches somewhat past the middle of the eye, and the upper jaw projects beyond the lower one. The fins are all well developed,

permitting an accurate enumeration of the rays. The longest spines in the first dorsal reach past the origin of the second dorsal when deflexed; the caudal fin is asymmetrically rounded, the longest rays being in the lower half of the fin; and the ventral and pectoral fins are rather long and coterminal, not quite reaching vent. The body almost everywhere is dotted with prominent black chromatophores. An indefinite brownish band is present on the back below the base of the dorsal fins, and another one extends along the lateral ventral edge from the origin of the anal to the base of the lower rays of the caudal. The spinous dorsal is almost wholly black; the second dorsal is colorless, except for an indefinite elongate dark band on the base of about the middle third of the fin; the caudal fin is colorless, with a white base, and sometimes with one or a few large black chromatophores; the anal fin is colorless, except for dark dots on its base; the ventral fins are wholly black; and the pectoral fins are plain translucent (fig. 11).

All the specimens at hand were caught among black, partly suspended vegetable debris, which they resemble in color. It seems probable that these fish are darker than they would have been had they been taken in a different environment.

This species is characterized at this size chiefly by the deep, strongly compressed body; the narrow, well-compressed head; the small elliptical pupil; the broad, asymmetrically rounded caudal; and by the black spinous dorsal and ventral fins.

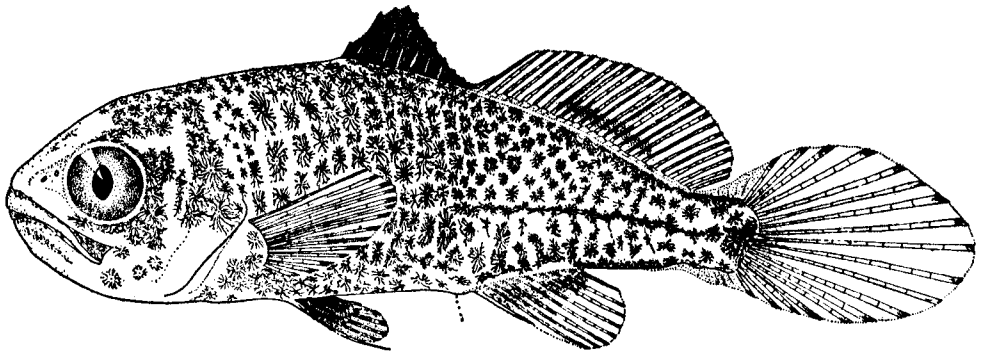

FIGURE 11.—*Menticirrhus saxatilis*. From a specimen 10 millimeters long. (Drawing by Miss Nell Henry.)

The specimens described in the foregoing paragraphs are the smallest ones taken. The confusion of this species with smaller specimens of the genus, identified and described as *americanus* is quite improbable, because of the rather pronounced differences among the species in specimens 10 millimeters in length, as shown by the descriptions and illustrations offered. Certainly some of the differences would be evident, also, in somewhat smaller specimens.

Specimens 18 to 20 millimeters long.—The body has become somewhat more slender since a length of 10 millimeters (no specimens between 10.5 and 17 millimeters in length having been collected) was attained, and it remains rather strongly compressed, the greatest depth being contained in the length to the base of the caudal about 3.25 to 3.4 times. The head has become broader, but it remains much deeper than broad. The mouth is slightly oblique and nearly terminal, the snout scarcely projecting beyond the upper jaw. A slight knob, the beginning of the characteristic barbel of the adult, is evident at the symphysis of the lower jaw. Scalation is nearly complete, and the lateral line is developed anteriorly to about the middle of base of second dorsal. The caudal fin is rather broadly pointed; the longest rays, which are shorter than the head, are in the lower half of the fin. The general color is

(of specimens taken in black vegetable debris) almost uniform dark brown, with a slight indication of a broad vertical bar, darker than the ground color, on the side under the spinous dorsal, and another one under the middle of the base of the second dorsal. The spinous dorsal and the ventral fins are black; the pectoral fins are colorless; the second dorsal and anal have at least a partly black base, the rest of these fins being colorless; and the caudal is colorless, except for a black blotch on the base (fig. 12).

The present species is deeper than either of the other two local species of the genus. Its elliptical pupil and rather bluntly pointed tail, which is shorter than the head, at once distinguish this species from *americanus*. The dark cross bars on the body, the black spinous dorsal, and the black ventral fins separate it from *littoralis*.

Specimens 30 to 35 millimeters long.—The body has continued to become more elongate and less strongly compressed. The depth remains proportionately a little greater than in the adult, it being contained in the length to the base of caudal 3.5 to 3.65 times. The mouth is nearly horizontal, inferior, and the snout projects moderately beyond it. The mandibular barbel is short, but plainly evident, and scalation is complete. None of the dorsal spines are produced, the longest reaching

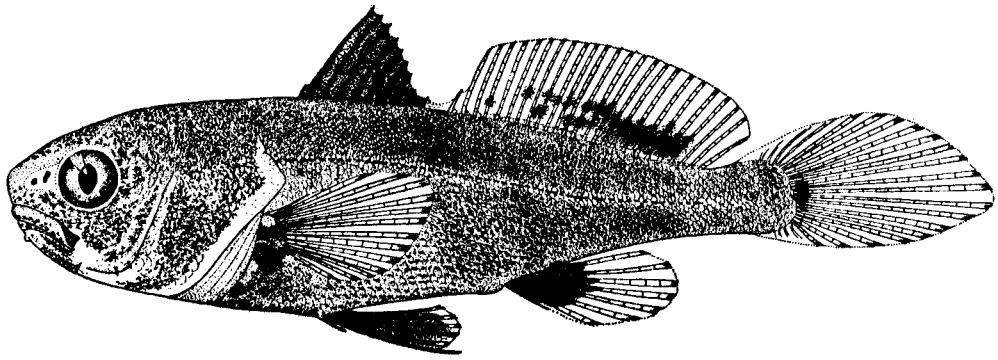

FIGURE 12.—*Menticirrhus saxatilis*. From a specimen 20 millimeters long. (Drawing by Miss Nell Henry.)

opposite the base of the first or second ray of the second dorsal when deflexed. The caudal fin is slightly angular, and the longest rays, which are in the lower half of the fin, are notably shorter than the head. The pectoral fins scarcely reach the tips of the ventrals, and the latter do not quite reach the vent. The body is quite fully pigmented; the ground color is silvery, brightest on lower parts of body, overlaid almost everywhere with dark brown dots. Dark bars are evident in the majority of the specimens at hand; the first one is on the posterior part of the head and runs obliquely downward and backward on the opercle; the second one crosses the nape and is parallel with the first one; the third one lies under the spinous dorsal and bends forward slightly, nearly or quite joining the second one on the middle of the side. The two together form a V, which is a recognition mark in the adult. Posterior to the bars described are dark blotches suggestive of bars. The spinous dorsal and the ventrals remain almost wholly black; the second dorsal and anal are black at the base or at least are dotted with black; the caudal fin bears two irregular dark spots on its base and is plain translucent elsewhere; and the pectoral fins are plain, more or less dotted with black at the base (fig. 13).

This species, like *littoralis*, continues to differ from *americanus* in the eliptical pupil and the short angulate caudal fin. It differs from both the other local species

in the deeper body; and from *littoralis* in the presence of large scales (which are not notably reduced) on the chest, and in the longer pectoral fins. This species, according to the specimens at hand, alone has definite dark bars (on anterior part of the body) at this size.

Specimens 50 to 60 millimeters long.—The body has continued to grow less compressed and somewhat more elongate, the depth now being contained in the length 3.8 to 4.1 times, which are the dominating proportions in the adult. The

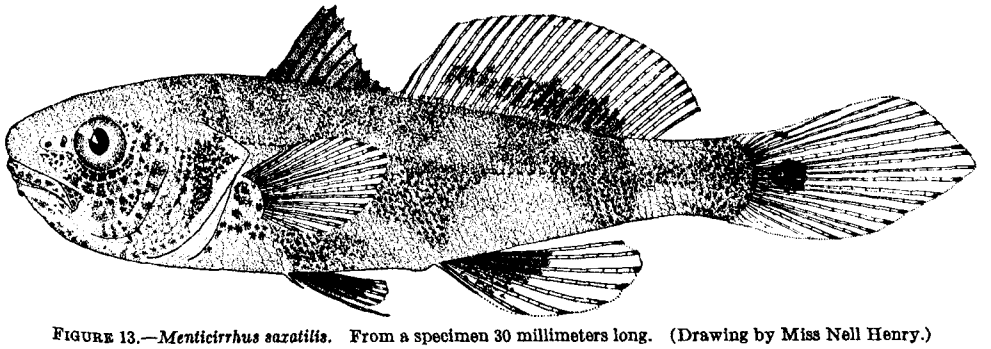

FIGURE 13.—*Menticirrhus saxatilis.* From a specimen 30 millimeters long. (Drawing by Miss Nell Henry.)

snout is conical, it projects much more strongly than in the smaller fish described in the foregoing section, and is somewhat longer than the eye. Although none of the dorsal spines are notably produced, the longest one reaches well past the origin of the second dorsal. The caudal fin has a slightly concave margin and the lower lobe remains notably longer and somewhat angulate. The color varies greatly among specimens. Some are dark brown, others silvery gray. However, all have rather definite oblique dark bars on the anterior part of the body and a few blotches poste-

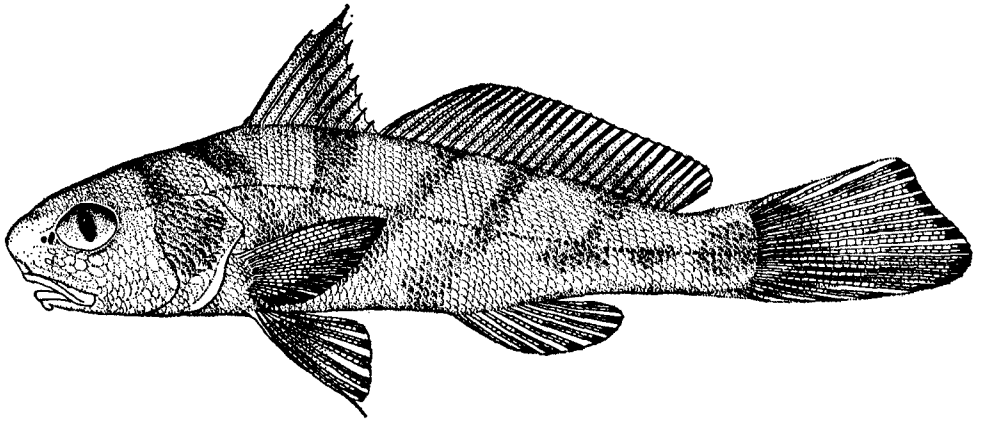

FIGURE 14.—*Menticirrhus saxatilis.* From a specimen 63 millimeters long.

riorly. The spinous dorsal and the ventrals remain almost wholly black in the darker specimens, but are only partly dusky in the lighter ones (fig. 14).

The characters of the adult are perhaps less fully developed in this species than in the other local forms at the length described. The third dorsal spine becomes notably produced when the fish reaches a length of about 85 millimeters, although not yet as long as in larger specimens. The caudal fin does not acquire fully the shape it has in full-grown fish until a length of about 120 millimeters is attained. However,

the fish resemble the adult sufficiently to be recognized readily. The characters that distinguish the species at this size are largely the same as those used in identifying the adult; namely, the small scales (91 to 96 vertical series above the lateral line), which are not notably reduced in size on the chest; the rather high spinous dorsal (the third ray later becoming conspicuously produced) with the longest spines reaching well past the origin of the second dorsal; the longer anal, typically with 8 soft rays; the moderately long pectorals, which usually reach to tips of ventrals; and the presence of rather definite black bars on the back and sides, the one crossing the nape and the one under the spinous dorsal nearly or quite meeting on the side to form a V above the pectoral. The small, vertically elongate, eliptical pupil remains conspicuous, as in smaller specimens, and readily distinguishes this species from *americanus*, although not from *littoralis*.

DISTRIBUTION OF THE YOUNG

Young under 10 millimeters in length were not taken. Those from 10 to 70 millimeters in length were all collected in the surf along the outer shores of the "banks." The larger ones were also taken there in part and in part in the estuary of Newport River. So far as known, the young dwell on or near the bottom like the adults.

GROWTH

The measurements obtained are inadequate to cast much light upon the rate of growth. However, specimens of the 0-class, 113 to 116 millimeters long, taken in July when very probably not over 3 months old, suggest rapid growth.

Hildebrand and Schroeder (1928, p. 291) report specimens, 35 to 154 millimeters in length, from Chesapeake Bay taken late in September, and others 50 to 185 millimeters long taken in October. If the larger fish are correctly assigned to the 0-class, a phenominally rapid growth must take place.

Welsh and Breder (1923, p. 192) state, "The growth of *Menticirrhus saxatilis* the first summer is exceedingly rapid." These authors record specimens of the 0-class from Woods Hole, Mass., as much as 100 millimeters long on September 1; others from Cape May, N.J., 90 millimeters long on August 8; and still others from Chesapeake Bay, 140 millimeters long on September 12. All the data that are available, therefore, point to a very rapid growth in this species during the first summer.

Very little is known about the growth after the first summer. The present investigation, being concerned almost wholly with the development of the young, has yielded virtually nothing on this phase of the life history. Welsh and Breder (1923, p. 194) state that from the examination of the scales of a small series of examples from New Jersey it appeared that a modal length of about 120 millimeters was attained by the first winter, the majority of the fish being 100 to 150 millimeters long. In the second winter the modal length was about 250 millimeters, and the third winter 350 millimeters. Then, the writers conclude that maturity is reached during the third or fourth summer. The earlier spawning season and the very rapid growth during the first summer further south, that is, in Chesapeake Bay and at Beaufort, suggests that maturity may be attained there a year earlier.

MENTICIRRHUS LITTORALIS (Holbrook)

Menticirrhus littoralis ranges from Chesapeake Bay southward to the Gulf coast, the exact limits of its southern distribution being undetermined. Its range northward does not extend as far as that of either of the other two local species of the

genus. Southward it probably extends further than that of *saxatilis* and equally as far as *americanus*. This species as a whole is of much less commercial importance than the others. At Beaufort it is much less numerous than *americanus* and about equally as common as *saxatilis*, its commercial value being small. This species evidently seldom enters Beaufort Inlet, as only one record (Bird Shoal, 1906) of its capture in the inside waters is at hand. The writers did not find it in the more or less enclosed waters of the vicinity. The young, ranging upward of about 15 millimeters, are common during the summer in the surf along the outer shores of the "banks" where they may be taken with small collecting seines in company with young pompano, spot, and occasionally with its congener, *saxatilis*.

SPAWNING

Smith (1907, p. 324) says, "At Cape Lookout spawning fish were found by the writer in June, and at Beaufort ripe eggs have been taken on several occasions between June 1 and 10." Unfortunately, the eggs are not described. If the eggs were taken in the tow during the present investigation, they were not recognized, and ripe fish were not seen. Neither did the larvae appear in the tow. The smallest specimens secured are 9 and 10 millimeters long, and were taken on June 20 (1932) with a bobbinet seine in the surf on Bogue Banks, opposite Fort Macon. Fish ranging from 15 to about 120 millimeters long are abundant there throughout the summer. Some of the fish taken in June that certainly belonged to the 0-class had attained a length as great as 75 to 80 millimeters. Examples evidently of the 0-class, caught during July, ranged from 11 to 58 millimeters (the larger individuals of the class being missing), those taken during August ranged from 15 to 98 millimeters, and those caught in September from 15 to 120 millimeters.

A collection made on June 10 includes specimens 53 to 57 millimeters long, and one made on June 20 contains specimens 75 to 80 millimeters long. It seems reasonable to assume that these rather large, well-developed specimens are 6 to 8 weeks old. If that be true then spawning probably begins not later than the 1st of May. Young only 15 millimeters long were taken as late as September 14. Fish of such a size probably were hatched in August. Although these data are not as complete as desirable, they do indicate rather strongly that spawning begins not later than the 1st of May and that it continues into August.

Although the eggs and small fry under 9 millimeters in length were not taken, it seems almost certain that spawning occurs only in the open outside waters. This conclusion is arrived at for the reason that the adults rarely enter the inside waters about Beaufort and, furthermore, the young of 9 millimeters and upward in length were found only in the surf.

DESCRIPTIONS OF THE YOUNG

Specimens 10 millimeters long.—The body is quite elongate, compressed, the greatest depth being contained about 3.6 to 4.0 in the length to base of caudal fin. The head is rather broad, more or less quadrate in cross section. Its width is equal to about three fourths its depth, and its length is somewhat greater than the depth of the body, being contained about 3.2 in the length to base of caudal. The interorbital is rather flat and broad. The eye is longer than the snout, and it has a very small, vertically slightly elongate pupil. The mouth is moderately large and oblique, the upper lip anteriorly is about on a level with the lower margin of the eye, and the

upper jaw projects beyond the lower one. The fins are all well developed and an accurate enumeration of the rays is obtainable. The longest spines in the first dorsal reach somewhat beyond the origin of the second dorsal when deflexed; the caudal fin is asymmetrically rounded, the longest rays being in the lower half of the fin; the ventral and pectoral fins are rather long and coterminal, not quite reaching the vent. The body is densely dotted with dark chromatophores, pigmentation in some specimens being almost general, and dark brown in color as seen with the unaided eye. The spinous dorsal, the ventrals, and the pectorals are colorless. The caudal fin, too, is colorless or at most with one to a few dark dots on the base. The posterior half of the base of the soft dorsal and most of the base of the anal are black, the amount of black present varying among specimens, the rest of these fins being plain colorless (fig. 15).

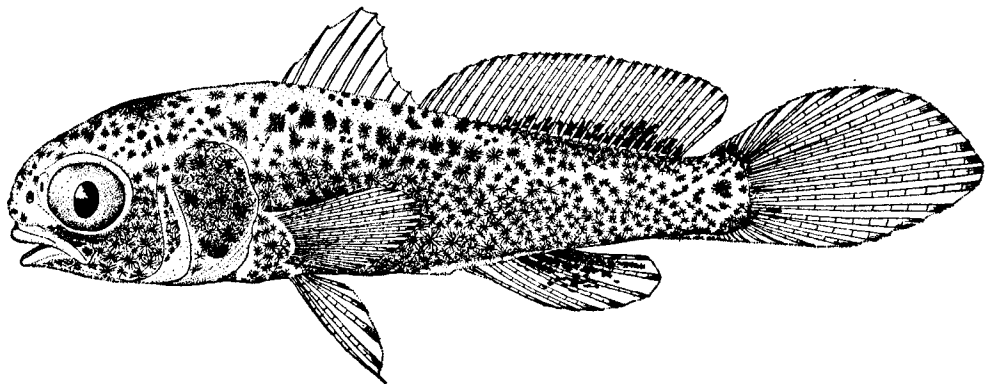

FIGURE 15.—*Menticirrhus littoralis*. From a specimen 11.9 millimeters long.

All specimens at hand of the size described were taken among black, partly suspended vegetable debris, which they resemble in color. Somewhat larger specimens caught in the same environment, too, are black, while specimens taken on white sand are pale silvery. It seems probable, therefore, that small fish, if caught in a different environment, too, would be paler in color.

This species is recognized, when about 10 millimeters long, chiefly by the slender body; the broad head, which is somewhat quadrate in cross section; the small elliptical pupil; the broad asymmetrically rounded caudal; and by the absence of black on the spinous dorsal and ventral fins.

The smallest specimen of this species at hand is 9 millimeters long. It does not differ noticeably from the 10-millimeter ones described in the foregoing paragraphs. It is quite unlikely that a confusion of this species has taken place with the smaller specimens of the genus identified and described as *americanus*. The very evident differences, existing at a length of 10 millimeters, as shown by the descriptions and illustrations offered, surely would be evident also in part in smaller specimens.

Specimens 13 to 15 millimeters long.—The body has become rather deeper and heavier posteriorly, although the length and the greatest depth remain proportionately about the same as in 10-millimeter fish. The head is more compressed and less evidently quadrate in cross section. The mouth is only slightly oblique, and the snout projects somewhat beyond the upper jaw. No pronounced changes in the fins have taken place. The caudal fin apparently has become slightly more pointed, but retains an asymmetrical shape. The body in the specimens at hand remains dark

brown. The spinous dorsal, the ventral, and pectorals remain colorless. The amount of black on the base of the soft dorsal and on the anal varies among specimens from a small spot on the base of each fin to a long band or blotch involving a considerable portion of each fin. The caudal fin is colorless, except for a pair of more or less triangular-shaped black spots on its base. The specimens described were taken among black vegetable debris and, therefore, may be generally darker in color than others would be if taken in a different environment.

In this species, as in *americanus*, moderately pronounced headway has been made toward acquiring the adult form, especially in the shape of the head, body, and mouth. The slender body, the elliptical pupil, the asymmetrically rounded caudal, and the absence of black on the spinous dorsal and the ventral fins serve to characterize *littoralis*, as in the 10-millimeter fish previously described.

Specimens 18 to 20 millimeters long.—The body has become only slightly more rounded and elongate since a length of about 15 millimeters was attained, the greatest

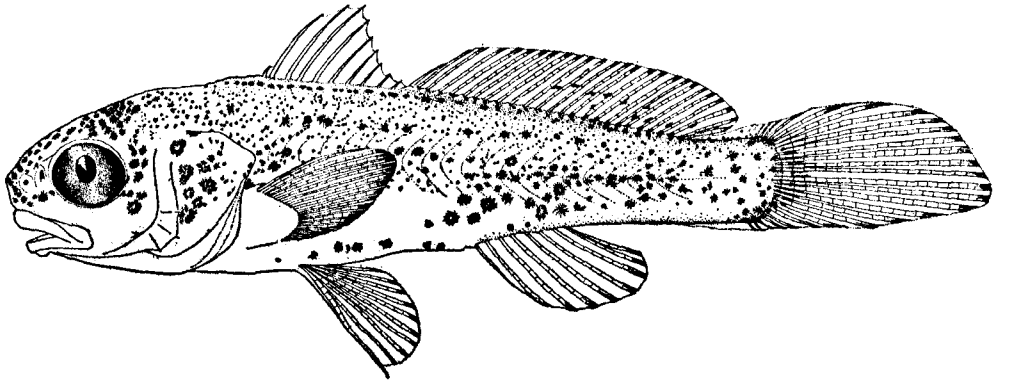

FIGURE 16.—*Menticirrhus littoralis*. From a specimen 19 millimeters long.

depth being contained in the length to the base of the caudal about 3.75 to 4.2 times. The head remains low and wide, its depth being only a little greater than its width. The mouth is nearly horizontal and inferior, and the rather conical snout, which is scarcely shorter than the eye, projects slightly. The development of the characteristic barbel of the adult at the symphysis of the lower jaw is indicated by a minute knob. Scalation is nearly complete (although not shown in the illustration), and the lateral line is developed anteriorly, extending to middle of base of soft dorsal. The caudal fin has become rather more broadly asymmetrically rounded, and the longest rays are shorter than the head. Pigmentation is very variable, depending upon the environment in which the specimens were taken. Some specimens are almost uniformly brown, while others are silvery with scattered brownish chromatophores. The spinous dorsal (except for a few black dots), the pectorals, and the ventrals in all specimens at hand remain plain translucent. The caudal fin is void of color except for a pair of dark blotches on the base, which may be separate or united. The dorsal and anal are largely black at the base in some specimens, whereas they bear only comparatively few dark points in others (fig. 16).

Specimens of *littoralis* of the size described remain more slender than either of the other two local species of the genus. The difference in this respect, however, is slight between *littoralis* and *americanus*, but comparatively great between *littoralis* and *saxatilis*. The strongly eliptical pupil and the short asymmetrically rounded caudal fin at once separate *littoralis* from *americanus*, although not from *saxatilis*. The

almost total absence of black on the spinous dorsal and ventral fins, also, aids in distinguishing *littoralis* from the other local species.

Specimens 30 to 35 millimeters long.—The body has become more rounded and has acquired virtually the form of the adult, the depth being contained in the length to the base of the caudal 4.05 to 4.3 times, which are the proportions found also in the adult. The mouth is inferior and horizontal, and the conical snout, which is now a little longer than the eye, projects notably beyond it. The mandibular barbel, although plainly visible, still has the appearance of a knob. Scalation is complete, and the scales on the chest are smaller than those on the sides and on the abdomen. The dorsal spines are short, the longest ones failing to reach the first soft ray of the second dorsal when deflexed. The caudal fin is slightly angular and the longest rays, which are in the lower half of the fin, are notably shorter than the head. The pectoral fins are short, failing by fully an eye's diameter to reach the tips of the ventrals, and the latter do not quite reach the vent. The ground color is silvery, overlaid on sides and back with grayish dots. Indications of dark blotches are present on the sides of some specimens, while others appear uniform silvery gray. The dorsal, caudal, and anal fins are more or less dotted with black, while the paired fins usually are plainly translucent (fig. 17).

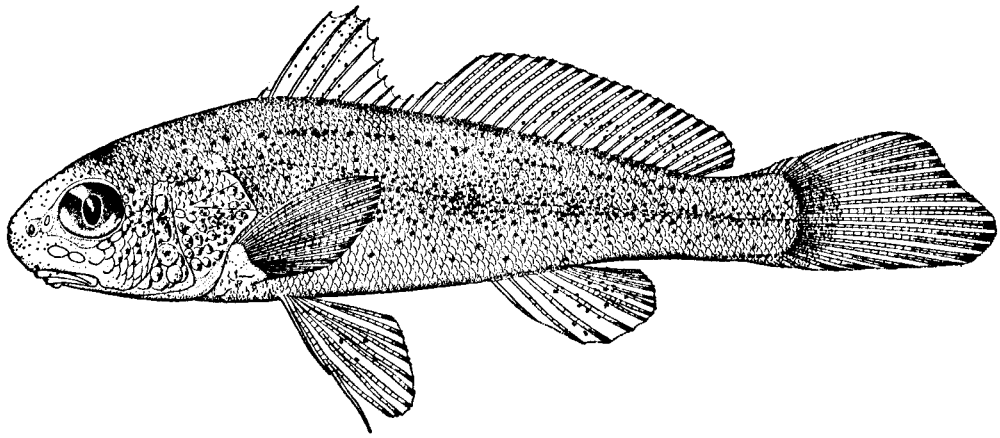

FIGURE 17.—*Menticirrhus littoralis*. From a specimen 30 millimeters long.

The attainment of virtually the adult form at so small a size is quite striking. While the body remains somewhat more slender than in the other two local species of the genus, the difference is slight between the present species and *americanus*. However, the eliptical pupil and the short angulate caudal fin have been retained and are useful in separating this species and *americanus*. The very short pectorals and the reduced scales on the chest distinguish the present species from both *americanus* and *saxatilis*.

Specimens 50 to 60 millimeters long.—The differences between specimens of this size and those described in the preceding section are not pronounced. The body has continued to become more rounded anteriorly and apparently proportionately not quite as deep, the greatest depth being contained in the length to the base of the caudal 4.3 to 4.4 times. These proportions are, also, common to the adult. The caudal now is shaped virtually as in the full grown fish, that is, its margin is concave and the lower lobe is longer and somewhat more sharply rounded than the upper one. The color is plain silvery gray, as seen with the unaided eye. Under magnification

dark points are evident on the sides and back, but they have become smaller and less numerous since a length of 35 millimeters was attained (fig. 18).

Specimens of the size described are virtually young adults and are readily recognized. The body remains slightly more compressed, however, and the caudal fin is less deeply concave and the lower lobe is more sharply rounded.

The principal characters that distinguish the adults of this form from the other local species of the genus are developed at this size, and are usable in making identifications. They are the rather large scales (72 to 74 vertical series above the lateral line), which are conspicuously reduced in size on the chest; the low dorsal spines, none being produced; the short anal, which typically has only 7 soft rays; the very short pectorals, which fail conspicuously to reach the tips of the ventrals; and the plain silvery gray coloration. The small, vertically elongate pupil still is conspicuous and readily distinguishes this species from *americanus*, although not from *saxatilis*.

DISTRIBUTION OF THE YOUNG

Young under 9 millimeters in length were not taken. Their habitat and distribution, therefore, remain unknown. Young ranging upward of 9 millimeters were

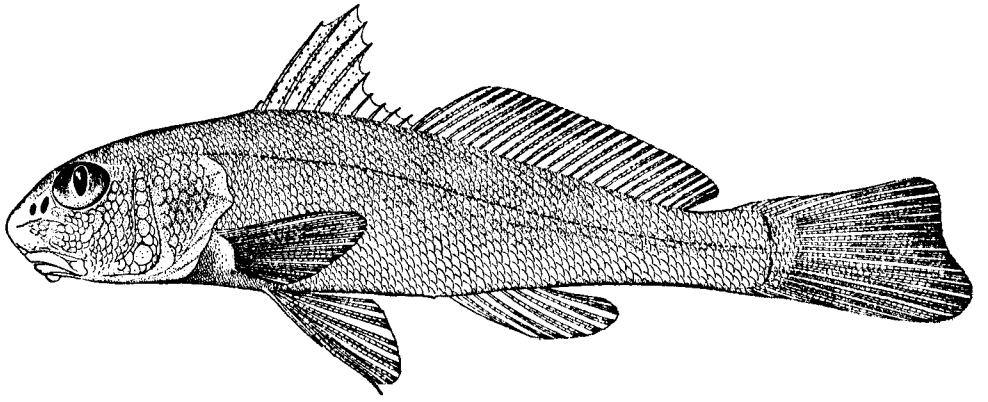

FIGURE 18.—*Menticirrhus littoralis*. From a specimen 60 millimeters long.

found only in the surf, at Cape Lookout and on the outer shores of the "banks." So far as known the young, like the adults, dwell on or near the bottom.

GROWTH

The measurements of 180 young taken during June, July, August, and September are entirely inadequate to cast much light upon the rate of growth. However, specimens of the 0-class, 98 millimeters long taken in August, and others 120 millimeters in length caught in September, when probably only about 3 or 4 months old, suggest rapid growth. Nothing is known concerning the rate of growth after the first several months.

STAR DRUM (Stellifer lanceolatus (Holbrook))

This small drum has no common name at Beaufort. The two names, "star drum" and "bullhead" occur in the literature. The species ranges from Chesapeake Bay to Texas and possibly to Mexico, its southern range of distribution not having been definitely determined. The species is recorded from Chesapeake Bay (Hildebrand and Schroeder, 1928, p. 282) from a single specimen. It is recorded

from North Carolina (Beaufort) by Smith (1907, p. 315), who refers to it as a "rare drum." However, during recent years it has proven to be rather common off Beaufort Inlet in water ranging from about 2 to 7 fathoms in depth. Here the star drum is sometimes taken in considerable numbers in trawls. Since specimens have been taken almost throughout the year, it obviously is a permanent resident, although quite evidently more numerous during the summer than during the winter. Only 3 small specimens were secured in the inside waters throughout several years of intensive collecting, indicating that this drum seldom crosses Beaufort Bar. It is reported as very common on the South Atlantic and Gulf coasts from South Carolina southward.

The species has no direct commercial value because of its small size, the maximum length attained being only about 165 millimeters (6½ inches). It no doubt enters into the food of other fishes to some extent, as it occupies areas frequented by such predatory species as the bluefish, weakfish, croaker, king whitings (or "sea mullet"), and flounders.

The star drum is the only species of the genus Stellifer recorded from the coast of the United States. The genus is represented by several species in tropical America. The adult star drum is recognized readily by the rather low head, broad interorbital, blunt snout, the slightly concave dorsal outline of the head, and the terminal or slightly inferior mouth. The spongy skull, with bony ridges and large caverns (readily perceptible to the touch), also is quite distinctive. The body is rather robust and elongate, the depth being contained in the standard length 3.0 to 3.3 times, and the length of the head is about equal to the depth. The caudal fin is pointed at all ages. The dorsal has X or XI–I, 21 or 24 rays, and the anal II, 7 or 8. The scales in the lateral series number about 47 to 50. The color is plain bluish gray above and silvery below.

SPAWNING

The star drum spawns during the summer. Young under 5 millimeters in length were taken at Beaufort in July, August, and September. The largest specimens of the 0-class taken in July (on the 25th day of the month) are 60 to 69 millimeters long. These large young quite probably are more than a month old. Only one ripe fish, a female taken August 4, 1914, was observed. It seems reasonable to assume from these data that spawning begins certainly not later than June, and probably as early as May, and that it extends through August. The eggs have not been studied.

The larvae were taken from Beaufort Inlet to Cape Lookout, that is, along Shackleford Banks, some rather near the shore and others several miles off shore, in the general vicinity inhabited more or less permanently by the adults. Besides the off-shore collections only one small lot of larvae was caught in the inside waters where they may have been carried by winds and tides. The indications, therefore, are that the young are hatched on the grounds regularly occupied by the adults and that no migration for the purpose of spawning takes place.

DESCRIPTIONS OF THE YOUNG

Specimens 1.8 to 2 millimeters long.—The head and trunk are short and moderately deep, compressed, and the tail is long and slender, an abrupt decrease in depth occurring at the vent. The distance from the snout to the vent is contained in the length to the end of the notochord about 2.4 times, distance posterior to vent (without finfold) 1.6 times, and the greatest depth about 3.1 times. The mouth is moderately large and oblique, and the snout is very short. The myomeres are too indistinct to enumerate accurately; about 25 can be counted, and only about 5 of them are in

advance of the vent. A small black spot is present on the median line of the abdomen immediately in advance of the vent, generally another elongate black spot is situated on the ventral outline of the tail at about midcaudal length. However, sometimes several small black spots occur on the ventral outline of the tail. The inner surface of the base of the primitive pectoral is black, and dark points are present on the sides along the upper margin of the abdomen. Three dark dots also are situated on the dorsal outline. The first is placed slightly in advance of the anterior margin of the eye, the next one is somewhat behind the posterior margin of the eye, and the third one is fully a half an eye's diameter behind the second one (fig. 19).

Specimens of this size differ notably from somewhat larger ones in the long slender tail, which becomes proportionately much shorter and stouter quite abruptly. The deep body, the moderately large oblique mouth, and the color markings are useful in identifying these small larvae with somewhat larger ones.

Specimens 2.5 millimeters long.—The fish has increased greatly in depth since a length of about 1.8 to 2.0 millimeters was attained, and the tail has become proportionately much shorter and stockier. The distance from the snout to the vent is contained 1.75 to 1.9 times in the length to end of the notochord, distance posterior to vent (without finfold) 2.0 to 2.3 times, and the greatest depth 2.3 to 2.5 times. The cavernous nature of the skull, characteristic of the adult, already is indicated by

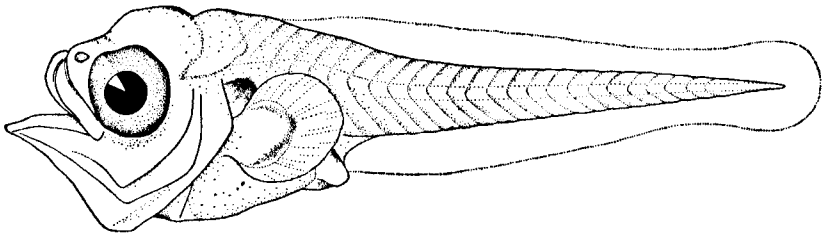

FIGURE 19.—*Stellifer lanceolatus*. From a specimen 1.8 millimeters long.

an apparently vacant space over the brain. (The outline of the brain is plainly visible because of the transparency of the coverings of the head.) The mouth is moderately large and oblique; the gape anteriorly is about on a level with the middle of the eye and the maxillary reaches under the pupil. Distinct teeth are present on the jaws, and a few spines have appeared on the preopercular margin. The myomeres are partly indistinct; about 8 can be counted in advance of the vent and about 17 behind it. A slight thickening of the vertical finfold is noticeable in those places where the soft dorsal, the caudal, and anal fins are developing. Slight indications of rays are present in the caudal fin (that is, below the end of the tail). The color markings of the smaller specimens described remain, though somewhat modified. A few dark points (more distinct in some specimens than in others) persist on the median line of the abdomen. The dark spot at about midlength of the ventral outline of the tail has become more distinct and quite elongate, and some specimens have a smaller spot in front of this one and another one behind it. The inner surface of the base of the primitive pectoral remains black. A few dark points persist along the upper margin of the abdomen, ending in a small dark spot dorsally of the base of the pectoral. These dark markings, in part at least, consist of dark membranes, visible through the body wall. The three dark markings on the head, noticed in smaller specimens, now have the appearance of dark cross partitions, lying below the surface of the skull (fig. 20).

The indications are that the fish when about 2.0 millimeters long (preserved specimens) virtually ceases to increase in length for a while. During the time it fails to grow in length it appears to increase greatly in robustness, and the caudal portion of the body becomes proportionately much shorter, as shown by the proportional measurements given in the foregoing description and by figures 19 and 20. Specimens 2.5 millimeters long have the appearance of being considerably older than those 2.0 millimeters long.

Specimens 3.0 to 3.5 millimeters long.—The fish has increased further in depth, the tail particularly having become much deeper, and the body, although rather robust, is compressed throughout. The decrease in depth immediately behind the vent, abrupt in younger fish, has become much less pronounced. The distance from the snout to the vent is contained 1.55 to 1.65 times in the length to the end of the notochord, distance posterior to vent (without finfold) 2.0 to 2.2 times, and the greatest depth 2.2 to 2.5 times. The notochord remains nearly straight in a specimen 3.0 millimeters long, but is bent upward quite sharply distally in a fish 3.3 millimeters long. A large vacant space exists between the brain and the cranium, and a few rather prominent spines are present on the preopercular margin. The mouth remains moderately oblique, the gape anteriorly being only a little higher than the lower

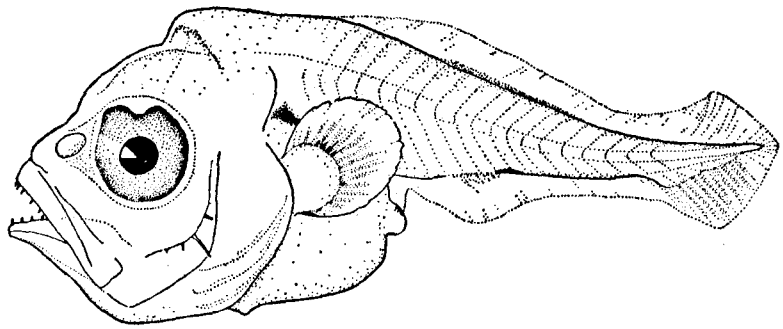

FIGURE 20.—*Stellifer lanceolatus*. From a specimen 2.5 millimeters long.

margin of the eye, and the maxillary reaches nearly opposite the middle of the eye. The caudal and pectoral fins contain well developed rays; the soft dorsal and anal bases are rather well outlined, but the rays are not fully differentiated; the spinous dorsal is not evident; and the ventral fins if present appear as mere tufts of membrane. Color markings on the chest and abdomen have increased in number and intensity. A short dark cross line, preceded by a median black spot, usually is present on the chest; a few indistinct dark points appear at the base of the ventrals; and a rather distinct short dark bar (sometimes consisting of a few dark points only) crosses the abdomen behind the ventrals. The elongate dark spot at about midlength on the ventral outline of the tail, mentioned in descriptions of smaller larvae, now is situated at or near the end of the base of the anal fin, and occasionally a black point is present directly over it on the dorsal outline. In some specimens, at least, a small dark spot has appeared also at the origin of the anal. The inner surface of the base of the pectorals remains black, and a dark shoulder spot is present as in the younger fish (fig. 21).

The most prominent advancement in the development since a length of about 2.5 millimeters was attained consists in the further deepening of the body, especially the caudal portion, causing a less pronounced break in the ventral outline at the vent.

Specimens 4.5 to 5.5 millimeters long.—The fish has become much more shapely than it was at a length of about 3.5 millimeters. It is quite deep and strongly compressed throughout, and the break in the ventral outline at the vent has almost disappeared, a space exceeding in length the diameter of the eye between the vent and origin of the anal being occupied by a transparent membrane. The distance from the snout to the vent is contained 2.0 to 2.3 times in the length to the base of the caudal, distance from vent to base of caudal 1.9 to 2.1 times, and the greatest depth 2.6 to 2.8 times. The cavernous nature of the skull is quite evident from the large vacant spaces occurring above the brain and around the snout. The eye and snout are of

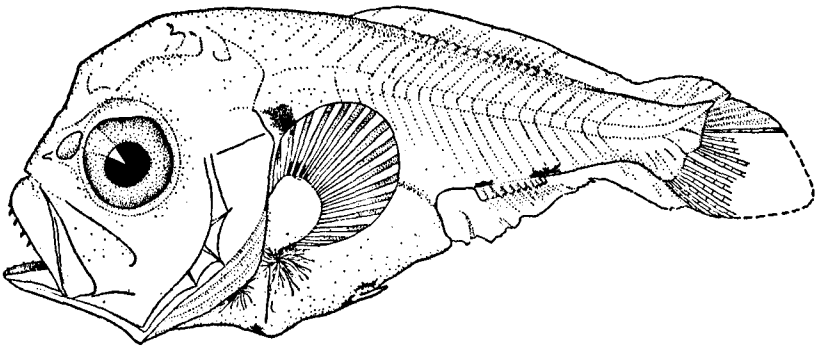

FIGURE 21.—*Stellifer lanceolatus.* From a specimen 3.3 millimeters long.

about equal length. The preopercular margin has several prominent spines at its lower angle. The mouth is oblique, the gape anteriorly is about on a level with the lower margin of the pupil, and the maxillary reaches below the middle of the eye. The fins, exclusive of the spinous dorsal and the ventrals which remain rudimentary, are quite well developed. About 22 rays can be counted in the soft dorsal and 10 in the anal (the spines and the soft rays not being differentiated in the latter). The caudal fin is moderately long and somewhat pointed. A few dark points remain on the median line of the chest and abdomen, but are less evident than in younger fish. The elongate black spot at the end of the base of the anal persists and is variable in

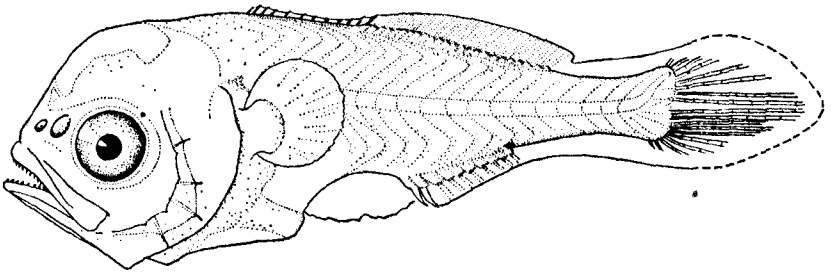

FIGURE 22.—*Stellifer lanceolatus.* From a specimen 5.6 millimeters long.

size and intensity among specimens. A slight dark spot remains evident at the origin of the anal in some individuals, though missing in others. The black on the inner surface of the base of the pectoral, prominent in the younger stages described, has disappeared entirely according to the specimens at hand. A slight shoulder spot and a few dark markings behind it, which extend to the vent, still persist. It is evident that the last-mentioned color markings are below the surface of the body, and apparently consist of a dark membrane on the dorsal wall of the abdominal cavity. A faint dark bar has appeared at the base of the caudal fin (fig. 22).

Specimens 7 to 8 millimeters long.—No pronounced changes in the proportions of the body have taken place since a length of about 4.5 to 5.5 millimeters was attained. The distance from the snout to the vent is contained 2.0 to 2.2 times in the length to the base of caudal; distance from vent to base of caudal 1.8 to 2.1 times; and the greatest depth 2.65 to 2.8 times. A slight concavity remains in the ventral outline of the body between the vent and origin of anal, which is occupied by a thin membrane, apparently a remanent of the finfold. Above this concavity in the ventral outline, the body is very thin and semitransparent. The snout remains short and narrow, its length being equal to the diameter of eye, and the profile ascends abruptly from its tip. Considerable advancement has been made in the development of the fins. The spinous dorsal is fairly well differentiated, although rather more closely connected with the soft dorsal than in the adult. About 12 spines and 24 soft rays may be counted. The anal fin consists definitely of 2 spines and 7 or 8 soft rays. The caudal fin is frayed in the specimens at hand, but it evidently is long and pointed. The ventral fins remain small. The dark markings present vary in size and number among specimens. Generally a few dark dots are present on the median line of the chest and abdomen. The spot at the end of base of anal, present in all the smaller larvae at hand, persists. Some specimens now have two spots at and behind the anal base, and each one may have a narrow vertical projection. Some specimens also

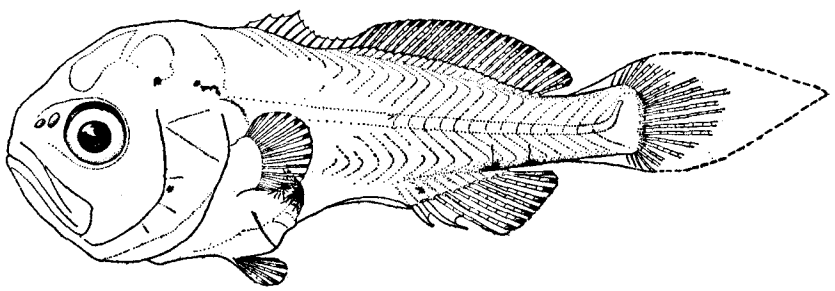

FIGURE 23.—*Stellifer lanceolatus.* From a specimen 9 millimeters long.

have a small black spot near the origin of the anal. A rather prominent dark spot is present above the vent, which often is more or less connected with other spots, reaching to an elongate, finely branched shoulder spot. A narrow dark bar at the base of the caudal is evident (fig. 23).

Specimens 10 to 13 millimeters long.—The proportions of the body remain about as in somewhat smaller specimens. The distance from the snout to the vent is contained 1.85 to 2.0 times in the length to the base of the caudal fin, distance from vent to base of caudal 2.05 to 2.15 times, and the greatest depth 2.6 to 2.75 times. A slight concavity remains evident in the ventral outline between the vent and the origin of the anal (which is occupied by a thin membrane as in smaller fish), and the distance between these two points exceeds the diameter of the eye. The snout has become broader and rounder; the mouth is less oblique and wholly below the lower margin of the eye; and the maxillary reaches nearly or quite to the posterior margin of the eye. In all the characters about the head, just mentioned, the fish is approaching the shape and form of the adult. The eye is unusually small. The cavernous nature of the skull, with its bony ridges, is quite prominent. The preopercular spines are smaller and more numerous than in younger fish. The fins are all well developed, the dorsal formula is X or XI–I, 23 or 24, and that of the anal II, 7 or 8. The caudal remains long and pointed, the longest rays being longer than the head. Little

advancement in pigmentation has taken place. The few dark markings usually present are shown in figure 24. Some specimens, however, have a series of 3 to 7 (instead of 1) dark spots on the side below the spinous dorsal, as well as several on the posterior part of the head and on the nape (fig. 24).

Specimens 18 to 20 millimeters long.—The fish has made considerable headway toward acquiring the form of the adult. Although the head has increased in width, it remains proportionately much more compressed than in the adult, its length is contained 2.55 to 2.75 in the total length without the caudal fin. The interorbital space has become relatively broad and is about 1.5 times as wide as the small eye. The snout is slightly longer than the eye and is contained 4.6 to 5.5 times in the head. The preopercular margin has 3 or 4 small spines, and 3 bony stays are partly embedded in the interopercle. A row of bony serrae are present at the shoulder. A slight concavity remains present between the vent and the anal fin, the membrane (remanent of the finfold) which occupied the concavity in smaller fish has disappeared, and the distance between the vent and origin of anal is now scarcely as long as the

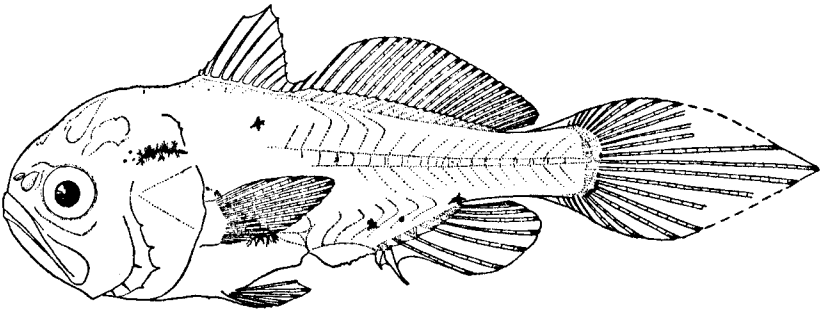

FIGURE 24.—*Stellifer lanceolatus*. From a specimen 13 millimeters long.

eye. The proportionate depth of the body remains the same as in fish 10 to 13 millimeters long. Much advancement in pigmentation has taken place. The dark spot near the end of the base of the anal, present in all younger fish, remains evident and is preceded (along the base of the anal) as well as followed (on the ventral outline of the peduncle) by a row of dark dots and spots. The characteristic elongate, slightly arched spot on the opercle, immediately in advance of the upper angle of the gill opening, remains prominent. The mouth is margined with black and numerous dusky markings occur on the head and nape, and on the upper parts of the sides. The markings are variable in size and intensity among specimens. One row of spots follows the base of the dorsal and another one parallels it about an eye's diameter lower on the side. Other scattered markings are present, and a dark bar is situated on the base of the caudal.

Specimens 25 to 30 millimeters long.—Although advancement toward the adult form has been rather rapid since a length of 18 to 20 millimeters was attained, the fish remains more compressed anteriorly and the snout is more pointed. The head is contained 2.8 to 2.9 times in the length to the base of the caudal, and the depth 2.7 to 3.1 times. These proportions are close to those of adult fish. The small eye is surrounded by a ridge which is not yet fully ossified, its longest diameter is contained 4.5 to 5.2 in the head; snout 4.25 to 4.5 times; interorbital 2.7 to 3.2 times; maxillary 1.8 to 1.95 times. The concavity between the vent and the anal, present in younger fish has disappeared, and the body in this region has thickened and no longer is semitransparent. Outlines of scales are present on most of the body. If scales

actually were developed they have been lost. Pigmentation has advanced rather rapidly. The chief color markings are shown in the accompanying illustration (fig. 25).

Specimens 40 to 50 millimeters long.—The head is lower and notably broader than in fish about 30 millimeters long. Although the snout is more rounded than in younger fish, it still remains narrower and rather more pointed than in the adult. The small eye, though lateral, is near the dorsal outline; the interorbital is broad, its width being contained 2.4 to 2.8 times in the head. Several bony ridges are present on the head among which caverns occur. The preopercle has a few small spines at the angle and the interopercular margin is strongly serrate, the spines at the angle being largest. The scapular spines have become much smaller. The caudal fin apparently remains rather longer and more pointed than in the adult, the longest rays being more than an eye's diameter longer than the head. Pigmentation is general. The

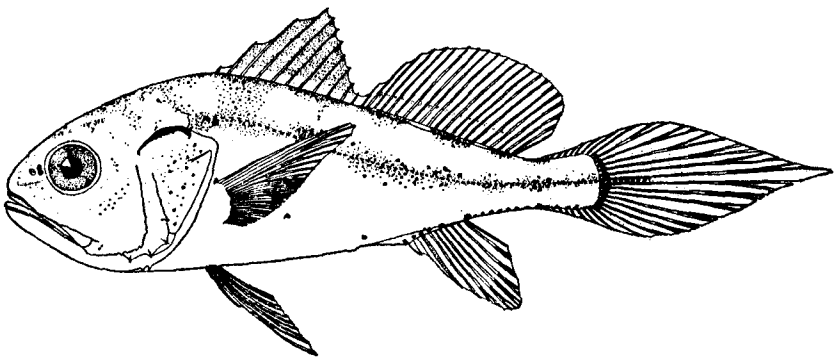

FIGURE 25.—*Stellifer lanceolatus*. From a specimen 29 millimeters long. (After Welsh and Breder.)

back of preserved specimens is light brown and the lower parts are silvery. The elongate dark spot on the upper part of the opercle and the dusky color around the mouth remain as in smaller specimens. Dark blotches, present in somewhat younger fish, along the back generally persist, but are less distinct, the color being more generally distributed as dusky points. The spinous dorsal is dusky, and all the other fins have dark dots, being very few, however, on the ventrals and pectorals. A dusky bar remains present on the base of the caudal fin.

Specimens 75 to 85 millimeters long.—Fish of this size are young adults, having the body proportions of full-grown fish. The head is somewhat depressed and its dorsal outline is slightly concave over and behind the posterior margin of the eye, as in the adult. The snout is broad, bluntly conical, and almost as broad as deep at anterior margin of the eye. The mouth is oblique, but wholly below the level of the lower margin of eye; the maxillary reaches about under posterior margin of the pupil. The small eye is shorter than the snout, and not as wide as the interorbital, its diameter being contained 4.4 to 4.8 times in the head. The preopercular spines are small, and those on the interopercle are strong, as in full grown fish. The scapular spines, described in younger fish, are now represented as serrations on an enlarged scale. The caudal fin remains rather pointed and is about as long as the head. The pectoral fins are long, being only a little shorter than the head. The color remains about the same, as in 40 to 50 millimeter fish. The dark points on the fins have become more numerous, however, and the anal and the tips of ventrals are quite dusky.

Specimens of this size have virtually all the characters of the adult and are easily recognized. Figure 26 illustrates the adult without indicating the scales.

DISTRIBUTION OF THE YOUNG

It has been shown (p. 76) that the young of the star drum in the vicinity of Beaufort apparently are hatched and live on the grounds occupied by the adults as a permanent residence, that is, the larvae were taken from Beaufort Inlet to Cape Lookout, as far as 7 to 12 miles off shore, and only one small lot was caught in the inside waters. Furthermore, all the young collected were taken on the bottom, showing that the young, like the adults, dwell on the bottoms. The star drum, therefore, appears to dwell at or near the bottom throughout life.

GROWTH

The number of young taken is insufficient to determine accurately the rate of growth even during the first several months of life. During July 122 young of the 0-class were caught, ranging in length from 2.5 to 69 millimeters, having an average length of 21.3 millimeters. Although no young were taken earlier in the season, it is believed that the larger specimens, as already explained (p. 76), are more than a month old and probably were hatched in May or June. In August 617 young were caught, ranging in length from 2.3 to 90 millimeters, with an average length of 49.3

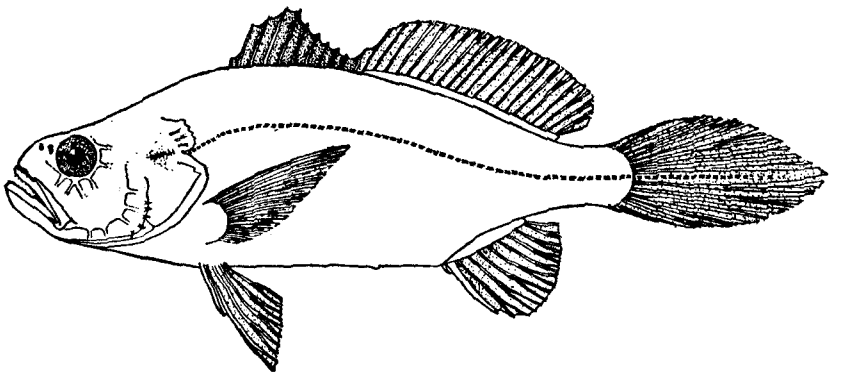

FIGURE 26.—*Stellifer lanceolatus*. From a specimen 164 millimeters long. Scales not indicated. (After Welsh and Breder.)

millimeters. Only 11 larvae, all less than 10 millimeters in length, were taken in September. During October 62 young, ranging in length from 38 to 112 millimeters, averaging 90.4 millimeters, were caught. The smaller young of the season obviously are missing in this catch, as the smallest specimen taken next month is 26 millimeters long. The largest one in the 0-class caught in November is only 91 millimeters, and the average length of 34 specimens taken is only 58 millimeters. It is obvious, therefore, that although the smaller ones are present the larger ones of the 0-class are missing in the catch for November. The number of specimens taken during the other months is too small to be worthy of consideration. From the data presented it is evident that some of the young reach a length as great as 100 to 125 millimeters (4 to 5 inches) during their first summer. Since the maximum length attained by the star drum is only about 6 inches, it seems probable that the fastest growing individuals reach maturity when about 1 year old. Others may require a year longer to reach that stage.

The foregoing analysis of the rate of growth is in general agreement with the data presented by Welsh and Breder (1923, p. 175), who found individuals of the 0-class varying from 10 to 40 millimeters in length (the smallest larvae of the season evi-

dently being missing) in a collection of fish made in Winyah Bay, S.C., in July (1915). From a collection from Fernandina, Fla., these writers determined that the fish reach a length of 50 to 90 millimeters by the first winter. These writers state that the 1-year-old fish are 70 to 100 millimeters long in July and that the same year class reaches a length of 80 to 140 millimeters by the second winter, and they conclude that maturity is reached at the age of 1 year.

BANDED DRUM (Larimus fasciatus Holbrook)

The banded drum, also known as "bastard drum", "bastard perch", and "chub", ranges from Cape Cod to Texas. According to published records, it occurs only as a straggler from Virginia northward, and is common from Cape Hatteras southward. The limit of its southward range apparently has not been determined definitely. The species is common off Beaufort Inlet, where it is a year-round resident, and where it sometimes is taken in large numbers in shrimp trawls in water ranging from a few to several fathoms in depth. According to the records at the Fisheries laboratory at Beaufort, the species does not enter the harbor nor adjacent sounds. Neither has it appeared in collections made with seines along the outer shores of the "banks."

The banded drum was first recorded from North Carolina by Smith (1907, p. 314), who reported it from "several specimens" with the notation, "It is not common anywhere." However, Welsh and Breder (1923, p. 170) state "* * * although stragglers have been taken as far north as Woods Hole, it is not found in abundance north of Cape Hatteras. South of this point and on the shores of the Gulf of Mexico it is one of the most abundant fishes, being taken in large numbers in the trawls of the shrimp fishermen." The species evidently did not appear often in the collections at Beaufort until the otter trawl came into use in about 1913 or 1914. We have no record of its capture with seines, probably because it does not frequent areas near Beaufort in which such nets commonly are operated.

The banded drum does not grow large enough to be of much direct commercial value. Comparatively few individuals attain a length as great as 8 inches. The largest one seen at Beaufort was 206 millimeters (8¼ inches) long. The species probably enters into the food of other fishes to some extent, as it occupies areas frequented by such predatory species as the bluefish, weakfish, croaker, king whiting ("sea mullet"), and flounder.

The banded drum is the only species of the genus occurring north of Florida. The adult is readily recognized by the deep compressed body (depth in standard length 2.6 to 2.8), the strongly oblique mouth, long dorsal fin (X–I, 24 to 27), short anal fin (II, 6 to 8), and by the 7 to 9 black crossbars. The skull is firm, without conspicuous caverns, and no barbels are present about the mouth.

SPAWNING

The banded drum evidently spawns throughout the summer. Young under 5 millimeters in length were taken in July, August, September, and October, and one specimen 12 millimeters long was taken on May 29 (1930). This specimen, according to measurements made of collections, belongs to a new year class. Furthermore, the largest young of the 0-class taken in July, as shown elsewhere (p. 91), were as much as 70 millimeters long and the average length of 87 specimens measured was 34 millimeters. Unless the rate of growth in this species were unusually rapid, the larger individuals certainly would be as much as 2 months old. It seems quite probable,

therefore, that spawning begins as early as May, even though no larvae were taken in June, and it extends through October, as some of the smallest larvae (1.9, 2.1, and 3.0 millimeters long) in the collection were taken on October 22 (1928).

The eggs, if taken, were not recognized. The larvae were caught in the tow in the same general vicinity where the adults are found throughout the year, that is, from Beaufort Inlet to Cape Lookout and as much as 12 miles offshore, beyond which collecting was not extended. It seems improbable, therefore, that a migration for the purpose of spawning takes place.

DESCRIPTIONS OF THE YOUNG

Specimens 1.9 to 2.0 millimeters long.—The body is moderately deep and robust for such a small fish, and the decrease in depth at the vent is not abrupt. The caudal portion is rather shorter than the rest of the body, the distance from vent to tip of notochord being contained 2.25 times in length without caudal fin membrane, and the greatest depth of body 4.15 times. Myomeres are partly indistinct; about 25 may be counted. The mouth is moderately large and oblique, the gape anteriorly being at or slightly above middle of eye, and the maxillary reaches about to the pupil. The eye is moderately small for such a young fish and does not exceed the snout in length. The color markings of preserved specimens consist principally of a dark spot at the vent, a larger and more distinct one at midcaudal length, and a third and smaller one about half-way between the last-mentioned spot and the tip of the notochord.

The smaller larvae of this species differ from related forms quite notably in having the caudal portion of the body rather deep anteriorly, thereby eliminating an abrupt decrease in the depth at the vent.

Specimens 2.3 to 2.6 millimeters long.—The head and trunk are deep, compressed, and the decrease in depth just posterior to the vent is less abrupt than in related species. The caudal portion of the body remains somewhat shorter than the rest of the fish, being contained in the total length without the caudal fin membrane 2.1 to 2.6 times, and the greatest depth is contained in the length 2.8 to 3.2 times. The mouth is moderately large, oblique, with the lower jaw projecting in advance of the upper one, the gape anteriorly being on or above the level of lower margin of pupil, and the maxillary reaches nearly or quite under anterior margin of pupil. Slight indications of rays are discernible in the vertical fin membranes, as well as in the pectorals. The color of preserved specimens is brownish. The air bladder may be seen as a small clear area, with a dark margin, situated above the base of the pectorals. The ventral outline of the abdomen is slightly dusky, with a small black spot just behind the gill membranes and another one usually present just behind the vent. Two or three black spots occur on the ventral outline of the tail. The first one, if present, is a short distance behind the vent; the second and more distinct one (sometimes quite elongate) is near midcaudal length, and the third one is about midway between the last-mentioned spot and tip of notochord. The inner surface of the base of the pectoral is black (fig. 27).

The head and trunk become abruptly deeper while the fish grows in length from about 1.9 to 2.5 millimeters.

Specimens 3 to 3.5 millimeters long.—The fish has become proportionately deeper and more robust, the greatest depth now being contained in the total length without the caudal fin membrane about 2.3 times. Although the tail remains much

more slender than the rest of the body, it has become proportionately deeper and rather shorter, its length being contained in the length of the body about 2.3 times. The mouth remains strongly oblique and the maxillary reaches about under the middle of the orbit. The eye is small, scarcely longer than the snout. The cranium is very transparent, permitting the lobes of the brain to be seen clearly. The fin membranes remain about as in the younger fish already described. A slight thickening of the membranes is discernible, however, in the places that will be occupied by the bases of the dorsal and anal fins. The color markings have not changed per-

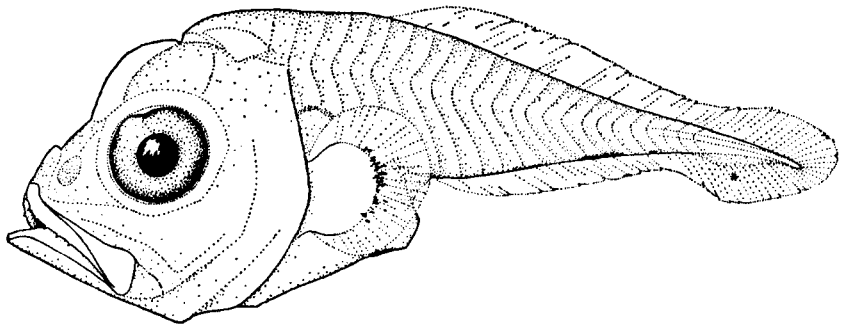

FIGURE 27.—*Larimus fasciatus*. From a specimen 2.5 millimeters long.

ceptibly, the most prominent ones being the dark spot on about midlength of the ventral outline of the tail, and the black inner surface of the base of the pectorals (fig. 28).

The dark color markings described, together with the very deep compressed body, serve as the principal diagnostic characters in the smaller larvae of this species.

Specimen 4.5 millimeters long.—The body is very deep and moderately compressed anteriorly, tapering rapidly behind the head. The break in the ventral outline behind the vent, very abrupt in the smaller specimens, is no longer pronounced. The caudal

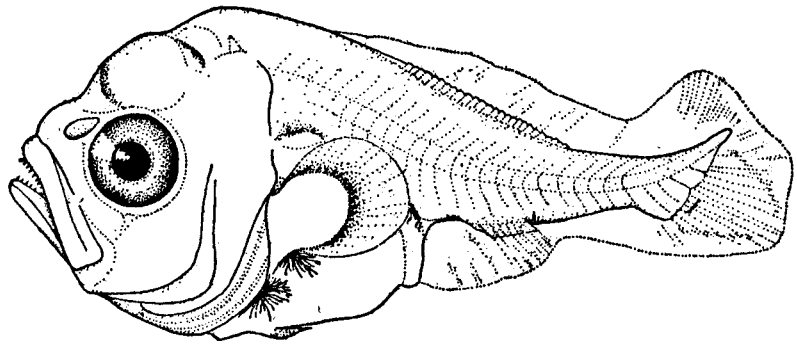

FIGURE 28.—*Larimus fasciatus*. From a specimen 3.4 millimeters long.

portion is notably shorter than the rest of the body, its length being contained about 2.6 times in the total length without the caudal fin, and the greatest depth is contained about 2.15 times in the length. The mouth remains strongly oblique, and the maxillary reaches under the middle of the orbit. The eye is comparatively small, being only a little longer than the snout, and is situated somewhat nearer to the dorsal than the ventral outline. The fins are fairly well developed, all of them, exclusive of the ventrals, having fairly well-developed rays. About 36 rays may be counted in the dorsal, and 7 in the anal. A structural differentation is not evident

between spines and soft rays. However, the rays in the anterior part of the dorsal, which will form spines, are shorter than the others. The color in spirits remains dark brown. The anterior part of the abdomen is dusky and the dark spot on the ventral outline of the tail, described in smaller specimens, is situated immediately behind the base of the anal. The inner surface of the base of the pectorals remains black, as in the smaller larvae (fig. 29).

The very deep compressed body, moderately large oblique mouth, the black spot behind the base of the anal, and the black inner surface of the base of the pectorals are the principal recognition marks.

Specimen 7 millimeters long.—The head and trunk remain deep and compressed, as in smaller specimens. The tail has become deeper, causing the fish to appear more shapely. It has decreased still further in proportionate length, the distance from the vent to the base of the caudal fin being contained in the total length without the caudal fin 3.8 times, and the greatest depth of the body is contained 2.35 times in the length. The mouth remains strongly oblique, the gape anteriorly being about on a level with the middle of the eye, and the maxillary reaches slightly beyond the middle of the orbit. The fins remain about as in the 4.5-millimeter fish already

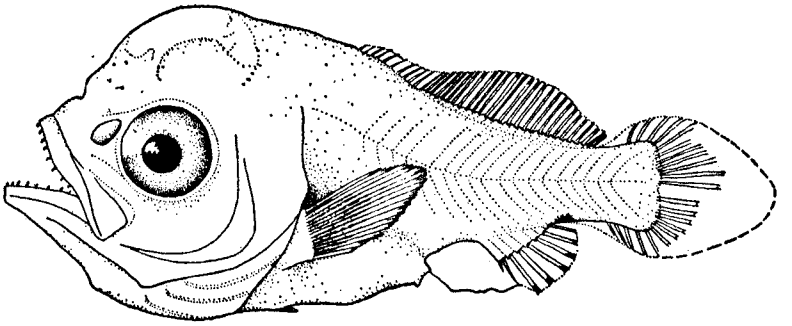

FIGURE 29.—*Larimus fasciatus.* From a specimen 4.5 millimeters long.

described, except that some of the anterior rays of the dorsal and the first one of the anal now resemble spines somewhat. The caudal fin is quite fully developed, but the exact shape cannot be determined as it is frayed at the tip in the single specimen of this size at hand. However, it very probably is pointed, as indicated in the accompanying illustration. The pectoral fins are long and reach the origin of the anal. Many black chromatophores are now present, as shown in figure 30. The characteristic black spot just posterior to the base of the anal, present in all the smaller specimens examined, persists. The inner surface of the base of the pectoral remains black, and the base of the ventral is dusky (fig. 30).

Specimens 9 to 10.5 millimeters long.—The body has become somewhat deeper, its greatest depth being contained about 1.9 times in the length. The dorsal outline is much more strongly curved than the ventral one. It ascends sharply anteriorly and descends strongly posterior to the origin of the dorsal. The mouth has become less strongly oblique, as the gape anteriorly is only a little above the lower margin of the eye. The spines and soft rays in the vertical fins are fully differentiated. The first dorsal consists of 10 spines, the second one (which is scarcely separated from the first one) has 1 spine and 26 or 27 soft rays, and the anal has 2 spines and 6 soft rays. The caudal fin is nearly as long as the head and is pointed. The ventral fins reach

almost to the origin of the anal, and the long pectorals reach to or past the middle of the anal base. Black pigment spots have increased greatly in number, as shown in figure 31. However, the spots vary in size and number among individuals, some examples having more and larger spots than the one illustrated. The black spot immediately behind the anal, present in the smallest specimens taken, persists, though it has become much more elongate and branched. The basal half of both the ventrals and pectorals is black (fig. 31).

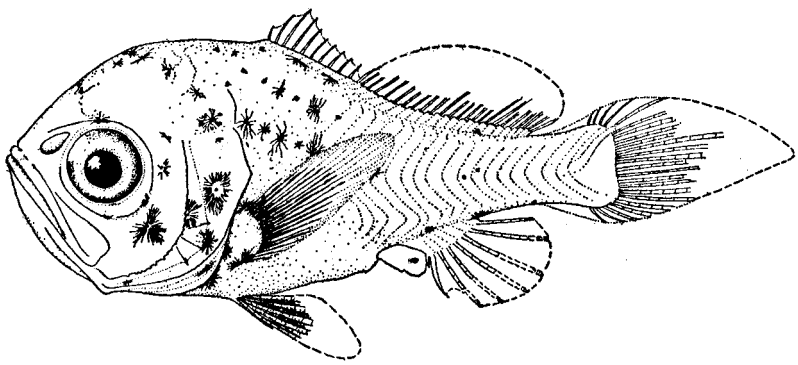

FIGURE 30.—*Larimus fasciatus*. From a specimen 7 millimeters long.

The deep compressed body, oblique mouth, the number of rays in the dorsal and anal fins, and the prominent black spots on the body distinguish specimens of this size from other local forms.

Specimens 15 to 17 millimeters long.—The body remains deep and compressed, although proportionately more slender than at a length of about 10 millimeters. The greatest depth, which falls under the origin of the dorsal, is contained about 2.4 times in the length. The vent is well posterior to midbody length, the tail (without

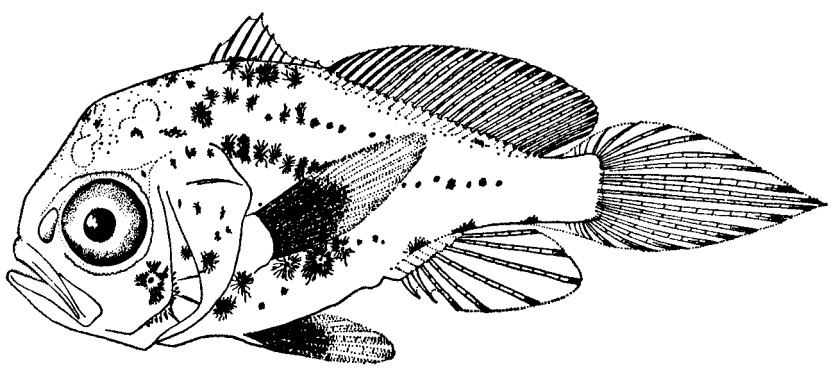

FIGURE 31.—*Larimus fasciatus*. From a specimen 10.5 millimeters long.

the fin) being contained in the length of the body about 3.15 times. The head is large and compressed. The preopercular margin has small serrae and three long spines at the angle. The eye is small, being scarcely longer than the short snout. The gape anteriorly is about on a level with the lower margin of the eye, and the maxillary reaches nearly opposite the posterior margin. Scales are present on most of the body, although not shown in figure 32. The dorsal and anal fins are rather high, the longest rays of the former reaching past the base of the caudal when deflexed, and those of

the latter about opposite it. The caudal fin is long and pointed (not round as shown by Welsh and Breder, 1923, p. 171, fig. 22), being longer than the head. The ventral fins, which have a strong spine, reach to or a little beyond the vent, and the pectorals reach opposite the anal base. Black pigment spots have increased in number as shown in figure 32. A concentration of spots, suggesting a broad black band, has taken place on the side below the base of the spinous dorsal. The black spots extend on the spinous dorsal, and the ventrals and pectorals are mostly black. A black spot at the end of the anal base, which serves as a recognition mark in the younger stages, is not evident in some specimens, though it persists in others (fig. 32).

Specimens 20 to 25 millimeters long.—The body is slightly more elongate than in the smaller fish described in the foregoing section, and has acquired proportions near those prevailing among adult fish, the depth being contained in the standard length 2.5 times. The head remains rather longer than in adults and is contained 2.7 times in the length. The eye is small, lateral, near the dorsal profile, and is a little longer than the very short snout, being contained in the head 3.2 to 3.6 times. The mouth virtually has the position it occupies in the adult; the gape anteriorly is a little above the level of the lower margin of the eye; and the maxillary reaches nearly to a vertical

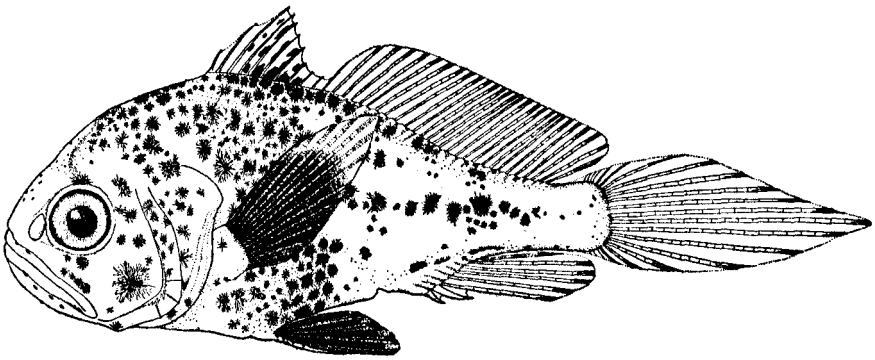

FIGURE 32.—*Larimus fasciatus*. From a specimen 17 millimeters long.

from the posterior margin of the eye, its length being contained 2.0 to 2.2 times in the head. The margin of the preopercle remains strongly serrate, but the long spines at the angle, present in somewhat smaller fish, have disappeared. The body is now fully covered with large scales. The fins remain about as in the smaller fish described in the preceding section. The caudal fin is notably longer than the head, and remains strongly pointed. The ventral and pectoral fins are long, the former reach a little beyond the vent and the latter opposite the anterior part of the anal base. Pigmentation has increased greatly, as shown in figure 33, although it is not yet general and complete. Indications of three dark crossbars are present. The anterior one, situated under the spinous dorsal, is broad and moderately distinct. The second one is situated under about the end of the anterior third of the soft dorsal, and the third one is under the posterior third of that fin. The posterior bars are narrower and much less distinct than the anterior one. A concentration of dark chromatophores occurs near the base of the caudal, forming a dark blotch. The ventral fins are almost wholly black, and the inner surface of the basal two-thirds of the pectorals also is black (fig. 33).

Fish about 20 to 25 millimeters long resemble the adults sufficiently to make identification comparatively easy. The chief diagnostic characters are the rather

short compressed body, the blunt head, short snout, strongly oblique mouth, the fin formulae (D. X–I, 24 to 27; A. II, 6 or 7), and the dark crossbars. Although only 3 bars are developed, whereas adults have 7 to 9, they are an aid in distinguishing the species.

Specimens 35 to 40 millimeters long.—The most evident advancement in the development since a length of about 25 millimeters was attained is in color. Pigmentation is general, and about seven dark crossbars are present. The broad one under the base of the spinous dorsal, present in smaller fish, shows indications of dividing into two narrower bars. The caudal fin remains nearly as long and pointed as in fish 25 millimeters long. The second anal spine has become very strong, as in the adult, and is only a little shorter than the snout and eye. The pectoral fins have become proportionately shorter and extend only to the tips of the ventrals, which scarcely reach the origin of the anal. The serrations on the preopercular margin have decreased in size, but remain somewhat more prominent than in the adult.

Specimens 60 to 65 millimeters long.—The proportionate depth (2.6 to 2.8 in the length) is about the same as in the fully matured fish, but the body remains more

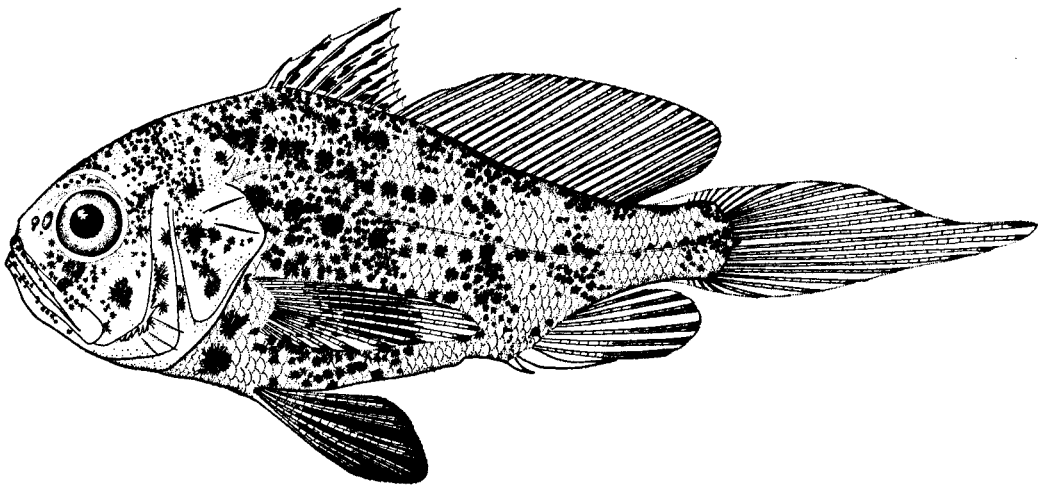

FIGURE 33.—*Larimus fasciatus.* From a specimen 24 millimeters long.

compressed. Specimens of this size differ from the adult conspicuously in the long pointed tail, the longest rays of which exceed the length of the head by at least an eye's diameter. The color pattern of the adult is quite fully developed. The ground color is silvery, the back in preserved specimens being slightly brownish. The sides have from about 7 to 9 dark bands. The spinous dorsal, the anal, ventrals, and pectorals are largely dusky to black, and the other fins are plain or somewhat punctulate with dusky.

The caudal fin generally does not acquire the characteristic shape it has in the adult (the upper lobe slightly concave and the lower one rounded) until the fish reaches a length of about 100 millimeters. In the adult, as in the young, the middle rays are the longest, but they do not exceed the head in length. When the fish reaches a length of about 100 millimeters the body has increased considerably in robustness, and this increase continues until the fish is full grown.

DISTRIBUTION OF THE YOUNG

It has been shown elsewhere (p. 85) that the young were taken in the general vicinity where the adults are permanent residents. The larvae, like the adults, apparently dwell at or near the bottom, for no young were taken in towings at the surface, whereas they appeared in bottom hauls 9 times (16 specimens, 1.9 to 15 millimeters long), notwithstanding that many more surface than bottom hauls were made. The eggs, although not taken, probably are pelagic, as in other sciaenids so far as known. If that be true the larvae must descend to the bottom very early, as already indicated. The banded drum, therefore, appears to be bottom dwelling almost throughout life.

GROWTH

The number of young fish measured is too small to cast much light upon the rate of growth. The range in length of 87 specimens of the 0-class, taken in July is from 3 to 70 millimeters, the average length being 34 millimeters. The range of 54 specimens taken in August is from 3 to 77 millimeters, with an average length of 54 millimeters. The only other month for which a considerable number of measurements is available is November. However, the larger young of the season obviously are missing, as the 215 fish measured range in length from 15 to only 63 millimeters, with an average length of 44.5 millimeters. The largest specimen, which evidently belongs to the 0-class, taken in October is 91 millimeters long, the largest one in February (no large ones of the 0-class having been taken in November, December, and January) is 113 millimeters, and the largest one in March is 123 millimeters long. While the data are quite incomplete, they do suggest a fairly rapid rate of growth, indicating that the largest young may reach a length of 120 to 125 millimeters (4¾ to 5 inches) when 1 year of age, although the average must be much smaller.

THE WEAKFISHES OR SEA TROUTS (Cynoscion nebulosus, C. regalis, and C. nothus)

Three species of sea trouts, namely *Cynoscion nebulosus*, *C. regalis*, and *C. nothus* occur on the coast of North Carolina. The two species named first are very important food fishes, as shown in the subsequent pages, whereas the last-mentioned one is of little value. The adults may be distinguished as shown by the following key.

KEY TO THE SPECIES

a. Soft dorsal and anal scaleless; gill rakers short, 8 on lower limb of first arch; body with round black spots ..... *nebulosus*

aa. Soft dorsal and anal covered with small scales; body without round black spots.

b. Anal fin usually with 12 soft rays, sometimes 11, infrequently 13; lower limb of first arch most frequently with 17 gill rakers, often with 16 or 18, infrequently with 15 or 19; caudal fin definitely emarginate in specimens 300 millimeters (12 inches) and more in length; upper parts of sides usually with dark greenish wavy oblique stripes or reticulations. *regalis*

bb. Anal fin usually with 9 soft rays, sometimes with 8 or 10; lower limb of first arch usually with 13 gill rakers, sometimes 12 or 14; caudal fin never definitely emarginate, the upper lobe in large specimens somewhat concave and the lower one rounded, pointed in fish under 200 millimeters (8 inches) in length; coloration generally plainer, seldom with dark wavy oblique lines or reticulations ..... *nothus*

The distinguishing characters of young *C. nebulosus* and *C. regalis* are pointed out in a separate paragraph following the descriptions of the different stages in the

development of *C. nebulosus*. Similarly, the distinguishing characters of *C. regalis* and *C. nothus* are shown in a paragraph following the descriptions of the various stages in the development of *C. nothus*.

CYNOSCION NEBULOSUS (Cuvier and Valenciennes)

SPOTTED TROUT; SPECKLED TROUT; SPOTTED WEAKFISH

The spotted trout ranges from New York to Texas and is commercially an important fish from Virginia southward to Texas. According to the statistical records [7] of this Bureau, the following catches were made by States: Virginia, 198,000 pounds; North Carolina, 694,309; South Carolina, 10,900; Georgia, 48,450; Florida, 2,790,566; Alabama, 105,981; Mississippi, 125,112; Louisiana, 387,101; and Texas, 1,043,353. This weakfish reaches a fairly large size. Individuals weighing 5 to 10 pounds are not unusual on the coast of North Carolina. The maximum weight attained, so far as known to the writers, is 16 pounds (Hildebrand and Schroeder, 1928, p. 298).

The spotted trout is a fish of superior flavor, and it always commands a good price. Its importance in North Carolina is greatly increased because it is caught in the shallow waters of the estuaries and sounds throughout the year. The catches made during the winter are of particularly great importance to the fishermen who depend on haul-net fishing. A catch of speckled trout during the winter, which is a very lean season with the haul-seine fishermen, often is a real "life saver." In fact, the speckled trout is of first importance to these fishermen in the vicinity of Beaufort. Even though the total annual catch is smaller than for the gray trout, the annual money value is greater, because of the higher price it commands in the market. Furthermore, much of the return, as already indicated, comes during the winter when it is badly needed.

Although the fish inhabit the shallow waters of the sounds and estuaries during the winter, they do at times become numb from the cold. For example, on January 7, 1926, fishermen are reported to have made good wages picking up numb and floating fish in North River. The weather had been rather unusually cold for a week or more, the air temperature having dropped to 12° F. on December 28. The water temperature at 4:30 p.m. at the laboratory pier, just off a moderately deep channel where the water undoubtedly was not as cold as in the shallow estuary of North River, was 55°, 57°, 53° F., respectively, on January 5, 6, and 7. Again on January 4, 1928, many numb floating speckled trout were seen in the vicinity of Beaufort. The senior author picked up several along the shores of Pivers Island, and commercial fishermen found it profitable to "gather" the fish. Perhaps many more fish were eaten by water fowl than were gathered by man. At least, the activities of the sea gulls were great around Pivers Island. January 4 was preceded by several days of exceptionally cold weather (for that vicinity), the air temperature reaching the low mark of 14° F. on January 2. The water temperature at 4:30 p.m. was 42°, 41°, and 39° F., respectively, on January 2, 3, and 4.

The numbed fish became quite active upon being taken into a heated room. It is thought, therefore, that they might have revived in nature with the return of warmer weather, if they had been left unmolested.

[7] Fisheries Industries of the United States, 1931. By R. H. Fiedler. Appendix II, Report, Commissioner of Fisheries, 1932 (1933), pp. 97–440.

Sometimes during cold weather the trout, although not numb enough to float, became quite helpless. The fish school more or less and if once found they are easily surrounded by a net. Fisherman often make large catches at such times.

According to Coker (in Smith, 1907, p. 313) speckled trout have not always been present in the shallow waters around Beaufort, N.C., during the winter. However, they have occurred there with a fair degree of regularity since 1914 when the senior author first began to make observations at Beaufort.

Pearson (1929, p. 190) reports that speckled trout in Texas mostly depart from the grassy areas during cold weather and seek the deeper holes and channels. At Beaufort the movement seems to be in the reverse direction.

It appears to be of interest to report a remarkable case of recovery from a very serious injury. This case is of special interest, as the speckled trout and other species of the genus Cynoscion in some localities are known as weakfish, presumably because they do not stand handling well and die quickly when caught. On June 27, 1927, a specimen of speckled trout that had had its tail severed from the body slightly behind the anal fin, was caught off Pivers Island. The wound had healed completely, and the stump of the tail, which was entirely without a fin, had become scaled over in part. The fish appeared to be healthy and in a well-fed condition.

The descriptions of the young fish, under 10 millimeters in length, that follow are based on specimens from Beaufort. In drawing up those of the larger fish, collections from the Gulf coast, made by Isaac Ginsburg and John C. Pearson, were used in addition to the specimens from Beaufort.

SPAWNING

Ripe fish, or fish with well-developed gonads, were not seen during this study Yarrow (Smith, 1907, p. 312) observed females with large roe in April at Beaufort. J. H. Potter, a local fish dealer of long experience, reported to the senior author that he saw a ripe female, from which eggs were "running", on June 10, 1915, the first and only fish of the genus he had ever seen with "roe of any size." Pearson (1929, p. 180), working on the coast of Texas says, "The spawning season of the trout begins in early spring (not before March) and continues as late in the summer as October. The spotted trout * * * are found in all stages of development throughout the spring and summer and probably spawn for weeks. The height of the spawning season occurs in April and May, however."

The young apparently are not numerous at Beaufort. Only 47 specimens 80 millimeters and less in length were secured during several years of rather intensive collecting, and generally only one to several specimens were taken at a time. Only 17 individuals under 5 millimeters in length were secured, and of these 6 were taken during June of 4 different years, namely, 1927, 1928, 1931, and 1932, and the other 11 were caught in one haul on August 26, 1929. No specimen less than 10 millimeters in length was caught during July. The largest specimen of the 0-class taken in June is 11 millimeters long, the largest secured during July is 71 millimeters, and the largest one taken in August is 150 millimeters in length. The size range of the limited number of specimens taken at Beaufort, therefore, suggests that spawning probably begins there in May and extends into August.

Pearson (1929, p. 180) has stated: "The spotted trout spawns largely, if not entirely, within the bays and lagoons along the coast of Texas * * *." Twelve of the 17 specimens under 5 millimeters in length, caught at Beaufort, are from stations

5 and 6 miles offshore, 1 was taken in the bight at Cape Lookout, and the remaining 3 were caught in the estuary of Newport River. Such small, comparatively helpless, young almost certainly had not voluntarily traveled far. However, they may at times be carried comparatively long distances by wind and tide. It is impossible to determine the exact spawning ground or grounds from the limited material secured at Beaufort. It seems probable that spawning may take place both in the inside and outside waters. The general scarcity of the young suggests that there is no important spawning ground in the vicinity of Beaufort.

DESCRIPTIONS OF THE YOUNG

Specimens 1.8 millimeters long.—The head and trunk are deep, and the caudal portion of the body is very slender, an abrupt break in the ventral contour of the body occuring at the vent. The vent in these small specimens is situated in advance of midbody length, the preanal distance being contained in the length to the tip of the notochord, 2.1 to 2.4 times, and the postanal distance 1.75 to 1.9. The greatest depth of the body is contained in the length about 3.1 times, and the depth behind the vent is scarcely greater than the diameter of the eye. The mouth is moderately

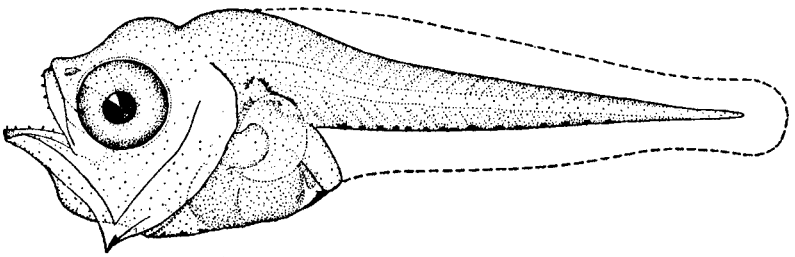

FIGURE 34.—*Cynoscion nebulosus*. From a specimen 2.0 millimeters long.

large and strongly oblique, the gape anteriorly being somewhat above the level of middle of eye, and it extends backward somewhat under the eye. The myomeres are indistinct anteriorly and posteriorly; about 25 may be counted. The vertical finfold is uninterrupted and is without indications of fin rays. The pectoral fin membranes are prominent, but the ventrals are not evident. Dark markings are present on the ventral outline of the chest and abdomen, with a prominent spot immediately in advance of the vent. A series of close-set black spots occupies the anterior half to two-thirds of the ventral outline of the tail. A few indefinite dark, probably subsurface, markings also are present above the abdominal mass (fig. 34).

The specimens described in the foregoing paragraph were taken in the same tow-net haul in which the somewhat larger ones, described in the next section were taken. The identification is somewhat uncertain because insufficient specimens are available and because of the darkened condition of some of the preserved ones, obliterating color markings. However, the larvae of nearly all the other local species of sciaenids are known. Therefore, the identification may be fairly definitely established through elimination.

The larvae of *C. nebulosus* at a length of 1.8 millimeters differ from those of *C. regalis* of the same length, so far as can be judged from the material available, in the rather deeper head and trunk, and apparently more slender tail, the decrease in depth at the vent being greater and more abrupt. The greatest depth of the body is contained in the total length to the tip of the notochord about 3.1 times in *C.*

nebulosus, whereas the greatest depth is contained about 4.0 to 4.5 times in the length in *C. regalis*. Another difference apparently exists in color, as the dark spots on the ventral outline of the tail are more prominent and in a much closer set series in *C. nebulosus* than in *C. regalis*.

Specimens 2.5 millimeters long.—The head and trunk are rather deep, and the caudal portion of body, although proportionately deeper than in specimens 1.8 millimeters long, remains moderately slender. The vent now is situated almost exactly at midbody length, and the greatest depth (measured somewhat behind the head) is contained about 2.6 times in the length to the tip of the notochord. The depth immediately behind the vent now is notably greater than the diameter of the eye. The mouth is large and strongly oblique, the gape anteriorly is only slightly below the level of the middle of eye, and the maxillary reaches nearly to the vertical from the posterior margin of the pupil. The myomeres are indistinct posteriorly, about 27 may be counted. The finfold remains continuous. However, a thickening of the tissues has taken place below the distal part of the notochord, and also farther forward, constituting respectively the primitive bases of the caudal and anal fins. The pectoral fin membranes are prominent, but the ventrals are not yet evident.

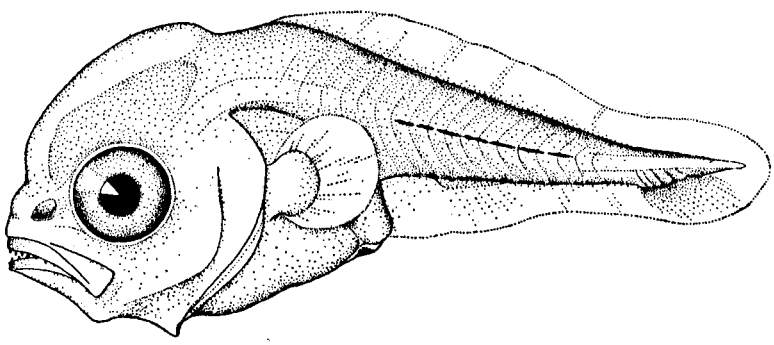

FIGURE 35.—*Cynoscion nebulosus*. From a specimen 2.5 millimeters long.

A black lateral stripe, consisting of nearly connected dashes, begins about at the vertical from the vent and extends nearly half the distance to the tip of the tail. The closely approximated dots, forming an almost continuous dark stripe along the ventral outline of the tail, although somewhat less distinct than in smaller specimens, remain present. Dark dots also remain evident on the ventral outline of the chest and abdomen (fig. 35).

The body proportions, according to the specimens at hand, are almost identical in *C. nebulosus* and *C. regalis* at this size. The chief diagnostic character is the dark lateral stripe, present in *C. nebulosus*, but wanting in *C. regalis*. The first-mentioned species, also, has more numerous and more closely approximated black spots of nearly uniform size, on the ventral outline of the tail. In *C. regalis* the spot at about midcaudal length already is somewhat larger than the others, a distinction that becomes more pronounced in somewhat larger specimens.

Specimens 3.0 to 3.6 millimeters long.—The body is quite elongate and compressed, the break in the ventral outline at the vent, abrupt in smaller specimens, no longer remains pronounced. The head and trunk now exceed the rest of the body in length, the preanal distance being contained in the length to the tip of the notochord 1.75 to 1.8 times, and the postanal distance 2.2 to 2.3 times, and the greatest depth is contained 3.4 to 3.6 times in the length. The large mouth remains strongly oblique,

the gape anteriorly being about at the level of the middle of the eye and the maxillary reaches to middle of pupil. The notochord is curved slightly upward distally, and rather definite rays (caudal fin) are present below the curved portion. The bases of the soft dorsal and the anal fins are rather definitely shown by the thickening of the tissues, though no rays are present. The pectoral fin membranes remain rather prominent as in smaller specimens, but no ventrals are evident. The black lateral stripe already present at a length of 2.5 millimeters, has become more prominent, and it extends from the shoulder nearly to the base of the primitive caudal fin, which (as already stated) is situated under the ventral side of the distal part of the notochord. The stripe is rather more continuous than in smaller specimens, but the dashes of which it is composed still are visible in some specimens. Furthermore, the line has slight vertical projections, making its edges somewhat ragged. The line extends forward faintly across the opercle and on the snout. Both the upper and lower lips are dusky. More or less black is present over the abdominal mass, which probably is subsurface. The dark markings along the ventral outline of the tail, distinct in the smallest specimens at hand, remain, and are nearly uniform in size. A few very small and indefinite dark points are evident on the ventral surface of the head and trunk (fig. 36).

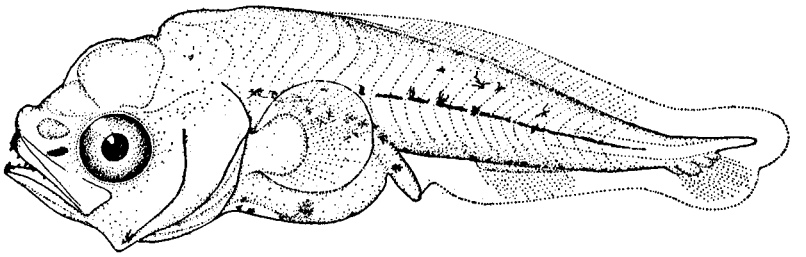

FIGURE 36.—*Cynoscion nebulosus*. From a specimen 3.2 millimeters long.

This species, at the length described, is distinguished from *C. regalis* principally by the black lateral line, which *C. regalis* does not possess. The first-mentioned species also has much more numerous black markings along the ventral outline of the tail, none of which are especially enlarged, whereas in *C. regalis* the spot lying at the posterior end of the base of the primitive anal is considerably larger than the others. *C. nebulosus*, at the size described, appears to be somewhat more slender, the greatest depth being contained 3.4 to 3.6 in length, compared with about 2.7 to 3.0 in *C. regalis*. Insufficient specimens are available, however, to determine definitely the relationship in this respect.

Specimen 7 millimeters long.—The body is quite elongate, compressed, and shapely for such a small fish. The dorsal profile anteriorly ascends rather gently and is moderately convex. The vent is situated much nearer the base of the caudal than the tip of the snout (preanal distance 1.6 times in standard length; postanal distance to base of caudal, 2.6 times), and the greatest depth is contained 3.3 times in the standard length. The snout is rather pointed and longer than the eye. The mouth is large, less strongly oblique than in smaller specimens; the gape anteriorly is almost on a level with the lower margin of the pupil; and the maxillary reaches about to the vertical from the posterior margin of the pupil. Although the caudal fin is well developed and apparently rather sharply rounded (the rays are broken in part and the exact shape cannot be determined), the upward curved tip of the notochord

remains visible. The anal and the soft dorsal are quite fully developed, but the spinous dorsal remains rudimentary. The anal consists of 11 soft rays, and the soft dorsal has 26 rays, formulae prevailing in adults. The pectoral fins, too, are developed, and have differentiated rays, but the ventrals are very rudimentary, that is, mere tufts of membrane less than half the length of the eye. A black lateral stripe persists, although rather less distinct than in smaller fish. A definite black band is present on the snout in advance of the eye, and indefinitely on the opercle behind the eye. Both lips are black. The black on the ventral outline, described in smaller specimens, now is confined almost wholly to the ventral surface of the caudal peduncle. Subsurface dark markings over the abdominal mass remain visible, although less distinct than in younger fish. Small dusky spots are scattered over the cranium, and a row of more or less definite black spots is present on the back and extends along the base of the dorsal fins (fig. 37).[8]

Only one specimen of the size described is at hand. This species is more slender and more shapely than *C. regalis* at this size (depth in standard length 3.3 times in the former and 2.8 in the latter), and the snout is more pointed. *C. regalis* is much

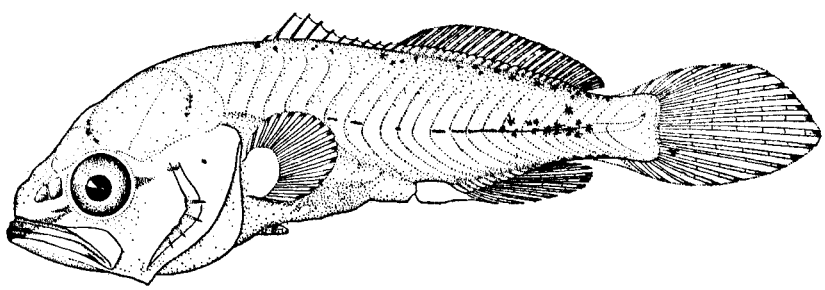

FIGURE 37.—*Cynoscion nebulosus*. From a specimen 7 millimeters long.

plainer in color, as it has no lateral stripe and no black markings on the head or back, and only a few on the ventral outline. The enlarged black spot near the middle of the base of the anal is quite distinctive, as no such spot is present in *C. nebulosus*. The enlarged spot on the anal base in *C. regalis* is present at a length of about 3.5 millimeters, and it serves as a mark of distinction in specimens ranging from that length to 7 millimeters and upward.

Specimens 10 to 12 millimeters long.—The fish is moderately slender, compressed, and shapely. The head is rather low, and pointed, its length is contained 2.7 to 2.85 times in the standard length, and the greatest depth 3.8 to 4.2 times. The snout is rather long, its length to tip of upper jaw being contained 3.5 times in the head, and the eye 4.2 to 4.4 times. The mouth is large, moderately oblique; the lower jaw projects rather prominently; the gape anteriorly is about on a level with the lower margin of the pupil; and the maxillary reaches slightly past middle of eye, its length being contained 2.25 to 2.9 times in the head. Small spines are present on the margins of the preopercle and interopercle. Two stained and cleared specimens have respectively 25 and 26 vertebrae. The fins are all developed, but the spinous dorsal remains quite low, the longest spines being shorter than the eye, and the ventrals, although having rays, also remain short, being equal to or scarcely longer than the eye. The

[8] The figure by Pearson (1929, p. 179, fig. 24) based on a specimen 7.8 millimeters long, presumably taken on the coast of Texas shows the body as being much more compressed and less shapely than in the Beaufort fish. Furthermore, the mouth is shown as less strongly oblique and the caudal fin as much more broadly rounded. Marked differences in color, also, are evident. If the figure is correct, much variation must exist among specimens. The figure certainly does not agree as to the shape of the body with a faded specimen from Texas examined by us.

caudal fin is moderately long and somewhat pointed, the longest rays being in the lower half of fin and much shorter than the head. Pigmentation has advanced little since a length of 7 millimeters was attained. A few additional dusky markings have appeared along the black lateral stripe, and the dusky markings on the head and back have increased somewhat in number and intensity (fig. 38).[9]

This species remains notably more slender than *C. regalis*, and the head is lower, and the snout more pointed (the depth in the former is contained 3.8 to 4.2 in the length and in the latter 2.95 to 3.0 times). The caudal fin is less sharply pointed and the rays are shorter than in *C. regalis*. The differences in color remain about as in 7-millimeter specimens. Although *C. regalis* now has a few dusky spots on the side and the back, they are not arranged in definite series. The characteristic dusky spot near the middle of the base of the anal remains in that species, and in some specimens a smaller one precedes it and another one follows it. No black spots occur on the base of the anal in *C. nebulosus*.

Specimens 16 to 20 millimeters long.—The body is quite slender and moderately compressed, the shape being close to that of the adult. The head is long and low, its length being contained 2.7 to 3.0 times in the standard length, and the greatest depth of the body 3.9 to 4.15 times. The snout is rather long and pointed, its length is contained 3.5 times in the head, and the eye 4.0 to 5.0 times. The mouth has ac-

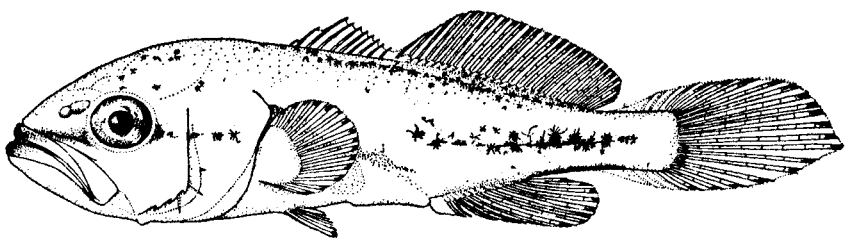

FIGURE 38.—*Cynoscion nebulosus*. From a specimen 11 millimeters long.

quired virtually the shape and position it has in adult fish. It is somewhat oblique, the gape anteriorly is scarcely above the lower margin of the pupil, and the maxillary reaches nearly opposite the posterior margin of the eye, its length being contained 2.2 to 2.8 times in the head. Scales are evident on the middle of the side from the shoulder nearly to the base of the caudal at a length of 16 millimeters; at a length of 20 millimeters the body is almost fully scaled. The spinous dorsal has increased greatly in height since a length of 12 millimeters was attained, and the longest spines are as long as the snout, therefore, proportionately about as long as in the adult. The caudal fin remains somewhat pointed and the longest rays are about as long as the head without the snout. The ventral fins have increased greatly in length since the fish attained a length of 12 millimeters, and now are fully twice as long as the eye. When the fish reach a length of about 16 millimeters the black lateral line, present in smaller fish, disappears or becomes laid over gradually by an indefinitely outlined dark band composed of numerous minute brownish or dark markings which extend forward on the side of the head and snout (quite indefinite on the head in some specimens), and backward on about the basal half of the caudal fin. Dark dots on the head and back have become much more numerous and those on the back form more

[9] The criticisms pertaining to Pearson's figure 24 (1928, p. 179), set forth in footnote 8, in general apply to his figure 25, with the addition that the origin of the spinous dorsal, which is shown as having its origin over the pre-opercular margin, actually has its origin slightly behind the vertical from the base of the pectoral, according to specimens from North Carolina as well as from Texas, which the writers were able to examine.

or less definite longitudinal bands than in smaller specimens. At a length of about 19 millimeters dark dots sometimes develop on the spinous dorsal (fig. 39).

This species continues to differ notably from *C. regalis* in the much more slender body (depth in standard length 3.9 to 4.15 times in *C. nebulosus*, 3.3 to 3.4 times in *C. regalis*), much lower head and more pointed snout, and in the much more prominently projecting lower jaw. The species also differ notably in color, as *C. nebulosus* is marked chiefly by dark longitudinal bands, whereas *C. regalis* has no longitudinal bands, but is marked anteriorly with indefinite broad dusky crossbars on the back, and posteriorly with lateral quadrate blotches. It is obvious that *C. nebulosus* acquires the shape and form of the adult at a smaller size than *C. regalis*.

Specimens 25 to 30 millimeters long.—No change of importance has taken place in the proportions of the body since a length of 16 to 20 millimeters was attained. The head is contained 2.7 to 2.9 times in the standard length and the depth 3.95 to 4.2 times.[10] The eye is small, being contained 4.25 to 5.0 in the head, the snout 3.25 to 4.5, and the maxillary 2.25 to 2.4 times. Gill rakers are well developed, 8 on lower limb of first arch. The body is fully scaled, and a sheath of scales is evident along

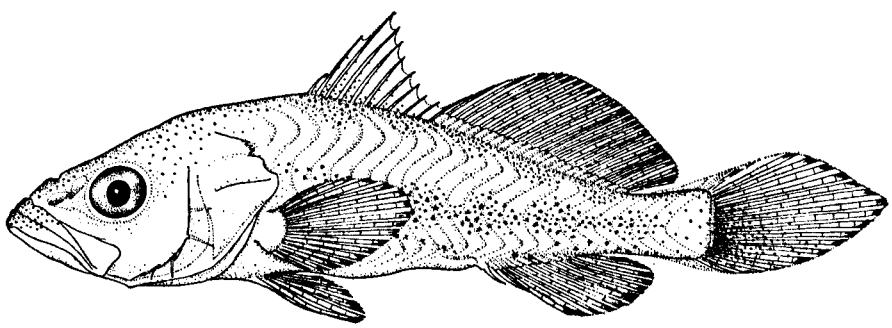

FIGURE 39.—*Cynoscion nebulosus*. From a specimen 20 millimeters long.

the bases of the dorsal and anal. The dorsal fins are moderately high, the longest rays and the longest spine being nearly equal in length and each is contained in the head about 2.5 to 2.8 times. The shape of the caudal remains unchanged, and the longest rays are about as long as the head. The ventral and pectoral fins are virtually equal in length and are contained 2.15 to 2.4 times in the head. A definite dark brownish band, with broken edges, extends from the snout along the side and on the caudal fin. The band is broken from the eye to the opercular margin where it forms more or less disconnected blotches. At the base of the caudal it is crossed by a pale line, and on the base of that fin it is darker and becomes somewhat pointed posteriorly. It is not definitely outlined, however, as most of the fin bears dark dots. The upper surface of the head is mostly brownish, and this color extends on the back as two indefinite bands, one on each side of the base of the dorsal fins. Posterior to the spinous dorsal the bands are more or less broken up into blotches. In some specimens the bands are more nearly continuous than in others. A few dark dots are present on the dorsal fins, being most numerous on the anterior margin of the spinous dorsal. Indications of scattered dark points also are present on the anal, but the pectorals and ventrals remain unmarked (fig. 40).

[10] Attention is called to figure 15 in Welsh and Breder (1923, p. 167) which is based on a specimen 28 millimeters long. This illustration appears to have been drawn from an abnormally deep fish. At least the body is shown as much deeper than in any of the specimens now at hand. Furthermore, the lower jaw projects too prominently, and the caudal fin has the longest rays in the lower half of the fin, and not in the middle as shown in the figure.

C. nebulosus remains more slender than *C. regalis* (depth in standard length of the former 3.95 to 4.2 and the latter 3.3 to 3.5), the head is lower and more pointed, and the mouth is less strongly oblique (the gape in *C. nebulosus* being wholly below the eye, whereas in *C. regalis* it is only a little below the middle of the eye anteriorly). The caudal fin is rather short and only moderately pointed in *C. nebulosus*, the longest rays being about as long as the head, whereas in *C. regalis* the fin is long, sharply pointed, the longest rays being notably longer than the head. The differences in color remain about as indicated for specimens 16 to 20 millimeters long.

Specimens 35 millimeters and upward in length.—The larger young of this species have been described adequately by Welsh and Breder (1923, pp. 164 to 169) and the descriptions by these authors were augmented with remarks on smaller fish by Pearson (1929, pp. 178 and 179). It does not appear essential, therefore, to draw up further descriptions. However, it does seem desirable, in the light of the study of large series of specimens, to include a discussion of the relationship of this species and *C. regalis*, as development proceeds.

The species are most readily separated by color, as the patterns are very different. However, evident structural differences also are present. In *C. nebulosus* the dark

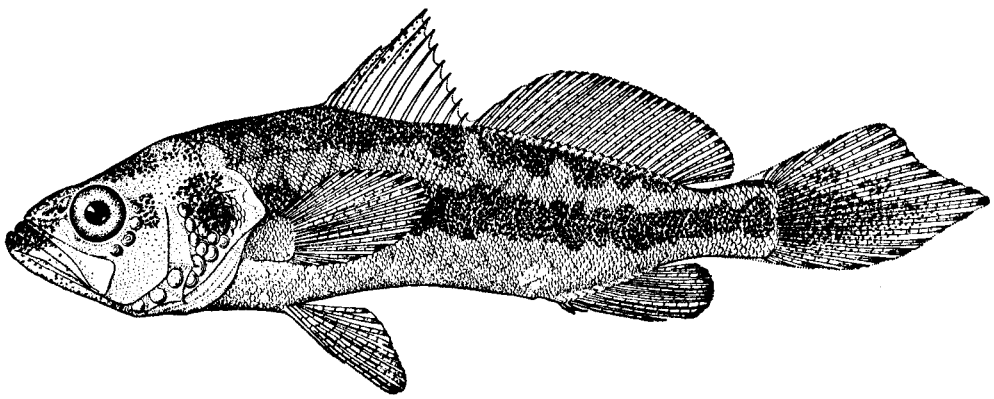

FIGURE 40.—*Cynoscion nebulosus*. From a specimen 27 millimeters long.

longitudinal bands, present in smaller specimens, begin to break up into spots when the fish are about 30 millimeters long. At a length of 35 to 40 millimeters, the band on the back is divided into more or less definite quadrate blotches, but the lateral band remains almost continuous. When the fish reach a length of about 60 to 70 millimeters the lateral band also becomes divided into spots, and the caudal fin, which previously was almost solidly black at the base, has become spotted. At about the same size spots develop between the bands, and at a length of 70 to 80 millimeters the entire upper half of the side bears indefinitely outlined spots, which are irregular in shape and variable in size. The spots (in preserved specimens) are rather more brownish in color than in younger fish. At a length of 110 to 120 millimeters, the characteristic small, roundish black spots of the adult, which occupy the upper two-thirds of the sides as well as the dorsal and caudal fins, are quite fully developed.

Specimens of *C. regalis*, 35 to 40 millimeters long, on the other hand, have broad dark crossbands on the upper part of the side, which extend to or somewhat below the lateral line. These bars disappear when the fish reach a length of about 70 to 80 millimeters. Specimens ranging from about 80 to 100 millimeters in length are almost plain grayish above and silvery below. The characteristic dark wavy lines

or reticulations of the adult begin to appear when the fish reach a length of about 100 millimeters, and at a length of about 120 to 130 millimeters the fish have acquired almost fully the color pattern of the adult.

C. nebulosus is more slender and more shapely than *C. regalis* throughout the younger stages. However, at a length of about 175 millimeters the differences in the shape of the body virtually have disappeared. It is evident from table 3 that *C. nebulosus* acquires the proportionate depth of the adult very early, that is, at a length of about 10 to 12 millimeters, whereas *C. regalis* is much deeper throughout the younger stages and does not have the proportionate depth of the adult until a length of about 175 millimeters is attained.

The shape of the caudal fin differs quite notably in the two species throughout the younger stages, that is, from a length of about 20 to 125 millimeters. During this entire period of development this fin, although pointed in both species, is notably longer in *C. regalis* than in *C. nebulosus*, the longest rays in the former being the middle ones, which are more or less filamentous in the younger stages, and equal to or longer than the head, whereas the longest rays in the latter are in the lower half of the fin and are not longer than the head. For some time during the course of development the upper lobe of the caudal fin in both species is slightly concave and the lower lobe more or less roundish. Although the fin must undergo a greater change in *C. regalis* to acquire the broadly concave outline which obtains in adults of both species, it is acquired somewhat earlier, that is, at a length of about 250 to 280 millimeters (there being much variation in the development among specimens), whereas this shape is not acquired by *C. nebulosus* until the fish is about 300 millimeters long.

The two species differ also in the number of gill rakers, *C. regalis* having 11 or 12 on the lower limb of the first arch, whereas *C. nebulosus* has only 7 or 8. The gill rakers are developed and can be counted readily when a length of about 26 millimeters is attained.

The species differ, furthermore, in that *C. nebulosus* has no scales on the fins throughout life, whereas *C. regalis* has minute scales on about the basal half of the soft dorsal, the caudal and the anal fins. The scales first appear when the fish are about 45 to 55 millimeters long.

TABLE 3.—*Proportionate depths of specimens of various size of Cynoscion nebulosus and C. regalis*

Total length in millimeters	C. nebulosus		C. regalis		Total length in millimeters	C. nebulosus		C. regalis	
	Depth in standard length	Number of specimens measured	Depth in standard length	Number of specimens measured		Depth in standard length	Number of specimens measured	Depth in standard length	Number of specimens measured
7	3.3	1	2.8	1	70–90	3.7–4.0	7	3.4–3.6	7
10–12	3.8 –4.2	3	2.95–3.0	3	120–130	3.8–4.1	5	3.5–3.6	5
16–20	3.9 –4.15	3	3.3 –3.4	3	150–175	3.9–4.25	4	3.5–4.1	4
25–30	3.95–4.2	6	3.3 –3.5	6	210–240	4.1–4.3	6	4.1–4.4	6
40–50	4.0 –4.25	6	3.3 –3.4	6					

DISTRIBUTION OF THE YOUNG

It has been stated elsewhere (p. 93) that the young under 5 millimeters in length, in the collection mostly were taken at off-shore stations. The larger ones of the same year class, ranging from 5 millimeters upward, however, were all caught in inside waters. The indications are, therefore, that the young, if actually hatched in part off shore, enter the inside waters soon afterward.

Only a few of the smaller larvae at hand were caught in surface towings, and all the larger ones were taken in bottom hauls. Therefore, the indications are that the young of this species are chiefly bottom dwelling.

GROWTH

The number of young of the 0-class, consisting of only 126 specimens taken and measured, is entirely too small to cast much light on the rate of growth. However, the measurements parallel those of *C. regalis* rather closely, and indicate that the fish grow rapidly during the first summer of life, attaining a modal length of about 170 millimeters (6¾ inches) when 7 or 8 months old. The size at which sexual maturity is reached remains unknown.

CYNOSCION REGALIS (Bloch and Schneider) GRAY TROUT; GRAY WEAKFISH

The gray trout ranges from Massachusetts to the east coast of Florida[11]. It is a commercially important species from Rhode Island to Florida. The States having the largest catches are New Jersey, with an average annual catch from 1928 to 1930 inclusive of 9,160,346 pounds;[12] Virginia, 12,710,389 pounds; and North Carolina, 4,415,059 pounds. This trout is reported to reach a maximum weight of 30 pounds. In Chesapeake Bay fish weighing 10 pounds are not particularly uncommon. However, at Beaufort fish weighing 6 pounds are considered large ones and 9-pound fish are exceptional.

The gray trout is a well-flavored fish and always commands a good price. This species and the spotted trout constitute the chief support of the haul-seine fishermen who generally go in pairs and fish the shallower inside waters in the vicinity of Beaufort. Their equipment consists of a small motor boat, which generally has a small cabin forward over the engine, a rowboat, and a 300 yard straight dragnet. Frequently two crews "pair", that is, they unite their gear and power by lashing their nets together and making long drags, using the power of their motor boats.

The gray trout is taken commercially at Beaufort from about March to December, the length of the fishing season varying according to the annual fluctuation in the mildness, or severity, and duration of winter weather, for the large fish leave when cold weather comes and return as early in the spring as the temperature of the water again becomes agreeable. The large fish evidently are more sensitive to temperature than the smaller ones. Whereas, the larger ones leave the shallow waters, as already stated, upon the approach of cold weather, the smaller individuals remain there, except during the brief cold snaps that occur locally. Small gray trout were taken many times during the winter in Newport River, for example, during the several years of the present investigation. They were common also off Bogue and Shackleford Banks in a few to several fathoms of water. However, they presumably withdraw to deeper and warmer water during cold snaps, but return within a few days after the temperature rises. Therefore they may make several migrations during one winter. The large fish, on the other hand, make only one migration

[11] In a study of the sea trouts of the Gulf coast, Ginsburg (1929, p. 83) found that the fish from that coast, formerly considered identical with the gray trout of the Atlantic coast, is a distinct species, which he named *C. arenarius*. Therefore, the range of the gray trout, previously thought to extend to Texas, is now restricted to the Atlantic coast.

[12] The statistics offered are taken from "Fisheries Industries of the United States", for the years 1929, 1930, and 1931. The "average annual catch" is the arithmetical average for the 3 years, 1928, 1929, and 1930. The gray trout and the spotted trout are listed separately only for 1930. The spotted trout is unimportant, from a statistical standpoint, in all the States named, exclusive of North Carolina in which this species constituted 22.7 percent of the catch in 1930. However, to make the figures comparable the entire catch of trout is considered for each State.

as already indicated, leaving the shallow waters in the autumn or early in the winter and returning early in the spring when low temperatures are not likely to recur.

Although the smaller gray trout generally migrate away from the shallow waters during cold snaps, they apparently do not always go early enough, for on January 14, 1927, quite a few dead and numb fish were seen along the shores of Pivers Island. A sample of 6 fish was gathered having a range in length of 122 to 182 millimeters. Several days of rather unusually cold weather preceded January 14. The water temperature at the laboratory pier, taken daily at 4:30 p.m., dropped to 41° F. on January 9, and it remained there until January 14 when it came up to 48° F. A temperature of about 41° F., therefore, probably is close to lethal.

SPAWNING

The spawning season of the gray trout is a moderately long one. Fish with well-developed roe (although not ripe) were observed as early as April 16 (1914), and as late as August 17 (1914). The young were taken first on May 25 (1932). However, they are rather large ones, ranging from 6.5 to 9 millimeters in length, and therefore may have been a few weeks old when caught. Larvae under 5 millimeters in length were caught during June, July, and as late as August 27 (1930). According to these data the spawning season at Beaufort begins in May and extends through June, July, and August.

The conclusion relative to the spawning period at Beaufort is in general agreement with statements by Welsh and Breder (1923, pp. 150–158), who say that the season is a protracted one, commencing in May and continuing until September. The great majority of the fish are reported, however, to spawn between the middle of May and the middle of June. These authors state, furthermore, that the spawning season is little affected by the latitude and that it occurs at about the same time from Cape Cod to the Carolinas. Higgins and Pearson (1927, p. 57) found virtually all mature females taken in pound nets in Pamlico Sound, N.C., in a spawning condition in the second week of June (1925) when they began their investigation, and by August 10 spawning had been completed.

It was noticed at Beaufort that the large fish develop roe earlier than the smaller ones. Among thousands of fish examined only large ones had gonads in an advanced state of development in April, whereas in August those fish that still contained roe were small ones, generally 15 inches and somewhat less in length.

In the vicinity of Beaufort spawning apparently takes place principally, if not wholly, at sea. This conclusion is arrived at from a study of the movements of adult fish and from a study of the distribution of the young. It has been stated elsewhere that the large fish return to the inside waters early in the spring from as yet a relatively unknown winter home. For a time these fish are quite abundant. However, within a month or two after their arrival, or about the latter part of May, the large fish become scarce and remain so until about July when they again increase in abundance. During two seasons (1914 and 1915) of almost ceaseless effort no females quite ripe were found among thousands of fish examined. Virtually all contained roe early in the spring. Later, when the large fish returned after a period of absence they had spawned. The explanation appears to be that the fish go out to sea to spawn and return to the estuaries and sounds when the process is completed.

The foregoing explanation of the scarcity of large fish in the inside waters during a period, which undoubtedly is the height of the spawning season, is substantiated in

a measure by the distribution of the young 10 millimeters and less in length, as shown by the collections. Young 5 millimeters and less in length were taken quite sparingly, as only 25 were secured, including 17 taken outside. The young ranging upward of 5 millimeters in length were taken much more abundantly. The collection contains 270 specimens 6 to 10 millimeters long, including 253 individuals taken off Bogue and Shackleford Banks and only 17 from Beaufort Harbor and adjacent waters. In explanation it may be stated that the foregoing results were secured, notwithstanding that many more hauls, using identical gear, were made in the inside than in the outside waters. It seems to be evident, therefore, that the young, 10 millimeters and less in length, are much more numerous off Bogue and Shackleford Banks than within the harbor and adjacent sounds and estuaries.

The bulk of the young undoubtedly remain in the general vicinity where they are hatched until the power to swim is developed. Occasionally the floating eggs and the helpless larvae no doubt are carried considerable distances by the wind and tide. It is possible that the comparatively few larvae taken in the inside waters were carried there involuntarily. The fins are entirely undeveloped until a length of about 6 millimeters is attained, and imperfectly until a length of at least 10 millimeters is reached. Prior to the rather full development of the fins the young fish probably cannot swim far, nor in a definite direction. Therefore, the majority of the young 10 millimeters and less in length would be expected to be found chiefly near the spawning ground.

The conclusion that in the vicinity of Beaufort spawning takes place principally, if not wholly, at sea, therefore, seems to be justified from the information given relative to the movements of the adults during the spawning season, and from the data presented concerning the distribution of the young.

DESCRIPTIONS OF THE EGGS AND YOUNG

The reader is referred to Welsh and Breder (1923, pp. 150–153) for descriptions of the eggs and their development, as well as for accounts of the newly hatched young. Descriptive notes and illustration of the development of the young are offered by Pearson.[13] They have been compared with specimens of similar sizes in our collection and found to be essentially correct. Accordingly, descriptions and illustrations are omitted in this paper. However, the diagnostic characters are shown in the accompanying keys.

Some remarks relative to the eggs of the gray trout seems to be in order, because of the extremely great variation in their diameter shown by Welsh and Breder and also by Pearson. It is believed that the eggs were taken numerous times off Beaufort Inlet, but were confused with those of the white perch, *Bairdiella chrysura*. However, near the close of the investigation it was noticed that the larger eggs, identified as perch eggs, had more numerous pigment spots on the yolk and these were particularly prominent on the embryo. It was noticed, also, that the newly hatched fish not only were larger as would be expected, but contained more pigment spots than those hatched from the smaller eggs. Furthermore, the larvae hatched from the larger eggs have two bars composed of dots slightly greenish in color in life on the caudal portion of the body; one of the bars being at about midcaudal length, and the other one, which is rather less distinct, about midway between the vent and the bar already described. The larvae hatched from the smaller eggs, on the other hand, have only one bar which is situated at about midcaudal length.

[13] Unpublished manuscript in the files of the Bureau of Fisheries.

The numerous dots on the egg and embryo are in general agreement with the illustrations given by Welsh and Breder (1923, p. 152) of the eggs of *C. regalis*, and the illustrations of the recently hatched young presented on page 155 of the work already cited contain suggestions of two crossbars on the caudal portions of the body, though less distinct than in the specimens observed by us.

Insufficient eggs of the larger type were secured, after the differences in pigmentation were noticed, to obtain a sufficiently large series of measurements to show the exact relationship in size. A sample of 205 eggs was taken at random from a towing made on June 3, 1930. Among this lot 25 eggs of the type described were found. These eggs ranged in diameter from 0.8 to 0.92 millimeter and the average was 0.84 millimeter. The smaller eggs, namely, those of the white perch, *Bairdiella chrysura*, had a range in diameter of 0.66 to 0.76 millimeter and an average of 0.69 millimeter. The last-mentioned proportions quite certainly are correct for Bairdiella, as the range of 97 eggs, spawned in the aquarium on 2 different dates, ranged in diameter from 0.66 to 0.72 millimeter and averaged 0.68 millimeter. Although the number of the larger eggs measured is quite limited, enough of the smaller ones were measured to show that two distinct groups were present.[14]

Kuntz (1914, pp. 4–10) states that the diameter of the eggs of Bairdiella ranges from 0.7 to 0.8 millimeter, thereby indicating that he may have measured eggs of two species. However, his description and illustrations of the development appear to be correct for Bairdiella.

Welsh and Breder (1923, p. 151, table 3) give measurements of eggs taken from 2 specimens of *C. regalis*, which show, as already stated, a comparatively large difference in the size of the eggs produced by the 2 examples. One of the fish had eggs ranging in diameter, according to 8 eggs measured, of 0.98 to 1.03 millimeters and, therefore, all larger than any measured at Beaufort. The other one had eggs ranging in diameter, according to 10 eggs measured, from 0.8 to 0.84 millimeter and, therefore, near the size of the eggs taken at Beaufort.

Pearson (MS.) working with specimens collected at the entrance of Chesapeake Bay, found even a larger range among eggs which he believed to be those of *C. regalis*. He remarks, however, that the eggs fall into two groups as to size. One of the groups ranged in diameter from 0.7 to 0.9 millimeter, with a mode at 0.83 millimeter, and the other one had a range in diameter of 0.9 to 1.13 millimeters, with a mode at 1.0 millimeter. Therefore, the range of the two groups of eggs combined is greater even than that given by Welsh and Breder (loc. cit.), as it extends from 0.7 to 1.13 millimeters.

The time during which Pearson took the eggs of both groups (the larger ones from April 24 to May 23 and the smaller ones from May 6 to July 24) quite probably covers nearly the entire spawning period of *C. regalis*. However, the pigfish, *Orthopristis chrysopterus*, and the perch, *Bairdiella chrysura*, too, spawn during this period, and their eggs fall into the range of the eggs measured, and are extremely similar in appearance. It has been stated already that the eggs of Bairdiella measured at Beaufort ranged in diameter from 0.66 to 0.76 millimeter and that they are similar in appearance during the cleavage stages to somewhat larger eggs believed to be the eggs of the gray trout. The eggs of the pigfish, according to Hildebrand and Cable (1930, p. 399), range in diameter from 0.7 to 0.8 millimeter, and therefore are more or

[14] The oil globule, too, was measured in each egg. There is definite overlapping and only an average difference appears to exist, the average in 100 perch eggs being 0.18 millimeter and in 25 trout eggs 0.2 millimeter.

less intermediate in size of the perch and the trout, but overlap somewhat with both species.

At Beaufort the eggs of the three species named often were taken in the same towing, assuming of course that the largest ones were trout eggs. The pigfish eggs, like those of the gray trout, are very similar to the perch eggs and are scarcely distinguishable (although their average size is larger), until the embryos become well developed. In the advanced embryonic stages the oil globule in the perch egg acquires greenish specks, whereas the oil globule generally remains clear in the pigfish, or at most it acquires only a few minute specks. Furthermore, the position of the oil globule in relation to the embryo is characteristic. In the perch (also the trout) it lies far behind the head, whereas in the pigfish it lies at or near the ventral surface of the head. The newly hatched fish, too, may be distinguished by the location of the oil globule within the yolk sac, as it retains the approximate position it has in the embryo, that is, it lies in the posterior part of the yolk sac in the perch (and trout), and in the anterior part of the yolk sac or under the head in the pigfish.

Pearson's (MS.) measurements, in the absence of descriptions of color marking and statements in regard to the position of the oil globule with respect to the embryo, suggest that he may have grouped the eggs of the pigfish, the white perch (also known as the yellow-tail perch), as well as those of the gray trout, all under *C. regalis*. All three species no doubt spawn in Chesapeake Bay or off the month of the bay during the period in which the eggs were taken by Pearson, as Hildebrand and Schroeder (1928, pp. 258 and 280) took spawning pigfish during June, and ripe perch during May in Chesapeake Bay, and Radcliffe (in Welsh and Breder, 1923, p. 151) took trout eggs there during the spring. Since Pearson does not list the eggs of the pigfish and the perch (both very common species in Chesapeake Bay), although they most probably were present among the trout eggs, lends support to the supposition that they may not have been distinguished.

Too much faith apparently should not be placed in the measurements of eggs, unless it is known definitely that the eggs were spawned in water of about even density. If preserved eggs are measured, it would seem necessary to use one preservative of uniform strength. Delsman (1931, p. 403) has shown that a comparatively large difference in size exists in the eggs of one species (*Cybium guttatum*), depending upon the density of the water in which they are taken. Eggs collected in the mouths of rivers where the water was brackish were larger, varying in diameter from 1.24 to 1.36 millimeters, than those taken in salt water, which had a range in diameter of 1.05 to 1.26 millimeters. Delsman concludes:

> So we easily came to the conclusion that the size of the egg depends on the salinity of the water, increasing or decreasing in proportion to the latter getting lower or higher. The same phenomenon has been observed in other pelagic eggs, the eggs of the Baltic Sea fishes, e.g., being bigger than the corresponding eggs of the North Sea.

Kuntz (1914, pp. 4–10), presumably Welsh and Breder (1923, p. 151), and the present writers measured live eggs, whereas Pearson measured preserved eggs. The present investigators are not aware of data that show how the eggs are affected by the commonly used preservatives. Pearson apparently assumes that some shrinkage takes place and, therefore, left the eggs "in preservative at least 6 months in order to obtain nearly the minimum shrinkage." However, he does not name the preservative, nor the strength at which it was used. The measurements made by Pearson and the other investigators, therefore, may not be directly comparable, although in general they are in agreement, as already stated.

The measurements made by us, which are shown in preceding pages, were all made in the laboratory with an eyepiece micrometer and are based on eggs taken at sea (exclusive of some perch eggs spawned in a tank, as stated in the text) and brought to the laboratory alive in water dipped up where the towings were made. The water used in the tank in which some of the perch eggs were spawned was pumped from underneath the laboratory pier at high tide when the salinometer readings generally average about 1.025, as compared with 1.03 off Beaufort Inlet. Therefore, all the measurements made at Beaufort are based on eggs spawned in salt water of rather high density.

It has been shown that the eggs of two examples of gray trout measured by Welsh and Breder (1923, p. 151) differed markedly in size. The writers assume that some fish simply have larger eggs than others, and do not state whether the eggs of both fish were spawned in water of about even density. According to our measurements, the eggs of any one species, when spawned in strictly salt water, are quite uniform in size. Our experience, and the information gained by Delsman (1931, p. 403) and others, relative to the difference in the size of the eggs of one species according to the density of the water in which the eggs are spawned, suggest that Welsh and Breder may have used water of very unequal density in which the eggs of the two samples of trout mentioned presumably were artificially spawned. Certainly we must consider the large variation in the diameter of the trout eggs given by the writers mentioned as unusual. In fact such a wide variation, under identical conditions, would suggest the presence of two races.

DISTRIBUTION OF THE YOUNG

It has been stated in the section of this paper dealing with the spawning (p. 104) of this species that the young, 10 millimeters and less in length, are much more numerous off Beaufort Inlet than in the harbor and adjacent sounds and estuaries. Somewhat larger fish, too, appear to be rather more numerous in the outside than the inside waters, although they tend to congregate and become abundant in certain restricted areas in the estuaries. For example, the young ranging from about 15 to 100 millimeters in length are very numerous above "cross rock" in Newport River during the summer or after the middle of June. The water is only a foot or two deep above cross rock at low tide and the bottom is very muddy. The water generally is brackish, but the density fluctuates greatly, depending upon the stage of the tide and the rainfall, as this mud flat is only a short distance from the mouth of the narrow channel of Newport River where this stream discharges fresh water into its estuary.

Pearson (MS.), too, found that young gray trout when about 8 to 10 millimeters long "settle on the bottom" in Chesapeake Bay in coves and creeks at Lynnhaven Roads and elsewhere.

Soft or muddy bottom seems to be preferred by the young during the first summer. Those that remain in the ocean, as well as those that enter the harbor, seem to seek muddy bottom. For that reason, presumably, the young are numerous in the vicinity of the sea buoy off Beaufort Inlet where the bottom is soft. It is presumed that the young fish find food abundant on the mud. However, the food requirements of the young under about 40 millimeters in length have not been studied. Larger ones, according to Welsh and Breder (1923, pp. 159–164), feed on a variety of forms, including copepods, amphipods, isopods, shrimps, crabs, worms, and fish.

The number of larvae, 5 millimeters and less in length, in the collection is too small to show the vertical distribution. Since the eggs are pelagic, the larvae would be expected to remain at or near the surface, at least, until the yolk is absorbed. The yolk sac contains an oil globule which persists until virtually all the yolk is absorbed (Welsh and Breder, 1923, p. 153, fig. 10). The oil globule almost certainly would keep the newly hatched fish at or near the surface. However, the indications are that the young fish in part, at least, go to the bottom very early, as the 25 specimens at hand having a range in length of 1.5 [15] to 5.0 millimeters were all taken in bottom hauls. The larger ones undoubtedly stay principally on the bottom, as all except 2 of a total catch of 270 specimens, 6 to 10 millimeters long, were caught in bottom hauls.

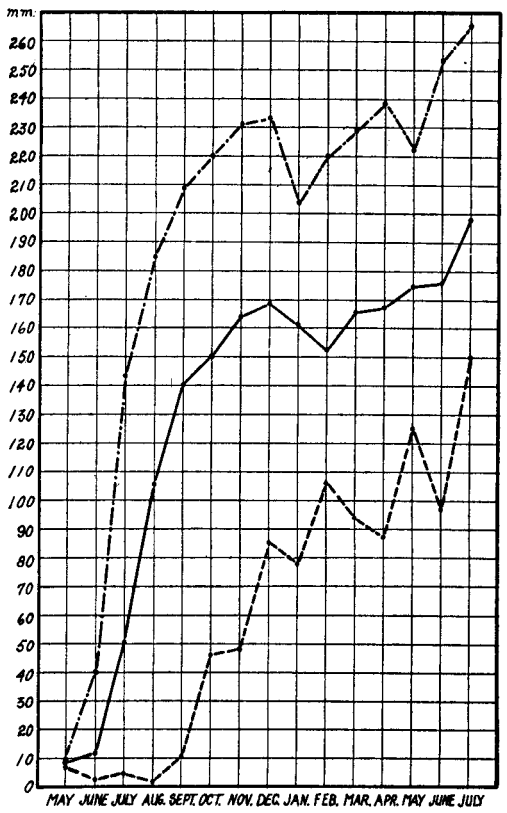

FIGURE 41.—Growth of *Cynoscion regalis* during first year or so of life. Solid line, average size; dot and dash line, maximum size; broken line, minimum size. (Graph based on table 5.)

It is stated elsewhere (p. 102) that the large fish leave the shallow waters during cold weather, whereas the smaller ones are more apt to remain. The young of the 0-class were taken throughout the winter. It seems significant, however, that the larger individuals are missing during the coldest months (see table 5), indicating that the largest young of the year probably follow the adults to a more agreeable habitat.

GROWTH

The study of the rate of growth was limited chiefly to the 0-class. The tables and graph presented herewith show quite conclusively that the rate of growth is very rapid during the first summer. The distinction between the 0-class and the 1-class is not very distinct after July, as some overlapping takes place, and it is probable that a few specimens may have been wrongly assigned in table 5. However, the specimens improperly placed are so few that the averages cannot be affected importantly, and therefore may be accepted as approximately correct.

The largest individuals of the 0-class, as shown by the accompanying tables and graph, already had attained a length of 215 to 220 millimeters (8½ to 8¾ inches) in October, and the average length of 914 fish measured was 150.4 millimeters (6 inches). In December a few individuals, apparently belonging to the 0-class, had attained a length as great as 220 to 233 millimeters (8¾ to 9¼ inches), and the average

[15] Specimens only 1.5 millimeters long in the present collection do not retain a yolk sac. Much shrinkage takes place in larval fishes during the hardening process if alcohol and formalin is used, as with the specimens at hand. Judging from the degree of shrinkage known to occur in some other species, as in the pigfish (*Osthopristes chrysopterus*), for example, it seems probable that the specimens of trout 1.5 millimeters long may have had a length of 2.5 millimeters before preservation. Welsh and Breder (1923, p. 153, fig. 10) show that the yolk sac is very small in live or fresh larvae when 2.2 millimeters long, and it would be expected to disappear very soon afterward.

length of 464 specimens measured was 168.8 millimeters (6¾ inches). The larger fish of the 0-class appear to be missing in the catches made during the winter, as the maximum and the average lengths of the specimens caught during January, February, and March were less than for December. (See table 5.) In April the largest individuals were 225 to 238 millimeters (9 to 9½ inches) long, and the average length of 1,455 fish measured was 167.2 millimeters (6¾ inches). Therefore, the fish caught in April were about the same size as those taken in December.

The data presented appear to show that some of the larger individuals of the 0-class, like virtually all the adults, leave the shallower water, in which the collections were made, during cold weather. The data appear to show, also, that fish grow little, if at all, during their first winter, for in April even the adult fish have returned, and the samples taken should represent the class correctly. After April growth appears to be fairly rapid, for in June (when many of the fish were a year old) the average length of 615 examples measured was 175.8 millimeters (7 inches) and the extremes in length extended from 97 to about 253 millimeters (4 to 10 inches). The length attained in June shows that some of the fish undoubtedly reach a marketable size [16] during their second summer.

The size attained by the young fish at Beaufort, as shown by the accompanying tables, is not in disagreement with published accounts. Eigenmann (1901, p. 47), working with fish at Woods Hole, Mass., states, "It seems very probable that the fish reaches a marketable size in about a year from birth." Welsh and Breder (1923, p. 157) have calculated the average length of fish hatched on June 1, based on "measurements of 10 large samples of young fish, taken at various times from July to March" to be 30, 80, 130, 170, and 180 millimeters (1¼, 3⅛, 5⅛, 6¾, and 7⅛ inches), respectively, on July 1, August 1, September 1, October 1, and November 1. These writers unfortunately do not name the localities in which the fish were caught. Therefore, the data cast no light on the rate of growth in different localities. No calculations were made by us that are directly comparable. However, the lengths given by the authors cited, in general, fall in with the larger individuals of the 0-class caught at Beaufort, N.C., on approximately the same dates.

TABLE 4.—*Length frequencies of 8,382 gray trout (Cynoscion regalis) under 380 millimeters in length*

Millimeters	May	June	July	August	September	October	November	December	January	February	March	April
0-4												
5-9	1	4	5	10								
10-14	8	25	164	25								
15-19		10	123	20	1							
20-24		7	29	5								
25-29		3	14	8								
30-34		1	23	10								
35-39			12	14	2							
40-44			11	7								
45-49		2	14	2	1							
50-54			17	2	3	3	1					
55-59			24	4		1						
60-64			30	2	2	2						
65-69			29	1	4	7						
70-74			27	5	6	9						
75-79			34	11	6	12						
80-84			55	11		2			2			
85-89			38	24	4	1			1			
90-94			47	23	12	3	1	1	1			1
95-99			38	47	9	2		1	2		1	
100-104		1	33	51	19		1	1			2	
105-109			32	54	21	6	1	6	1		2	1
110-114		1	21	81	11	9	6	2	2	1	3	1
115-119			18	58	30	21	9	5	2	2	2	3
120-124			11	49	34	16	3	3	1	6	1	13
		1	12	31	37	16	9	6	1	11	1	26

[16] The legal minimum size limit in North Carolina in 1925 is given as 9 inches by Higgins and Pearson (1927, p 49, fig. 8).

TABLE 4.—*Length frequencies of 8,382 gray trout (Cynoscion regalis) under 380 millimeters in length*—Continued

Millimeters	May	June	July	August	September	October	November	December	January	February	March	April
125–129	1	1	5	37	33	17	8	8	1	7	2	29
130–134		3	4	25	42	19	13	12	4	11	1	32
135–139	3	4	1	16	30	22	25	13	9	11	2	32
140–144	3	14	2	25	33	62	34	13	25	25	2	60
145–149	2	21		29	28	102	63	11	38	26	9	76
150–154	7	41	3	21	24	139	76	30	60	32	27	125
155–159	5	23	5	20	22	121	87	26	68	26	19	181
160–164	4	47	23	34	18	109	75	41	75	40	33	228
165–169	9	40	18	26	21	66	76	38	57	21	30	184
170–174	14	55	18	18	20	42	73	56	42	26	32	147
175–179	9	46	12	6	11	21	33	43	28	27	25	110
180–184	7	43	8	5	23	27	23	40	18	16	26	82
185–189	4	42	12	3	14	15	23	28	26	12	17	40
190–194	4	47	19	5	14	16	20	28	11	3	19	32
195–199	4	53	14	4	6	6	10	10	7	6	9	11
200–204	5	41	21	3	4	6	3	20	4	3	8	14
205–209	2	25	25	14	3	6	5	10			3	3
210–214	4	19	23	9	3	2	2	4			4	10
215–219	1	17	25	6	6	4	2	5			1	7
220–224	2	13	17	6	8	2	1	2		2	1	3
225–229		5	17	7	13		1				1	2
230–234		4	7	3	10	5	1	1				1
235–239			5	4	10	2						1
240–244		3	2	9	10	2		1				5
245–249		1	1	9	7	3	1					2
250–254		3	1	9	7	5	1	1				2
255–259			2	9	6	1						2
260–264			2	10	6	3		1				1
265–269			1	2	4	2						
270–274		1	4	6	3	1						
275–279			2	4	1	4	1					1
280–284			10	5	2	3						1
285–289				1								
290–294			10	2	2	1						
295–299			4	4	1	2	1	1				
300–304			16	6	1							
305–309			1	9								
310–314			12		1							
315–319			12	9	2	2						
320–324			15	1								
325–329				3		1	1					
330–334			13	1								
335–339				5								
340–344			12	3								
345–349				2								
350–354			7	3								
355–359			1	2								
360–364			13	1								
365–369			5	3								
370–374			16									
375–379			3									

TABLE 5.—*Monthly summaries of length measurements of 7,883 gray trout (Cynoscion regalis) during the first 12 to 14 months of life (based on table 3)*

Month	Fish measured	Smallest	Largest	Average	Month	Fish measured	Smallest	Largest	Average
May	8	6.5	9	8.1	January	486	78	204	161.5
June	52	2.3	40	11.5	February	311	106	220	152.5
July	873	4.4	143	50.4	March	281	94	229	165.5
August	820	1.7	185	105.4	April	1,455	87	238	167.2
September	548	10.5	209	140.3	May	90	125	222	174.6
October	914	46	220	150.4	June	615	97	253	175.8
November	685	48	231	164.1	July	281	150	265	197.9
December	464	85	233	168.8					

CYNOSCION NOTHUS (Holbrook) BASTARD TROUT

The bastard trout ranges from Chesapeake Bay to the southwestern coast of Texas. Although it was described (from South Carolina) as early as 1860, its exact status as a species was not well understood until recently. For a time its validity was doubted by some writers (Coles, 1916, p. 30, and Welsh and Breder, 1923, p. 169), probably because plain colored *C. regalis* were thought to be *C. nothus*. However,

Hildebrand and Schroeder (1928, p. 299) obtained two specimens of true *C. nothus* from Chesapeake Bay, and thereby were enabled to show definitely that this is a valid species. Finally Ginsburg (1929, p. 71–85), who examined many specimens, shows the relationship of *C. nothus*, *C. regalis*, and *C. arenaris* (a Gulf coast species) in great detail. The fishermen and fish dealers of Beaufort and Morehead City recognize *C. nothus* as distinct from *C. regalis*, giving it the name "bastard trout" because it is supposed to be a cross of *C. regalis* and some other species. The diagnostic characters of the bastard trout are given in the key to the species.

It has been found during recent years that the bastard trout is rather common off Beaufort Inlet during the summer. However, no specimens were taken during the winter, probably because the fish migrate to warmer water. This trout certainly is not a regular inhabitant of the inside waters of the vicinity, as no adult specimen and only 4 young were taken there during 5 years of rather systematic and extensive collecting. The young, all taken in 1 tow-net haul, may have drifted in with the tide, as explained elsewhere.

The bastard trout appeared rather frequently during the summer, sometimes in considerable numbers, in a collecting trawl hauled in a few to several fathoms of water off Shackleford and Bogue Banks. At times, particularly during the early part of summer, catches of about 100 pounds a day were taken in a commercial pound net operated for a few years off Bogue Banks. It cannot be said, however, that this species is of much commercial importance on the coast of North Carolina. Further southward, and particularly on the Gulf coast, it seems to be more important.

The bastard trout apparently does not grow large. The largest individual seen at Beaufort was only 228 millimeters (9¼ inches) long.

This species is closely related to *C. regalis*, and the separation of the young prior to the development of the anal fin, that is, specimens under about 6 millimeters in length, may be difficult. It is thought, however, that the position of the color markings, which differ somewhat in specimens 9.5 millimeters long (the smallest *C. nothus* recognized), as pointed out on page 113, would aid in separating the smaller young. The position of the color markings in all the specimens at hand of this group under 9.5 millimeters in length agree with *C. regalis*. It is concluded, therefore, that specimens of *C. nothus* under 9.5 millimeters in length are missing.

The descriptions of the young that follow are based on specimens collected at Beaufort, exclusive of the account of fish 75 millimeters and upward in length, which is based in part on specimens from Beaufort and in part on specimens from the Gulf coast.

SPAWNING

No ripe fish, so far as known, have been observed, and if the eggs have been taken in the tow they were not recognized, therefore, the only clue to the time and place of spawning is furnished by the collection of young fish. The smallest young taken were secured on August 8, 1930, and the smallest specimen in that collection is 9.5 millimeters long. The largest specimen taken the same month, which certainly belongs to the 0-class, is 88 millimeters long. No specimen of this year class less than 39 millimeters and none exceeding a length of 95 millimeters were taken during September. However, in October 30 specimens 17 to 25 millimeters in length were secured, and the largest one of this year class is only 80 millimeters long, showing that the larger young are missing in the collection. In November, when numerous specimens of the 0-class were taken, the range in length extends from 19 to

147 millimeters. It seems reasonable to conclude from the range in size of specimens taken during four summer and fall months, when the rate of growth no doubt is rapid, that spawning very probably begins in May or June (for specimens 80 to 88 millimeters long, such as were taken on Aug. 14, 1930, quite probably are 2 to 3 months old), and that it extends at least through August (as 30 specimens 17 to 25 millimeters long, were taken on Oct. 30, 1929).

It probably may be assumed that spawning takes place at sea at Beaufort in the general vicinity inhabited by the adults. At least, that is where all the young in the collection, exclusive of one small collection consisting of 4 specimens 9.5 to 12 millimeters long, were taken. It is thought that the 4 specimens of young, too, were hatched at sea, but that they had drifted in part with the tides and probably in part had swum to the place of capture, namely, near the mouth of Core Creek in Newport River. The presence of these four fish in the inside waters is interesting, not only because no other young were taken there, but because no adults were caught in the inside waters.

DESCRIPTIONS OF THE YOUNG

Specimens 9.5 to 11.0 millimeters long.—The body is rather deep and compressed, the depth being contained 3.0 to 3.25 in the standard length. The head

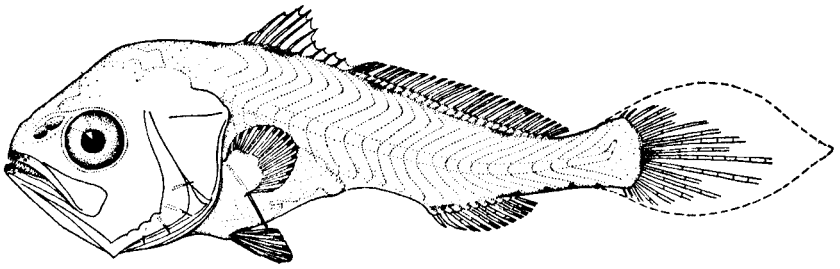

FIGURE 42.—*Cynoscion nothus*. From a specimen 10.5 millimeters long.

particularly is short and deep, being contained 2.85 to 3.0 times in the length. The snout, too, is rather short and blunt, and is about as long as the eye, 3.7 to 4.4 times in the head. The mouth is large, quite strongly oblique; the gape anteriorly is scarcely above the lower margin of the eye; the lower jaw projects only slightly; and the maxillary reaches nearly opposite the posterior margin of the eye, 1.65 to 1.85 in the head. The fins are all developed and a definite enumeration of the rays is obtainable. The anal consistently has 9 articulated rays in the 4 specimens of this size at hand (although in larger specimens only 8 rays sometimes are present), and the dorsal fin has 28 or 29 rays. The caudal fin is frayed in the specimens at hand, and its exact shape cannot be determined. However, it evidently is quite long and pointed. The ventral fins are small, scarcely as long as the eye. Preserved specimens are very plain in color. A few dusky markings are evident along the ventral outline of the caudal peduncle, and an elongate dusky spot is present at the base of the anterior rays of the anal and similar spots at the end of that fin. A dusky spot is situated just in advance of the spinous dorsal, another one is under the base of the spinous dorsal, a third one is situated under the anterior rays of the soft dorsal, and a fourth one is near the end of the base of this fin. The jaws anteriorly are slightly dusky (fig. 42).

This species is closely related to *C. regalis* from which it is distinguished, at the size described, chiefly by the shorter anal fin, which has 9 (sometimes 8) rays, where-

as *C. regalis* has 11 to 13. According to the preserved specimens at hand, *C. nothus* is somewhat plainer in color and some of the markings present are a little differently placed. *C. regalis* at a length of 9 to 11 millimeters has numerous dusky dots on the side, which *C. nothus* does not possess. *C. regalis* generally has more numerous spots on the back also. On the other hand, *C. nothus* has two elongate dusky spots at the base of the anal, one being below the anterior rays and the other one at the base of the last rays, whereas only one spot placed near the middle of the anal base is present in *C. regalis*.

The specimens described are the smallest ones of the species recognized. It is possible that this species and *C. regalis* are so similar in the younger stages that they were not recognized as distinct. Identification apparently would be somewhat uncertain until the anal fin is developed sufficiently to permit the enumeration of the rays. However, it is thought that the markings on the ventral surface of the tail might be useful in separating the species, since the spots appear to be a little differently placed in the two species, as already stated. In the younger specimens the markings are quite uniformly placed, and the large spot near midcaudal length (being the one that is situated below the base of the anal when that member becomes developed) is steadfastly present and is thought to be diagnostic for *C. regalis*.

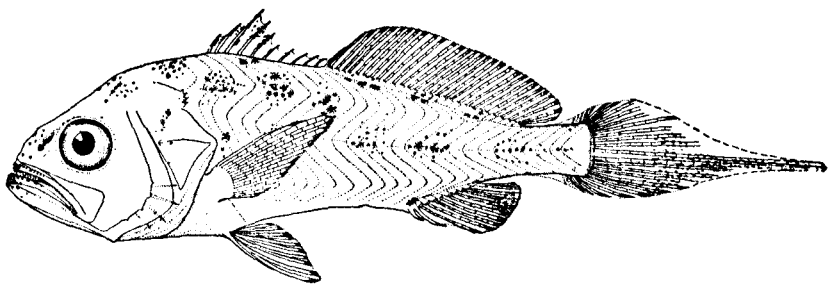

FIGURE 43.—*Cynoscion nothus*. From a specimen 26 millimeters long.

Specimens 24 to 26 millimeters long.—The fish has become more shapely since a length of 9 to 11 millimeters was attained (no specimens of intermediate sizes are at hand), that is, the head and trunk are not as disproportionately deep in comparison with the tail as in the smaller fish. The greatest depth is contained 3.2 to 3.6 times in the standard length, and the head now is considerably longer than deep, its length being contained 2.5 to 2.7 times in the standard length. The snout is a little sharper than in smaller fish; its length remains about equal to the diameter of the eye, and is contained 3.7 to 4.3 times in the head. The mouth is moderately oblique; the lower jaw projects little; and the maxillary reaches to or a little beyond the posterior margin of the pupil, 2.0 to 2.2 in the head. Gill rakers are developed, 11 were counted on the lower limb of the first arch in each of two specimens. Scales are evident on the side, though the sides are not completely covered. The caudal fin is sharply pointed and the middle rays are much longer than the head. The ventral fins have increased greatly in length and are about twice as long as the eye. Dark color markings have become much more numerous; the markings (chromatophores) mostly remaining small and rather scattered, and are present on the sides, on the head, on the back, and along the ventral outline. In some specimens congregations of dark marks are present along the lateral line, forming indefinite quadrate spots. In some specimens a concentration of dark markings, also, has occurred on the back

where they form saddle-like blotches. A dark cross line is present on the base of the caudal fin and a few dark dots have appeared on the spinous dorsal (fig. 43).

This species is very close to *C. regalis*, differing (in addition to having fewer anal rays) chiefly in color. In general, the individual markings (chromatophores) are smaller and form less definite blotches. Furthermore, blotches on the back and in the lateral line, if present, are separate, whereas in *C. regalis*, blotches somewhat similarly placed, are connected and form more or less definite crossbands, at least on the anterior part of the body. The indications are that *C. nothus* has the middle rays of the caudal more strongly produced, though this cannot be determined definitely because this fin is more or less damaged in all the specimens at hand.

Specimens 40 to 46 millimeters long.—The body has become deeper posterior to the ventral fins, and the head is rather more pointed. The proportions, measured as in the smaller specimens, have not changed greatly. The head is contained 2.5 to 2.75 in the standard length, and the depth 3.2 to 3.6 times. The eye and snout are of about equal length and are contained 3.7 to 4.3 in the head. The mouth remains quite oblique, the gape anteriorly being somewhat above the lower margin of the eye, and the maxillary reaches about opposite the posterior margin of the pupil, it being contained 1.9 to 2.2 in the head. The body is fully covered with scales and small scales also are evident on the base of the soft dorsal and on the anal. The caudal fin remains long and pointed, the middle rays being much produced and nearly an eye's diameter longer than the head. The body has become more definitely blotched, the blotches consisting chiefly of a series along the lateral line and another on the back. In the majority of specimens examined the blotches are separate, but in some examples the ones on the anterior part of the back tend to unite with those on the side to form cross bars. Dark dots are present on both dorsals, the caudal, and occasionally on the anal.

This species continues to differ from *C. regalis* in color, the body generally being blotched, or if suggestions of crossbars occur they are present anteriorly only, and are less distinct than in *C. regalis*. The caudal fin is notably longer and more sharply pointed in *C. nothus*, the longest rays being nearly an eye's diameter longer than the head, whereas in *C. regalis* none of the rays exceed the length of the head. In the proportional measurements given in the foregoing description the two species are almost identical at a range in length of 40 to 46 millimeters.

Specimens 75 millimeters and upward in length.—The depth is contained 3.4 to 4.0 times in the standard length in specimens 75 to 90 millimeters long, and these proportions prevail in adult fish, also. However, the body remains notably more compressed, its greatest width being somewhat less than the length of the maxillary. The fish apparently increase in robustness very gradually as long as growth continues. At a length of 150 millimeters the width of the body is about equal to the length of the maxillary, and in larger fish the width exceeds the length of the maxillary. The head is contained 2.9 to 3.0 times in the length in fish 75 to 90 millimeters long, as compared with 3.2 to 3.4 in specimens ranging from 150 to 200 millimeters in length. Therefore, the head remains proportionately longer, as usual, in the smaller fish. The mouth virtually has attained the position and nearly the proportions of the adult in specimens only about 40 millimeters long, described in the foregoing section, and the two large recurved canines in the upper jaw, characteristic of this genus, slightly evident at a length of 45 millimeters, are prominent in specimens 75 millimeters long. Small scales are present on the basal portion of the fins, exclusive of the spinous dorsal, at a length of 75 millimeters (and earlier in some

specimens), and they are extended almost all over the fins by the time the fish reach a length of about 125 millimeters, apparently increasing in density with age.

The caudal fin remains pointed in specimens 75 millimeters long and the longest rays (although proportionately shorter than in smaller fish) are about equal to the length of the head. This fin is still moderately pointed in fish 150 millimeters long, but the longest rays then are notably shorter than the head. The caudal does not acquire the shape it has in adults, that is, with the upper lobe slightly concave and the lower one rather sharply rounded, until the fish reach a length of about 200 millimeters.[17]

The blotches present in the smaller fish described in the preceding section become less distinct at a length of about 60 millimeters. In the preserved specimens examined only traces are left in fish 75 millimeters long, and soon afterward they disappear and the fish are plain grayish above and silvery below. Only large specimens (of the preserved material examined) 200 millimeters and upward in length have traces of oblique lines running along the rows of scales above the lateral line. The dark

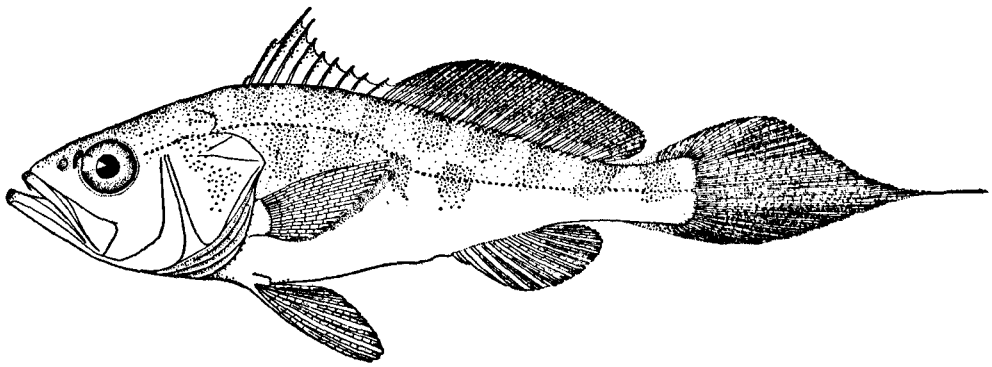

FIGURE 44.—*Cynoscion nothus*. From a specimen 67 millimeters long.

cross line on the base of the caudal, present in small fish, has disappeared in specimens about 60 millimeters long. Dark dots on the dorsal and caudal fins increase rapidly in number as growth proceeds. In specimens about 100 millimeters long the caudal fin is quite dusky and distally almost black. The dorsal fins, too, are densely dotted and soon become dusky in color, and the spinous dorsal has a black margin (fig. 44).

This species and *C. regalis* resemble each other closely. Beside the difference in the number of anal rays, the slight difference in the number of gill rakers, and vertebrae, pointed out elsewhere, it is evident that almost throughout life (that is, after the caudal fin becomes developed) *C. nothus* has a longer and more sharply pointed caudal fin, which never becomes truncate as in *C. regalis*. Although the fins, exclusive of the spinous dorsal, become covered with small scales in both species, those of *C. nothus* appear to be more densely scaled in adult specimens.

DISTRIBUTION OF THE YOUNG

It has been pointed out elsewhere (p. 111) that no young under 9.5 millimeters in length were taken. Therefore, the early stages remain unknown. It has been stated, also (p. 112), that all the young collected, exclusive of four specimens, were caught in the

[17] The shape of the caudal, because the fin was frayed in the specimen drawn, is incorrectly shown as round for the adult in Hildebrand and Schroeder (1928, p. 299, fig. 175). It is correctly indicated in Ginsburg's figure (1929, p. 81, fig. 5), which shows the upper lobe to be slightly concave and the lower one rather sharply rounded.

general vicinity (off Beaufort Inlet) inhabited by the adults during the summer. It is quite certain, therefore, that at least the larger young occupy the same grounds with the adults.

Both young and adults were taken only with an especially adapted otter trawl, which, of course, was hauled on the bottom. If the larvae of this species behave like those of the gray and the spotted trout, as would be expected, they may occur at the surface when very small, but soon descend to the bottom.

GROWTH

An insufficient number of young fish was caught to determine accurately from length measurements the rate of growth of the 0-class. Specimens that definitely belong to this year class were taken only during August, September, October, and November. In August 54 young, ranging in length from 9 to 88 millimeters, with an average length of 61.1 millimeters, were measured. In September only 15 specimens, 31 to 95 millimeters in length, averaging 57.2 millimeters, were measured. The smaller young obviously are missing in the collection for September, as the fish caught during October consisting of 179 specimens, contain fish ranging in length from 17 to 80 millimeters, averaging only 46.5 millimeters in length. The larger young of the 0-class obviously are missing in the collections made in October. In November, only, a sufficient number of specimens was taken and measured to give reliable information. The 486 specimens of the 0-class measured, range in length from 19 to 147 millimeters, and have an average length of 75.8 millimeters.

Since this fish quite certainly is a smaller species than the other local species of this genus (as pointed out on p. 111) a slower rate of growth would be expected, and that is what the limited number of measurements appears to indicate. Instead of attaining a length of about 170 millimeters (6¾ inches) during the first 7 or 8 months of life, as in *C. regalis*, and probably in *C. nebulosus*, this species appears to reach a length of only about 75 millimeters (3 inches). The size at which sexual maturity is reached remains unknown.

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RACES OF HERRING, CLUPEA PALLASII IN SOUTHEASTERN ALASKA

By GEORGE A. ROUNSEFELL
and EDWIN H. DAHLGREN

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 17

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1935

For sale by the Superintendent of Documents, Washington, D. C. - Price 10 cents

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RACES OF HERRING, *CLUPEA PALLASII*, IN SOUTHEASTERN ALASKA[1]

By GEORGE A. ROUNSEFELL, Ph. D., *Associate Aquatic Biologist*, and EDWIN H. DAHLGREN, *Junior Aquatic Biologist, United States Bureau of Fisheries*

CONTENTS

	Page
Introduction	119
Spawning and feeding localities	120
Analysis of vertebral counts	123
Discussion of factors influencing vertebral count distribution within a population	123
Existence of races proven by heterogeneity of samples from all localities	124
Homogeneity of material from individual localities	129
Segregation of races	129
Analysis of growth rates	133
Analysis of year classes	138
Tagging	138
Summary	140
Literature cited	140

INTRODUCTION

The reasons underlying this attempt to study the individuality and distribution of each population of herring are many, and for the most part, rather obvious. When a locality where herring have been abundant fails to produce its wonted supply, a question always arises as to the causes of such a failure. Aside from natural fluctuations in abundance or unusual unavailability to the fishermen, the apparent causes are migration or depletion. Without an intimate knowledge of the herring stocks either explanation is possible. For example, Whale Bay (Rounsefell, 1930, p. 238) on the outer coast of Baranof Island, produced a tremendous run of herring in 1925 but failed the following year. No herring have been caught in this bay since that time. It is now practically certain that this temporary run was caused by the summer herring schools that normally congregate about Cape Ommaney shifting farther north. On the other hand, the failure of the once important fishery in Kootznahoo Inlet, on Admiralty Island, may be fairly ascribed to depletion of the stocks from overfishing (Rounsefell, 1931, p. 35–36).

Only by an intimate knowledge of the areas inhabited by each stock of herring is it possible to know whether fishing in one area is affecting the supply in another. It may now be said with certainty, for instance, that the heavy fishing in lower Chatham Strait can in no wise be blamed for the scarcity of herring tvat has been noticeable for several years in the "inside" waters of Behm Canal, Ernest Sound, Zimovia Strait, and upper Frederick Sound (Rounsefell, 1930, p. 236, 237 and 307;

[1] Bulletin no. 17. Approved for publication, Oct. 4, 1934.

Rounsefell, 1931, p. 35–36). The herring of these "inside" waters belong to populations quite distinct from those of Chatham Strait.

It is well known that different populations may exhibit different structural peculiarities owing to differences in environment or to differences in heredity arising during long periods of isolation. The study of the individuality of the populations has been based largely on these structural differences. Whether the differences in the characters chosen are due to heredity or to environment has not been considered as being of great importance, as long as the characters are fairly stable within each population so that significant differences indicate very slight intermingling, if any, between adjacent stocks of herring.

Success has finally been achieved for the direct method of tracing migrations by the release and recovery of tagged herring (Rounsefell and Dahlgren, 1933). This method may be called the direct method of racial investigation in contradistinction with the indirect method in which the movements or lack of movement of a population are inferred from the statistical analysis of morphological characters. Owing to the newness of this method which was first attempted in 1932, only a few results have been attained. Yet these few results offer such corroboration of our racial work as to inspire confidence in our results.

In the determination of the individuality of populations by indirect methods it was deemed advisable, profiting by the experience gained in the preliminary racial work (Rounsefell, 1930), to concentrate on vertebral counts. This was the more necessary, owing to the difficulty of securing enough samples of fresh herring from various localities in the nearly perfect condition necessary for body measurements. The rates of growth and relative abundance of year classes have also been employed as indicators of populational differences.

SPAWNING AND FEEDING LOCALITIES

At the present time there are 3, or perhaps 4, spawning areas in southeastern Alaska, where the herring may be counted upon to spawn in abundance each spring. (See fig. 1.) Of these, the spawning grounds in Sitka Sound, on the outside of Baranof Island are probably the largest. Those at the entrance to Klawak Inlet in San Alberto Bay are undoubtedly a close second, and those centering near Juneau in Stephens Passage are easily third. The spawning grounds in Kootznahoo Inlet were once of great importance but have declined.

As indicated in figure 1, there are a number of minor spawning grounds, a few of which were considered of importance in the past. There are certainly additional localities, not noted, where a few herring occasionally spawn.

It may be of interest to note here the distances between the four major spawning grounds. These distances, measured approximately from the centers of spawning, are as follows: Sitka to Craig (Klawak Inlet), 120 miles; Sitka to Kootznahoo Inlet, 70 miles by Peril Strait; Sitka to Kootznahoo Inlet, 140 miles by Cape Ommaney; Sitka to Juneau, 150 miles by Icy Strait; Sitka to Juneau, 120 miles by Peril Strait; Juneau to Kootznahoo Inlet, 65 miles; Craig to Kootznahoo Inlet, 140 miles; and Craig to Juneau, 210 miles.

It is difficult to theorize as to the significance of the considerable distance between any major spawning grounds. It may mean that some of the minor spawning grounds are used merely by occasional schools straying from the main body of herring of any particular race. On the other hand it may indicate that there are two kinds or types

of herring populations. One type would be those races inhabiting the major spawning grounds, and, by inference, some of the minor spawning grounds of importance in the past. This type of race might be rather migratory in its habits, thus accounting for the distances between major spawning grounds. Many of the minor spawning grounds might then be inhabited by herring of local character, rather nonmigratory in habits. Such a type is suggested by the herring found spawning at the head of Gut Bay (see fig. 2) in the middle of June, at least 6 weeks after the normal cessation of spawning at Craig and Sitka. Such small bodies of herring might seldom stray from a single inlet or fiord. Possibly a herring population may change gradually from a nonmigratory to a migratory habit, or vice versa, according to its abundance, as spatial considerations are known to affect the migrations of mammals.

There are two quite distinct herring fisheries in southeastern Alaska—the minor fishery for halibut bait, carried on during the halibut fishing season throughout the whole area; and, secondly, the major fishery of the herring plants which produces salt herring and fish meal and oil. The second fishery operates only from June 1 to September 30 and its fishing operations are confined to the western portion of southeastern Alaska.

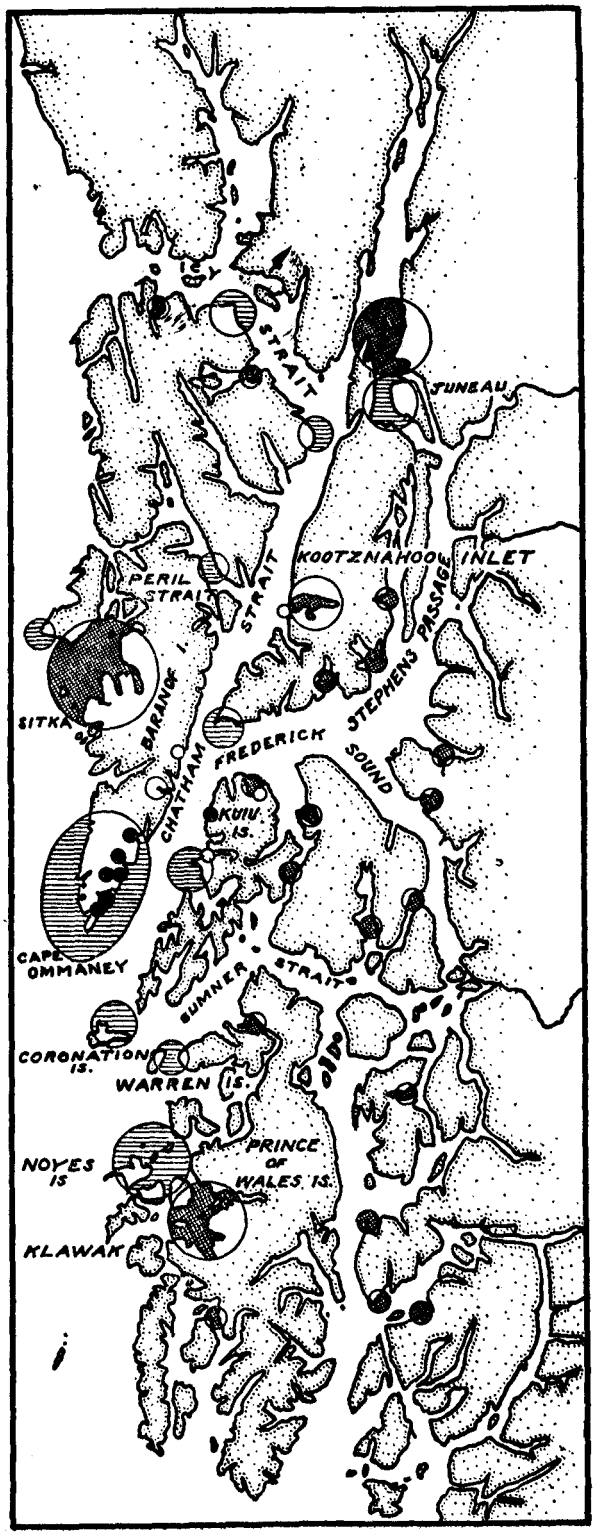

FIGURE 1.—Southeastern Alaska, showing spawning grounds and feeding grounds of herring. Cross-hatched areas indicate spawning grounds; horizontally barred areas indicate feeding grounds of importance to summer fishery of salt herring and fish oil and meal industry. The importance of both types of areas is roughly proportional to size of circles. Black dots show location of 7 herring plants operating in 1934; small circles give location of 4 herring plants remaining inactive in 1934.

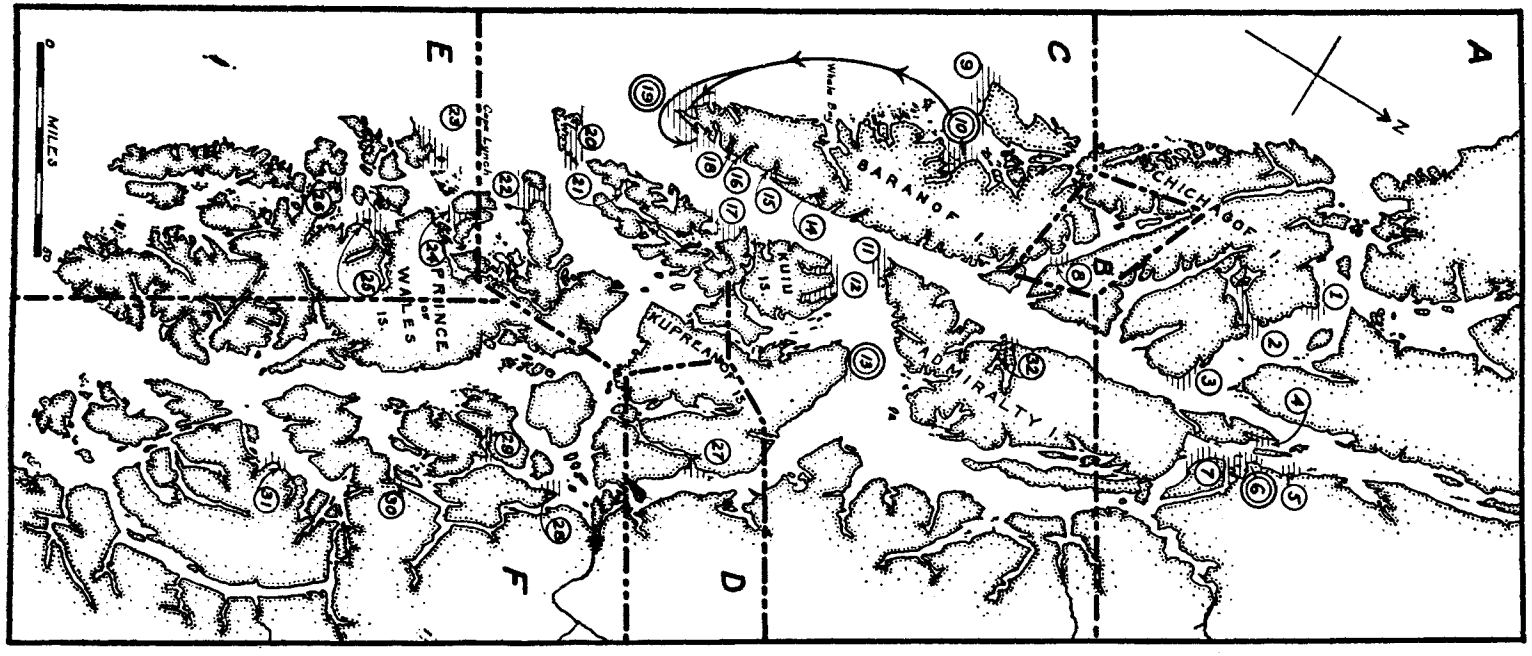

FIGURE 2.—Map of Southeastern Alaska. Heavy dot-and-dash lines separate areas whose herring populations have been shown to be independent. Circles indicate localities from which samples of not less than 50 vertebral counts were obtained from any 1-year class. Double circles indicate localities in which herring were also tagged and released. Main bodies of water are Chatham Strait—east of Baranof and Chichagof Islands; Icy Strait—north of Chichagof Island; Frederick Sound—south of Admiralty Island; Stephens Passage—east of Admiralty Island; Sumner Strait—north of Prince of Wales Island; Keku Strait—between Kupreanof and Kuiu Islands; Wrangell Narrows—very narrow channel east of Kupreanof Island and Clarence Strait east of Prince of Wales Island. Localities numbers in circles are as follows: 1. Point Adolphus, Icy Strait; 2. Hoonah, Icy Strait; 3. Point Augusta, Icy Strait at junction with Chatham Strait; 4. Barlow Cove, vicinity of Juneau; 5. Eagle Harbor, vicinity of Juneau; 6. Auke Bay, vicinity of Juneau (tagging locality); 7. Douglas Island, vicinity of Juneau; 8. Todd, Peril Strait; 9. Cape Edgecumbe, Kruzof Island; 10. Sitka, in Sitka Sound (tagging locality); 11. Point Gardner, junction of Chatham Strait and Frederick Sound (tagging locality); 12. Meade Point, Frederick Sound between Security and Saginaw Bays; 13. Cape Bendel, Frederick Sound (tagging locality); 14. Gut Bay, Chatham Strait; 15. Deep Cove, Chatham Strait; 16. Port Herbert, Chatham Strait; 17. Tebenkof Bay, Chatham Strait; 18. Big Port Walter, Chatham Strait; 19. Cape Ommaney, includes Larch Bay west of cape and Port Alexander and Port Conclusion east of cape (Port Conclusion a tagging locality); 20. Coronation Island, junction of Chatham Strait and Sumner Strait; 21. Kell Bay, Affleck Canal; 22. Warren Island. entrance to Sumner Strait; 23. Noyes Island, includes small islands between the Pacific and the Gulf of Esquibel; 24. Culebra Island, Gulf of Esquibel; 25. Klawak, San Alberto Bay; 26. Port Estrella; 27. Petersburg, junction of Wrangell Narrows and Frederick Sound; 28. Wrangell, eastern end of Sumner Strait; 29. Anita Bay, Zimovia Strait; 30. Santa Ana Inlet, Ernest Sound; 31. Frances Cove, Behm Canal, and 32. Favorite Bay, entrance to Kootznahoo Inlet, Chatham Strait.

This fishery has not in recent years been conducted eastward of a line from Juneau to Klawak, or south of Noyes Island. So closely is this fishery identified with Chatham Strait, the great waterway that extends with its continuation, Lynn Canal, for two-thirds the length of southeastern Alaska, that if a straight line is drawn down Chatham Strait and extended southward it will be noted that the summer fishery operates on both sides of this line from Noyes Island to Juneau, a distance of 180 miles, yet practically the entire catch is made within 35 miles of this line, the only exception being occasional fishing in Sitka Sound 65 miles from the line through Peril Strait.

These summer feeding grounds fished by the herring plants are shown in figure 1. The importance of each to the fishery is roughly indicated by the size of the circles. The most important fishing ground, by far, is the area surrounding Cape Ommaney, the southern tip of Baranof Island. This is due largely to the abundance of herring around the cape, but also, in some measure, to the proximity of the herring plants. Of the herring plants now in operation the one farthest from the cape is that at Washington Bay, on Kuiu Island, 35 miles distant; all of the others are on the eastern side of Baranof Island, 25 miles being the greatest distance any of them are from Cape Ommaney. (See fig. 1.)

The area along the north shore of Noyes Island, including the waters surrounding the Maurelle Islands, is another great herring feeding ground. Tebenkof Bay, Coronation Island, and Warren Island also contribute a share of the catch, but their importance fluctuates, some years being practically blanks (Rounsefell, 1931). The feeding grounds at the juncture of Frederick Sound and Chatham Strait were once important fishing grounds but have declined tremendously (Rounsefell, 1931, pp. 33 and 34) and are now of minor importance. The feeding grounds in Icy Strait and near Juneau in Stephens Passage are heavy producers of herring on occasion, but are too distant from the plants to warrant fishing when herring are abundant elsewhere.

Analyses of the catch statistics to determine the relative abundance on these various spawning and feeding grounds cannot be accurately made without knowledge of the interrelationships of the populations inhabiting different areas. The next section takes up a discussion of the methods of determining the individuality of these populations by means of the vertebral count.

ANALYSIS OF VERTEBRAL COUNTS

DISCUSSION OF FACTORS INFLUENCING VERTEBRAL COUNT DISTRIBUTIONS WITHIN A POPULATION

In an earlier report on the herring of Prince William Sound (Rounsefell and Dahlgren, 1932) it was shown that a high negative correlation (in that case -0.85) exists between the average temperature during the developmental period and the average number of vertebrae in different year classes or "brood years" of herring from the same locality. Comparison of the means of samples of herring without division into year classes is thus shown to introduce variation other than that expected in random sampling. Therefore all of our samples have been divided into year classes so that only vertebral counts of herring hatched during the same spring are compared.

The vertebral count of samples of a year class caught in any one year could not be compared with samples of the same year class taken during ensuing years without showing that there was not, due to selection, a tendency for the mean vertebral count to rise or fall with advancing age. To determine this point, samples of

the 1926 and 1927 year classes from eight localities, caught in their fourth summer, were compared with samples of the same year classes from the same localities taken during their fifth summer (neglecting samples of less than 25). Between the two series the average difference in vertebral count was 0.042, which was obviously of no significance as the chances were 1 in 8 that the means were the same.[2] (See table 1.)

Having thus failed to note any correlation between age and number of vertebrae in our samples, the means of the 4-year-olds of each year class were compared with the means of the 5-year-olds for the same year classes in each of the eight localities. Of these eight comparisons, none showed a significant difference,[3] although one might be regarded as doubtful, the chances being 1 in 25 that the two means are the same.

TABLE 1.—*Means of vertebral counts of 1926 and 1927 year classes from various localities compared at 4 and at 5 years of age*

Locality	Year class	Mean		Difference	Locality	Year class	Mean		Difference
		Age 4	Age 5				Age 4	Age 5	
Inside Cape Ommaney	1926	52.411	52.408	0.003	Hoonah	1926	52.364	52.474	−0.110
Larch Bay	1927	52.573	52.750	−.177	Petersburg	1927	52.488	52.408	.080
Do	1926	52.478	52.433	.045	Do	1926	52.147	52.253	−.106
Coronation Island	1926	52.404	52.482	−.078					
Point Gardner	1926	52.472	52.464	.008	Average		52.417	52.459	−.042

To determine if sex had any effect on the number of vertebrae, the mean vertebral count for both sexes was determined for each of a series of 24 samples of the 1926 year class caught during the summer of 1930 at Larch Bay, containing 491 males and 493 females. The mean of the 24 unweighted means for males was 52.431; for females, 52.435. The difference between these means was of no statistical significance. In making this comparison, the means of the males and of the females were not weighted because the presence of more than one population amongst the samples would then cause a weighting of the data according to the number of individuals in the samples.

EXISTENCE OF RACES PROVEN BY HETEROGENEITY OF SAMPLES FROM ALL LOCALITIES

Proof of the existence of independent stocks of herring is furnished by an analysis of the averages of all samples of vertebral counts of herring of the 1926 year class in southeastern Alaska. (See table 3 for total samples of each locality.) The object of this analysis is to prove whether or not all of the samples could have been drawn from the same population. From localities where many samples are available some of the samples are statistically different from others. This is to be expected according to the laws of probability. Before comparing the samples of one locality with those from another, it is essential that it be known whether any differences found may be due merely to such expected random variation or may be ascribed to a difference between the populations from which the samples are drawn. Therefore, it was necessary to test the data as a whole to determine if all of the samples could have been drawn from one population.

[2] Quoting from Fisher (1930, p. 111), "In cases in which each observation of one series corresponds in some respects to a particular observation of the second series, it is always legitimate to take the differences and test them * * *". In this method the test shows whether the mean difference differs significantly from 0, which is taken successively as each mean of the first series. t is the mean difference divided by its standard error, which in this case was 1.54 which yields a probability of 0.12 or approximately 1 to 8.

[3] This method of comparison is explained by Fisher (1930, p. 107), see section on "Segregation of races." Probability was 0.04 or 1 to 25.

The method used in testing the homogeneity of the means of all of the samples is merely an extension of the method of comparison of two means to the comparison of several means. This method is called the "Analysis of variance" by Fisher (1930, p. 196). Wollaston (1933) in an article in the Journal du Conseil, with a foreword by R. A. Fisher, expounds the use of this method and its applicability to herring race problems. Quoting from Wollaston:

There are two fundamentally different ways of approaching observational scientific data. The first is to lay out the data as graphically as possible and see what they suggest; the second, to formulate, without examining the data in detail, hypotheses which the data may be expected to prove or disprove, and then to test the agreement of the data with the hypotheses. The first result remains but a suggestion, and the actuality of the suggested phenomena cannot be stated in terms of probability. The second allows definite statement of probability that the hypotheses are true or not true. The great majority of fishery workers, including Dr. Schnakenbeck in his work criticized in this paper, have adopted the first way. His conclusions may be right, but his method of approach, which I will call the *a posteriori* method, includes no test whatever as to the probability of his being right.

* * * * * * *

Sound statistical tests of probability can *only* be applied to data treated in the second way. It is even better to formulate hypotheses to be tested by the data before these are collected than to do so before they are worked up. The research can then be given the exactness of pure experimental science, giving equally definite positive or negative results.

* * * * * * *

The main object of this paper is to introduce into fishery research some of the most important methods developed by R. A. Fisher, of Rothamsted Laboratory. These are offered as alternative and far preferable to empirical methods which take no account of the variability which occurs between samples drawn from a larger population. For the purpose in question I have used the data collected by Dr. Schnakenbeck from the North Sea, and I propose to show that Dr. Fisher's methods are perfectly adequate to deal with such data and to extract all the information from them which they are capable of giving. As I have not had access to subsidiary data, collected by other workers and used by Dr. Schnakenbeck in his report, it cannot be said definitely whether these would have modified my conclusions and brought them more nearly into line with Schnakenbeck's. It is hoped that all available data bearing on the herring race question will eventually be combined in a complete statistical analysis on the lines laid down here. This must be considered merely as an introduction to such analysis.

* * * * * * *

Though the mathematical theory on which the present paper is founded is somewhat advanced, the methods introduced herein are very simple in application. The first part deals almost exclusively with Fisher's methods for finding the best-fitting Curve of Error to fit to highly grouped data. Readers who have not to deal with such data may prefer to omit this part. The second part (from p. 23 on) deals with Fisher's method of the Analysis of Variance, which is of almost universal application in testing the significance of variations in any phenomenon under different conditions. There is no other method so ideally fitted for this kind of test. This second part will be therefore found worth reading by anyone who is engaged in fishery research and who is not familiar with Fisher's work. Every step in the application of the method to the present problem is shown in detail, and described as far as possible in nonmathematical language.

* * * * * * *

We have then an ideal set of conditions for the application of Fisher's Analysis of Variance,[4] which is a powerful weapon for distinguishing between real differences between samples and those which are probably due to variation "within samples."

[4] The term "Analysis of Variance" is somewhat misleading. It is the total sum of squares which is analyzed. If, however, each estimate of variance is considered as weighted by its degrees of freedom, the term Analysis of Variance is quite correct, as will be seen later.

This is not the place to give a full description of the Analysis of Variance, but I propose to discuss shortly in nonmathematical language the assumptions on which it is founded, since I did not myself find Fisher's own description (Fisher (4)) very easy to follow, nor do I consider that the logical bases of the method were sufficiently emphasized in the work cited.

Supposing then for the moment that every single one of our vertebral counts is a sample from a strictly normal population of vertebral counts, we can take *at random* from the whole set of counts any given number of counts n_1', and calculate for the set the mean number $\bar{x}_1$, and the variance, $\frac{S(x_1-\bar{x}_1)^2}{n_1}$ where $n_1=n_1'-1$. This variance, which we will call S_1^2, is an *estimate* of the variance σ^2 of the whole population, founded on the number of degrees of freedom n_1. The term degrees of freedom means the number of ways in which the frequencies of the counts may be varied at will, provided that given fixed relations between the data are adhered to. In calculating S_1^2 we have used $\bar{x}_1$ as an estimate of the true mean, $\bar{x}_1$ being calculated from the data themselves. As $\bar{x}_1$, or the sum of all the n_1' x_1's, is fixed, only $n_1'-1$ of them may be varied at will, the last being fixed by the sum of the $n_1'-1$, whatever its value.

We can take any other random sample of n'_r counts and obtain another estimate s^2_r of the variance σ^2, based on n_r degrees of freedom. We can also obtain s^2_t from our total set of N' counts and this is an estimate of σ^2 based on $N'-1$ degrees of freedom. All these values of s^2 may be shown to be *efficient* estimates of σ^2, provided that our total set of counts is normally distributed, and our choice of subsamples is strictly random and not influenced in any way by the counts themselves. Besides these groups of counts chosen singly, we may separate all the counts into any number of n's of sets, containing, say, n'_1, n'_2 . . . n'_r counts, and find their means $\bar{x}_1$, $\bar{x}_2$ . . . $\bar{x}_r$. Then, if $\bar{\bar{x}}$ be the grand mean of all the counts,

$$\frac{n'_1(\bar{x}_1-\bar{\bar{x}})^2+n'_2(\bar{x}_2-\bar{\bar{x}})^2+\ . \ . \ . \ +n'_r(\bar{x}_r-\bar{\bar{x}})^2}{n'_s-1}$$

or

$$\frac{Sn_p(\bar{x}_p-\bar{\bar{x}})^2}{n'_s-1}$$

is an estimate of σ^2, based on n_s degrees of freedom. We have here assumed that the individual counts in each set are concentrated at their means, and used the weighted means instead of the individual counts. This is perfectly allowable if the sets are random samples from a normal population.

Thus we may *analyse* the total sum of squares in many ways on the assumption of normal distribution, the various sums of squares being divided (within errors of random sampling) proportionately to the degrees of freedom involved.

Fisher has shown that if

$$z=\log_\epsilon\sqrt{\frac{s^2_m}{s^2_n}} \text{ or } 1/2(\log_\epsilon s^2_m-\log_\epsilon s^2_n)$$

when s^2_m and s^2_n are two estimates of σ^2 based on m and n degrees of freedom respectively, then z is distributed in a known manner. If the value of z, found from two estimates of σ^2, calculated from data, lies too far away from the centre of this distribution, it may be reasonably concluded that s^2_m and s^2_n are *not* estimates of the *same* variance σ^2, indicating that the samples from which they were calculated were not randomly chosen but show an effect of the method of choice. This is the fundamental principle of the Analysis of Variance, but some of its applications involve very complex parceling of the data into groups, and groups within groups. In all these cases, the method is used to test suspected effects of particular ways of parceling the data, causing differences between some groups or means etc., and others, allowance being made automatically for variance *within* groups, i. e., for differences between the parcels which could arise by chance. The z-test offers a sound criterion for judgment as to whether the suspected effects are real or not, without personal opinions having the slightest influence on our judgment. The distribution of z is a function of n_m and n_n, the degrees of freedom involved in the two estimates of σ^2 to be compared. Fisher has tabulated (4) the 5% points and 1% points in the z-distribution for various values of n_m and n_n. If our value of z lies outside the 5% points, the two variances s^2_m and s^2_n are considered significantly different; if z is outside the 1% point, the difference is considered doubly significant, as a value of z beyond our value would only occur by chance, if s^2_m and s^2_n are not really different, 1

in 20 times in the former case and 1 in 100 times in the latter. The main advantage of using variance as a measure of variability lies in the additive property of the sums of squares, and of the degrees of freedom. Thus we may add together $S(x_m-\bar{x}_m)^2$ and $S(x_n-\bar{x}_n)^2$ and obtain an efficient estimate of σ^2 founded on n_m-n_n degrees of freedom, or we may divide our whole sample of counts into n'_s sets, with n'_1, n'_2 . . n'_r counts in the different sets, as we did when considering weighted means and obtain

$$\frac{S(x_1-\bar{x}_1)^2+S(x_2-\bar{x}_2)^2+\ldots+S(x_r-\bar{x}_r)^2}{n+n_2+\ldots n_r}$$

or $\frac{SS(x_p-\bar{x}_p)^2}{N'-r}$ as an estimate of σ^2 based on $N'-r$ degrees of freedom. This last estimate is usually called the variance "within classes" while that based on weighted means is called the variance "between classes." It should be mentioned that, in adding the sums of squares about the group means and dividing by the total number of degrees of freedom involved, we are assuming that the variances *within* the different groups are not significantly different. If significant differences are suspected, the *z*-test should be applied, since the Analysis of Variance is not sound if such differences are found.[5]

To clarify the exact steps in testing the data on the hypothesis of homogeneity, the following table has been inserted:

TABLE 2.—*Analysis of vertebral counts of samples of the 1926 class year from Noyes Island (see 23, fig. 2) to illustrate method of testing for homogeneity of the population*

A	B	C	D	E	F	G
June 21, 1930	51.786	14	—0.402	0.161604	2.262456	6.357
Do	52.250	24	.062	.003844	.092256	12.500
June 23, 1930	52.348	23	.160	.025600	.588800	15.217
June 24, 1930	52.226	31	.038	.001444	.044764	13.419
Do	52.000	9	—.188	.035344	.318096	2.000
June 27, 1930	51.857	7	—.331	.109561	.766927	2.857
June 28, 1930	52.240	25	.052	.002704	.067600	10.560
July 18, 1930	52.231	39	.043	.001521	.059319	16.923
July 28, 1930	52.214	14	.026	.000676	.009464	4.357
Total		186			4.209682	84.190

NOTE.—General mean, 52.188; column A, date of sampling; column B, mean of sample; column C, number in sample; column D, column B minus general mean; column E, column D squared; column F, column C times column E; and column G, sum of squared deviations from mean of sample.

Variance	Degrees of freedom	Sum of squares	Mean square	Log$_e$ mean square
Between arrays	8	4.209682	0.5262	—0.6420
Within arrays	177	84.190	.4756	—.7433

Difference	0.1013
Observed *z* (half of difference) [6]	.0507
Calculated *z* for probability of 0.05 [6]	.3322

[5] The variance "within classes" is the weighted mean of all the sample variances, the weights being the numbers of counts in the samples, less one in each case.

[6] The value of observed *z* being less than that of calculated *z* (methods of calculating *z* are given by Fisher, 1930, p. 201) at a probability of 0.05 shows the population to be homogeneous.

TABLE 3.—*Vertebral distributions for various year classes from all localities*

[Data from 1928 to 1931; no samples under 50 included]

Locality	Year class	Number of vertebrae [1]									No.	Mean	$S(x-\bar{x})$ [2]
		47	48	49	50	51	52	53	54	55			
Vicinity of Juneau	1923	1		2	4	75	446	334	45	2	909	52.370	541.802
Sitka Sound	1923					1	21	38	8		68	52.779	29.691
Vicinity of Juneau	1924			1		7	31	31	4		74	52.392	51.635
Wrangell	1924				1	12	32	13	2		60	52.050	36.850
Sitka Sound	1924					2	24	33	3		62	52.597	24.919
Fish Egg Island	1924					7	51	24	5		87	52.311	42.621
Vicinity of Juneau	1925			1	1	15	61	54	4	1	137	52.328	92.219
Petersburg	1925					16	61	43	4		124	52.282	65.121
Wrangell	1925				1	27	104	50	5		187	52.166	95.861
Tebenkof Bay	1925		1			5	29	44	7		86	52.570	85.081
Cape Ommaney	1925						25	42	3		70	52.686	21.086
Vicinity of Juneau	1926				1	37	183	150	18		389	52.378	207.450
Point Augusta	1926					9	53	40	2		104	52.337	45.221
Hoonah	1926					4	37	26	4		71	52.423	33.324
Point Adolphus	1926					8	27	18	2		55	52.255	30.436
Favorite Bay	1926					2	27	25	3		57	52.509	24.246
Point Gardner	1926					10	89	81	9		189	52.471	85.090
Petersburg	1926			1	3	64	274	144	7	1	494	52.178	250.324
Wrangell	1926				3	37	67	35	1		143	51.958	87.748
Jamestown Bay	1926			1		8	37	36	4	1	87	52.414	63.103
Cape Edgecumbe	1926					21	84	81	7		193	52.384	101.627
Deep Cove	1926					9	48	26	3		86	52.267	40.849
Port Herbert	1926				1	7	66	37	5		116	52.328	55.552
Big Port Walter	1926					4	36	44			84	52.476	28.952
Tebenkof Bay	1926				3	24	197	171	16		411	52.421	198.180
Cape Ommaney	1926			3	10	141	1,013	877	97	2	2,143	52.423	1,107.123
Coronation Island	1926					22	221	186	19	1	449	52.457	199.403
Warren Island	1926		1	1	1	21	190	145	8		367	52.357	156.371
Kell Bay	1926			1		9	36	27	1		74	52.230	45.095
Noyes Island	1926				1	25	100	58	2		186	52.188	88.414
Port Estrella	1926					8	34	11		1	54	52.111	27.333
Meade Point	1926					2	20	25	4		51	52.608	24.157
Vicinity of Juneau	1927			1	1	11	77	64	11	1	166	52.440	108.898
Point Augusta	1927					6	28	26	7	1	68	52.544	48.868
Hoonah	1927			1	3	20	97	83	15	1	220	52.395	158.595
Point Adolphus	1927				1	7	32	27	1		68	52.294	36.118
Todd	1927			1		13	75	62	9		160	52.394	102.194
Petersburg	1927			1	1	29	245	212	36	2	526	52.487	291.407
Wrangell	1927					6	30	23	5		64	52.422	37.609
Anita Bay	1927					2	29	24	4		59	52.508	26.746
Port Herbert	1927					13	23	18	6		60	52.283	50.183
Gut Bay	1927			1		5	46	21	5		78	52.295	48.218
Cape Ommaney	1927				1	11	134	193	22	1	362	52.627	162.655
Warren Island	1927					1	37	41	3	1	83	52.590	34.072
Culebra Island	1927				1	4	27	21	2		55	52.346	30.436
Noyes Island	1927					17	104	81	3		205	52.342	86.098
Klawak	1927					6	33	19	1		59	52.254	25.186
Hoonah	1928					2	24	47	11		84	52.798	39.560
Anita Bay	1928					20	113	63	4		200	52.255	85.995
Santa Ana Inlet	1928					13	80	40	4		137	52.255	60.058
Frances Cove	1928					11	71	32	2		116	52.216	45.612
Gut Bay	1928					4	26	24	4		58	52.483	30.483
Gut Bay	1929					10	28	26			64	52.250	32.000
Cape Bendel	1929				1	16	107	63	7		194	52.304	93.057

[1] Excluding the hypural.

In using this method, as pointed out by Wollaston, the distribution of the variances of the samples must approach normality. Accordingly, before analyzing these samples their variances were tabulated, table 4, and the 4 samples indicated were discarded, their variances obviously being far outside of the normal range. A test of the homogeneity of the remaining 158 samples, comprising 5,964 vertebral counts showed definitely that these samples could not all have been drawn from the same population, since the observed z of 0.3387 far exceeds 0.1256, the value of z calculated at a probability of 0.01.

Therefore, it must be concluded that the herring of southeastern Alaska are composed of more than one population.

TABLE 4.—*Frequency of variances of 162 individual samples of the vertebral count from various localities in southeastern Alaska*

Variance	Number	Variance	Number	Variance	Number	Variance	Number
0.1600–0.2300	1	0.5600–0.6300	19	0.9600–1.0300		1.3600–1.4300	[1] 2
0.2400–0.3100	16	0.6400–0.7100	15	1.0400–1.1100		1.4400–1.5100	[1] 1
0.3200–0.3900	25	0.7200–0.7900	9	1.1200–1.1900		1.5200–1.6000	
0.4000–0.4700	38	0.8000–0.8700	3	1.2000–1.2700	[1] 1		
0.4800–0.5500	30	0.8800–0.9500	2	1.2800–1.3500			

[1] These samples omitted in analysis of variance.

HOMOGENEITY OF MATERIAL FROM INDIVIDUAL LOCALITIES

Evidence tending to prove a lack of admixture in the samples from the individual localities is shown in table 5, in which a test of the homogeneity of samples of the vertebral count of the 1926 year class has been made for each of the 7 localities from which sufficient data were available for such a test. In contrast to the results obtained when the southeastern Alaska material was considered as a whole, none of the 7 localities have an observed z exceeding the value of the calculated z at a probability of 0.05, indicating the homogeneity of the population sampled in each locality.

However, the observed z for the Warren Island samples, 0.2768, is only slightly less than that of the calculated, 0.3448, for a probability of 0.05. Therefore the Warren Island samples must be regarded with some suspicion, especially as the proportion the observed z forms of the calculated z is larger in the Warren Island samples than in those from the other localities.

TABLE 5.—*Analysis of variance of vertebral count samples of the 1926 year class from various localities in southeastern Alaska taken from 1929 to 1931, inclusive*

Locality	Mean	Number	Number of samples	Mean square		Observed z	Calculated z for probability of 0.05 [1]
				Between arrays	Within arrays		
Cape Ommaney	52.423	2,143	60	0.6465	0.5247	0.1044	0.1414
Tebenkof Bay	52.421	411	19	.4215	.4862	.0714	.3279
Coronation Island	52.457	449	12	.3828	.4467	.0785	.4409
Warren Island	52.357	367	8	.8397	.4829	.2768	.3448
Point Gardner	52.471	189	6	.6426	.4474	.1810	.4052
Noyes Island	52.188	186	9	.5262	.4756	.0507	.3322
Vicinity of Juneau	52.378	389	11	.6977	.5304	.1370	.3054

[1] The observed value of z is less than the calculated value at a probability of 0.05 in every case, thus showing that the population of each locality is homogeneous.

SEGREGATION OF RACES

Since the above evidence supports the hypothesis that the population of each locality is homogeneous, the vertebral counts from each locality have been compared to those of adjacent localities. (See fig. 3 and tables 3 and 6.) Only counts of fish of the same year class have been compared, necessitating the limiting of samples to those containing 50 or more counts. Smaller samples were not used, owing to the probability that occasional errors enter into our age determinations.

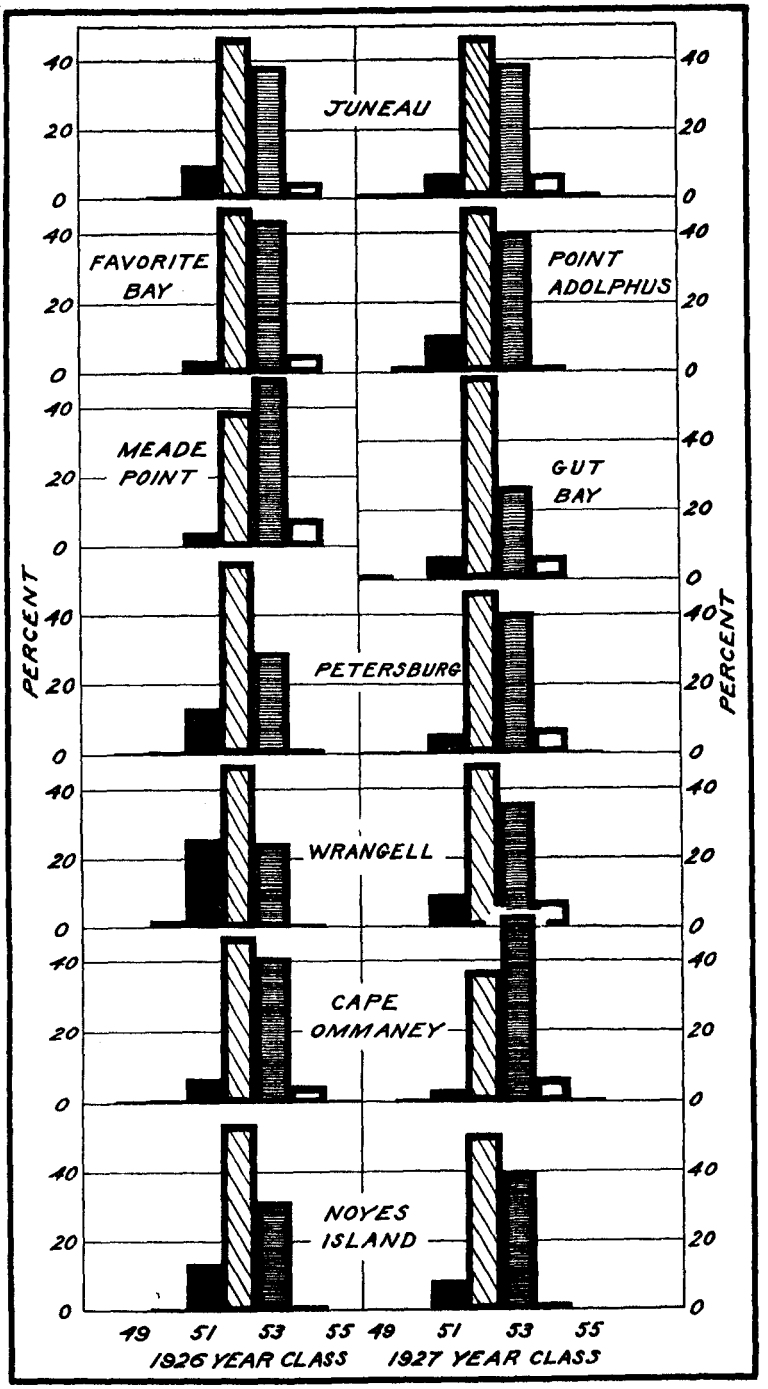

FIGURE 3.—Percentage vertebral count distributions of 1926 and 1927 year classes from some of chief localities.

TABLE 6.—*Comparisons of the means of the vertebral counts of each year class in southeastern Alaska*

Localities compared	Year class	Difference between means	Summation of populations	Standard error of difference between means	Difference between means divided by standard error
Juneau and Point Augusta	1927	0.104	234	0.119	0.87
Do	1926	.041	493	.079	.52
Juneau and Hoonah	1927	.045	386	.086	.52
Do	1926	.045	460	.094	.48
Juneau and Petersburg	1927	.047	692	.068	.69
Do	1926	.200	883	.049	[1] 4.08
Do	1925	.046	261	.097	.47
Juneau and Point Gardner	1926	.093	578	.062	1.50
Hoonah and Point Adolphus	1927	.101	288	.114	.89
Do	1926	.168	126	.129	1.30
Hoonah and Point Augusta	1927	.149	288	.118	1.26
Do	1926	.086	175	.104	.83
Favorite Bay and Point Augusta	1926	.172	161	.109	1.58
Favorite Bay and Point Gardner	1926	.038	246	.101	.38
Todd and Point Augusta	1927	.150	228	.118	1.27
Todd and Gut Bay	1927	.099	238	.110	.90
Point Gardner and Petersburg	1926	.203	683	.060	[1] 4.88
Point Gardner and Meade Point	1926	.137	240	.107	1.28
Point Gardner and Deep Cove	1926	.204	275	.088	[2] 2.32
Point Gardner and Tebenkof Bay	1926	.050	600	.060	.83
Meade Point and Petersburg	1926	.430	545	.104	[1] 4.13
Meade Point and Tebenkof Bay	1926	.187	462	.103	1.82
Meade Point and Deep Cove	1926	.341	137	.122	[1] 2.80
Tebenkof Bay and Deep Cove	1926	.154	497	.082	1.88
Tebenkof Bay and Port Herbert	1926	.093	527	.072	1.29
Tebenkof Bay and Big Port Walter	1926	.055	495	.081	.68
Tebenkof Bay and Cape Ommaney	1926	.002			
Do	1925	.106	156	.134	.79
Tebenkof Bay and Coronation Island	1926	.036	860	.046	.78
Deep Cove and Port Herbert	1926	.061	202	.099	.62
Port Herbert and Gut Bay	1927	.012	138	.146	.08
Port Herbert and Big Port Walter	1926	.148	200	.094	1.57
Big Port Walter and Cape Ommaney	1926	.053	2,227	.079	.67
Cape Ommaney and Port Herbert	1927	.344	422	.098	[1] 3.51
Do	1926	.095	2,259	.068	1.40
Cape Ommaney and Deep Cove	1926	.156	2,229	.079	[2] 1.97
Cape Ommaney and Coronation Island	1926	.034	2,590	.037	.92
Cape Ommaney and Warren Island	1927	.037	445	.080	.46
Do	1926	.066	2,510	.040	1.65
Cape Ommaney and Meade Point	1926	.185	2,194	.102	1.81
Cape Ommaney and Point Gardner	1926	.048	2,332	.053	.91
Cape Ommaney and Jamestown Bay	1926	.009			
Cape Ommaney and Cape Edgecumbe	1926	.039	2,336	.053	.74
Cape Ommaney and Gut Bay	1927	.332	440	.087	[1] 3.82
Jamestown Bay and Cape Edgecumbe	1926	.030	280	.099	.30
Jamestown Bay and Favorite Bay	1926	.095	144	.134	.71
Jamestown Bay and Point Adolphus	1926	.159	142	.141	1.13
Cape Edgecumbe and Favorite Bay	1926	.125	250	.107	1.17
Cape Edgecumbe and Point Adolphus	1926	.129	248	.112	1.15
Coronation Island and Kell Bay	1926	.227	523	.086	[1] 2.64
Coronation Island and Warren Island	1926	.100	816	.047	[2] 2.13
Coronation Island and Noyes Island	1926	.269	635	.059	[1] 4.56
Warren Island and Kell Bay	1926	.127	441	.086	1.48
Warren Island and Culebra Island	1927	.244	138	.120	[2] 2.03
Warren Island and Noyes Island	1927	.248	288	.084	[1] 2.95
Do	1926	.169	553	.060	[1] 2.82
Warren Island and Wrangell	1927	.178	147	.117	1.52
Do	1926	.399	510	.068	[1] 5.87
Warren Island and Meade Point	1926	.251	418	.103	[2] 2.44
Warren Island and Petersburg	1927	.103	609	.086	1.20
Do	1926	.179	861	.046	[1] 3.89
Culebra Island and Noyes Island	1927	.004	260	.102	.04
Culebra Island and Klawak	1927	.092	114	.132	.70
Noyes Island and Klawak	1927	.088	264	.096	.92
Noyes Island and Port Estrella	1926	.077	240	.108	.71
Wrangell and Petersburg	1927	.065	590	.098	.66
Do	1926	.220	637	.069	[1] 3.19
Do	1925	.116	311	.084	1.38
Wrangell and Anita Bay	1927	.086	123	.132	.65
Santa Ana Inlet and Anita Bay	1928	.000			
Santa Ana Inlet and Frances Cove	1928	.039	253	.082	.48

[1] Statistically significant.

[2] Approaching statistical significance.

Any two means are compared by dividing their difference by the standard error estimated by the formula

$$\sigma=\sqrt{\frac{S(x-\bar{x})^2+S(x'-\bar{x}')^2}{n_1+n_2}\left(\frac{1}{n_1+1}+\frac{1}{n_2+1}\right)}$$

if $x_1, x_2 \ldots\ldots\ldots, x_{n_2}+1$ and $x'_1, x'_2 \ldots\ldots\ldots x'_{n_2}+1$ be two samples,

and $$\bar{x}=\frac{1}{n_1+1}S(x),\ \bar{x}'=\frac{1}{n_2+1}S(x')$$

Of the 71 comparisons between the mean vertebral counts given in table 6, 36 are between localities not over 25 miles apart, and the remaining 35 are from localities over 25 miles apart.

The results of the comparisons are listed in table 7.

That there is such close agreement between the results of the two group of comparisons is surprising considering the difference in distance. The median distance apart in the close group is only 17 miles as contrasted with 52 miles in the group of distant comparisons. These results tend to indicate that ordinarily there is probably little intermingling between herring of different races, the boundaries between racial areas being quite abrupt.

TABLE 7.—*Summarized comparisons of vertebral counts*

Distance apart in miles	Probability of means being the same		
	0.99–0.05	0.05–0.01	0.01 or less
0–25	27	3	6
26 and over	26	2	7

The mean vertebral counts of herring from Petersburg, in the northern entrance to Wrangell Narrows, for instance, differ by over 4 standard errors from those of Juneau, Point Gardner, or Meade Point, by 3.89 standard errors from Warren Island, and by 3.19 from those of Wrangell. This is rather definite evidence that herring do not migrate through Wrangell Narrows or Dry Strait, and that migrations in Frederick Sound must be largely confined to that body of water.

The samples taken in the area south of Sumner Strait and east of Clarence Strait, including Wrangell, Anita Bay, Santa Ana Inlet, and Frances Cove, do not differ amongst themselves, so that, until additional evidence is collected, it can only be assumed that the herring of these localities may intermingle. That this group of herring does not intermingle with herring of the outer coast through Sumner Strait is clearly indicated by a difference between the Warren Island and Wrangell averages of 5.87 standard errors.

On the west coast of Prince of Wales Island the means of the samples from 4 closely adjacent localities, Klawak, Port Estrella, Noyes Island, and Culebra Island, do not differ amongst themselves, but differ from those of the localities to the north. The agreement of the herring of the adjacent localities (captured during the summer months) with those taken while spawning, on the important spawning grounds near Klawak, is quite in keeping with expectations. Noyes Island differs from Coronation Island by 4.56 standard errors and from Warren Island by 2.82 and 2.95 standard errors in the 2 available comparisons. However, Warren Island and Culebra Island differ by only 2.03 standard errors which gives a probability of 0.04 of the populations

being the same. This is not sufficiently great odds to be able to state definitely that Warren Island and Culebra Island represent distinct populations. Thus while the significant differences between Warren Island and Noyes Island and between Coronation and Noyes Islands tend to indicate the lack of migration across Iphigenia Bay, the lack of a statistically significant difference between Warren Island and Culebra Island averages does not confirm this view.

A test of the homogeneity of the Prince of Wales Island samples with the Warren Island data included, made by above-described methods, yielded an observed z of 0.3247 which happens to be exactly the same as the calculated z for a probability of 0.01, thus indicating that this group of samples is not all drawn from one population. The same test made without the Warren Island samples gives an observed z of 0.0248 which is many times less than the calculated z of 0.4420 for a probability of 0.05. Therefore, it must be concluded that the data point to the lack of migration between localities lying north and those lying south of Cape Lynch (Iphigenia Bay).

Samples from Warren Island, at the mouth of Sumner Strait, differ from those of Meade Point, near the mouth of Frederick Sound, by 2.44 standard errors which yields a probability of 0.014. Even if this difference were significant, it could not be assumed to give definite information on migration through Keku Strait as neither locality is very close to the entrance to this channel. It does, however, suggest that the herring at the mouth of Frederick Sound do not migrate to the ocean by this route.

A sample from Kell Bay, in Affleck Canal, differs significantly in vertebral count from Coronation Island, but does not show a significant difference from Warren Island, which is about the same distance as Coronation Island from the mouth of the canal.

The vertebral count comparisons of table 6 also indicate differences between the Cape Ommaney herring and those from Port Herbert and Gut Bay, but not from those caught in Big Port Walter. The Big Port Walter herring also do not show differences from Port Herbert. Therefore these localities cannot be classified without more material.

ANALYSIS OF GROWTH RATES

In analyzing the growth rates from the various localities for racial purposes no data were used except those from freshly caught purse-seined specimens, all of which were obtained during the summer months.

Many of the body length distributions are slightly skewed, and in addition cover a wide range, with a tendency in a few cases for slight modes to form near the upper or lower range of the distribution. These disturbing factors are probably caused in large measure by errors in age reading whereby a length distribution may contain a few fish belonging to younger or older age groups. Since these doubtful measures near the extremes of the range exert a large influence in the determination of the arithmetic mean, whereas, being of doubtful authenticity they should not carry as much weight as the more centrally located items, it was decided not to use the arithmetic mean but to employ the median for the measure of central tendency. In keeping with the use of the median the interquartile range has been used as the measure of dispersion.

To gain an insight into the growth increments during the summer months the data have been grouped by 10-day periods. (See table 8.) For Larch Bay 5-year-olds

(herring in their fifth summer) taken during 1930, a consecutive series of 8 periods shows no consistent changes in length during the first 5 periods (from June 21 up to and including Aug. 10). There is an abrupt increase in length, however, between the fifth and sixth periods, the fish of the last three periods averaging about a half centimeter greater in body length. Such a sudden increase in length can scarcely be ascribed to growth but is probably due to an influx of new schools of herring onto the fishing grounds.

That such a sudden change in body length is not due to growth is supported by the Noyes Island data, in which both the 4- and 5-year-olds taken toward the end of July were considerably smaller than those taken during the last of June, the largest difference, that between the 5-year-olds, being 6 millimeters.

TABLE 8.—*Body lengths in various localities for 1929 and 1930 by 10-day periods*

Locality	Age	Date	Number of specimens	Median	Q_1	Q_3	Q_3-Q_1
		1929					
Larch Bay	4	June 11-20	226	199.2	193.7	204.6	10.9
Port Alexander	4	June 1-10	212	193.5	188.0	198.7	10.7
Do	4	June 11-20	190	194.5	189.7	200.1	10.4
Do	4	June 21-30	68	198.7	193.8	204.5	10.7
Tebenkof Bay	4	....do	226	199.6	195.1	204.6	9.5
Do	4	July 1-10	131	200.9	196.6	206.0	9.4
Do	4	July 11-20	51	203.4	199.3	207.6	8.3
Do	4	July 21-31	39	202.4	198.3	206.1	7.8
Big Port Walter	4	May 31	85	191.7	185.1	198.3	13.2
Off Port Herbert	4	June 1-10	60	194.5	187.7	202.0	14.3
Deep Cove	4	June 11-20	87	190.4	185.1	197.1	12.0
Hoggatt Bay	4	....do	38	194.2	187.4	198.0	10.6
Coronation Island	4	....do	147	203.4	199.2	208.5	9.3
Affleck Canal	4	June 1-10	74	186.9	183.7	191.0	7.3
Port Estrella and Culebra Island	4	June 8-12	95	185.9	178.8	190.9	12.1
Point Gardner	4	July 1-10	59	200.0	195.8	204.9	9.1
Do	4	July 11-20	65	201.2	196.3	205.1	8.8
Do	4	July 21-31	37	201.6	198.1	208.9	10.8
Favorite Bay	4	....do	57	201.8	192.8	205.3	12.5
Point Adolphus	4	....do	44	184.5	175.5	189.5	14.0
Douglas Island	4	....do	36	187.5	179.5	191.0	11.5
		1930					
Larch Bay	4	July 21-31	65	204.6	198.1	208.9	10.8
Do	4	Sept. 1-10	132	206.4	201.5	211.5	10.0
Port Alexander	4	June 21-30	34	194.8	191.1	200.0	8.9
Off Port Herbert	4	July 11-20	47	198.4	194.3	208.1	13.8
Warren Island	4	July 1-10	37	197.8	194.8	204.4	9.6
Do	4	July 21-31	28	196.0	191.5	202.0	10.5
Noyes Island	4	June 21-30	121	192.8	188.3	197.2	8.9
Do	4	July 11-20	53	187.6	181.3	190.7	9.4
Do	4	July 21-31	34	188.5	181.3	190.4	9.1
Todd	4	June 1-10	160	176.0	169.5	181.9	12.4
Larch Bay	5	June 21-30	80	210.8	204.2	214.8	10.6
Do	5	July 1-10	98	213.0	206.8	217.4	10.6
Do	5	July 11-20	157	212.1	207.4	218.0	10.6
Do	5	July 21-31	284	211.5	206.1	218.1	12.0
Do	5	Aug. 1-10	46	212.9	208.8	217.3	8.5
Do	5	Aug. 21-31	67	219.1	213.2	223.0	9.8
Do	5	Sept. 1-10	334	216.0	210.7	222.0	11.3
Do	5	Sept. 11-20	38	216.5	207.3	222.7	15.4
Port Alexander	5	June 11-20	70	211.8	206.1	214.8	8.7
Do	5	June 21-30	145	209.9	200.1	214.7	14.6
Do	5	Aug. 21-31	43	213.3	209.8	219.6	9.8
Off Port Herbert	5	July 11-20	63	207.1	201.7	210.8	9.1
Coronation Island	5	....do	68	215.2	209.5	218.8	9.3
Do	5	July 21-31	188	214.7	209.3	220.4	11.1
Do	5	Aug. 11-20	48	212.5	204.8	217.2	12.4
Warren Island	5	June 21-30	38	212.2	209.5	218.9	9.4
Do	5	July 1-10	119	209.1	203.9	212.8	8.9
Do	5	July 11-20	162	211.1	205.3	215.5	10.2
Do	5	July 21-31	51	213.0	208.4	217.3	8.9
Noyes Island	5	June 21-30	134	204.5	199.6	210.8	11.2
Do	5	July 11-20	39	197.1	193.9	201.8	7.9
Point Gardner	5	July 1-10	29	214.0	209.8	217.8	8.0
Cape Edgecumbe	5	....do	195	213.6	208.0	218.8	10.8

Because of these large variations in the size of herring of the same age taken from the same locality, it was adjudged unwise to attempt any careful statistical com-

parisons between localities. The medians and quartiles are given for each month in table 9. Figures 4, 5, and 6 give the length distributions for some of the localities. In these figures the lengths have been grouped by 3-millimeter categories and smoothed once by three's. The figures and the table reveal at once that the herring from 4

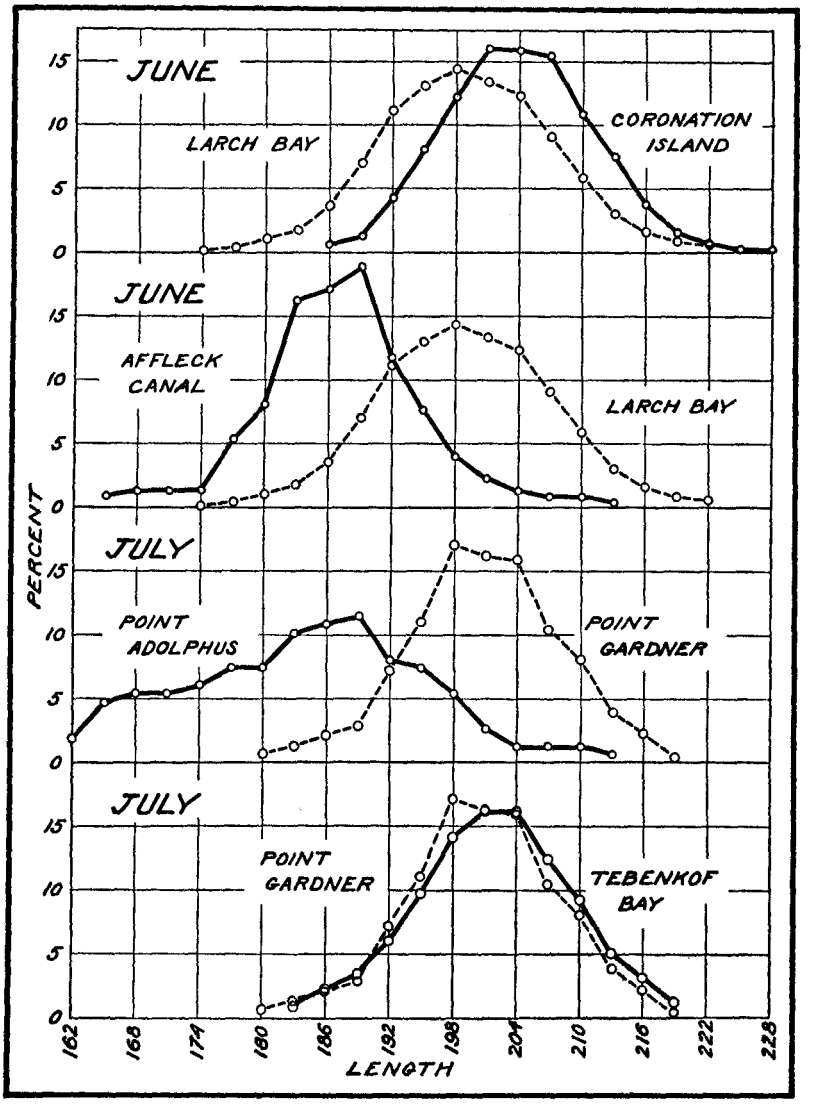

FIGURE 4.—Percentage length distributions, grouped by 3-millimeter categories and smoothed once by three's for herring of 1926 year class caught in 1929 (their fourth summer).

localities: The Noyes Island area (including Culebra Island and Port Estrella), the Douglas Island-Icy Strait area, Affleck Canal (Kell Bay) and Peril Strait (Todd) are all much slower growing than those of the other localities. These differences are so great that we have considered these 4 localities to represent groups of fish separate from the neighboring stocks or populations. The Peril Strait herring appear to be the slowest growing of any we have so far encountered in Alaska, the median of the 4-year-olds taken in June 1930 being only 176.0 millimeters.

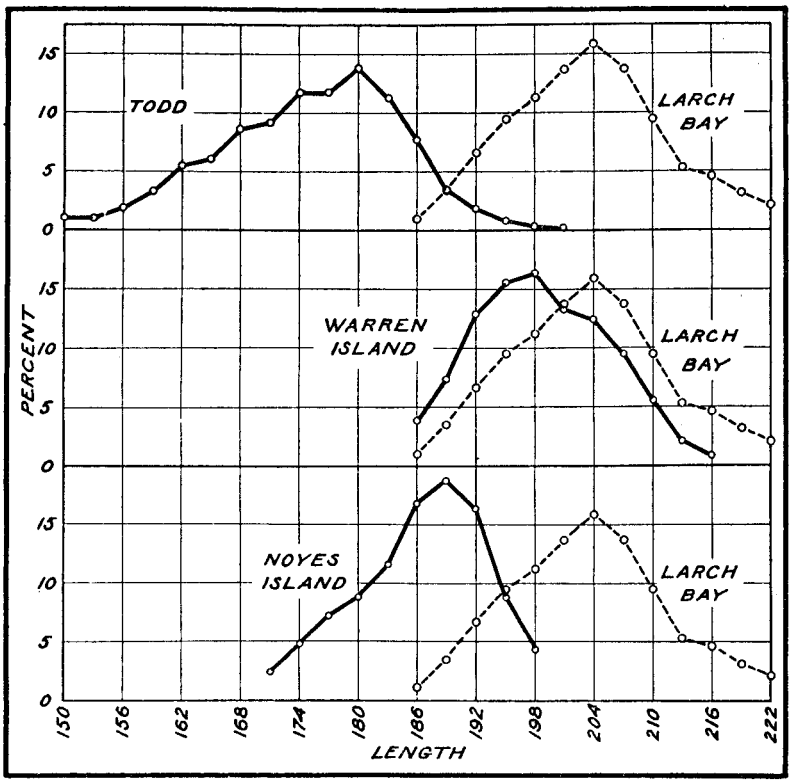

FIGURE 5.—Percentage length distributions, grouped by 3-millimeter categories and smoothed once by three's for herring of 1927 year class caught in 1930 (their fourth summer).

TABLE 9.—*Body lengths in various localities for 1929 and 1930 by months*

Locality	Age	Date sampled		Number of specimens	Median	Q_1	Q_3	Q_3-Q_1
		Year	Month					
Larch Bay	4	1929	June	226	199.2	193.7	204.6	10.9
Port Alexander	4	1929	do	470	194.2	189.4	200.1	10.7
Tebenkof Bay	4	1929	do	226	199.6	195.1	204.6	9.5
Do	4	1929	July	221	202.0	197.2	206.3	9.1
Big Port Walter	4	1929	May 31	85	191.7	185.1	198.3	13.2
Off Port Herbert	4	1929	June	60	194.5	187.7	202.0	14.3
Deep Cove	4	1929	do	87	190.4	185.1	197.1	12.0
Hoggatt Bay	4	1929	do	38	194.2	187.4	198.0	10.6
Coronation Island	4	1929	do	147	203.4	199.2	208.5	9.3
Affleck Canal	4	1929	do	74	186.9	183.7	191.0	7.3
Port Estrella and Culebra Island	4	1929	do	95	185.9	178.8	190.9	12.1
Point Gardner	4	1929	July	161	200.8	196.4	205.7	9.3
Favorite Bay	4	1929	do	57	201.8	192.8	205.3	12.5
Point Adolphus	4	1929	do	49	185.8	176.1	191.4	15.3
Douglas Island	4	1929	do	71	188.3	182.4	198.1	15.7
Larch Bay	4	1930	do	96	203.5	197.3	207.9	10.6
Do	4	1930	September	152	206.4	201.4	211.6	10.2
Port Alexander	4	1930	June	45	196.8	191.8	201.9	10.1
Off Port Herbert	4	1930	July	47	198.4	194.3	208.1	13.8
Warren Island	4	1930	do	80	197.7	193.8	204.5	10.7
Noyes Island	4	1930	June	121	192.8	188.3	197.2	8.9
Do	4	1930	July	87	187.8	181.3	190.5	9.2
Todd	4	1930	June	160	176.0	169.5	181.9	12.4
Larch Bay	5	1930	do	80	210.8	204.2	214.8	10.6
Do	5	1930	July	539	212.0	206.8	217.9	11.1
Do	5	1930	August	113	216.3	211.5	221.0	9.5
Do	5	1930	September	372	216.0	210.6	222.1	11.5
Port Alexander	5	1930	June	215	210.4	204.2	214.8	10.6
Do	5	1930	August	43	213.3	209.8	219.6	9.8
Off Port Herbert	5	1930	July	63	207.1	201.7	210.8	9.1
Coronation Island	5	1930	do	256	214.8	209.3	219.8	10.5
Do	5	1930	August	48	212.5	204.8	217.2	12.4
Warren Island	5	1930	June	38	212.2	209.5	218.9	9.4
Do	5	1930	July	332	210.4	204.9	214.9	10.0
Noyes Island	5	1930	June	134	204.5	199.6	210.8	11.2
Do	5	1930	July	54	198.5	194.7	206.0	11.3
Point Gardner	5	1930	do	29	214.0	209.8	217.8	8.0
Cape Edgecumbe	5	1930	do	195	213.6	208.0	218.8	10.8

That the northern slow-growing group of herring found in Icy Strait and the vicinity of Juneau all belong to the same race cannot be assumed from growth rates. A test of the homogeneity of the vertebral count distributions in this area (see *A*, fig. 2) gives an observed z (see illustration in section on vertebrae) of 0.4069. The

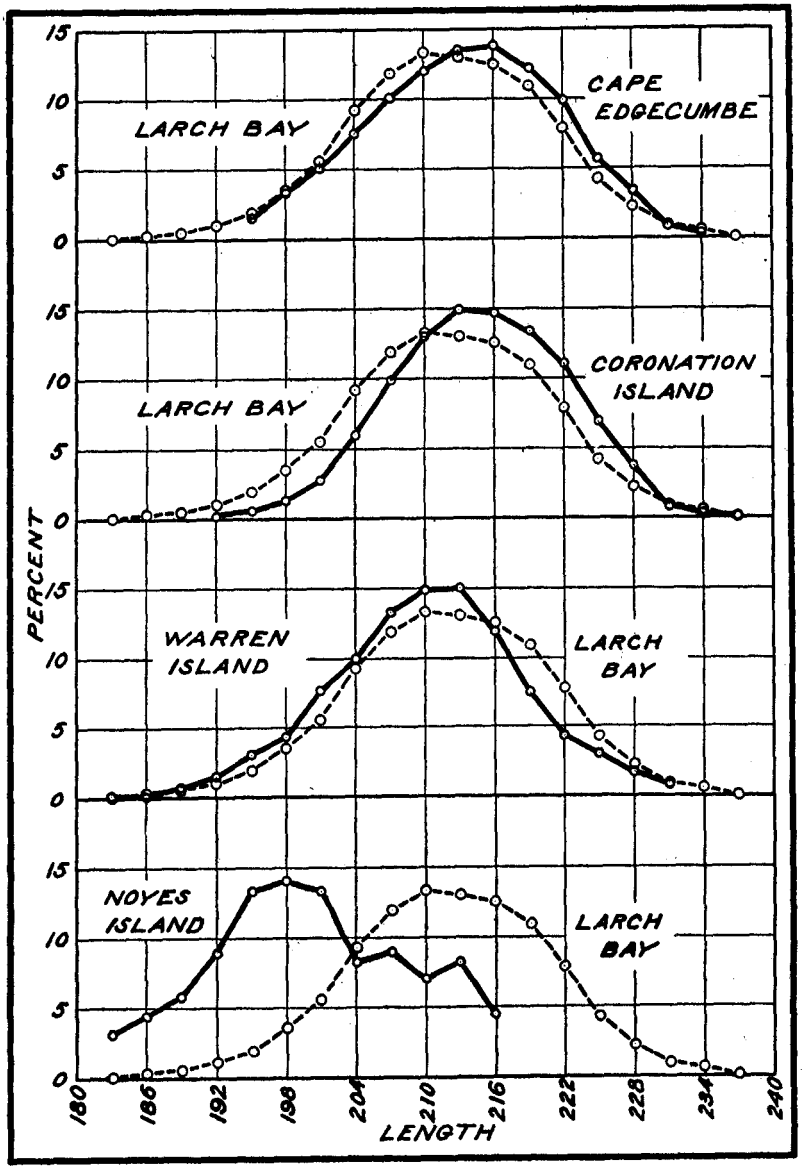

FIGURE 6.—Percentage length distributions, grouped by 3-millimeter categories and smoothed once by three's, for herring of the 1926 year class caught in 1930 (in their fifth summer).

calculated z for a probability of 0.05 is 0.3388, and for a probability of 0.01 it is 0.4909. Therefore, in this case, the observed z is large enough to be of doubtful significance. In this test the mean square between the arrays 0.2268 is less than that within the arrays 0.5117 which may indicate a difference in variance. It must be realized that no definite conclusions as to the racial homogeneity of this area can be reached without further data.

ANALYSIS OF YEAR CLASSES

Differences in the relative proportions of different year classes present in the populations may be of value as an indication of the extent of intermingling. The relative abundance of any particular year class in the catch is influenced chiefly by three factors: First, the relative number of larvae of that year class hatching and surviving through the juvenile period until of an age or size to enter the catch; second, by the rate of natural mortality; and third, by the increased rate of mortality induced by the fishery. However, the relative abundance of any particular year class in the catch may change during the season. Such a progressive change from younger to older age groups is apparent as the season advances, for instance, in Prince William Sound. Owing to such fluctuations in the relative proportions of each age group present at any particular time, only the major differences between localities can be emphasized without further data.

In figure 10 are given histograms of the percentage age distributions for the major fishing grounds during the 1929 and 1930 seasons. Several features are worthy of emphasis. These are (1) the approximate equality of the 1926 and 1927 year classes at Noyes Island as contrasted with the overwhelming dominance of the 1926 year class at most of the other localities, (2) the great dominance of the 1927 year class at Todd, (3) the dominance of the 1923 year class at Douglas Island and Favorite Bay, (4) the large percentage of the catch older than the 1923 year class at Douglas Island.

These salient facts all support the indications given by the analyses of the vertebral counts and of the growth rates which separate the Noyes Island area, Todd, and the Juneau-Icy Strait area (including Douglas Island) as independent of neighboring areas. Whether Favorite Bay is independent of Point Gardner we hesitate to say without further data.

TAGGING

Curtailment of fishing operations during 1932 and 1933, due to economic conditions, and an increased abundance in the Cape Ommaney tribe of herring, owing to the accession to the catch of certain dominant year classes, caused fishing during 1932 to be carried on almost wholly in the area between Noyes Island and the lower end of Baranof Island. During 1933 the boats did not fish farther south than Warren Island. This condition, which was in contrast to the widespread fishing conducted for several years previously, made our tagging work of less value than it would have been under normal conditions, as obviously the presence of tagged herring cannot be detected where no fishing operations are being conducted. However the results are presented for what they are worth. For a full discussion of tagging methods and manner of recovery of the tags, see Rounsefell and Dahlgren (1933).

During the fishing season of 1933 (June 1 to September 30) 101 belly tags and 7 opercle tags were recovered from 2,499 of the former and 1,470 of the latter affixed to herring released at Jamestown Bay (Sitka) between April 21 and April 25, 1933. All of these tags were recovered around Cape Ommaney, between Larch Bay and Port Alexander, giving the first definite proof of a migration of some length, as it is approximately 66 miles by water from Jamestown Bay to Port Alexander.

On the other hand, out of 996 belly tags and 824 opercle tags affixed to herring released at Cape Bendel, just under 60 miles from Port Alexander, on August 17, 1932, not a tag has been recovered. This may be considered rather definite evidence of a lack of migration between Cape Bendel and Cape Ommaney.

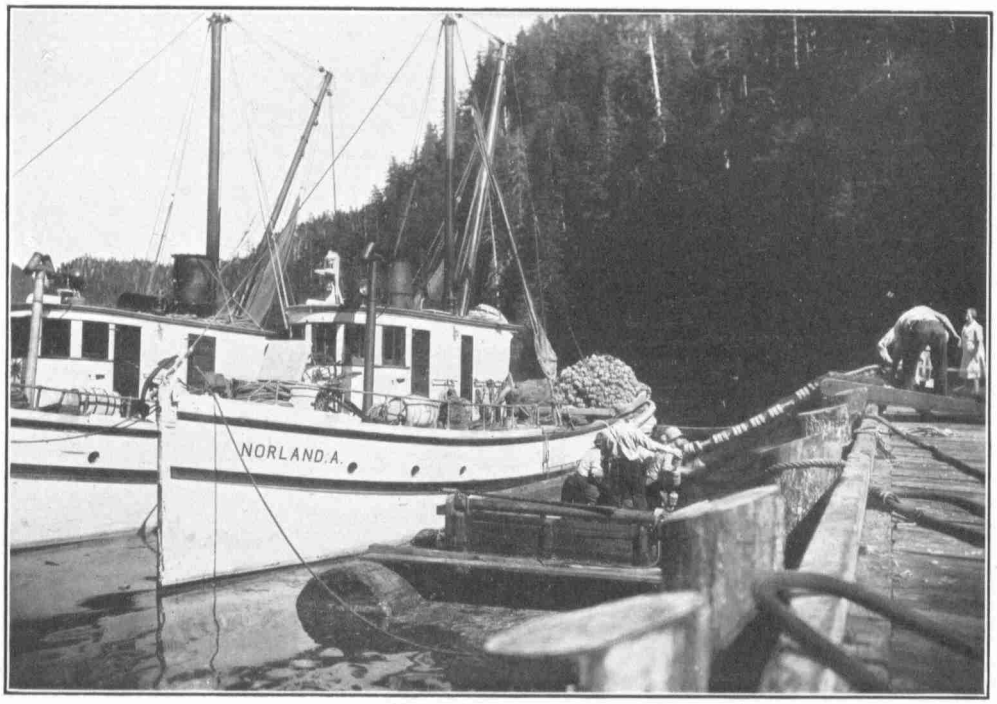

FIGURE 7.—BLUESTONING A SEINE.

At frequent intervals throughout the season a seine is dipped into a solution of copper sulphate to kill the marine growths that cause the web to rot.

FIGURE 8.—THE SCIENTIFIC VESSEL "HERON" AT ANCHOR IN PORT CONCLUSION.

Note the live box used in tagging operations moored astern. The acquisition of this motor launch in 1932 permitted the carrying out of the herring tagging program.

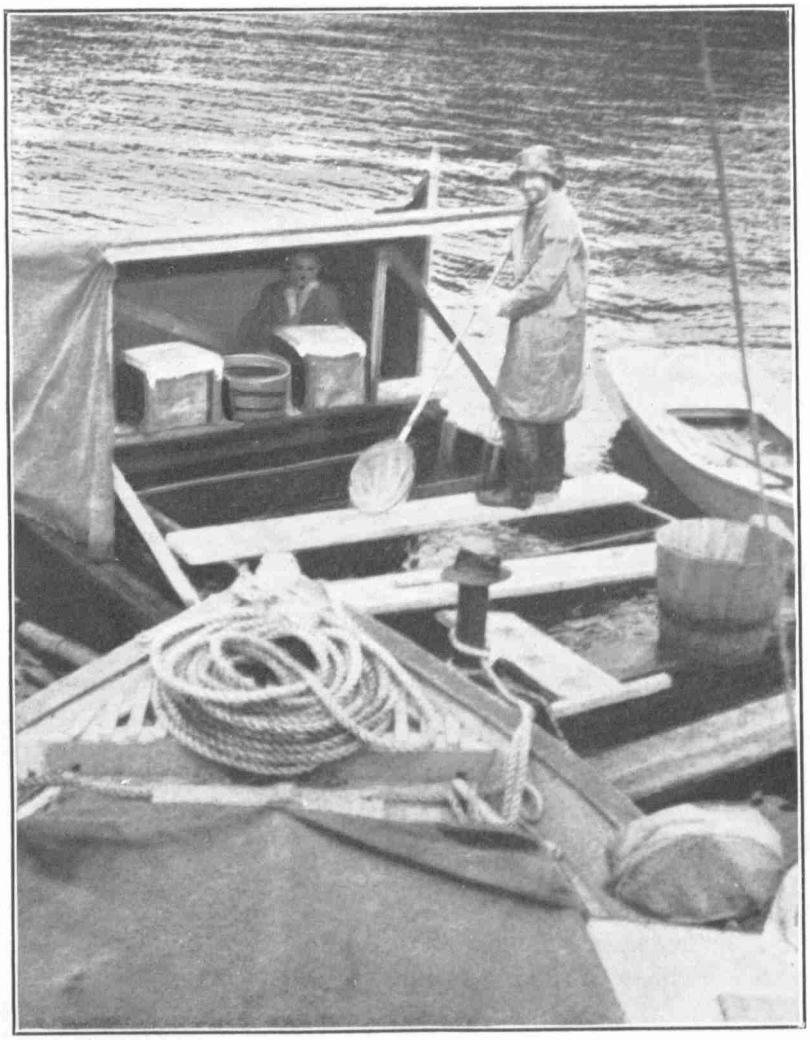

FIGURE 9.—HERRING TAGGING OPERATIONS.

The tagging live box is filled with herring which the man with the net dips a few at a time into the half barrel of sea water under the shelter. From this half barrel the herring are removed one at a time by hand and placed on damp cheesecloth stretched over a frame. A sharp arrow-pointed knife is used to puncture a small hole through the wall of the belly and the flat metal tag is inserted within the body cavity of the herring, the small wound healing completely within a few days.

In another tagging experiment at Auke Bay near Juneau, 800 belly tags and 772 opercle tags were affixed to spawning herring released on May 3, 4, and 5, 1933.

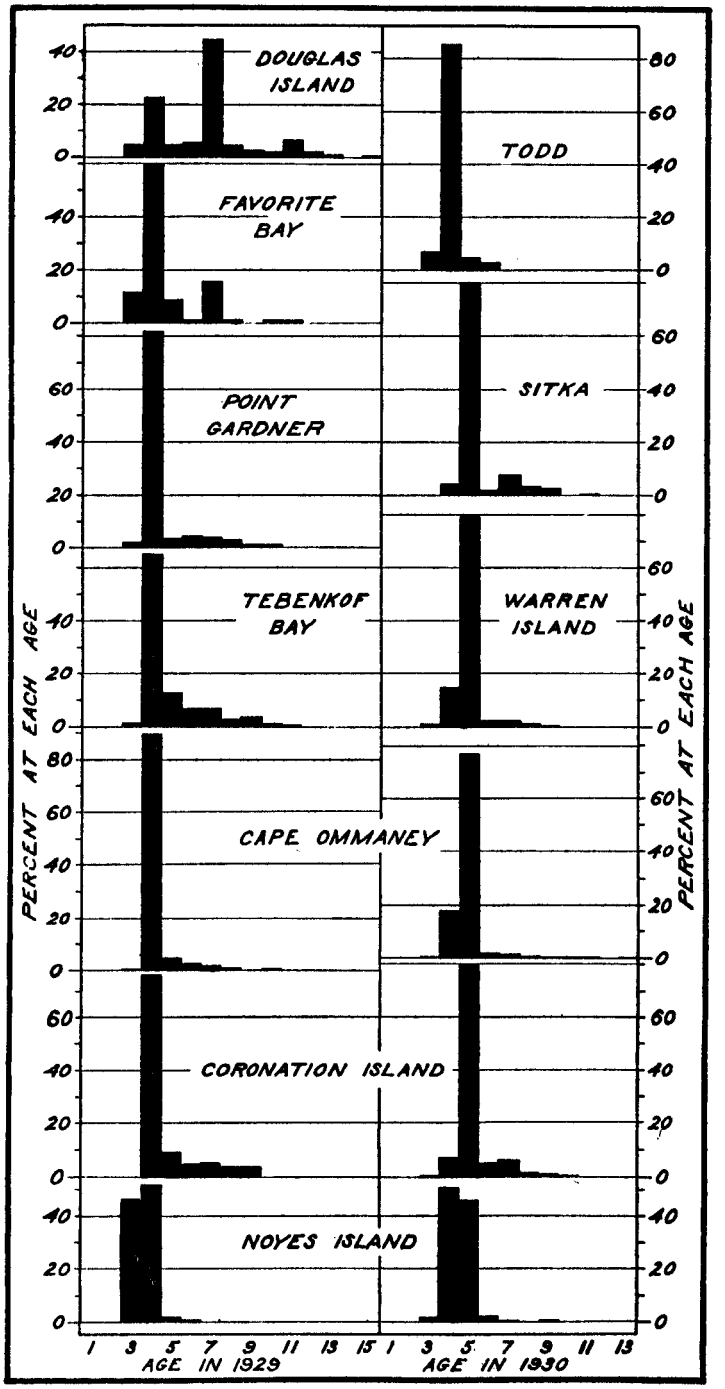

FIGURE 10.—Percentage age distributions of herring taken during 1929 and 1930 in some of the principal fishing grounds.

No recoveries have been made, supporting the previous conclusion of a lack of migration between Juneau and Cape Ommaney.

SUMMARY

The results so far attained in determining the herring populations and the areas inhabited by them serve to show the immense complexity of the problem. Although much remains to be done, the present work has set apart some of the chief areas and answered many pressing questions. It must be borne in mind that where morphological differences have not been shown we can only assume that the populations are the same, until such time as we obtain evidence to the contrary. Such evidence may come from tagging experiments. It must be further noted that the area boundaries shown in figure 2 are merely lines across which neighboring populations do not migrate according to positive evidence. They are not intended to convey the impression that each area necessarily contains only one race. Indeed, the section on tagging shows that area *C* very probably does contain more than one race. With these restrictions in mind the following results are listed:

1. Differences in vertebral count between Wrangell and Warren Island herring indicate that there is no migration through Sumner Strait.

2. Differences in vertebral count between Petersburg and Wrangell herring show a lack of intermingling through Dry Strait or Wrangell Narrows.

3. Differences in vertebral count between Point Gardner and Petersburg show no migration through Frederick Sound.

4. Differences in growth rate and vertebral count indicate a lack of migration along the outer coast between localities lying north and those lying south of Cape Lynch (Heceta Island).

5. The presence of very slow-growing herring in Peril Strait indicates a distinct race and shows a lack of migration through this waterway.

6. Differences in growth rate and vertebral count indicate that the herring of Icy Strait and the vicinity of Juneau do not migrate down Chatham Strait or through Stephens Passage. Failure to recover any of the herring tagged at Auke Bay in the Cape Ommaney fishery tends to confirm this view.

7. A difference of 2.44 standard errors, giving a probability of 0.014 between the mean vertebral counts of Warren Island and Meade Point indicates that there is probably no migration through Keku Strait.

8. Failure to recover any of the tagged herring released at Cape Bendel in the Cape Ommaney fishery indicates a lack of migration between lower Chatham Strait and Frederick Sound.

9. Recovery of tagged herring proves that the great spawning grounds in Sitka Sound are the mainstay of the tremendous herring fishery at Cape Ommaney.

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EFFECTS OF CRUDE OIL POLLUTION ON OYSTERS IN LOUISIANA WATERS

By Paul S. Galtsoff, Herbert F. Prytherch
Robert O. Smith, and Vera Koehring

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 18

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1935

For sale by the Superintendent of Documents, Washington, D. C. - Price 20 cents

EFFECTS OF CRUDE OIL POLLUTION ON OYSTERS IN LOUISIANA WATERS[1]

By PAUL S. GALTSOFF, Ph. D., HERBERT F. PRYTHERCH, Ph. D., ROBERT O. SMITH, and VERA KOEHRING, Ph. D., *United States Bureau of Fisheries*

CONTENTS

	Page
Foreword	144
Introduction (P. S. Galtsoff and H. F. Prytherch)	144
Preliminary field investigations, 1933 (H. F. Prytherch)	146
Survey of oyster bottoms in areas affected by oil-well pollution, 1934 (R. O. Smith)	150
Methods	150
General conditions	150
Lake Barre	152
Lake Felicity and Lake Chien	152
Terrebonne Bay	153
Timbalier Bay	153
Lake Raccourci	154
Lake Pelto and Pelican Lake	154
Examination of oyster beds at mouth of Bayou Grey and Little Lake	155
Conclusions	156
Experimental studies of the effect of oil on oysters	158
Review of the literature (P. S. Galtsoff)	158
Survival of oysters in oil-polluted water (H. F. Prytherch)	159
Experiments with surface film of oil	160
Survival of oysters in sea water passed through oil	161
Immersion of oysters in oil	162
Effect of oil on glycogen content of oysters	163
Experiments with brine	164
Effect of brine on glycogen content of oysters	167
Effect of oil on feeding of oysters (P. S. Galtsoff and R. O. Smith)	167
Effect on the adductor muscle	167
Effect of oil and oil well bleed-water on the rate of feeding of oysters	170
Carmine cone method	171
Drop counting apparatus	172
Preparation of water-soluble fraction of oil	174
Results obtained with the cone method	174
Results obtained with the drop-counting method	183
Effect of bleed water on the rate of feeding	188
Effect of consecutive treatments	191
Effect of crude oil on diatoms (P. S. Galtsoff and V. Koehring)	193
Method	194
Effect of heavy surface layer of oil on Nitzschia culture	196
Effect of oil held on the bottom	197
Effect of water-soluble fraction of oil	199
Effect of oil held in collodion bags	200
Effect of brine on Nitzschia	200
Discussion and conclusions (P. S. Galtsoff)	204
Bibliography	208

[1] Bulletin no. 18. Approved for publication, June 3, 1935.

FOREWORD

The mortality of oysters in Louisiana waters in 1932–33, coincident with the development of oil wells in the coastal areas of the State, brought up again a question as to the possible effect of oil on marine life. In the spring of 1933, at the request of the Louisiana Conservation Department, Dr. H. F. Prytherch was detailed by the United States Bureau of Fisheries to make an investigation in the Terrebonne Parish and adjacent territory with the view of determining the probable cause or causes of the mortality. In 1934, in an attempt to carry out a more comprehensive study, the Bureau obtained from the Civil Works Administration approval of a project to investigate the oil-pollution problem in Louisiana and to carry out both laboratory and field experiments in order to determine the effect of oil on oysters. Unfortunately, out of the $42,000 allotted for this project only an amount of $3,000 was made available, and after the completion of a preliminary hydrographic survey of Timbalier and Terrebonne Bays and adjacent bodies of water the field work was discontinued. Laboratory experiments on the effect of oil on oysters and oyster food were carried out, however, at Beaufort, N. C., Woods Hole, Mass., and Washington, D. C.

Although the exact cause of the mortality of oysters has not been determined, the reports of the field and laboratory investigations throw considerable light on the conditions of oyster beds in Louisiana waters and on the possible effect of oil pollution on oysters.

INTRODUCTION

By P. S. Galtsoff and H. F. Prytherch

The fact that the discharge of oil into natural waters may be detrimental to aquatic life has been recognized for a long time and was a subject of lengthy discussion before the numerous governmental committees (Oil Pollution in Navigable Waters, 1926; Pollution of Navigable Waters, 1930) attempting to remedy the situation by proper legislative action. In view of the widespread oil pollution of coastal waters, especially in the vicinity of large cities and industrial centers, and the interest in this problem shown by many Federal and State agencies, it is surprising to learn that there has been very little direct experimentation on the effect of crude oil or its derivatives on fresh-water or marine organisms and that most of the statements appearing in the minutes of official hearings are based primarily on field observations and frequently represent opinions and assumptions not corroborated by direct evidence.

It is true that in the case of gross pollution conditions in the affected body of water may be such as to make any deeper investigation superfluous. However, when pollution is light or only temporary, the lack of knowledge of the toxic properties of oil and of the manner in which it may affect various organisms, constitutes a serious handicap in developing efficient methods of protection. In the case of the location of oil fields in the coastal area, the question arises as to whether or not the coastal fishery and the oil industry can coexist. The problem is of particular importance in south Louisiana waters where the production of oil has increased rapidly from a total output of 5,032,400 barrels in 1927 to 15,540,341 barrels in 1933, according to Dabney (1934). Drilling operations have been extended to within a few miles of the Gulf of Mexico, particularly in Terrebonne Parish, where, according to the statistics of the Louisiana Department of Conservation, there were 17 wells in opera-

tion in 1933, having a total average daily output of 6,961 barrels. In this parish most of the wells are not located on land, but are situated in the open waters of Lake Barre, Lake Pelto, and vicinity, which constitute one of the most important oyster-producing regions of the State. Pollution of the water has occurred as the result of oil-well operations, and coincident with this condition there has been a high mortality of oysters particularly during the winter of 1932–33 and to a lesser degree during the previous winter. The aggregate losses of the oyster planters, alleged to have been caused by oil-well operations, have been estimated at several hundred thousand dollars.

In January 1933 the Louisiana Department of Conservation received reports of an extensive and serious mortality of oysters in the Lake Barre and Lake Pelto region, which were corroborated by immediate field surveys of its Bureau of Research and the State Department of Health. The chemical studies of pollution and subsequent field and laboratory experiments conducted by these departments are reported briefly by Gowanloch (1934). Similar chemical and biological field investigations were also made by chemists of the Texas Co. and by Dr. C. E. Coates, Dr. A. R. Choppin, and Dr. W. H. Gates of the chemistry and zoology departments of Louisiana State University. In May 1933 the cooperation of the U. S. Bureau of Fisheries was requested by the Louisiana Department of Conservation, following which, field studies were made by Dr. H. F. Prytherch in May, June, and September of the oyster mortality in Terrebonne Parish in relation to oil-well operations in this region. At the Bureau's laboratories in Washington, D. C., and Beaufort, N. C., a series of experiments have been conducted by the authors to determine the effect of different grades of crude petroleum and accompanying brine waters on the survival, feeding, and food of the oyster.

There is no doubt that unavoidable pollution of water by oil and bleed water incidental to drilling operations constitutes a serious danger to local oyster, shrimp, and fishing industries from the point of view of a fisherman, it being immaterial whether pollution has actually destroyed the stock of fish and shellfish or rendered them unmarketable on account of oily taste and emaciated condition of the flesh. In both cases the industry sustains economic losses. Of course, in case of oyster or other mollusks there is a possibility of transplanting the stock to other areas unaffected by pollution. So far as the Louisiana coastal section is concerned, this appears to be only a palliative, for it is but a question of time until the development of oil fields will spread all along the coast and most of the oystermen in the State sooner or later will face the problem which at present confronts the industry in Timbalier and Terrebonne Bays and Lake Pelto, the sites of the present extensive drilling operations.

The questions to which the oyster industry desires to receive a competent answer can be formulated as follows: Whether the unusual mortality which occurred in Louisiana in 1932–33 is attributable to the discharge of oil and bleed water, and how further development of the oil resources of the coastal section may affect the cultivation of oysters. The marine biologist called to provide an answer finds himself in a difficult situation. As often happens in the case of an unusual mortality among fish or oysters, he is requested to investigate the cause or causes of it several weeks or months after death has occurred, and when the conditions responsible for the mortality have already changed or disappeared. There is a general and well understandable tendency on the part of a layman to attribute his troubles to unusual activities or events that occurred in the affected area. The concurrence of the two phenomena, however, does not constitute in itself a proof that one is the cause of the other.

There are two aspects in the study of mortality problems in relation to pollution of water. One is to determine the cause of the mortality, that occurred some time ago, the second is to find out how the pollutant agent may affect marine life and what are the expectations of the fishing industry if the pollution is permitted to continue. From the point of view of conservation, the second problem is of far greater importance, while the parties involved in the controversy regarding the causes of mortality are primarily interested in the first one. Although the present report fails to give a definite answer to the first question, it supplies sufficient data regarding the possible dangers of oil pollution to oysters.

One must bear in mind that actual conditions in the sea may be much more complex than they appear to a casual observer. There is a possibility, for instance, that because of unfavorable meteorological conditions, attacks of parasites, or other unknown factors, oysters already have become weakened or diseased. In that case an additional adverse factor, as for instance a small concentration of a toxic substance in the water, may have been responsible for the mortality, although under more favorable circumstances the oysters might have been strong enough to withstand it. Being ignorant of the past history of the case and not being able to duplicate conditions that existed at the time of greatest mortality, the biologist is unable to determine with certainty the cause of it. He can provide, however, sufficient evidence regarding the toxicity of the suspected pollutant, the manner in which it affects the organism, its fate in the ocean, and from all this information provide a substantial basis for outlining the methods and policies of future conservation.

These considerations and the lack of funds to carry out field observations on the large scale contemplated in the original project, made it necessary for the authors to concentrate their attention on the experimental studies of the effect of oil on the behavior of the oyster and on the growth of diatoms, which constitute the principal part of the oyster diet.

It was thought desirable, however, to present first the preliminary field observations made by H. F. Prytherch in 1933 and the result of the survey made by R. O. Smith in March and April 1934.

PRELIMINARY FIELD INVESTIGATIONS, 1933

By H. F. Prytherch

Terrebonne Parish includes practically the whole oyster-producing region between Barataria Bay and the Atchafalaya River and is the westernmost section in which good oysters are obtained in considerable quantities. According to the Bureau's fisheries statistics for 1930 (Fiedler, 1932), this parish exceeded all others in oyster production and furnished over 360 thousand bushels, valued at $156,213, or approximately 30 percent of the total State crop. Virtually all of the oysters produced here come from private beds, leased from the State, most of which formerly were natural beds that had become depleted through overfishing and the destruction of small seed (spat) by natural enemies. Through the leasing and cultivation of these areas production has been maintained and a better grade of oysters produced.

The usual procedure is to stock the leased areas with seed obtained from natural beds in other coastal sections such as Sister Lake, Bay Junop, Barataria Bay, etc. The seed are planted quite densely at reported concentrations of 700 to 900 barrels per acre which does not allow a great deal of room for subsequent growth and increase in volume. This practice, however, has been generally successful for many years and is apparently caused by the fact that the oyster beds are elevated to some extent

above the surrounding bottom and occupy but a very small percentage of the total acreage of those inshore waters. When the oysters reach marketable size they are removed from the growing areas, culled, and either shipped directly to market or temporarily stored in convenient protected areas near the oyster camps. It was during these operations that the oysters died in greatest numbers, as a result primarily of a weakened condition of the adductor muscle and its failure to maintain closure of the shell in air or water. During shipment the oysters opened quickly and spoiled because of evaporation and the loss of shell liquor, while a high percentage of those transplanted to storage areas soon succumbed to the attacks of crabs, small fish, etc., because of their inability to close the shell. The mortality was greatest during the winter months and occurred on beds located at distances ranging from approximately one-half mile to 9 miles from the Barre oil wells and 1 to 5½ miles from the Pelto wells as shown in figure 1.

During the periods from May 23 to June 1, and from August 31 to September 2, 1933, field observations were made of the oyster mortality in Lake Barre, Lake Pelto, and vicinity in relation to existing hydrographical and biological conditions and particularly in respect to pollution of these waters by oil-well operations. These studies were made several months after the mortality was at its peak and after pollution of the water by oil, hydrogen sulphide, and natural gas had been considerably reduced by action of the Louisiana Conservation Department.

Oil production at Lake Barre and Lake Pelto began in June and September 1929, respectively. The most important wells are those at Lake Barre, 14 of which were in operation on June 1, 1933, with a production on that day of 9,987 barrels of oil according to a report received from the Texas Co. These wells were also producing at that time from 6,500 to 7,000 barrels of brine or "bleed water" daily which after being combined and chlorinated (since February 1933) for removal of hydrogen sulphide was emptied into the bay. Samples of this effluent were found to have a salt concentration of 123 parts per thousand as compared with 15 to 22 per thousand for the surrounding waters. They became quite turbid soon after exposure to air or chlorine through the formation of colloidal suspensions of iron and sulphur, and gradually were covered with a thin film of oil after coalescence of finely divided particles. The daily output of the Lake Pelto wells was much less, amounting to only 57 barrels of oil and 650 to 750 barrels of brine, the latter having a salt concentration of 98 parts per thousand.

Studies were made at 27 stations throughout this region as to the condition of the water and its bearing on the reproduction, growth, and mortality of oysters on both natural and planted beds, located in the immediate vicinity and at varying distances from the oil wells. Particular attention was also paid to the abundance and activities of natural enemies of the oyster and to other marine organisms, particularly mollusks, which might be affected by oil-well pollution.

The following observations were made in respect to the oyster-oil well situation in Terrebonne Parish.

1. Random samples of oysters from planted beds in Lake Barre, Lake Pelto, Timbalier Bay, and vicinity, showed that a high percentage of the oysters had died previously on all but three of these leased areas. The mortality on the various beds ranged from approximately 50 to 95 percent as shown in figure 1 and in virtually every case included only the larger and older oysters of marketable size. Many of those surviving were in poor condition and exhibited retarded and abnormal shell growth during the preceding period.

2. No evidence of unusual mortality or retarded growth was found on the beds at stations 23 and 24 in Lake Felicity, on 2 adjacent plantings at station 16 in Lake Pelto, or on a small natural oyster bed, at station 25, which is located at a distance of approximately 500 yards from the Barre wells. Adult oysters were also growing on the piling of these wells and showed a general vertical distribution extending from 1 to 2 inches above the bottom to nearly the surface of the water. The shells of the latter measured from 2½ to 3½ inches and indicated continuous rapid growth over a preceding period of at least 1 year.

3. The oyster beds in Lake Barre and Timbalier Bay are located at distances varying from approximately 500 yards to 9 miles from the numerous Barre wells. Those in Lake Pelto lie within a radius of from 1 to 5½ miles from wells in that region. The previous observations failed to show any direct relation between the degree of oyster mortality on these beds and their distance from the oil wells.

4. Oysters in all localities contained a considerable amount of ripe spawn. A heavy spawning had already occurred several weeks prior to June 1 and was still in progress at that time.

5. Tow-net collections of microscopic marine life revealed an abundance of healthy oyster larvae as well as those of other bivalve mollusks. In the immediate vicinity of the oil wells the free-swimming larval stages of the oyster were plentiful at all ages from 1 day old to setting size.

6. Examination of old shells and those of live oysters showed that intensive setting or attachment of oyster larvae had already occurred (1) on the natural beds, (2) on the planted beds where the mortality occurred, and (3) on the piling of the oil wells and other submerged objects nearby. Heavy setting was still in progress at the time of the investigation as shown by maximum concentrations ranging from 200 to 500 spat per shell on those collected at the Lake Barre and Lake Pelto wells.

7. The spat or minute seed oysters found throughout Terrebonne Parish were of varying ages and size, ranging from 1 day old or recently attached specimens with a diameter of one seventy-fifth of an inch to those 2 or 3 weeks of age having a diameter of approximately one-fourth to one-half inch. It was evident that metamorphosis of the oyster from the larval to spat stages had been successfully completed and that the growth obtained subsequently under existing conditions was rapid and to all appearances normal. No indications of unusual mortality of spat were observed. Spat collected at the Lake Pelto oil well at depths varying from a fraction of an inch to 2 feet above the bottom were in good condition, as were those found on oysters in the test boxes at the Lake Barre oil wells and on the adjacent natural bed. Though setting and spat production is heavy throughout this region only a small percentage survive because of the attacks of natural enemies such as crabs and the borer (*Purpura haemostoma*).

8. Three natural enemies of the oyster, the borer, *Purpura;* the boring clam, *Martesia;* and the boring sponge, *Cliona,* were found to be abundant on many of the planted beds. There was no evidence of the destruction of adult oysters by the borer. The shells of approximately 50 to 75 percent of the dead oysters examined showed heavy infestation of the boring clam and boring sponge. The numerous small tunnels and perforations made by these organisms had caused partial disintegration and weakening of the shells, interfered with normal shell growth, and, apparently, had been a serious drain upon the vitality of the oyster. Serious sponge attack and perforation of the shell by the boring clam were found in many instances at the point of

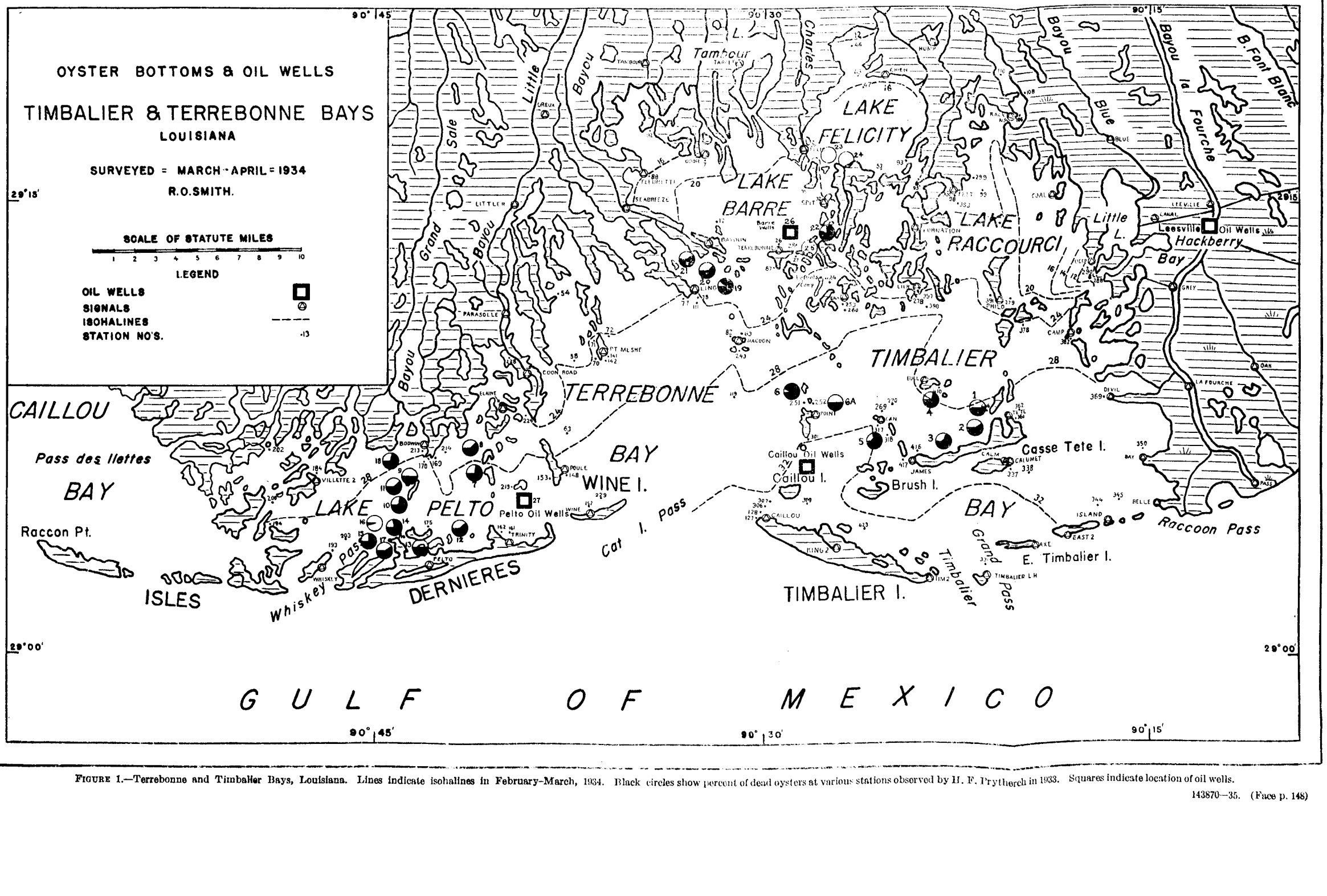

FIGURE 1.—Terrebonne and Timbalier Bays, Louisiana. Lines indicate isohalines in February–March, 1934. Black circles show percent of dead oysters at various stations observed by H. F. Prytherch in 1933. Squares indicate location of oil wells.

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muscle attachment. There was no evidence of a mortality of these natural enemies or of impairment of their growth and reproduction on many areas where a high percentage of the oysters had died previously.

9. A small percentage of the dead oysters and those in a weakened and dying condition showed no serious shell injury by the boring sponge and boring clam. There was one case in particular at station 6 where 95 percent of the oysters had died on a temporary storage bed and were free of shell infestations of these organisms. This bed is located approximately 5½ miles south of the Barre wells.

10. The field studies at the 27 stations in Terrebonne Parish failed to disclose any direct evidence of the destruction of marine animals or plants by oil-well pollution. As indicated previously, conditions throughout this region and in the immediate vicinity of the oil wells were found to be decidedly favorable for reproduction of adult oysters and for the development, attachment, and growth of oyster larvae and spat. Several other mollusks such as the boring clam, shipworm, mussel, *Crepidula*, *Anomia*, and the common borer showed no evidence of unusual mortality and were found to be reproducing and growing throughout this region in an apparently normal manner.

Barnacles and green algae were abundant on the piling of the oil wells and were thriving on submerged cross beams at the Barre well at a distance of 5 feet from the bleed-water discharge where they were subjected continually to a mixture of this effluent and sea water. Blue crabs were observed feeding on these forms at the latter location during the period that the effluent and oyster samples were being collected.

Many species of fish such as trout, croaker, alligator gar, bonnet head shark, channel bass, and bluefish were caught or observed at the Pelto well within 100 feet of the bleed-water discharge. At the Barre well many schools of immature fish, measuring from approximately one-half inch to 3 inches were actively swimming and feeding at distances ranging from 3 to 25 feet from the effluent discharge.

11. *Hydrographical observations.*—Determinations of water temperature, specific gravity, and hydrogen-ion concentration were made at all stations during the period, May 23 to June 1. The records of water temperature give an average of 28.1° C. (86.6° F.) and range from 27° to 29° C.

Measurements of specific gravity at surface and bottom, corrected to 17.5° C., range from 1.0118 to 1.0174 with an average figure of 1.0143. When converted into terms of salinity (grams of salt per 1,000 grams of sea water) the concentration of salts shows a variation of 15.41 to 22.77 per mille, with an average of 18.69 per mille. These salinities are favorable for oyster growth and reproduction and correspond to those found on some of the best oyster-producing areas in this country. The present records of specific gravity have been compared with those obtained in 1906 and 1907 by the United States Bureau of Fisheries (Moore and Pope, 1910) and the Gulf Biologic Station (Cary, 1907) and show that the salt content of the water in Terrebonne Parish was essentially the same in 1933 as at that time.

The observations of hydrogen-ion concentration (as expressed in pH) show an average pH of 8.3 and range from 8.2 to 8.6. These also compare favorably with the Bureau's records of this factor in other oyster-producing regions. Water samples, collected in the immediate vicinity of the Barre and Pelto wells (100 and 300 feet from brine discharge pipes) showed no appreciable difference in hydrogen-ion concentration and salinity at surface and bottom, and no noticeable increase in these factors as compared with conditions on the various oyster beds.

SURVEY OF OYSTER BOTTOMS IN AREAS AFFECTED BY OIL WELL POLLUTION 1934

By Robert O. Smith

METHODS

The survey vessel was a standard oyster and shrimp lugger, 36 feet in length, with 24 inches draft, and a maximum speed of 10 miles per hour. The vessel had been reconstructed to carry scientific equipment and to provide living accommodations for 4 persons.

A total of 423 stations approximately half a mile apart were made. At each station a sample of bottom water was taken for specific gravity; the depth, bottom temperature, and character of the bottom were observed. Occasional surface samples were taken for comparison. An average of 3 minutes was required for these observations at each station. The water samples were taken with a Galtsoff sampler, using a 1-liter Wolff bottle. Depths were measured with a 16-foot sounding pole marked in conformity with Coast and Geodetic Survey practice. Bottom temperatures were read from a Bureau of Fisheries surface thermometer in brass cup case. Bottom water samples at each station were placed in citrate of magnesia bottles and the specific gravities of all were measured by hydrometer at the end of the day's run. Conversion of specific gravity to salinity was made from Knudsen's table.

The stage of the tide throughout the hydrographic work is given as at Wine Island unless otherwise stated.

All locations refer to the Coast and Geodetic Survey progress sketch of Terrebonne and Timbalier Bays prepared February 1934, under the direction of Lt. W. D. Patterson, chief of party. Prior to this work no accurate chart of the region existed. Without this chart, and the signals erected in preparing it, this survey could not have been made, for there are no natural landmarks, no trees, and only occasional human habitation in the form of fishing camps.

GENERAL CONDITIONS

The area covered by the survey extended from Timbalier Bay on the east to Pelican Lake on the west, including approximately 400 square miles (fig. 1). The examination of beds and hydrographic survey began February 19, 1934, and continued to March 15. Two days, March 27 and 28, were spent in Barataria Bay and Lake Washington.

The bottom over this entire area is exceedingly level. There are very few gullies or reefs except where islands are in the process of being broken down. The bottom, composed of soft black mud and mixed with broken shell, was devoid of vegetation at the time of the survey. On account of the shallowness of the water, rarely over 6 feet, moderate winds churn the bays from top to bottom, so that the water is seldom clear except at the passes during flood tide. The oyster reefs are limited to sections where the bottom is comparatively firm. This condition occurs usually only about the margin of the bays or around islands.

The mean range of tide at Wine Island, near the center of the area, is 1.3 feet. Usually there is only 1 high and 1 low tide daily. However, the actual change in

water level is largely determined by the direction and velocity of the wind. Northerly winds drive the water out, while southerly winds pile it up inside. In either case the difference caused by wind may exceed 1 foot under ordinary conditions and as much as 10 feet during a hurricane. Since the land elevation above mean high water seldom exceeds 2 feet, it is evident that even moderate winds result in considerable wash from the marshes.

On many of the beds the oysters were found to be quite variable in fatness. In general, it appears that accumulation of glycogen occurred very late during the winter of 1933–34. Many oystermen stated that their oysters were in better condition during the latter part of March than at any time previously in the season. It is possible that the customary planting level of 600 to 800 barrels (1,500 to 2,000 bushels) per acre is excessive at times for the amount of food available.

Two previous surveys of the area made, by Moore in 1898 (1899) and by Moore and Pope from 1906 to 1909 (1910), were not sufficiently detailed to permit direct comparison of hydrographic data. However, it seems safe to say that except for the elimination of extraordinary fluctuations in density resulting from crevasses, the salinity observed in 1934 appears to be much the same as during the 1909 survey.

In 1898 the water in Terrebonne Bay was found to be fresher than in Timbalier Bay, an observation not borne out by our determinations, as the salinity now is approximately the same in both bays. It is said that owing to the freshness of the water no oysters were found in Terrebonne Bayou above Lake Lagraisse prior to 1883. It was also stated in 1898 that considerable changes in topography were occurring in Terrebonne Bay. Such changes consisted in the tearing down of large amounts of marsh land then present in Terrebonne and Timbalier Bays, and separating Terrebonne Bay from Lake Barre. It was at one time possible to go from Houma to Timbalier Island by land. Undoubtedly this continued destruction of land area has been one of the most important factors bearing on oyster culture in the region, for the absence of obstructing land permits the rapid mixing of Gulf water with the fresh water from the bayous and serves to maintain a relatively high salinity (16 parts per million, February 1934) to the upper parts of Lake Barre and Lake Felicity.

At the time of the 1898 survey market oysters were no longer produced in Barataria Bay, which includes Lake Washington (Grand Ecaille), and only a few dead reefs existed there as evidence of previous importance. The chief oyster-producing region was Terrebonne Bay, which included Lake Pelto. Since then the beds in Barataria Bay have been rehabilitated and extended so that at present some of the finest oysters are produced here. Although Terrebonne Parish still is foremost in quantity, the quality is in general inferior to Barataria Bay.

Insofar as shape, growth, and quality are concerned, observations just made are in almost complete agreement with the early survey, and such discrepancies as exist may be caused in part by confusion in identifying localities from the local names in use at that time.

An effort was made to obtain a definite record of sudden and unexplained losses of oysters in the past. No such occurrences were found other than the occasional killing of oysters said to have been caused by freshets due to breaks in the levee.

LAKE BARRE

The lake has an area of about 40 square miles and contains relatively few reefs, mostly on the southern side.

Mortality of oysters was reported in 1932–33 only from the southeast side of the bay at Lafont's camp (fig. 1), about a mile from Barre operations of the Texas Co. The loss was estimated by the fishermen to have been about 75 percent.

When visited during February and March 1934, oysters were still dying as evidenced by many clean paired shells and occasional dying or newly dead oysters. The dying individuals were very thin and watery as though they had slowly starved to death. The majority of oysters have the shells honeycombed by boring sponge, boring clam or worm, and the interior of the shell usually has from 1 to 6 mud inclusions covered by a thin layer of shell.

Out of 40 stations made on 2 days, February 19, from 11 a. m. to 6 p. m. and February 20 from 9 to 10 a. m., 14 stations were made on flood tide and 20 on ebb. Salinities varied from 16 parts per thousand at Signal Odor to 32 parts per thousand at the Barre wells of the Texas Co. Isohaline contours (fig. 1) indicate that fresh water from Bayou Terrebonne enters the lake at Seabreeze and is deflected down along the islands formerly paralleling the course of the bayou. Salt water from the Gulf is crowded somewhat to the western side of the bayou by fresh water from Lake Felicity.

Temperatures on the bottom at stations on February 19 ranged from 61° F. at 11 a. m. to 60° F. at 5:30 p. m. (16.1°–15.5° C.). On February 20, the temperature had fallen to 55° F. (12.7° C.).

LAKE FELICITY AND LAKE CHIEN

Depths in this section varied from 4 to 6 feet, with a depth of 7 feet in the channel at Seabreeze.

Lake Felicity has an area of about 20 square miles, and Lake Chien, which opens into it on the north, covers about 4 square miles. Although the reefs entirely surround these lakes, production of oysters is mostly limited to their northern and southern shores. Oysters were examined at three places: at the point where Lake Chien joins Lake Felicity; on the northwest shore of Felicity; and on the southeast side of Felicity where it joins Bay Jacko. The oysters observed were not high-grade shell stock, being more suitable for seed or steaming, according to size. No mortality was reported as having occurred in these waters, and samples taken in February contained no shells from recently dead individuals.

Owing to the low specific gravity, drills are not bothersome, so that the area is valuable for seed production. The entrance to the lake is about 4 miles from the nearest oil wells.

Eighteen stations were made in the 2 lakes, from 9:30 a. m. to 3:15 p. m. February 20. Although the survey was carried on mostly during flood tide, the prevailing north wind very probably prevented a normal high tide. The salinity varied from 10 parts per thousand at the head of Lake Chien, to 20 parts per thousand at Grand Pass Felicity on the southwest side of Felicity. The depth varied from 5.5 to 7 feet, but the depth over the reefs around the shore is 2.5 to 4 feet. A depth of 25 feet with a strong current was found in Grand Pass Felicity on the southwest side where Felicity joins Lake Barre. The bottom temperature varied from 54° to 57° F. (12.2°–13.9° C.).

A number of reefs are said to be present in Bay Jacko, but the water was too shallow for the survey boat.

TERREBONNE BAY

This bay covers an area of about 100 square miles, exclusive of bayous, small lakes, and bays. Natural reefs are limited by soft bottom to bayous and the shores of islands in the bay. The section affected by mortality lies between Lake Barre and Terrebonne Bay. The heaviest losses in this region occurred in the vicinity of Lafont's camp, as mentioned above. At the time of this survey, in February 1934, the better oysters were watery. Whether or not this is the usual condition during late winter could not be ascertained.

This area is said to have produced large numbers of high quality oysters in the past. At present (1934) most of the oysters are used for steaming.

At the 99 stations which were occupied on February 26–27 and March 5 and 8, salinities varied from 22 parts per thousand south of the Texas Co.'s wells, to over 32 parts per thousand near the west end of Timbalier Island, and less than 30 at the east end of Wine Island. The opening between these islands is known locally as Cat Island Pass and is by far the largest pass in this region, being about 5.5 miles across. Isohalines show that the western side of the bay is slightly fresher than the east side, due apparently to drainage from Bayous Terrebonne and Little Caillou.

Bottom temperatures on February 26–27 varied from 51° to 59° F. (10.6°–15° C.); on March 5 they averaged 64.5° F. (18.0° C.); on March 8 the average was 70° F. (21.1° C.).

The depth varied from 4 to 10 feet. The lower part of the bay will average 8 feet although there is a channel up to the Texas Co.'s wells through which 10 feet may be carried. The upper part of the bay is mostly 5 to 6 feet deep.

TIMBALIER BAY

This bay has an area of approximately 230 square miles, bisected by a string of islands lying in an east to west direction. Practically all of these islands have oyster beds around them. The bottom, except about Philobruis, is soft mud.

The quality of the oysters varies greatly in the different sections of the bay. On the eastern side, including Devils Bay north through Jacks Camp Bay to Little Lake, excellent shell stock occurs, though on March 24, at the mouth of Bayou Grey and approximately 5 miles from the Leesville wells, the oysters had a pronounced oily taste. At Philobruis, 9 miles from the Leesville wells, oysters are of good quality for shell stock, no oily flavor could be detected, and no mortality was reported or observed. Practically the entire area between Philobruis and the eastern shore of the bay is covered with oyster reefs, all leased. Sponge, boring clam, and conchs are common. Most of the marketable oysters are between 2 and 3 years of age.

The greatest mortality was reported in the vicinity of the islands Castete and Bull, about 14 miles from the Leesville wells, and 9 from the Barre wells. Dredgings made on March 13 consisted of about 90 percent shell. Numerous clean paired shells found at this station indicated that oysters continued to die. As a result of the mortality during the winter of 1932–33, no fresh plantings were made by the leaseholders in 1933. Local setting does not survive, so that seed must be brought from Lake Felicity or from the Louisiana marshes to the east of the Mississippi River.

One hundred fifty-five stations were occupied during the 5 days of March 8, 12, 13, 14, and 15. The salinity varied from 22 parts per thousand at Philobruis,

to 32 parts per thousand at Timbalier Lighthouse (fig. 1). All but 25 samples were taken on flood tide.

The bay is very shallow. On the western and southern sides, the depth ranges from 5.5 to 7 feet. The center and northeast sections are shallower, ranging from 3 to 6.5 feet, but much of it on the eastern side does not exceed 4.5 feet.

On March 8, the botton temperature averaged 71.5° F. (21.7° C.); March 12, 61° F. (16.1° C.); March 13, 65° F. (18.3° C.); March 14, 62° F. (16.6° C.); March 15, 64.5° F. (18.0° C.).

LAKE RACCOURCI

Lake Raccourci, which lies north of Timbalier Bay, has an area of approximately 25 square miles. The depth varies from 2.5 to 4.5 feet. The bottom is soft mud mixed with small clam shells. There are no reefs in the center of the lake. A few oysters are to be found about the entire shore line, but the chief beds are at the northern end and at Philobruis on the southern boundary. At the time of the survey, March 9, 1934, the beds at the upper end of Lake Raccourci were not being worked. No mortality was observed. The salinity varied from 18 parts per thousand in Bay Courant above Lake Raccourci, to 22 parts per thousand at Philobruis. Boring sponge and boring clam were present.

Thirty stations on flood tide and 8 on ebb tide were occupied on March 2, 9, and 14. The bottom temperature on March 2 averaged 63° F. (17.2° C.); on March 9 and 14, the average temperature was 61.5° F. (16.4° C.); and 64.5° F. (18.0° C.), respectively.

LAKE PELTO AND PELICAN LAKE

Lake Pelto extends along an east and west line from Wine Island on the east where it connects with Terrebonne Bay, to Pelican Lake on the west. It connects with the Gulf at the southwest through Whiskey Island Pass. The lake is about 5 miles wide and covers an area of 50 square miles. Oil wells are located at the eastern end of the lake about equidistant from the north and south shores. The few oysters found in this lake were of good appearance and flavor, and some from the western end were equal to any produced in the region. Extensive losses have been reported throughout the lake except along the northern shores and at the extreme western end. The greatest damage, amounting in certain cases to complete destruction of the beds, has occurred about the centrally located islands and along the southern shore within a radius of 5 miles of the oil wells. Of natural enemies, the boring sponge was most abundant, there were some boring clams and some drills. Most of the oysters in this region have very dark gills.

Sixty-two stations were made on Lake Pelto on March 6 and 7. Salinity varied from 26 parts per thousand along the northern shore, to 30 parts per thousand along the southern shore. Bottom temperature varied from 64° to 71° F. (20.0°–21.6° C.) on March 7. The average depth through the center of the lake is about 7 feet. The greatest depth measured was 12.5 feet at Wine Island Pass.

Pelican Lake is situated at the northwest end of Lake Pelto. The area is about 9 square miles. The oysters were fairly fat, well flavored and of medium size. No mortality had occurred here according to the oystermen, and no clean shells were found on the reefs. The bayous leading off from the lake are well populated with coon oysters. The planted beds are limited to firm bottom around the shore and about the islands. Boring sponge was abundant, boring clams common, and there

were a few drills, though the actual abundance of the latter is difficult to determine until they begin to assemble for the spring spawning around the first of April.

On March 7, 9 stations, all on flood tide, were made from Bay Round to the head of Pelican Lake. The salinity varied from less than 24 parts per thousand at the head of the lake to 28 parts per thousand where Bay Round joins Lake Pelto. The average depth in Pelican Lake at three-quarters flood was 3 to 4 feet. In Bay Round, depths of 7 to 9 feet were found. The bottom temperatures on March 7 in Pelican Lake varied from 67° to 69° F. (19.4–19.6° C.). These high temperatures ended March 8, and by the morning of March 9 the temperature was down to 61° F. (16.1° C.) and only rarely exceeded 65° F. (18.3° C.) during the remainder of the month.

Production of oil at Lake Pelto was discontinued April 1, 1934. The total production from this dome is not known, but at the time the survey began (February 1934) only about 40 barrels per day were reported. No oil was produced in Bay Saint Elaine until the first of April 1934, but gas was piped from here to the Lake Pelto wells for fuel.

Bay Saint Elaine lies to the north of Lake Pelto at the eastern end. The area is about 4 square miles, but the shape is so irregular and there are so many marshy islands within that the actual extent of the bay is difficult to determine.

Few, if any, oysters were being marketed from this bay at the time of the survey. Coon oysters were abundant in places and seemed to grow rapidly.

Four stations were made on March 7. Salinities varied from 18 parts per thousand, at the head of the bay where bayou Little Caillou empties into it above Coon Road, to 24 parts per million at signal Elaine. The bottom temperature ranged from 69° to 72° F. (20.5°–22.2° C.), an increase of about 2 degrees per mile from the lower to the upper end. The depth was generally about 5 feet, but at station 225 east of signal Elaine the depth was 16 feet.

EXAMINATION OF OYSTER BEDS AT MOUTH OF BAYOU GREY AND LITTLE LAKE

On March 24, 1934, a trip to the beds was made by oyster lugger from Leesville. Thirteen wells were then in operation along the bayou below Leesville. The surface of the bayou was covered with oil for a distance of 3 miles below the wells. There was a flood tide, with a strong wind from the southeast.

Adult oysters, which had been on the bedding grounds 3 months, had a strong oily flavor. There had been some mortality as evidenced by recently dead paired shells. All shells were covered with a brownish black coating of a tarry consistency. When the bottom was stirred by tongs, an oily patch appeared on the surface. The oysters were of good shape but watery. There was very little gonad development. It was stated that ordinarily the oysters were very milky at that time.

On March 28, 1934, an examination was made of water conditions in Lake Washington, with reference to their bearing on oyster culture. At the time of the survey, there were 44 sulphur wells in operation, each producing 12 tons of crude sulphur per hour. Very little effluent found its way into the lake. The bottom over a short radius around the point of entry of the effluent was covered with a thick brownish layer of diatoms of undetermined species. There was a strong odor of hydrogen sulphide in the air, but the mud samples had very little odor, though they were quite oily.

Based on conditions existing on March 28, there was no evidence that the operation of the sulphur wells had an injurious effect on oysters.

On July 4, 1933, an oil well was out of control for 36 hours, during which time it was estimated that some 3,000 barrels of oil flowed into the lake. No appreciable quantity of oil was lost subsequently. One of the leases was reported to have been heavily covered with oil, and until November oysters were unmarketable on account of the oily flavor.

On March 28, 1934, a combined sample of three-quarters bushel was tonged from these beds. Some of the oysters had a slight oily taste. The tonging caused patches of oil to appear on the surface of the water, indicating that some oil still was held by the mud.

CONCLUSIONS

The purpose of the survey described above was to supply a knowledge of the local and general factors in the environment of the oyster beds in Terrebonne Parish and adjacent territory which might have a bearing on the problem of pollution.

The hydrographic data show that conditions of salinity, current, and temperature were, at the time of the survey, suitable for growing oysters throughout the area covered, and it has not been possible to assign the mortality to any known disturbance of the natural conditions on the oyster beds. Bearing this in mind, special attention was given to several factors whose combined effect would tend to magnify the action of any polluting substance. Among these may be mentioned the shallowness of the water. Even moderate winds stir the bays from top to bottom so that the water carries much suspended matter. Any polluting substance is quickly and thoroughly mixed with the water and is adsorbed by suspended matter; it may be transported over wide areas and deposited on the bottom far from the source of pollution.

In general, mortality has been higher on soft, muddy bottom than on hard ground or reefs. The significance of this is not known, but there is no evidence that silting is directly responsible for the mortality observed. Probably because of the decomposition of the organic matter, a muddy bottom presents a less favorable habitat for oysters than that found on hard ground.

In 1934, oysters on many of the beds throughout the region did not become fat until February or March, which points to a possible scarcity of food organisms during the fall and winter, or to a disturbance in the functioning of the oysters' organs of feeding. Overcrowding would tend to aggravate this situation. The oystermen state that from 600 to 800 barrels, i. e., 1,500 to 2,000 bushels, are planted per acre. While this quantity may be supported so long as conditions remain normal and the food supply adequate, it is obvious that should mortality begin in such a concentration it is likely to result in the loss of a considerable number of the oysters.

No direct evidence was found that the mortality had been caused by any known natural enemies, although they may have an indirect effect by increasing calcium metabolism or competing for food, and, in some cases, possibly a direct injury by attack or the secretion of poisonous substances, for boring clams, sponges, and worms are abundant in parts of Lake Barre, Timbalier Bay, Terrebonne Bay, and Lake Pelto. The borer has not been included in the above consideration of enemies because its habits, range, and destructiveness are well known, the damage done by it is fairly constant, and its depredations can be eliminated as a cause of the unusual mortality.

Crude oil pollution has been suspected as the chief cause of the mortality. No information is now available upon which to base an opinion as to the validity of this belief. Light films of oil were observed to be generally present in the vicinity of the Lake Barre wells, and below Leesville to the mouth of Bayou Grey. Whether or not this oil was harmful to oysters could not be determined in the short time allotted to the survey. But regardless of any alleged toxicity of oil to oysters, two facts should be borne in mind. First, oil in water is quickly taken up by oysters, imparting an oily taste to the flesh which renders the meat unsalable. Second, the effect of oil pollution will last over a long period, for the oil is carried to the bottom by suspended mud particles and released from time to time by storms, tonging, or dredging.

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EXPERIMENTAL STUDIES OF THE EFFECT OF OIL ON OYSTERS

REVIEW OF THE LITERATURE

By PAUL S. GALTSOFF

So far as the author was able to ascertain, the literature on the subject is rather meager, comprising less than a dozen papers. On the basis of a small number of experiments with water-gas tar carried out in 1912 at the United States Bureau of Fisheries station at Woods Hole, Mitchell (1914) arrived at the conclusion that in constantly renewed sea water tar shows no noticeable effect on oysters. Fatal effects are produced however, when considerable quantities of water-gas tar are in intimate contact with oysters kept in stagnant water.

Orton (1924) when studying the causes of the unusual mortality among oysters in England during 1920 and 1921, made a few experiments with oil and arrived at the conclusion that the petroleum residue is not seriously poisonous to oysters, as all of them kept in a jar covered with a thick film of oil survived at least 7 weeks. Similar results were obtained in the laboratory of the Scottish Biological Association (Orton, 1924). Examination of water made by the Government chemist (Orton, l. c., p. 42) showed that the sample of water in which the oysters were kept contained traces of the original petroleum waste in solution and in addition small quantities of substances of an acidic character. The latter, probably naphtenic acids which exist in certain petroleums, may have been present originally in the petroleum waste used in Orton's experiments or may have been derived from the waste by some chemical or biological action of the sea water.

Contrary results were obtained by Leenhardt (1925) who showed that the mortality of both European and Portuguese oysters (*Ostrea edulis* and *Gryphea angulata*) kept in water covered with petroleum increases in proportion to the amount of the latter. Thus, no mortality was observed in the oysters kept for a month in water containing from 0.01 to 0.05 percent petroleum. When the quantity of petroleum was increased to 0.1–0.5 percent only 2 or 3 oysters out of a dozen survived. In the water containing 2 percent petroleum all oysters died within 1 week. Although Leenhardt states that water was changed and presumably the oysters did not suffer from lack of oxygen it is not clear how often the water was renewed. From the observations that the same mortality occurred in the oysters that never were in direct contact with petroleum as in those which were periodically covered with it, simulating the conditions on tidal flats, Leenhardt concluded that oil contains a substance soluble in sea water, and poisonous to oysters. Unfortunately both Orton's and Leenhardt reports are very brief and fail to give all the details of the experiments.

More comprehensive investigation on the effect of oil on fish was carried out by Roberts (1926) who demonstrated that oil extracts (gas oil, Diesel oil, 600 seconds and 1,500 seconds oil) prepared by shaking 100 cc of oil with 2,000 cc of boiled and filtered river water are toxic to brown trout. He attributed the toxicity to both soluble toxic substances and emulsions. Mention should be made also of the work of Stephen (quoted from Roberts, 1926) who described the adverse effect caused by a film of paraffin 0.03 mm in thickness on pelagic larvae of plaice and flounders; and of the experiments of Jee and Roberts (1923) with fresh-water shrimp killed by contact with fuel oil, and with caddis larvae and fresh-water shrimp killed by

immersion in a fuel oil extract. Gardiner (1927) found that the aqueous extracts of tar were completely without effect on freshly fertilized eggs and on "eyed" ova of trout, and that the resistance of trout alevins to the toxic action of phenol decreased with age. Alevins 60–66 days old were quite unaffected by 2-hour immersion in a solution of 40/100,000 phenol, whilst fry 110–115 days old were unable to withstand more than 15 minutes immersion.

Elmhirst (1922) found that oil in water had no effect on a number of bottom organisms (Purpurea, Serpula, Authozoa, Ascidia, Mollusca) and many planktonic forms although the latter were killed when they came in direct contact with oil.

According to James (1926), under conditions approaching those prevailing in nature, a 0.1 percent dilution of light or heavy bunker oil exerts no effect on the development of cod eggs, but toxic effect of the same oils becomes apparent under conditions of limited circulation and aeration. Slight injurious effect is exerted by the same oils upon larval flounders. He rightly states that further research should be based upon more specific knowledge of the physical and chemical phenomena accompanying oil pollution.

Considerable discrepancies in the results of the experiments mentioned in this brief revue may be attributed to various causes, namely, differences in the chemical composition of oils used, defects in experimental technique and small number of observations. It has been the purpose of the present experiments to obtain a better understanding of the effect of oil and brine on oysters and to carry them on a more comprehensive scale than has been done before. The experimental investigation comprises two distinct parts; a study of the effect of oil and bleed water on mortality, rate of feeding and behavior of the adductor muscle of the oyster; and a study of the effect of oil on the growth of a diatom. For the latter experiments the culture of a single species of *Nitzchia closterium* E. was used. It is believed that the results obtained with this planktonic species which occurs in the normal habitat of the oyster, are applicable to other planktonic diatoms.

Most of the experiments on oysters were carried out at the United States Fisheries laboratory at Beaufort, N. C. Studies on diatom growth were made at the Bureau of Fisheries laboratory in Washington and Woods Hole, Mass. Since the experiments carried out by the authors were performed at different times and under different conditions, the results of their investigations are presented separately under their respective names.

SURVIVAL OF OYSTERS IN OIL-POLLUTED WATER

By Herbert F. Prytherch

The plan and purpose of these experiments was to expose oysters to high concentrations of the principal polluting substances from the oil wells in order to determine their effect on growth and survival. The oysters were subjected to crude petroleum, sludge, brine-effluent water, and hydrogen sulphide, samples of which, with the exception of H_2S, were collected previously at the wells by the author and stored in glass containers. These studies were conducted at the United States Fisheries Biological Station at Beaufort, N. C., and involved the use of several

different methods and apparatus, a description of which is furnished with each series of experiments. Special studies were also made of the changes in glycogen content of oysters after continuous exposure to three different grades of crude petroleum and varying concentrations of brine water from the Barre wells. The glycogen analyses were performed by P. S. Galtsoff.

EXPERIMENTS WITH SURFACE FILM OF OIL

The shell movements of the oyster indicate whether it may or may not be feeding and also reflect quite accurately its reactions to environmental conditions. Graphic records were obtained of the shell movements of one representative oyster in each of the experimental and control jars. For this purpose adult oysters of approximately the same age and size were immobilized in a horizontal position by cementing the lower valve to a brick or piece of slate. The upper valve was free to move, and, by means of a simple arrangement of levers and pen, its movements were transmitted and recorded continuously on a revolving smoked drum as shown in figure 2.

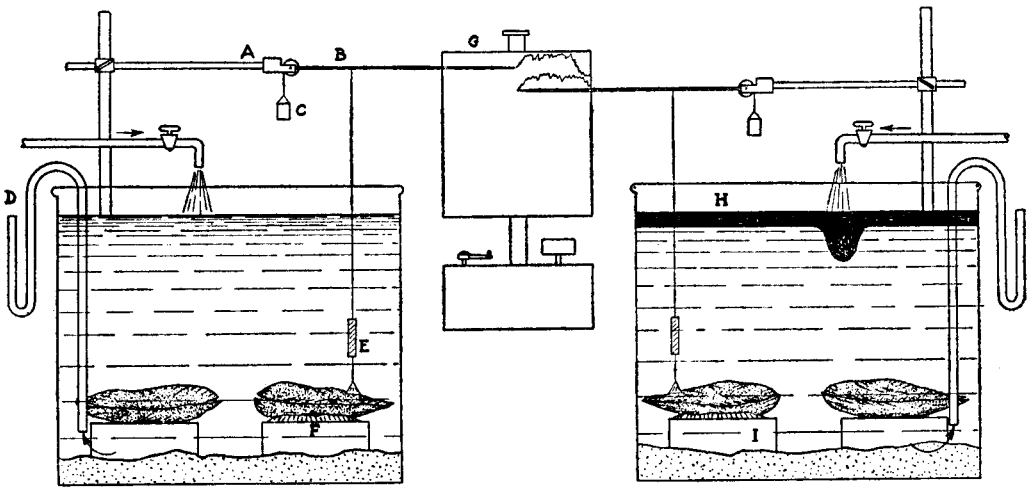

FIGURE 2.—Diagram showing arrangement of apparatus for obtaining comparative records of shell movements of oysters in sea water (control) and in sea water passed through oil (experimental). A, light muscle lever; B, aluminum pen; C, counterbalance weight; D, constant level arrangement; E, rubber universal joint and light rod connecting upper valve of oyster to recording pen; F, oyster cemented to brick (control); G, kymograph; H, layer of oil; and I, experimental oyster.

A series of experiments was arranged, employing 5 glass jars of 6-liter capacity, in each of which 2 small and 2 large adult oysters were placed, 1 of the latter being attached to the recording apparatus. Four of the jars were covered with a heavy surface layer (50 cc) of the following oils and sludge—grade A and grade B crude petroleum from the Barre wells, a composite sample of crude petroleum from the Pelto wells, and basic sludge collected from the storage tanks at the Barre wells. Each experimental jar was supplied with running sea water, which was introduced above the oil film at the rate of 8 liters per hour as shown in figure 2. This series of experiments was conducted from July 3 to September 4, 1933, during which time the surface layer of oil and sludge was renewed weekly. The temperature of the water ranged from 24.8° C. to 28.5° C., and the salinity from 32.7 to 33.4.

The results of these studies are shown in table 1. All of the large adult oysters survived, and those attached to the recorder and exposed to oil and sludge showed essentially the same behavior as the control in respect to shell movements and ability

to maintain closure when kept in air for over 72 hours after completion of the experiment. Records of shell movements of these oysters made for 2 days before exposure to oil and sludge showed no noticeable differences in comparison with those obtained during and at the end of the experiment. Examination of table 1 shows that the experimental oysters were open on an average of 10 to 13.6 hours daily as compared with 11.2 hours for the control specimens. This difference, however, is not significant if allowance is made for the individual variations in oysters in respect to duration of open periods. For example, in other experiments 16 control oysters in running sea water (temperature 22° to 30° C.) showed an average daily open period ranging from 7.5 to 14.2 hours. Hopkins (1931) states that oysters at Beaufort, N. C., averaged between 10 and 14 hours per day open in running water.

TABLE 1.—*Length of time oysters remained open in running sea water passed through surface layers of oil and sludge*

[July 3 to Sept. 4, 1933]

Specimen	Medium	Total hours open	Average number of hours per day open	Percent of time open
No. 1 (control)	Running sea water—no oil	719	11.2	46.8
No. 2 (experimental)	Running sea water—Barre oil A	783	12.2	51.0
No. 3 (experimental)	Running sea water—Barre oil B	664	10.3	43.2
No. 4 (experimental)	Running sea water—Pelto oil	641	10.0	41.7
No. 5 (experimental)	Running sea water—Barre sludge	870	13.6	56.6

During the last 2 weeks of the experiments 7 of the small adult oysters died, the losses occurring as follows: Control, 2; Barre oil A, 1; Barre oil B, 2; Pelto oil, 2; Barre sludge, 0. Similar losses have occurred in previous experiments not involving oil pollution and are believed to be due to the fact that these oysters were collected from a densely populated bed near the laboratory and consequently were not in as good condition as the larger oysters which were obtained from planted beds.

SURVIVAL OF OYSTERS IN SEA WATER PASSED THROUGH OIL

According to Gowanloch (1934) the toxicity of Louisiana crude petroleum can be demonstrated by continuously exposing oysters to sea water passed through a heavy layer of oil. A similar series of experiments was conducted at the Beaufort laboratory using a large wooden tank having 4 watertight compartments in each of which were placed 25 small, adult "coon" oysters from a bed adjacent to the laboratory and 25 large oysters obtained from planted beds in Newport River. The arrangement of the equipment in one of experimental compartments is shown diagrammatically in figure 3. One compartment was used as a control and the other 3 supplied with the same amount of running water at the rate of 20 liters per hour, which was passed through 1 liter samples of the following oils: Barre grade A, Barre grade B, and Pelto composite. The experiment was in operation from March 26 to July 27, 1934. At the completion of the experiment it was found that there was little difference in the survival of the large adult oysters in the control and experimental jars, though the small oysters exposed to oil showed a slightly greater mortality than the controls. The results of this series of experiments are given in the following table (table 2). In reviewing the results, consideration must be given to the possibility that certain compounds in the oil may reduce the oxygen content of the inflowing water and that the oil itself may

act as a filter and prevent many food organisms from reaching the oysters in the experimental tanks.

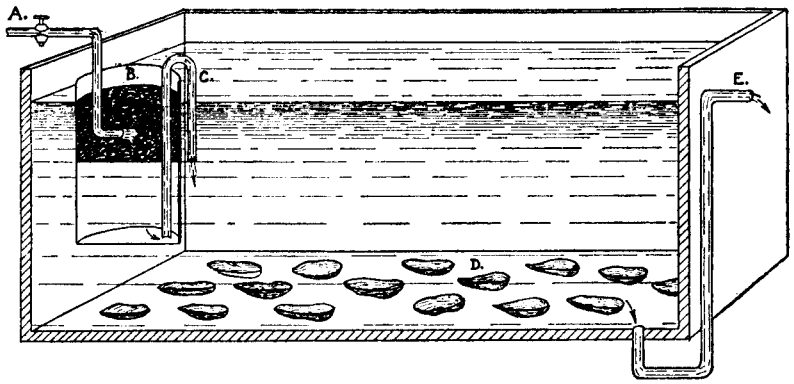

FIGURE 3.—Cross section of apparatus used to expose oysters to sea water passed through oil and smudge. A, sea water intake; B, glass cylinder containing 1 liter of oil; C, siphon tube; D, oysters; and E, overflow.

TABLE 2.—*Survival of oysters in sea water passed through oil*

	Total number of live oysters				Percent survival according to size	
	Apr. 30	May 30	June 30	July 27	Large	Small
Tank no. 1 (control—no oil)	50	39	29	23 (12 large, 11 small)	48	44
Tank no. 2, Barre oil A	50	37	24	18 (11 large, 7 small)	44	28
Tank no. 3, Barre oil B	50	38	29	21 (11 large, 10 small)	44	40
Tank no. 4, Pelto oil	50	36	25	do	44	40

IMMERSION OF OYSTERS IN OIL

The purpose of these experiments was to immerse oysters in crude petroleum at regular intervals in order to determine if they would be killed by direct exposure to oil or would subsequently recover from such severe treatment. By means of an artificial

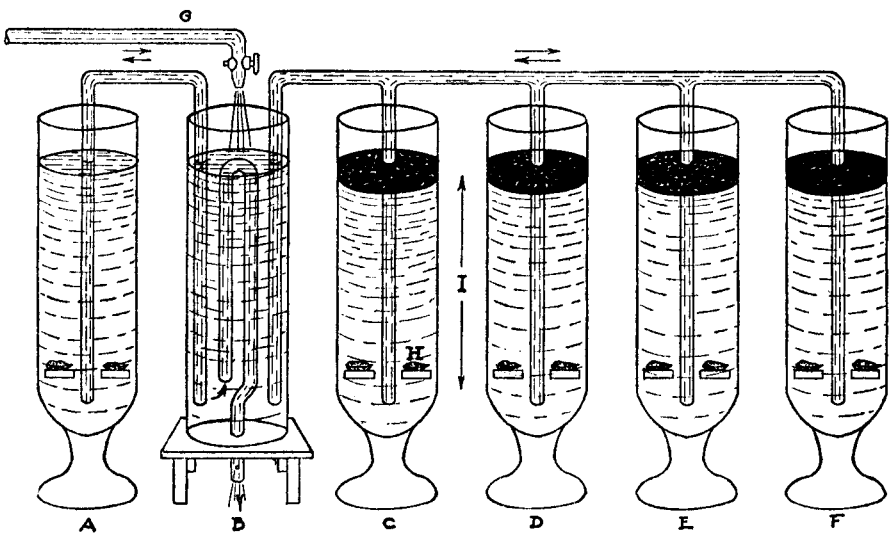

FIGURE 4.—Diagram of apparatus used to immerse oyster in oil at regular intervals. A, control jar; B, automatic siphon jar; C-F, experimental jars containing different grades of petroleum and sludge; G, sea water intake; H, oysters (4 per jar); I, vertical movement of oil layer during each artificial tidal cycle.

tidal arrangement a heavy surface film of oil was made to cover completely the oysters at intervals of 1 and 2 hours. The equipment used, as shown in figure 4, consisted of

5 tall hatching jars of 5 liter capacity, in each of which 4 adult oysters were elevated above the bottom by a 3-inch layer of clean oyster shell. An additional jar containing an automatic siphon arrangement was connected with each hatching jar by glass and rubber tubing so as to bring about the filling and emptying of these jars at regular intervals. One control and 4 experimental jars were used in each series of experiments, each of the latter containing a heavy surface layer (50 cc) of the following: Barre oil grade A, Barre oil grade B, Pelto oil (composite sample), and Barre sludge. After the experiments had been in progress for approximately 3 weeks, 50 cc of each of the above oils and sludge were added to each experimental jar, respectively.

Four separate and complete series of experiments were conducted during the period from September 20, 1933, to January 3, 1934, in which a total of 64 oysters were completely immersed in oil at intervals of 1 and 2 hours over a period of 6 to 8 weeks. The results of these studies are given in table 3. In the first series (1 hour interval), which was conducted in the early fall at fairly high water temperatures, there was a loss of 31.25 percent of the oysters exposed to oil and 50 percent of the control oysters. In the second series the losses in the control and experimental jars were the same amounting to 25 percent. In the third and fourth series (2 hours exposure interval) not a single specimen died in either the control or experimental jars or during the subsequent period of 3 months when they were returned to natural conditions in the harbor. During the course of the experiments it was frequently observed that the oysters kept the shell open when covered with oil and that the formation of new shell was much greater in the experimental oysters than in the controls.

In order to test further the toxicity of water contaminated with oil and sludge, the overflow from all jars used in series 1 and 2 was passed into a tank containing 22 seed oysters, 22 clams (3 species), 4 gastropods (2 species), and 6 anemones, none of which died during the course of the experiments. In the third and fourth series the overflow water was passed into a tank containing approximately the same number and kind of marine organisms as the former and in addition 6 small fish (Fundulus, Hypsoblennius), all of which survived and appeared to be in a healthy condition.

TABLE 3.—*Survival of oysters after immersion in oil and sludge at regular intervals of 1 and 2 hours over periods of 6 to 8 weeks*

Conditions	Series no. 1 (Sept. 20 to Oct. 31)		Series no. 2 (Sept. 20 to Oct. 31)		Series nos. 3 and 4 (Nov. 2 to Jan. 3)		Total results (Sept. 20 to Jan. 3)	
	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental
Number of oysters used	4	16	4	16	8	32	16	64
Number of times oysters immersed in oil	0	1,008	0	1,008	0	720	0	720-1,008
Number oysters alive at end of experiment	2	11	3	12	8	32	13	55
Percent survival by jar:								
Control	50		75		100		81.2	
Barre oil A		75		75		100		87.5
Barre oil B		75		50		100		81.2
Pelto oil		50		75		100		81.2
Barre sludge		75		100		100		93.7
Percent survival, total	50	68.7	75	75	100	100	81.2	85.9

EFFECT OF OIL ON GLYCOGEN CONTENT OF OYSTERS

This series of experiments was conducted to determine the effect of 3 different grades of crude petroleum on the glycogen content of oysters over a period of 4 weeks (Dec. 6, 1933, to Jan. 4, 1934). Two hundred and ten oysters of uniform age and size were used, of which a representative sample of 10 oysters was taken for glycogen

analysis at the beginning of the experiment. The experiments were conducted in a specially constructed wood tank having 4 compartments of equal size in each of which 50 oysters were placed. Each compartment had a capacity of 135 liters and, by means of an automatic siphon arrangement similar to that shown in figure 7, received an equal amount of sea water, which was completely renewed every 3 hours during the course of the experiment. One compartment was used as a control and the other 3 covered with a heavy layer of crude petroleum (2 liters each) of the following grades: Barre oil, grade B; Barre oil, grade A; and Pelto oil composite sample. The oil completely covered the surface of the 3 experimental tanks and during each low-water interval was approximately one-half inch above the oysters. At the end of each week 10 oysters were taken from each compartment and analyzed for glycogen content by P. S. Galtsoff.

The results of this experiment, given in the following table, indicate a slight decrease in the glycogen content of oysters kept in oil-polluted water.

TABLE 4.—*Effect of heavy surface layer of oil on glycogen content of oysters*

[Experiment G 1]

Item	Percent glycogen, fresh basis					
	Dec. 6	Dec. 13	Dec. 20	Dec. 28	Jan. 4	Average
Control	1.72	2.81	2.68	2.67	1.62	2.30
Barre oil B	(1.72)	1.89	1.82	2.56	2.54	2.10
Barre oil A	(1.72)	1.62	1.57	1.98	2.22	1.82
Pelto composite	(1.72)	1.69	.....	1.42	2.29	1.80

EXPERIMENTS WITH BRINE

The principal effluent from the oil wells in Lake Barre and Lake Pelto is the brine water that is separated from the petroleum. The quantity discharged daily, at the time of the oyster mortality, varied from approximately 5,000 to 7,000 barrels for the Barre wells and from 650 to 750 barrels for the Pelto wells. The composition of petroleum brines, according to Clark (1924), has been found in many instances to be quite similar to that of ocean water although modified by local conditions and differing in concentration. Such waters have been variously interpreted, sometimes as fossil sea water which was entrapped in the original sediments, and sometimes as derived by leaching from beds of salt.

Analyses of the brines from the Barre and Pelto wells are given in table 5, together with those of 3 samples of sea water which were collected from the following localities: (1) Oyster bed of St. Pierre, west of Barre walls, where a high mortality of oysters occurred, (2) oyster bed at Sea Breeze where no mortality occurred, and (3) Gulf of Mexico in ship channel at Buoy No. 3. These analyses, prepared by the Port Arthur laboratory of the Texas Co., show that the brines are quite similar to the sea water found in this region in respect to the presence and relative amounts of the different salts but differ as to their concentration. The samples of Barre brine that were used in the subsequent experiments showed a salt concentration of from 122.8 to 123.5 parts per thousand, while those from the Pelto wells varied from 97.0 to 98.5 parts per thousand. The salt content of the water over the oyster beds is considerably lower and was found, during the field survey in May 1933, to vary from 15.41 to 22.77 parts per thousand, with an average of 18.69.

TABLE 5.—*Analyses of brines from oil wells at Lake Barre and Lake Pelto, and sea water from oyster beds and Gulf of Mexico*

Constituents	Barre brine	Pelto brine	Oyster bed, Lake Barre	Oyster bed, Sea Breeze	Gulf of Mexico
pH value	7.0	7.5	8.1	7.9	8.7
Specific gravity 60° F./60° F.[1]	1.109	1.0735	1.016	1.009	1.016
	Parts per 100,000	*Parts per 100,000*	*Parts per 100,000*	*Parts per 100,000*	*Parts per 100,000*
Suspended matter[1]	5.6	3.70	1.0	1.2	1.3
Ash of suspended matter[1]	1.5	.40	None	.4	.7
Iodine adsorption as hydrogen sulphide (H_2S)[1]	.29	5.34	.046	.039	.12
Alkalinity as calcium carbonate ($CaCO_3$)[1]	33.5	31.2	10.8	11.2	9.9
Silica (SiO_2)[2]	14.0	6.4	5.0	2.5	1.5
Iron and aluminum oxides (R_2O_3)[2]	20.9	68.0	8.3	4.9	1.7
Manganese oxide (Mn_3O_4)[2]	1.1		.7	.6	.3
Calcium oxide (CaO)[2]	474.0	395.0	34.0	24.0	38.0
Magnesium oxide (MgO)[2]	225.0	320.0	123.8	86.4	125.3
Alkalies calculated as sodium oxide (Na_2O)[2]	7,190.0	4,460.0	735.5	570.6	873.4
Sulphur trioxide (SO_3)[2]	24.8	27.0	130.0	88.2	131.5
Chlorides as chlorine (Cl)[2]	9,831.5	9,526.0	1,151.3	786.5	1,150.9
Silica (SiO_2)[3]	14.0	6.4	5.0	2.5	1.5
Iron and aluminum oxides (R_2O_3)[3]	20.9	68.0	8.3	4.9	1.7
Manganese oxide (Mn_3O_4)[3]	1.1		.7	.6	.3
Calcium chloride ($CaCl_2$)[3]	938.2	744.6	67.3	47.5	75.2
Calcium sulphate ($CaCO_4$)[3]		44.9			
Magnesium chloride ($MgCl_2$)[3]	532.0	756.0	292.4	204.1	296.0
Sodium chloride (NaCl)[3]	13,523.7	9,526.0	1,197.2	947.3	1,455.0
Sodium sulphate (Na_2SO_4)[3]	36.3		230.6	156.4	233.1
Additional chloride from alkali chlorides as chlorine (Cl)[3]	632.4		164.4	29.5	
Total of calculated solids	15,698.6	11,145.9	1,965.9	1,392.8	2,062.8
Residue on evaporation (160° C.)	16,370.0	11,124.0	2,120.0	1,419.0	2,050.5
Residue after gentle ignition	15,804.0	10,238.0	1,908.0	1,281.5	1,914.5
Mineral matter as sulphates	19,484.0	12,380.0	2,427.0	1,672.5	2,471.5

[1] On sample as received.
[2] On sample after boiling, filtering, and making to original volume with distilled water.
[3] Probably combined as indicated.

The purpose of the present experiments was to determine the effect of high concentrations of brine on the shell movements and survival of oysters. Nine large adult oysters were used, each of which was cemented to a brick by the lower valve and connected with a graphic recording apparatus as shown in figure 2, in order that an accurate record of their reactions might be obtained. Each oyster was placed in a shallow glass jar and covered with 4,000 cc of either sea water or a brine-sea water mixture, which was renewed daily. The experiments were conducted for a period of over 3 months—from January 12 to April 16, 1934.

In the experimental jars the oysters were subjected to different mixtures of brine and sea water which contained 12.5, 25, 50, and 100 parts per thousand of Barre brine and 25 and 50 parts of Pelto brine. The former mixtures contained, 1.53, 3.07, 6.15, and 12.30 grams of brine salt per liter and the latter 2.45 and 4.90 grams. During the course of the experiments the average salinity of these solutions was respectively as follows: 33.30, 34.44, 36.71, and 41.25 for those containing Barre brine, and 33.81 and 35.46 for those containing Pelto brine. In the control jars the oysters were kept in normal sea water having an average salinity of 32.17. The temperature of the water in the experimental and control jars was the same and ranged from 4.2° to 23.6° C., while these studies were in progress. Temperature fluctuations of as much as 5 to 13 degrees occurred daily as each new supply of cold harbor water became warmed to room temperature.

The results of the experiments are shown in table 6. None of the oysters died while exposed to brine or during a subsequent period of 1 month when they were kept in running sea water. An examination of the data presented in table 6 shows that oysters remain open for longer periods of time in sea water to which brine has been

added and that this reaction can be correlated with the amount of brine present and salt content of the water. The three control specimens were open an average of 7.26 hours daily as compared with daily open periods ranging from 8.5 to 11.8 hours in experimental specimens subjected to brine in amounts varying from 12.5 to 100 parts per thousand.

In many instances the brine was added when the oysters were open and had been feeding for a short period, which caused one or two partial contractions of the adductor muscle but did not produce closure of the shell or appear to have any noticeable effect upon its subsequent movements. With the exception of specimen no. 7 all of the experimental oysters showed normal records as to the number of shell movements or muscular contractions per hour as compared with their respective records prior to the first addition of brine, and those of the control specimens. In the case of specimen no. 7 there were frequent, nearly complete, contractions of the muscle which might be attributed not only to the higher concentration of brine but also to the high salinity of the water which was considerably greater than that found in the natural environment of the oyster. In spite of such abnormal muscular activity this oyster was able to maintain shell closure for periods ranging from 24 to over 96 hours toward the end of the experiment and subsequently recovered completely in running water.

TABLE 6.—*Comparison of length of time oysters remained open in normal sea water and brine-sea water mixture*

Specimen	Medium	Average salinity	Total hours open	Average number of hours per day	Percent of time open
CONTROL					
No. 1	Normal sea water	32.17	648	7.2	30.0
No. 2	do	32.17	806	8.9	37.0
No. 3	do	32.17	513	5.7	23.7
EXPERIMENTAL	BARRE BRINE				
No. 4	12.5 parts per thousand	33.30	927	10.3	42.9
No. 5	25 parts per thousand	34.44	1,026	11.4	47.5
No. 6	50 parts per thousand	36.71	1,053	11.7	48.7
No. 7	100 parts per thousand	41.25	1,062	11.8	49.1
	PELTO BRINE				
No. 8	25 parts per thousand	33.81	765	8.5	35.4
No. 9	50 parts per thousand	35.46	819	9.1	37.9

One purpose of the experiments with brine was to determine its effect upon the holding power of the oyster muscle, since loss of this function was apparently the immediate cause of the oyster mortality in Terrebonne Parish. Consequently all of the specimens were kept in air for a period of 96 hours, at an average temperature of 19° C., after completion of the experiments during which time they were able to keep the shells tightly closed and later showed no serious effects of such treatment when returned to running water. This test was again repeated 10 days later with the same result.

The previous experiments indicate that the brine waters from the Lake Barre and Lake Pelto oil wells do not affect the muscular mechanism of the oysters in relatively high concentrations provided the quantity present does not increase the salinity beyond the limits favorable for the growth of this shellfish. Since these effluents are greatly diluted before reaching the oyster beds, and since no significant

increase in the salt content of the water was found on these beds during previous field investigations, it is probable that the oysters in this region were exposed to much lower concentrations of brine than those used in the experiments. This is also indicated by the fact that the Barre brine, in concentrations of 50 parts per thousand, was found to be toxic to the boring sponge, whereas a prolific growth of this organism was found on a high percentage of the oysters in the vicinity of the oil wells.

EFFECT OF BRINE ON GLYCOGEN CONTENT OF OYSTERS

During the period from February 7 to March 8, 1934, studies were made of the changes in glycogen content of oysters kept in sea water to which brine water from the Barre wells had been added in varying amounts. Two hundred and ten oysters were used, of which a representative sample of 10 oysters was taken to determine their glycogen content at the beginning of the experiment. For this experiment a 4-compartment wooden tank was arranged as follows: Compartment 1, 50 oysters as control in 135 liters of sea water; compartment 2, 50 oysters in a mixture of 130 liters of sea water plus 5 liters of brine; compartment 3, 50 oysters in a mixture of 125 liters of sea water plus 10 liters of brine; and compartment 4, 50 oysters in a mixture of 120 liters of sea water plus 15 liters of brine. The water in all compartments was changed once each week and continuously aerated during the course of the experiment. The salinity of the water in the different compartments was as follows: Compartment 1 (control), salinity 31; compartment 2, salinity 34.5; compartment 3, salinity 38.7; and compartment 4, salinity 42.8.

At the end of each week 10 oysters were taken from each compartment and analyzed for glycogen content by P. S. Galtsoff. The results obtained are given in the following table:

TABLE 7.—*Effect of different concentrations of Barre brine on glycogen content of oysters*

[Experiment G 2]

Date	Percent glycogen, fresh basis					
	Feb. 7	Feb. 14	Feb. 23	Mar. 1	Mar. 8	Average
Control	2.16	3.33	2.74	1.93	4.36	2.90
Brine, 5 liters	(2.16)	2.66	4.77	2.92	3.24	3.15
Brine, 10 liters	(2.16)	3.06	3.38	5.26	2.92	3.35
Brine, 15 liters	(2.16)	1.71	3.15	2.65	2.25	2.38

THE EFFECT OF OIL ON FEEDING OF OYSTERS

By PAUL S. GALTSOFF and R. O. SMITH

EFFECT UPON THE ADDUCTOR MUSCLE

It has been established that oysters have a well-developed chemical sense and are sensitive to a wide variety of chemical substances (Hopkins, 1932). When an irritating chemical solution is brought in contact with the tentacles, situated along the free border of the mantle at the edge of the shell, they retract sharply. The reaction may spread to the mantle, which contracts, and to the adductor muscle, the response of which to stimulation according to Hopkins (1932) "bears a relationship to concentration similar to that of the tentacular reaction, but the reaction time is longer."

Sharp contraction of the adductor muscle caused by a sufficiently strong concentration of an irritating substance produces a twofold effect: The oyster snaps its valves to expell the irritating substance from the inhalent chamber and then keeps the valves tightly closed to protect itself from further irritation or injury. Since feeding can take place only when the muscle is relaxed and the valves are open, the number of hours the oyster remains open determines to a certain extent the duration of feeding. One must bear in mind that the principal organs of feeding of an oyster are the gills, the function of which consists of filtering large quantities of water and in carrying microscopic food particles toward the mouth. (For a detailed description of the function of gills see Galtsoff, 1928.) Obviously the gills can function only when the valves are open.

The presence of a toxic or irritating substance may affect the adductor muscle which will cause the oyster to close, therefore reducing the number of feeding hours and the quantity of food consumed by it, or it may have direct harmful effect on the delicate ciliary mechanism of the gill. In both cases the feeding of the organism is impaired. The effect of oil on ciliary activity of the oyster is discussed later. At present we are interested only in its effect on the muscular activity.

Records were obtained of the behavior of the adductor muscle of oysters subjected to Pelto oil. Immobilized oysters were attached to 24-hour recording instruments in such manner that every shell movement was transmitted and reproduced graphically upon charts which were divided into hours. The number of hours of activity and the number of closed hours were counted for each day.

The running water, supplied to 4-liter dishes containing 2 mounted oysters, flowed through a layer of oil and out from a siphon. Fifty cc of Pelto oil was used to form the surface layer. As the force of the inflow caused globules to be constantly forced down into the water, much of the oil driven into the water gradually adhered to the sides of the dish and to the mounted oyster. Some oil was also lost occasionally through the outflow, and fresh oil, therefore, frequently was added so that a heavy surface film was always maintained. The oysters were so placed in the dishes of running water that the upper valve was less than an inch below the surface of the oil.

TABLE 8.—*Average number of hours oysters remain open*

IN RUNNING SEA WATER UNDER OIL

Oyster no.	Dates	Days	Hours	Temperature range	Oyster no.	Dates	Days	Hours	Temperature range
	1933			° C.		1933			° C.
13y	June 30–July 12	12	8.6	23–26	406	Aug. 18–25	7	10.8	25–28
Do	July 12–23	11	12.1	22–25	Do	Aug. 25–29	4	8.9	28–30
Do	July 23–Aug. 5	13	8.5	27–30	Do	Aug. 29–Sept. 9	7	11.0	26–29
Do	Aug. 5–12	7	12.2	24–27	Do	Sept. 9–15	6	11.6	28–30
13x	June 31–July 12	11	10.8	23–26	Do	Sept. 15–20	5	12.5	25–28
Do	July 12–19	7	9.5	22–25	Do	Sept. 20–Oct. 2	12	8.5	24–27
Do	July 19–Aug. 2	14	16.6	25–28	169	Aug. 8–17	9	8.2	26–29
354	July 10–23	13	7.3	23–26	Do	Aug. 17–24	7	10.5	24–27
Do	July 23–Aug. 4	12	9.9	26–29	Do	Aug. 24–Sept. 5	8	11.0	26–29
Do	Aug. 4–16	12	8.5	24–27	Do	Sept. 5–13	8	10.2	24–27
Do	Aug. 16–27	11	8.6	25–28	Do	Aug. 18–24	6	10.2	24–27
Do	Aug. 27–Sept. 14	14	10.3	26–29	Do	Aug. 24–Sept. 7	11	7.1	26–29
Do	Sept. 14–26	10	11.5	24–27	Do	Sept. 7–14	7	8.3	27–30
150	July 18–24	6	12.4	25–28	Do	Sept. 14–29	13	8.2	24–27
Do	July 24–Aug. 3	10	13.7	27–30					
Do	Aug. 3–17	14	13.1	24–27	7		292	[1] 10.5	22–30
406	Aug. 13–18	5	8.2	26–29					

[1] Average.

TABLE 8—*Average number of hours oysters remain open*—Continued

IN RUNNING SEA WATER

Oyster no.	Dates	Days	Hours	Temperature range	Oyster no.	Dates	Days	Hours	Temperature range
	1931			° C.		1931			° C.
119	July 19–27	8	11.2	28–30	84	Sept. 2–10	5	10.0	22–25
Do	July 27–Aug. 4	8	12.4	27–30	Do	Sept. 10–21	7	9.0	23–26
Do	Aug. 4–12	8	9.0	27–30	Do	Sept. 21–29	6	7.0	22–25
Do	Aug. 12–20	8	9.1	27–30	121	Sept. 2–10	8	12.0	22–25
Do	Aug. 20–26	6	6.2	27–30	Do	Sept. 10–18	8	11.5	23–26
Do	Aug. 26–Sept. 2	7	7.0	28–30	Do	Sept. 19–27	8	10.0	22–25
Do	Sept. 2–9	4	7.0	22–25	311	Sept. 2–10	8	10.0	22–25
Do	Sept. 9–18	8	6.0	22–25	Do	Sept. 10–18	8	6.4	23–26
Do	Sept. 18–26	8	6.0	22–25	Do	Sept. 19–27	8	6.0	22–25
170	May 31–June 5	5	14.0	22–25		1932			
Do	June 5–13	8	10.4	24–27	68	July 25–Aug. 1	8	12.0	27–30
Do	June 13–22	9	11.1	24–27	Do	Aug. 1–9	8	12.4	27–30
Do	June 22–27	5	9.2	26–29	Do	Aug. 9–17	8	12.1	27–30
Do	June 27–July 3	6	9.0	27–30	Do	Aug. 17–25	8	9.0	28–30
Do	July 3–9	6	12.1	28–30	121	June 20–27	7	8.3	25–28
P	Aug. 21–25	4	10.7	24–27	Do	June 27–July 4	7	9.3	27–30
R	do	4	11.9	24–27	Do	July 4–10	6	11.7	28–30
84	July 19–27	8	8.5	28–30	124	June 25–July 2	7	15.0	27–30
Do	July 27–Aug. 4	8	13.0	27–30	Do	July 2–10	8	14.3	28–30
Do	Aug. 4–12	8	14.0	27–30					
Do	Aug. 12–19	7	10.0	27–30					
Do	Aug. 19–26	7	10.0	27–30	10		292	[1] 9.6	22–30
Do	Aug. 26–Sept. 2	7	10.4	28–30					

[1] Average.

The behavior of the oysters left in running water under oil was compared with that of the specimens kept in clear sea water under the same conditions—mounting, attachments to recording apparatus, volume of dishes, rate of flow of water, and temperature.

In view of the finding by Hopkins (1931) that temperature is one of the factors determining the length of time during which oysters remain open, the comparison between normal and experimental oysters was made for the same ranges of temperature. In presenting the results of the experiments (table 8) the average number of hours of activity of oysters during June, July, August, and September of 1931 and 1932 was compared with the activity of oysters left under oil in July and September 1933. By examining table 8 one can detect no significant difference in muscle behavior of the two groups of oysters. The number of hours of activity per day varied between 8.9 and 12.2 in the oysters kept under oil and between 8.8 and 11 in the untreated oysters. No significant differences are apparent in the average of 292 days of untreated oysters compared with the averages of 292 days of oysters kept under oil. The average numbers of hours of activity per day for the whole range of temperature 22°–30° C. were 9.6 hours for the untreated and 10.5 hours for the experimental oysters.

The question may arise that the difference in the muscular activity of oysters kept under oil and under normal laboratory conditions was unnoticeable because of the wide temperature fluctuations during the experiment. That this is not the fact can be seen from table 9 in which the average number of hours the oysters were open are computed for various temperature ranges. On account of daily temperature fluctuations in the laboratory water supply it was necessary to group the results of the observations into six overlapping classes. The results indicate very clearly that under the conditions of the experiments oil had no effect on the number of hours the oysters were open.

TABLE 9.—*Average number of hours of activity of the oysters*

Item	Temperature ranges, ° C.					
	22–25	23–26	24–27	25–28	26–29	27–30
In running sea water, under oil	10.8	8.9	10.3	12.2	10.5	10.2
In running sea water	8.8	9.0	11.0	8.3	9.2	10.2

In another set of experiments, simultaneous observations were taken on oysters kept under oil and in the control tanks. In these experiments water was supplied at the uniform rate of flow of 6 liters per hour to each of the oysters kept in glass aquaria tanks. Experimental tanks contained enough oil to make a layer 1 centimeter thick. The amount of oil varied from 300 to 350 cc. Water was not permitted to pass through the oil layer, both the intake and out-take tube of the siphon being kept under it. The results presented in table 10 are similar to other experiments. There was no significant difference between the behavior of the oysters under oil and in the controls, the average number of hours of activity being 11.2 and 11.8 respectively.

TABLE 10.—*Average number of hours of activity of oysters under oil and in controls*

Experiment number	Date	Number of days	Temperature range (° C.)	Average number hours per day open		Kind of oil
				Experimental	Control	
1	Oct. 11–30	20	16–22	5.75	7.25	Pelto.
2	Oct. 19–24	6	18–22	11.9	9.5	Do.
3	Oct. 26–31	6	16–20	12.2	16.0	Do.
4	Nov. 1–7	7	18–21	11.6	12.8	Do.
5	Nov. 11–16	6	11–18	16.6	10.6	Do.
6	Nov. 19–25	7	11–17	9.6	10.6	Barre.
7	Dec. 7–16	10	10–15.5	13.8	17.2	Do.
8	Dec. 5–16	12	10–17	8.5	10.5	Barre sludge.
Average		[1] 74		11.24	11.83	

[1] Total days.

The results of these observations show that presence of oil in the water failed to interfere with the muscular activity of the oyster and did not reduce the duration of their feeding.

EFFECT OF OIL AND OIL WELL BLEED WATER ON THE RATE OF FEEDING OF OYSTERS

The purpose of the experiments here described was to determine the effect of various concentrations of the water soluble fraction from crude oil and oil well bleed water on the rate of feeding of oysters. The importance of this matter from a practical standpoint can scarcely be overestimated.

Growth and fattening of oysters depend on three major conditions: 1. Abundance of food organisms in the water; 2, percentage of time the shell of the oyster is open; and 3, rate of flow of food-bearing water through the gills. It is obvious that no matter how abundant food may be in the water, or how long the shell is open, very little food will be available to the oyster unless a current is maintained through the gills. Consequently, any substance which slows down the filtering activity of the gills acts to reduce the quantity of nourishment available to the oyster. In an extreme condition, a substance which reduces the rate of flow might eventually cause the death of oysters without ever being directly toxic.

All experiments reported below were made during November and December 1933 and from June through September 1934. It was thus possible to observe the reaction of oysters to the experimental fluids over a temperature range of from 10 to 30 degrees centigrade and water salinity varying from 27.5 to 36.6 parts per million.

The crude oil, collected by the Louisiana Department of Conservation from the Lake Barre and Lake Pelto wells of the Texas Co. in Terrebonne Parish, was shipped to the laboratory and kept in glass containers. The feeding activity of the oyster was determined by measuring the rate, and quantity of water pumped through the gills by the ciliated epithelium.

CARMINE CONE METHOD

The carmine-cone and the drop-counting methods developed by P. S. Galtsoff were used. The data obtained by these methods may be expressed as volume of water pumped or work performed. The carmine cone method, while not so accurate as the drop counting, has the advantage of being simpler and is better suited for experiments extending over several days. It has been fully described by Galtsoff (1928). Only a brief résumé follows.

The oyster is prepared by carefully forcing the valves apart and inserting a short piece of glass rod to hold them open. A 4-inch piece of gum rubber tubing of ⅛ inch inside diameter is pushed a short distance into the outlet of the gill chamber. Cotton is then used to close the opening between the valves so that no water can escape from the exhalent chamber except through the tube.

The oyster is placed in an enameled rectangular tray approximately 14 inches by 20 inches by 2½ inches, having a capacity of 7 l. A constant level arrangement maintains the level at 5 l (5.25 quarts). An inverted T-tube is supported so that one of the arms may be connected to the prepared oyster and the other with a 20 cm piece of glass tubing of 6 mm bore, marked off with a 10-cm interval. The shank of the inverted T is connected to a glass funnel by a short length of rubber tubing. The funnel contains a suspension of carmine in sea water.

In operation, laboratory supply sea water flows through the tray at a rate of about 200 cc per minute. This flow is stopped at the beginning of an experiment.

Circulation and aeration are accomplished by a stream of air bubbling through an inclined piece of glass tubing about 18 inches in length and ½ inch in inside diameter.

After a preliminary period of half an hour to allow the oyster to adjust itself to the new conditions, it is considered ready for the experiment. A small amount of freshly made carmine suspension is admitted from the funnel and forms at the axis of the tube a cone which is carried out by the current from the oyster. By means of a stop watch, a measurement is made of the time, in seconds and tenths, required for the tip of the cone to traverse the graduated 10-cm. distance. As the mean velocity of the whole cross-sectioned area of the tube is one-half of the velocity at the axis (Galtsoff, 1928), the rate of discharge of water can be easily computed. No such computation was regarded necessary for the purpose of the present experiments, the results of which are presented as velocities of current in millimeters per second.

Each time 10 or more readings were made and the average taken as representative of the velocity of current of water at the axis of the tube. Observations are made

at 30- to 60-minute intervals, and are continued for from 2 to 4 hours, the average rate of flow for this period being considered as the normal rate of pumping. The flow of sea water is then cut off, if it has not already been stopped, and a predetermined amount of sea water is siphoned off and immediately replaced by the same amount of oil extract, prepared in the manner described below. The solution is allowed to remain in the tray from 1 to 24 hours, during which time measurements of the rate of flow are made, first at 15-minute intervals, later at 30- and 60-minute intervals. Measurements on controls run for the same period of time. The total elapsed time for these experiments, from preparation of the oyster to removal from the tray, averages 26 hours.

Treatment with soluble fraction is followed by fresh sea water, measurements being made hourly to indicate the rate and extent of recovery. The plugs, tubing, and glass rod are then removed; and the oyster, suitably marked for future identification, is returned to the large laboratory aquarium.

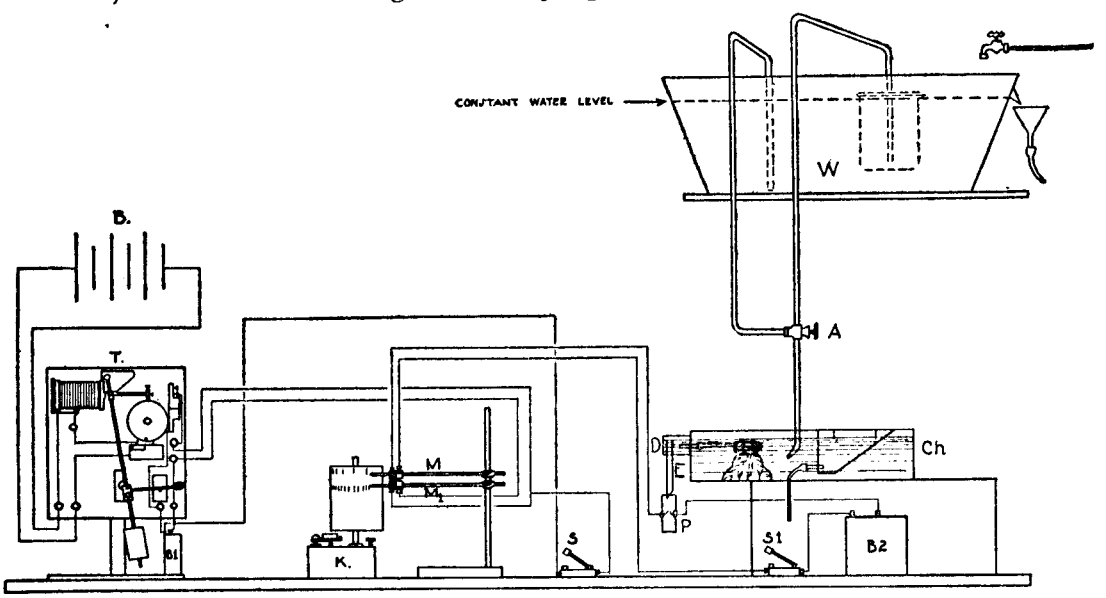

FIGURE 5.—Drop counting set-up for the determination of the rate of flow of water through the oyster gills. W, water supply tank; A, 3-way stop cock; Ch, experimental chamber (made of celluloid) provided with constant level arrangement; D, small cell connected to the chamber; E, overflow; P, drop counter; S, key switch connecting the signal magnet (M_1); S_1, key switch connecting the circuit in the drop counter and 45 volt "B" battery (B_2); K, kymograph; T, electric clock; B, storage battery; B_1, 2-volt dry cells for operation of the signal magnet (M_1); and M, signal magnet connected with a drop counter P.

DROP-COUNTING APPARATUS

The apparatus is illustrated in figure 5. There are three main parts:

1. Supply (*w*), experimental chamber (*Ch*) and recording apparatus (*k*). A three-way stopcock (*A*) supplies either laboratory sea water or a test solution. A constant level device maintains equal pressure for both liquids, delivering 200 cc per minute to the experimental chamber. Temperature fluctuations are kept within 1° C. of the laboratory sea water.

2. Experimental chamber (*Ch*) consists of a celluloid box of 1,500 cc capacity with a small cell (*D*) of the same material attached to its wall and connected through the side by a short piece of glass tubing. An overflow tube (*E*) in the center of the small cell drains through the bottom. The height of this tube must be so adjusted that when the two chambers are connected the water in both of them remains in

equilibrium. A constant level is maintained in the large chamber (*Ch*) by means of an overflow which is so adjusted that the water content of the chamber after the oyster is placed in it will be approximately 1 l. Before beginning an experiment the stopcock (*A*) supplying sea water is turned on and the levels are carefully checked. After the equilibrium has been established a single drop added to the small chamber immediately overflows through the tube (*E*). The oyster, prepared in the same manner as for the cone method, is then placed in the large chamber; and the rubber tubing introduced in the exhalent chamber of its gills is connected to the small horizontal glass tube. Water pumped by the gills will immediately overflow through tube (*E*). An electric stirrer and thermometer are kept in the large chamber.

3. Recording apparatus. Two platinum contact wires sealed in the glass tubing (*P*) are placed under the overflow tube (*E*) so that each drop makes a contact which activates a small signal magnet registering on the smoked revolving drum of a spring kymograph (*K*). Current for operating the magnet is supplied by a 45-volt radio B battery. An electric clock (*T*) operates another signal magnet which records on the drum time intervals of 1 second. Into this circuit is connected a key switch (*S*) and a 2-volt dry cell to mark the time of changing from laboratory supply to test solution and vice versa. Another switch (S_1) disconnects the circuit in the drop counter when the kymograph is not in operation. The kymograph was set to make 1 revolution in 5 minutes.

Since the pumping activity of the oyster transfers liquid (sea water or test solution as the case may be) from the large chamber to the smaller, it is necessary to have a continuous flow into the large chamber to maintain the level, otherwise additional work will have to be done by the gill cilia in raising water from the large chamber into the smaller. The change from sea water to test solution therefore is made instantaneously by a twist of the three-way stopcock (*A*). As soon as the shift is made the oyster is subjected to a gradually increasing proportion of test solution. This solution was allowed to flow into the experimental chamber for 5, 10, or 15 minutes as noted in the tables under the heading "Duration of test solution."

At the rate of 200 cc per minute, from 12 to 15 minutes were required to change the liquid completely in the experimental chamber, so that the oyster was rarely if ever subjected to the full concentration of test solution shown in the tables under the heading "Percent soluble fraction or bleed water." The percentage given in this column represents the concentration of the test solution, not the percentage to which the oyster was subjected. In experiment 55, table 17, for example, it should be understood that the figures do not show the effect of 10-percent bleed water remaining on the oyster for 10 minutes. It does show the effect of gradually replacing sea water with a 10-percent brine solution, the maximum concentration reached being unknown, but somewhat less than 10 percent. The same remarks apply to drop-counting experiments in which water soluble fraction of crude oil was used instead of bleed water.

In the experiments using the cone method the specific gravity of the test solution was brought, as nearly as possible, within ± 0.0002 of the laboratory supply sea water at the time of the experiment. This was not practicable when using the drop-counting apparatus, but in all cases the difference in specific gravity between the laboratory sea water and the test solution was kept as low as possible. Specific gravity determinations were made by Knudsen hydrometers certified by the National Bureau of Standards. Hydrogen-ion concentration was checked with a Hellige-Klett color disk.

No change in pH of sea water was found after stirring with oil, the average both before and after stirring being 7.6.

As in the case of crude oil, bleed water from the Barre and Pelto wells of the Texas Co. was furnished through the courtesy of the Louisiana Department of Conservation.

When received, the bleed water had a disagreeable oily odor, was slightly brown in color, had a pH of 7.1–7.6, and a specific gravity of 1.1064 (17.5°C). A small amount of brown flocculent precipitate present in the bottom of the bottle was left undisturbed when taking a sample of brine for the experiments.

The brine was mixed with distilled water, laboratory sea water, or both just before the beginning of an experiment. The percentage of dilutants was varied in order to keep the specific gravity of the test solution as near that of the laboratory sea water as possible and avoid confusing the results through change in density.

PREPARATION OF WATER SOLUBLE FRACTION OF OIL

The soluble fraction solution was made by placing 6 liters of crude oil and 3 liters of laboratory supply sea water in a glass jar and stirring violently for 30 minutes. The mixture was allowed to stand overnight so that the two fluids would separate as completely as possible. However, only 2,500 to 2,900 cc of soluble fraction solution were recovered from the 3 liters of sea water added. This preparation was regarded as a stock solution from which all other dilutions were made. In the following discussion and in the tables the undiluted solution is called 100 percent soluble fraction. The authors were not in a position to make a chemical analysis of the extracts they used, but due care was exercised in using exactly the same method of preparation. There is a possibility that because of the variation in temperature and salinity of water, the actual amount of substances extracted from the crude oil varied in different samples.

RESULTS OBTAINED WITH THE CONE METHOD

Experiments using the cone method were begun in the early part of June 1934, and completed in the middle of September of that year. The percentages of soluble fraction used were 1, 5, 10, 20, 40, 50, 80, and 100. Since the Pelto wells were no longer producing when this work began, Barre crude oil was used. During the course of investigations, 62 experiments were performed with the cone method. The results of these experiments are summarized and presented in table 11, which contains the essential information regarding the conditions under which the experiments were carried out. The hydrogen-ion concentration of the oil extract was slightly higher than that of the natural sea water. At Beaufort the pH of the water was 7.8. After dilution with distilled water to adjust the salinity, the pH of the sample was as low as 7.6. In Beaufort experiments the observed differences between the sea water and soluble fraction did not exceed 0.3 pH. In a test made at Woods Hole the pH value of the oil extract was 7.4 as compared with the pH 8.3 of the natural sea water. This extract was obtained by stirring oil and water for 24 hours and permitting them to separate in 3½ days. Sea water, the pH of which was reduced by the addition of 0.1 N HCl to 7.4, decreased the ciliary motion by 13.7 percent. The oil extract of the same pH completely inhibited the ciliary mechanism.

TABLE 11.—*The effect of water-soluble fraction of Lake Barre oil on the rate of pumping of water by the gills of the oyster*

[Cone method, Beaufort, 1934]

Experiment no.	Date	Average velocity, current		Effect of treatment (percent)	Duration of test in hours	Specific gravity, 17.5° C.		Increase in specific gravity due to washing	Number of times oil washed	Temperature (° C.)	
		Before	During			Laboratory sea water	Soluble fraction			Beginning	End
CONTROL											
92	June 5	27	38	140.0	59	1.0211				25.0	25.4
98	June 13	29	36	124.1	24	1.0243				25.4	23.7
115	June 27	44	43	97.7	25	1.0257				27.9	28.8
121	July 9	34	30	88.2	43	1.0272				27.6	25.8
139	July 25	51	54	105.8	25	1.0272				27.2	26.0
151	July 31	44	62	140.9	24	1.0270				27.2	26.4
161	Aug. 9	77	75	97.4	24	1.0274				27.4	25.6
179	Aug. 29	44	45	102.3	48	1.0270				25.7	23.9
Average		43.7	47.8	112.0							
1 PERCENT SOLUBLE FRACTION											
135	July 19	47	58	123.4	22	1.0279	1.0275	0.0002	2	27.7	28.9
146	July 27	36	42	116.6	24	1.0274	1.0281	.0009	5	26.9	27.3
154	Aug. 2	54	46	85.2	24	1.0273	1.0274	.0000	21	27.6	27.0
158	Aug. 7	54	48	88.8	24	1.0273	1.0275	.0003	17	26.1	26.7
164	Aug. 13	41	28	68.3	24	1.0277	1.0277	.0004	25	27.7	28.0
168	Aug. 15	58	57	98.3	18	1.0280	1.0281	.0002	19	28.4	28.1
174	Aug. 18	83	81	97.6	18	1.0275	1.0277	.0004	20	28.7	27.7
Average		53.3	51.4	96.9							
5 PERCENT SOLUBLE FRACTION											
106	June 21	67	71	105.9	24	1.0259	1.0259	.0002	4	27.4	27.5
107	do	41	33	80.5	24	1.0259	1.0259	.0002	4	27.2	27.6
138	July 23	46	49	106.5	24	1.0273	1.0275	.0003	1	26.8	27.4
144	July 26	36	41	113.9	18	1.0272	1.0279	.0003	4	27.2	28.0
150	July 31	46	34	73.9	18	1.0270	1.0274	.0006	16	26.8	26.1
157	Aug. 8	61	49	80.3	18	1.0273	1.0275	.0003	17	26.8	26.5
182	Sept. 5	38	45	118.4	18	1.0231	1.0232	.0003	29	25.5	25.3
Average		47.8	46.0	97.0							
10 PERCENT SOLUBLE FRACTION											
104	June 20	59	35	59.3	18	1.0258	1.0259	.0001		27.5	27.2
105	do	28	16	57.1	18	1.0258	1.0259	.0001		26.9	26.8
112	June 26	45	44	97.7	14	1.0259	1.0259			27.9	27.0
113	do	62	42	67.7	12	1.0259	1.0259			27.9	27.6
116	June 27	47	44	93.6	18	1.0257	1.0259		2	28.0	28.3
117	June 28	40	31	77.5	24	1.0249	1.0250			28.2	28.5
170	Aug. 15	59	50	84.7	24	1.0280	1.0281	.0004	19	27.9	27.4
176	Aug. 30	39	28	71.8	24	1.0269	1.0267	.0007	28	23.0	22.0
Average		47.4	36.2	76.2							
20 PERCENT SOLUBLE FRACTION											
99	June 14	47	39	83.0	20	1.0239	1.0251	.0004	1	25.1	26.4
122	July 9	64	42	65.6	18	1.0274	1.0270	.0004	15	27.6	26.7
123	do	52	10	19.2	18	1.0274	1.0270	.0004	15	27.7	27.1
137	July 23	43	13	30.2	24	1.0273	1.0275	.0003	1	27.5	25.8
163	Aug. 13	36	24	66.6	24	1.0277	1.0277	.0002	25	28.2	27.5
175	Aug. 17	40	13	22.5	18	1.0275	1.0277	.0004	20	28.6	27.4
178	Aug. 29	41	9	21.9	18	1.0270	1.0267	.0002	22	25.3	20.4
Average		46.1	21.4	45.6							
40 PERCENT SOLUBLE FRACTION											
125	July 12	74	22	29.7	24	1.0276	1.0274		16	26.4	27.9
126	do	46	21	45.7	18	1.0276	1.0274		16	26.5	27.7
129	July 16	37	13	35.1	23	1.0275	1.0276	.0003	17	28.4	29.6
142	July 25	51	26	51.0	12	1.0272	1.0281	.0005	4	26.7	26.3
153	Aug. 2	74	41	55.4	24	1.0273	1.0274	.0006	16	27.7	27.6
166	Aug. 13	52	11	21.1	18	1.0277	1.0276	.0003	10	27.7	27.9
Average		55.7	22.3	39.7							
50 PERCENT SOLUBLE FRACTION											
128	July 16	58	33	56.8	24	1.0275	1.0276	.0003	17	28.5	29.1
152	Aug. 1	58	22	37.9	24	1.0277	1.0275	.0006	21	27.8	26.3
160	Aug. 7	112	19	16.9	24	1.0273	1.0275	.0002	17	27.3	26.9
173	Aug. 17	74	15	20.2	18	1.0275	1.0277	.0004	20	28.1	26.9
183	Sept. 4	34	12	35.3	24	1.0230	1.0232	.0003	29	24.9	26.1
Average		67.2	20.2	33.4							

TABLE 11.—*The effect of water-soluble fraction of Lake Barre oil on the rate of pumping of water by the gills of the oyster*—Continued

[Cone method, Beaufort, 1934]

Experiment no.	Date	Average velocity, current		Effect of treatment (percent)	Duration of test in hours	Specific gravity, 17.5° C.		Increase in specific gravity due to washing	Number of times oil washed	Temperature (° C.)	
		Before	During			Laboratory sea water	Soluble fraction			Beginning	End
80 PERCENT SOLUBLE FRACTION											
143	July 26	63	0	0	18	1.0272	1.0271	0.0004	13	27.4	28.2
165	Aug. 13	66	27	40.9	24	1.0277	1.0276	.0003	10	27.4	27.0
171	Aug. 15	85	1	1.2	24	1.0280	1.0281	.0002	19	28.2	28.2
172	Aug. 16	53	2	3.8	18	1.0277	1.0279	.0001	26	28.7	28.2
177	Aug. 29	62	0	0	18	1.0270	1.0267	.0002	22	25.3	21.6
185	Sept. 6	115	11	9.5	24	1.0238	1.0241	.0003	24	25.1	22.8
Average		74.0	6.8	9.2							
100 PERCENT SOLUBLE FRACTION											
131	July 18	76	0	0	1	1.0277	1.0274	.0001	18	27.9	27.8
136	July 23	61	0	0	1	1.0273	1.0275	.0003	12	27.8	28.2
140	July 25	59	0	0	2	1.0272	1.0272	.0000	20	27.1	27.2
147	July 30	64	0	0	4	1.0275	1.0274	.0006	6	27.4	27.1
156	Aug. 3	75	0	0	4	1.0275	1.0275	.0000	7	27.7	27.0
162	Aug. 8	51	28	54.9	2	1.0274	1.0276	.0002	23	27.1	25.9
167	Aug. 14	54	11	20.4	6	1.0276	1.0278		18	28.6	28.0
181	Sept. 4	95	23	24.2	24	1.0230	1.0233	.0002	23	24.5	25.2
Average		66.9	7.8	12.4							

One of the difficulties encountered in these experiments lies in the seasonal fluctuations in the laboratory sea water. In preparing soluble fraction there was a slight increase in the specific gravity of water owing to washing with oil. However, the solution used in various experiments was not always heavier than the laboratory sea water used in the same experiment. This was caused by daily fluctuations in the salinity and the necessity of preparing soluble fraction solution in advance of the experiment. The specific gravity of the laboratory sea water used during each experiment and the specific gravity of soluble fraction solution are given in separate columns. They correspond to the measurements of velocity of current before and after treatment. In making up various concentrations of soluble fraction, efforts were made in each experiment to adjust the specific gravity of the solution, by diluting it with sea water of high or low salinity, as close as possible to that of the laboratory sea water. However, this was not always feasible. A complete record of several experiments with 20-, 50-, and 100-percent soluble fraction are given in figures 6 and 7. The vertical lines in these figures indicate time when the laboratory sea water was replaced with soluble fraction of oil.

The figures of the velocity of the current produced by the gills are the averages of 10 or more readings in millimeters per second. They all represent the velocity at the axis of the tube. In the case of the controls, there is no acutal distinction between the periods marked "Before treatment" and "During treatment." Separation has been made aribitrarily on a time basis. To provide a basis for comparison, at least 3 readings were made during a period of 2 or more hours before treatment. The change in efficiency of the ciliary motion, designated in table 11 as "Effect of treatment", is expressed by the ratio of the average velocity of the current during treatment divided by the average velocity before treatment and multiplied by 100.

The effect of changes in specific gravity on the activity of gill cilia has not been studied. However, there was relatively little change in the salinity of the laboratory

sea water from day to day, and this factor is not believed to have affected the results. In most experiments the specific gravity of the test solution was brought within ±0.0002 of the specific gravity of the laboratory sea water so as to avoid stimulation by salinity changes during the course of an experiment. Complete data of the specific gravity of the laboratory water and of the solution of soluble fraction used in the experiments are given in the table.

Fluctuations in temperature may be disregarded insofar as they might influence the results obtained with different concentrations of soluble fraction. The maximum difference in average temperature between the several groups of experiments is 0.9° C. This comparatively slight variation was made possible by using 4 sets of apparatus at a time so that 4 experiments could be run simultaneously. By arranging to have a different concentration of soluble fraction in each tray, the experiments at various concentration levels were carried along together so that seasonal changes in temperature did not affect one group of experiments more than another. Temperature fluctuations during the course of individual experiments were usually less than 2° C.

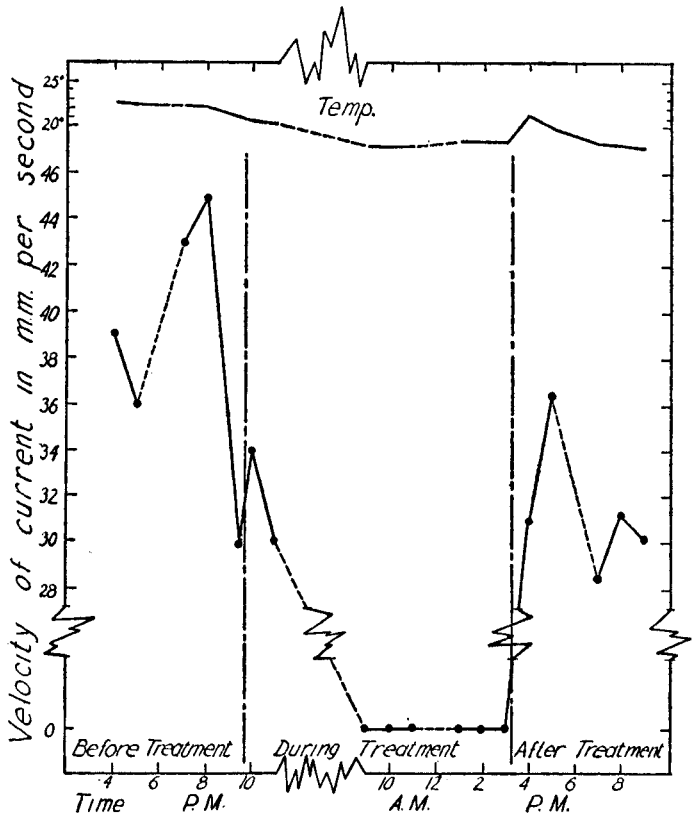

FIGURE 6.—Effect of water soluble fraction on rate of flow of water. Exp. 178.

In 5 of the controls (table 11) the rate of flow increased slowly during the course of the experiments. Two others showed a very slight decrease in rate, and in 1 experiment (no. 121) in which there was no aeration or circulation of water the decrease amounted to 11.8 percent. The characteristic gradual increase in rate of pumping is attributed to recovery from the mechanical stimulation of the plugging operation. The controls cover the period from June 5 to August 29, and except for the first experiment, no. 92, all were subjected to the same range of salinities and temperatures as the experimental oysters. On the average for all the 8 controls there was an increase in the velocity of current which amounted to 12.0 percent. The average duration of test for controls was 34 hours; for experimental oysters, 20.5 hours. The total elapsed time during which each oyster was plugged averaged approximately 6 hours more than the duration test.

In experiments extended from July 19 to August 18, 7 oysters were subjected to a 1-percent soluble fraction solution for from 18 to 24 hours. During this time the specific gravity of the laboratory sea water was very high, ranging from 1.0273 to 1.0280 (17.5°). Water temperature averaged 27.6° C.

The average rate of pumping during treatment, as compared with the rate before treatment, showed a reduction of 3.1 percent (table 11). This is insignificant by itself insofar as indicating any effect of 1-percent soluble fraction solution is concerned. However, this reduction in rate of flow is 15.6 percent lower than the control average during the treatment period.

The greatest decrease in rate of flow resulting from this treatment was found in experiment 164, in which the reduction in rate amounted to 31.7 percent. This maximum effect was obtained with soluble fraction from a sample of oil washed 25 times, the increase in specific gravity caused by washing being 0.0004. If the

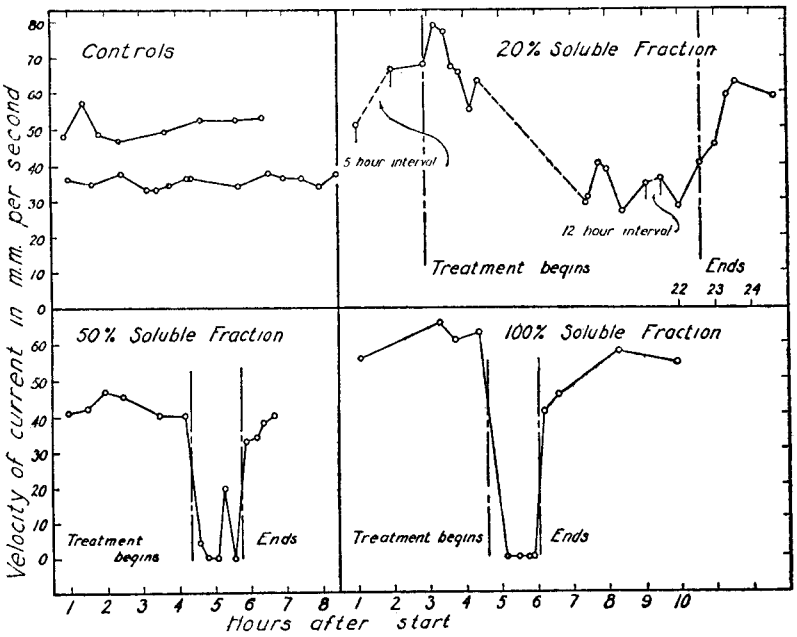

FIGURE 7.—Effect of water soluble fraction on rate of flow of water.

effect of the soluble fraction was owing to mineral salts taken up from the oil by the sea water, it would be expected that the inhibiting power of the soluble fraction on rate of flow would gradually diminish as the salts were exhausted, and that the increase in specific gravity of the sea water after washing with oil would likewise decline. However, this was not the case and the inhibiting effect of the oil extract did not diminish with subsequent washing of the sample.

Except for experiment 164, the effect of treatment with 1 percent soluble fraction gives percentages closely comparable with similar figures for the control experiments. However, considering the orderly decrease in rate of flow caused by treatment with increasing percentages of soluble fraction, it is believed that a 1 percent soluble fraction exerts a definite though slight inhibiting effect on the ciliated epithelium of the gills.

Seven experiments were made with 5 percent soluble fraction solution between June 21 and September 5. The average temperature was 26.8° C., and the specific

gravity ranged from 1.0231 to 1.0273 (17.5° C.). The average rate of flow during treatment is 97.0 percent of the rate before treatment. It would appear that 5 percent soluble fraction is no more toxic to oysters than 1 percent, over a period of 24 hours. However, on closer examination we find an interesting situation in this group. Of the seven experiments, four show an average increase of 11.2 percent during treatment, comparable to 12.0 percent shown by controls. The remaining three experiments have an average rate of 78.2 percent during treatment, comparable to the rate obtained with 10 percent solutions.

In considering factors which might be responsible for the effect, or lack of it, a comparison was made between the conditions of the two groups of experiments.

The average temperature of the four experiments in which an increased rate of flow resulted from treatment is 26.7°. The average for the three experiments whose flow was reduced during treatment is 26.9°. This difference of 0.2° between the averages for the two groups is less than the fluctuations generally found during the course of an experiment. It is obvious that temperature differences could have no connection with the disparity in effect of the soluble fraction solution.

Also, the effect of the soluble fraction has no apparent relationship with the specific gravity of the laboratory sea water. In experiment 182, the low specific gravity of 1.0231 was accompanied by an increase of 18 percent in rate of flow during treatment. In experiment 144, the high specific gravity of 1.0272 was associated with an increase in rate of flow of 13.9 percent during treatment. Consequently, there is no evidence that an increase or a decrease in rate of flow during treatment has any connection with a high or low specific gravity of the sea water, though this statement is intended to apply only to the limits of salinity occurring in these experiments.

The difference in specific gravity between the laboratory sea water and the soluble fraction was, in most experiments, not over 0.0002. Where the difference exceeded this figure, notably in experiment 144, in which the difference was 0.0007, the effect is negligible compared with fluctuations in experiments where differences in specific gravity were not present. For example, experiments 106 and 107 were carried on simultaneously. They received soluble fraction prepared from the same sample of oil and sea water, were treated for the same length of time and the soluble fraction was adjusted to the same specific gravity as the laboratory sea water. Yet oyster 106 increased the rate of flow during treatment by 5.9 percent, while oyster 107 reduced its flow 19.5 percent.

Since there is no intergrading effect between the two groups of oysters used in these experiments, the inference can be drawn that 5 percent solution exerted a definite effect on one group of them which comprised specimens more sensitive than the others. In other words, this concentration may be regarded as a threshold of inhibitory action.

These results are based on treatments extending only for 18 or 24 hours. It is possible that the same depression of the efficiency of ciliary motion may be reached with smaller concentrations acting over a longer period of time.

Ten percent soluble fraction solution very definitely inhibited ciliary activity and resulted in an average decrease in rate of pumping during treatment of 23.8 percent. (Table 11.)

There is no relationship between the increase in the specific gravity of the undiluted oil extract and the effect on rate of flow during treatment. In experiment

104, the increase in specific gravity caused by washing was 0.0001, and the rate of flow during treatment was only 59.3 percent of the normal rate before treatment, while in experiment 176, the increase in specific gravity was 0.0007, and the rate of flow during treatment was 71.8 percent of the normal.

The difference in specific gravity between the laboratory sea water and the test solution was held within close limits, not exceeding 0.0002 in any experiment in this group. The specific gravity of the sea water was high in all experiments, ranging from 1.0249 to 1.0280. There is no apparent relationship between a high specific gravity and effect of the soluble fraction, for the greatest reduction in rate of flow, 42.9 percent, occurred in experiment 105, in which the specific gravity was considerably lower than in experiment 170, specific gravity 1.0280, the reduction in flow during treatment for the latter experiment amounting to only 15.8 percent.

Fluctuations in temperature may be disregarded as factors influencing the rate of flow during the experiments, the maximum difference in temperature at the beginning and end of an experiment in the 10 percent group not exceeding 1.0° C. The time of treatment in this group varied from 12 to 24 hours. Within these limits the duration of treatment does not appear to be a factor in determining the effect. Three experiments, 104, 105, and 116, were carried on for 18 hours. The first two showed the greatest, the last one next to the least effect for the group.

Seven experiments were made with 20 percent soluble fraction solution. These were well distributed over the period from June 14 to August 29. The average temperature of the water in these experiments was 27.1° C. Specific gravities ranged from 1.0239 to 1.0277. The average reduction in rate of flow resulting from this treatment amounted to 54.4 percent.

In the experiments with 20 percent solution (figs. 6 and 7) the difference in specific gravity between the laboratory sea water and the test solution was not held to as low limits in all cases as was done in the experiments with 10 percent solution. The maximum difference in specific gravity occurred in experiment 99, where the test solution was higher by 0.0012. This increase in specific gravity of the soluble fraction solution apparently was not of serious proportions in this case, for the reduction in rate of flow during treatment was only 17 percent, the lowest for the group. Consideration was given to the possibility that the comparatively slight effect of soluble fraction in experiment 99 might be due, in part, to the relatively low salinity of the laboratory sea water, 1.0239, for the other experiments in this group were made when the specific gravity was at or above 1.0270. However, an examination of the control and other experiments does not support this contention. While most of our experiments were made with sea water of higher salinity than is found over many oyster beds, nevertheless it may be stated that within the range of specific gravities used the effect of the soluble fraction is independent of the salt content of the sea water.

Increase in specific gravity of the sea water after washing with oil has no bearing on the effect of the 20 percent soluble fraction. In experiments 122 and 123 (table 11), two oysters were treated with portions of the same soluble fraction for 18 hours. The increase in specific gravity following washing with oil was 0.0004. The rate of flow of oyster 122 was reduced 34.4 percent during treatment. The reduction in rate for oyster 123 was 80.8 percent. Oyster 99 was treated for 20 hours with a different sample of soluble fraction having the same increase in specific gravity after washing and the reduction in rate of flow was 17 percent, comparable to the effect in experiment 122. Oyster 163, treated for 24 hours with soluble fraction having an increase in

specific gravity of 0.0002, half that of experiment 122, showed a decrease in rate of flow of 33.4 percent, almost exactly the same as no. 122. Finally, oyster no. 178 (fig. 6), treated for 18 hours with soluble fraction having an increase in specific gravity of less than 0.0002, had the rate of flow reduced 78.1 percent, a figure of the same order of magnitude obtained in experiment 123.

Fluctuations in temperature are not significant insofar as their effect on the rate of flow is concerned. Experiments 122 and 123, as mentioned above, were carried on simultaneously. The temperatures differ little in the two experiments, but the effect of the soluble fraction is not at all comparable in amount. It might appear that the temperature drop of nearly 5° C. in experiment 178 is partially responsible for the relatively large decrease in rate of flow. Actually, this is not the case as can be seen by examining figure 6 which presents a complete record of the experiment.

Six experiments were made with 40 percent soluble fraction, from July 12 to August 13. The average temperature of the water in these experiments was 27.2° C. Specific gravities of the laboratory sea water were very high, with little fluctuation, the range being from 1.0272 to 1.0277 (17.5° C.).

Except in experiment 142 (table 11), in which the decrease in rate of flow during treatment was almost the smallest in the group, the difference in specific gravity between the sea water and the soluble fraction was kept within 0.0002. The greatest increase in specific gravity of the sea water due to washing (0.0006) occurred in experiment 153, which was least affected by treatment. The maximum reduction in rate of flow following treatment was found in experiment 166, and the soluble fraction used here was a mixture from two oils which had been washed 10 and 24 times respectively.

Five experiments were made with 50 percent soluble fraction solution from July 16 to September 4. The average temperature of the laboratory sea water during this period was 27.3° C. The specific gravity of the sea water varied but little in July and August, 1.0273 to 1.0277; but in the last experiment on September 4 it had fallen to 1.0230.

The average rate of flow during treatment dropped 66.6 percent. There is relatively little difference in the effect of 40 and 50 percent soluble fraction. The experiments in the two groups have been separated chiefly to emphasize the close agreement between them.

The main interest of the experiments with 50 percent soluble fraction is the lack of any definite relationship between the effect of the soluble fraction and specific gravity (table 11, fig. 7). The reduction in rate of flow was practically the same in experiment 152, with the high specific gravity of 1.0277, and in experiment 183, with the low specific gravity of 1.0230.

Six experiments were made with 80 percent soluble fraction solution from July 26 to September 6. The average temperature of the laboratory sea water during this time was 27.0° C. Five of the experiments were carried on during July and August, when the specific gravity of the laboratory sea water ranged from 1.0270 to 1.0280. At the time of the last experiment on September 6, the specific gravity had fallen to 1.0238. The maximum difference between the specific gravity of the laboratory sea water and the soluble fraction was 0.0003.

The effect of 80 percent soluble fraction was to reduce the activity of the ciliated epithelium 90.8 percent. The drop in pumping activity is 24.2 percent greater than was found with 50 percent soluble fraction.

In experiments 143 and 177 of this group we find, for the first time, the pumping immediately stopped on addition of the soluble fraction, and not beginning again until the test solution was replaced with fresh sea water. As in previous experiments, an extreme effect is probably attributable to poor condition of the oysters, for the difference between the specific gravities of the laboratory sea water and the soluble fraction was very small, 0.0001 in experiment 143 and 0.0003 in experiment 177. Nor can the stoppage of flow be attributed either to an increase in specific gravity of the sea water after washing with oil, or to the number of times the oil was washed.

The least effect of 80-percent solution occurred in experiment 165, in which the reduction in flow amounted to 59.1 percent. This relatively small effect is doubtless also due to the condition of the oyster, no. 165, being for some reason better able to withstand the test solution than any of the others in the group.

Eight experiments were made with 100-percent soluble fraction (table 11, fig. 7). The average temperature of the laboratory sea water for all experiments was 27.3° C. The specific gravity was high, 1.0272 to 1.0277, except in the last experiment, where it was 1.0230.

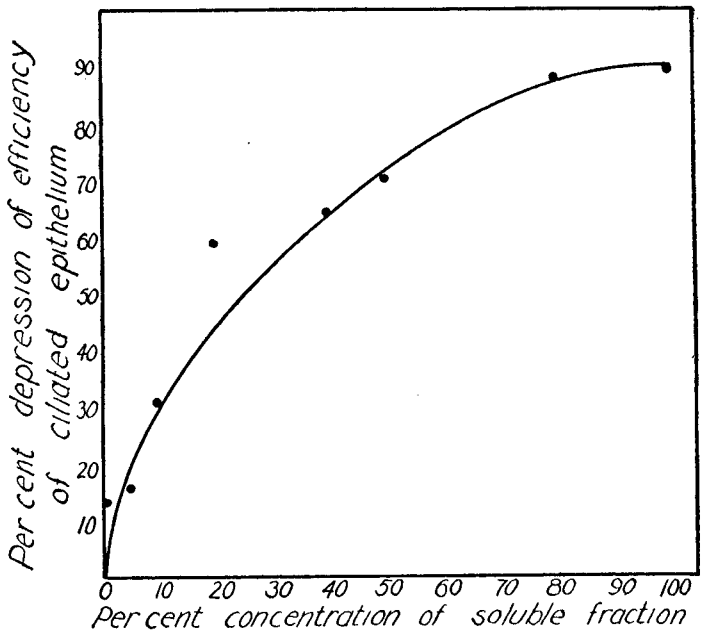

FIGURE 8.—Depression of rate of pumping of gills caused by various concentrations of water soluble fraction of oil.

The average reduction in ciliary activity amounted to 87.6 percent. In five experiments there was a complete cessation of pumping.

The results of all the experiments with the cone method show, without any doubt, that the presence of the water-soluble fraction of crude oil exerts an inhibiting effect on the efficiency of the ciliary motion of the gill epithelium, the work of which is interfered with in such a way that less water is pumped through the gills, and consequently the rate of feeding of an oyster is decreased. The decrease in efficiency of the epithelium is directly proportional to the increase in concentration of the soluble fraction. This is clearly seen from an examination of figure 8, which shows the percentage of depression caused by various concentrations. The values plotted in the figure are the averages, recalculated from the data given in table 11, based on the efficiency of the ciliary motion in the controls as 100 percent.

A relatively high degree of depression caused by the 20-percent solution may be considered as a breaking point in the curve, but so small a number of observations is not sufficient to determine this point with certainty. Regardless of the graphical interpretations that can be made concerning the shape of the depression curve, one

fact is clear: That a concentration between 20 and 30 percent soluble fraction will, on the average, reduce the rate of feeding of the oyster to one-half its normal value.

RESULTS OBTAINED WITH THE DROP COUNTING METHOD

Two series of experiments were made with the water-soluble fraction of crude oil, using the drop counting technique previously described.

The first group of 12 experiments (table 12) represents winter conditions, as they cover the period of November and December 1933. Two Louisiana crude oils were used, one from the Lake Barre wells, the other from the Pelto wells. Both fields are located in Terrebonne Parish and are operated by the Texas Co.

In the second series (table 13) are 19 experiments completed during May 1934, using only Lake Barre oil. The results of all experiments are summarized in these tables, which give the rate of pumping, in drops per minute, before, during, and after treatment. A column marked "Effect of treatment" gives the percent of the normal rate of flow obtained by dividing the average rate of flow during treatment by the average rate before treatment, making it possible to evaluate the inhibiting effect of oil extract on various oysters. In table 14 the results of the experiments are presented in a more detailed manner, showing for every 5-minute interval, the average number of drops of water per minute passed by the gills.

Heavy type indicates observations made when the soluble-fraction solution was running through the experimental chamber.

In both series of experiments a full-strength solution was used. There was a slight increase in the specific gravity of the sea water after it was stirred with oil, but there was no correlation between the specific gravity of the extract and its toxicity.

TABLE 12.—*The effect of soluble fraction of crude oil of Lake Pelto and Lake Barre wells on the rate of pumping of water by the gills of the oyster*

[Drop counting method, winter experiments, Beaufort, 1933]

Experiment no.	Date	Drops per minute			Effect of treatment	Duration test in minutes	Specific gravity, 17.5° C.		Temperature, ° C.		pH soluble fraction	Increase in specific gravity of soluble fraction	Recovery time		Source of oil
		Before treatment	During treatment	After treatment			Laboratory sea water	Soluble fraction	Beginning	End			Percent	Minutes	
					Percent										
60	Nov. 28	92.0	109.6	95.2	119.1	5	1.0261	1.0277	13.6				128	5	Barre.
60A	do	65.8	41.3	69.7	62.8	5	1.0261	1.0262	15.0	15.1	7.3	0.0001	116	30	Do.
62	Dec. 1	31.2	19.0	27.0	61.1	5	1.0261	1.02638	15.4	15.2	7.3	.00028	93	15	Do.
63A	Dec. 4	112.2	92.0	108.2	82.0	5	1.0262	1.0262	17.4	17.3	7.3		107	15	Do.
64A	Dec. 5	77.2	30.0	71.5	38.9	5	1.0260	1.0260	16.5	16.3			97	15	Do.
65A	Dec. 7	41.4	46.6	39.0	112.7	5	1.0265		14.8	14.8			123	5	Pelto.
66	Dec. 11	36.0	35.0	39.5	97.2	10	1.0267		13.2	13.5			145	5	Do.
67	do	60.5	54.7	58.2	90.4	10	1.0267		13.8	14.1			103	20	Do.
68	Dec. 12	67.2	52.0	57.2	77.4	10	1.0267		11.8	11.6			77	10	Do.
69	Dec. 15	77.0	60.4	79.6	78.4	10	1.0267	1.0279	12.3	12.5	7.5	.0012	109	15	Do.
70	Dec. 21	[1]120.7	0	36.5	[1] 30.2	15	1.0256	1.0260	15.6	16.5	7.6				Do.
70A	Dec. 22	[1] 83.5	0	64.9	[1] 77.7	15	1.0256		15.0	15.4					Sea water.
Average		66.0	54.06	62.2	82.0				14.48				109.8	13.5	

[1] Numbers omitted in making average.

TABLE 13.—*The effect of soluble fraction of Lake Barre oil on the rate of pumping of water by the gills of the oyster*

[Beaufort, 1934, spring experiments]

Experiment no.	Date	Average number drops per minute			Effect of treatment	Duration of test in minutes	Specific gravity, 17.5/17.5° C		Increase in specific gravity of soluble fraction	Temperature, ° C.		Number of washings	Recovery time	
		Before treatment	During treatment	After treatment			Laboratory sea water	Soluble fraction		Beginning	End		Percent	Minutes
CONTROLS					*Percent*									
73	May 9	44	40	38	91	78	1.0234	----------	----------	21.7	22.0	----------	----------	----------
74	May 10	121	128	134	106	71	1.0237	----------	----------	21.6	21.5	----------	----------	----------
84	May 16	139	141	137	101	92	1.0242	----------	----------	20.9	21.15	----------	----------	----------
86	---do----	115	114	115	99	55	1.0242	----------	----------	21.3	21.45	----------	----------	----------
SOLUBLE FRACTION														
71	May 7	109	49	73	45.0	5	1.0223	1.0177	0.0007	21.5	21.5	1	72	35
72	May 9	128	71	119	55.0	4	1.0234	1.0177	.0007	20.9	20.9	1	87	30
75	May 10	132	69	64	52.0	9	1.0237	1.0177	.0007	21.6	21.7	1	42	10
76	---do----	124	98	122	79.0	10	1.0237	1.0122	.0115	21.7	21.9	----------	92.3	20
77	---do----	129	85	99	66.0	8	1.0237	1.0244	.0007	21.9	22.1	1	62.9	10
78	May 14	141	13	129	9.2	8	1.0242	1.0247	.0008	22.1	22.4	1	96	30
79	---do----	136	19	106	14.0	8	1.0242	1.0249	.0007	22.4	22.7	2	102	30
80	---do----	146	27	105	18.5	8	1.0242	1.0247	.0005	23.3	23.3	3	75	30
81	May 15	156	94	132	60.3	8	1.0242	1.0250	.0008	22.9	22.5	3	87.9	20
82	---do----	133	85	119	64.0	8	1.0242	1.0246	.0004	22.5	22.4	4	91	15
83	---do----	126	33	100	26.2	20	1.0242	1.0245	.0003	22.3	22.6	4 and 5	93	10
85	May 16	133	31	107	23.3	23	1.0242	1.0244	.0002	21.1	21.3	5 and 6	79.1	20
87	May 17	87	27	55	31.0	24	1.0241	1.0243	.0001	19.1	19.1	6 and 7	64.1	30
88	May 21	154	42	103	27.3	38	1.0242	1.0245	.0005	24.2	24.3	8 and 9	70	20
89	May 22	126	38	93.5	30.2	12	1.0230	1.0237	.0007	24.8	24.8	9 and 10	68	15
Average	----------	130.6	52.0	101.6	40.0	-------	--------	--------	---------	22.1	------	----------	78.7	21.6

NOTE.—Averages do not include controls or experiment no. 76, which was made with dilute sea water.

The column in table 13, marked "Number of washings" refers to the number of times the same oil has been stirred with sea water. In the winter experiments, the oil was used only once, then discarded. In the spring experiments as many as 10 extractions were obtained from a single sample of oil without exhausting its toxicity.

One must bear in mind that because the oysters in these experiments are kept in running water, which is gradually replaced by the solution, the duration of each test lasted only a short period of time, varying from 4 to 38 minutes, depending on the amount of solution available. In figure 9, representing the results of three experiments, the time when the treatment began is marked with a vertical line. It has been estimated that the sea water in the experimental chamber (fig. 5, *Ch*) was completely replaced in 12 minutes, and that the same period of time was required to replace the oil extract with normal sea water, but there was no means of checking the exact concentration of solution in the chamber at the beginning and end of the test.

A decrease in the rate of pumping of water, caused by the oil extract, is noticeable almost immediately upon the beginning of treatment, and continues as long as the toxic substances are present in the water. There was a wide difference in the sensitivity of various oysters. While in some of them the pumping was completely inhibited, in others it was only slightly depressed (table 14).

The average rates of flow of water, in drops per minute, were computed from the kymograph data. The time during which the record was taken varied for the period "Before treatment", from 20 to 45 minutes; "During treatment", from 15 to 45 minutes; and "After treatment", from 15 to 90 minutes. It is believed that these periods are of sufficient duration to eliminate the effects of accidental stimulation and other possible disturbances.

Although both the winter and spring experiments show a depression in the rate of flow following treatment, the effect is much greater in the spring series. The average depression in rate of flow resulting from treatment for the winter series is 18 percent. For the spring series it is 60 percent. This difference in the levels of depression for the two groups is presumably a function of temperature, and is due to the direct relationship existing between temperature and rate of motion of the lateral gill cilia. It will be noted (table 12) that the average rate of flow before treatment in the winter series is 66 drops per minute, while in the spring series the average is 130 drops per minute. The average temperature at the beginning of the experiments for the winter series is 14° C., while the spring average is 22° C. Thus an average increase of 8° C. in temperature approximately doubles the rate of pumping while the depressing effect of the soluble fraction solution is trebled.

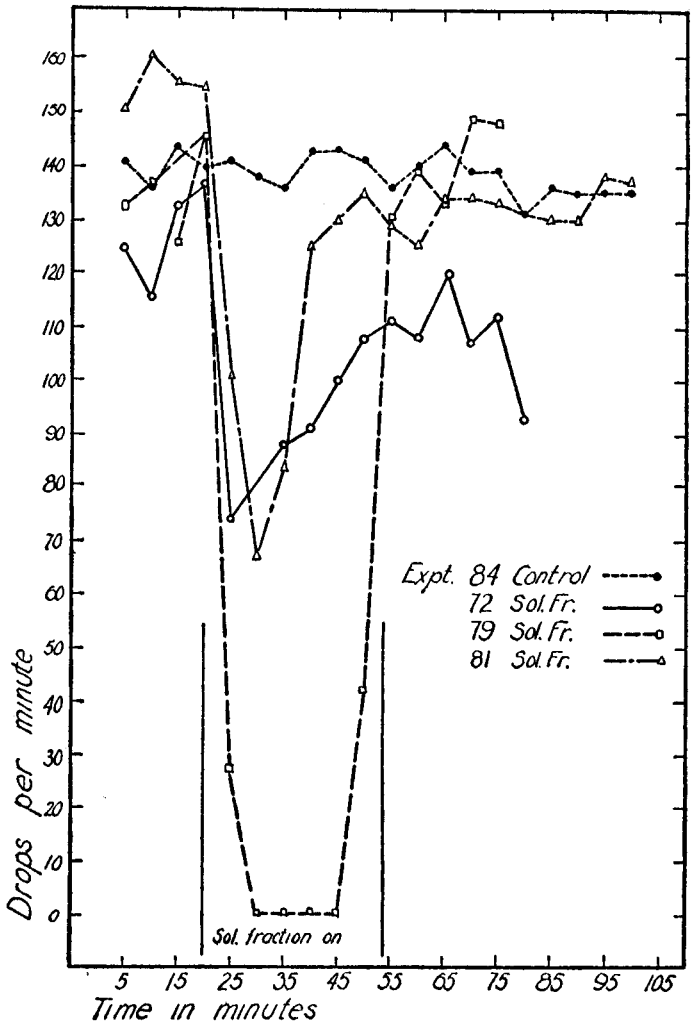

FIGURE 9.—Effect of water soluble fraction of Lake Barre oil on the activity of the ciliated epithelium. Drop counting method.

TABLE 14.—*The effect of soluble fraction of crude oil from Lake Barre and Lake Pelto wells on the rate of pumping of water by the gills of the oyster*

[Detailed record of the experiments. Figures printed in heavy type represent observations made when oysters are in solution of soluble fraction]

Experiment no.	Date	Crude oil	Time of treatment	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
				Drops per minute, average by 5-minute intervals																	
				5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
	1933		*Min.*																		
60	Nov. 28	Barre	5	94	92	91	87	**96**	**110**	118	101	104	98	91	88						
60A	do	do	5	61	64	64	65	**75**	**29**	37	58	61	69	73	76						
62	Dec. 1	do	5	34	35	31	30	**24**	**13**	18	26	29	27	25							
63A	Dec. 4	do	5	115	114	113	118	**101**	85	90	101	120	106	100	107						
64A	Dec. 5	do	5	80	81	74	**75**	**76**	**14**	14	62	75	75	68	68						
65A	Dec. 7	Pelto	5	44	42	40	39	**42**	**42**	51	47	44	40	34	38						
66	Dec. 11	do	10	35	35	40	34	**39**	**22**	**27**	52	45	38	38	37						
67	do	do	10	63	59	64	56	**57**	**53**	**52**	57	61	62	54	56						
68	Dec. 12	do	10	70	72	59	68	**81**	**31**	**44**	52	51	54	56	68						
69	Dec. 15	do	13	65	81	80	82	**81**	**73**	**40**	35	73	84	83	72						
70	Dec. 21	do	15	119	122	121	121	**1**	**1**	**1**	0	0	29	42	39	52					
70A	Dec. 22	Sea water	15	80	83	85	86	**2**	**2**	**2**	25	25	28	75	91	91					
	1934																				
73	May 9	Control		46	49	46	36	45	42	42	43	40	36	35	32	42	38	41	39		
74	May 10	do		127	128	118	126	106	127	126	120	134	117	142	**144**	116	141	126	144		
84	May 16	do		141	136	144	140	141	138	136	143	143	141	136	140	144	139	139	131	136	135
86	do	do		123	122	104	113	117	117	109	112	113	114	116	117						
71	May 7	Barre	5	118	115	111	107	104	103	**49**	40	58	63	64	67	71	78	70	77		
72	May 9	do	5	125	116	133	137	**74**	32	88	91	100	108	111	108	118	107	112	93		
75	May 10	do	10	**122**	**54**	45	55	54	45	43	47	52	56	48	44	44	56	65	69	107	
76	do	do	12	124	**129**	**106**	**71**	88	104	114	105	136	114	138	140						
77	do	do	10	123	**125**	**72**	64	80	76	83	67	86	94	66	100	107	110	120	110	118	
78	May 14	do	10	148	136	149	123	**53**	**0**	0	0	119	220	131	136	129	114	140	133	137	
79	do	do	10	146	**77**	**0**	0	0	0	42	130	139	133	149	148						
80	do	do	10	153	**103**	**4**	0	0	0	6	78	109	105	133	139	147	143	144	149		
81	May 15	do	8	151	161	156	155	**101**	**67**	84	125	130	135	129	125	134	134	133	131		
82	do	do	8	133	131	135	132	**61**	**44**	117	120	121	117	117	120						
83	do	do	20	120	127	126	130	**80**	**27**	**36**	**21**	**1**	108	117	102	89	100	98	95	97	
85	May 16	do	24	137	133	129	134	**104**	**39**	**31**	**12**	**0**	0	71	102	105	99	104	112	119	
87	May 17	do	24	87	87	87	85	**64**	**45**	**32**	**21**	**1**	2	37	52	54	55	56	45	60	
88	May 21	do	38	151	155	154	156	**120**	**69**	**54**	**52**	**49**	**34**	**2**	**0**	**0**	29	82	107	108	
89	May 22	do	12	118	130	131	128	127	127	121	125	**85**	**15**	**16**	37	84	86	84	90	95	

The effect of temperature on the rapidity of recovery is equally striking. The oysters in both winter and spring experiments show, after treatment with soluble fraction solution, a fairly steady rise in the rate of pumping but this initial rise is followed by a slight drop (fig. 9). The significance, if any, of this peak in the recovery curve is not known. However, it is useful in demonstrating the relation of temperature to rate and extent of recovery. In table 12, the column headed "Recovery time", shows the percent of recovery at the peak as compared with the average rate before treatment. The time in minutes extends from the moment of turning off the test solution to the point where the peak occurs. For the winter series, the average recovery at the peak was 109 percent in an average time of 13.5 minutes. The spring series averaged only 78 percent recovery at the peak in an average time of 21.6 minutes (table 13).

Results of the experiment carried out at Woods Hole, Mass., in which a solution of water-soluble substances present in Pelto oil was prepared by allowing them to diffuse through a collodion sack suspended in the sea water are similar to those obtained at Beaufort with soluble fraction prepared by shaking oil with the sea water. The sack, about 1 inch in diameter and 7 inches high, was made by dipping a glass test tube of corresponding size into a solution of Merck's collodion (reagent quality) and drying it for 1 minute. The membrane was carefully examined under a microscope and tested against leakage. Fifty cubic centimeters of oil were poured into the sack and the latter was kept suspended for 4 days in 4 liters of sea water which was gently agitated by means of an electric stirrer with glass rod. The specific

gravity of the water (at 17.5° C.) at the beginning and at the end of this period was 1.02455 and 1.02461, respectively. This slight increase in the specific gravity may be attributed either to the evaporation of water or to the dialysis of substances present in the oil.

An oyster was mounted in the usual manner and placed in a celluloid tank of 1,830-cc capacity used for measuring the rate of flow of water through the gills. Water was supplied at the rate of 100 cc per minute and the entire volume of the tank could be renewed in 20 minutes. Drops of water filtered by the oyster gills were recorded by means of an electric drop counter. The record of this experiment is presented in table 15 which shows the average number of drops per minute delivered by the gills before, during, and after the addition of the water soluble fraction of the oil. During this period the temperature varied between 21.5 and 21.8° C.

TABLE 15.—*The effect of water soluble fraction of Pelto oil obtained by dialysis through a collodion membrane on the rate of flow of water through the gills of the oyster*

Time	Drops per minute	Remarks	Time	Drops per minute	Remarks
12:05–2:25	[1] 208	Sea water.	4:07–4:08	105	Sea water replaced by solution—Continued
2:30		Solution turned on.	4:08–7:10		Left in solution.
2:50	96	Sea water replaced by solution.	7:10–7:11	53	Solution turned on.
2:53–2:54	96	Do.	7:11–7:12	52	Do.
3:20–3:21	90	Do.	7:12–7:13	60	Do.
3:22–3:23	66	Do.	7:15		Sea water turned on.
3:23–3:24	90	Do.	7:50–7:51	99	Do.
3:24–3:25	108	Do.	NEXT DAY		
4:00–4:01	10	Do.			
4:01–4:02	14	Do.			
4:03–4:04	72	Do.	9:15–9:16	66	
4:05–4:06	106	Do.			
4:06–4:07	107	Do.			

[1] Average.

By examining this table one notices that the presence of the water soluble fraction of Pelto oil greatly interferes with the normal activity of the gill epithelium. The rate of flow of water becomes less regular and decreases about 50 percent. A 3-hour exposure in this solution causes further inhibition of the ciliary motion of the epithelium, the activity of which was not fully restored even when the oyster was placed back in natural sea water.

On account of the limited amount of crude oil available in the laboratory experiments, it was necessary in preparing the water soluble fraction to use the same sample of oil several times. It was noticed that subsequent 30-minute stirrings of 2 volumes of crude oil with 1 volume of sea water did not exhaust the potency of the sample in inhibiting the work of the ciliated epithelium. Table 15 shows the percentage of depression in rate of flow of water caused by 10-, 20-, and 40-percent solutions of the extract. It will be observed that after 28 washings, there was no decrease in the toxicity of the extract.

TABLE 16.—*Showing no decrease in toxicity of a sample of oil due to repeated washings with sea water*

Number of washings	Percent depression	Number of washings	Percent depression	Number of washings	Percent depression
10 PERCENT		20 PERCENT		40 PERCENT	
2	6.7	1	17.0	4	50.0
19	10.3	1	69.5	9	54.3
28	29.1	8	34.0	9	70.5
		8	80.6	10	79.0
		13	68.0	16	45.0
		22	77.0		
		25	35.0		

This observation has an important bearing on the problem of oil pollution of natural waters, indicating that oil floating on water or absorbed in mud will, for a long time, remain a source from which toxic substances diffuse into the water. It seems probable that the toxic effect is not due to the mineral salts which occur in the crude oil and which doubtless will be leached out by subsequent washings, but to the organic compounds which gradually dissolve in the sea water.

TABLE 17.—*The effect of oil well bleed water on the rate of pumping of water by the gills of the oyster*

[Drop counting method]

Experiment no.	Date	Drops per minute			Effect of treatment	Bleed water on—	Percent bleed water	No current for—	Specific gravity 17.5/17.5		Temperature, °C.		pH bleed water solution	Source bleed water
		Before treatment	During treatment	After treatment					Sea water	Bleed water	Beginning	End		
						Min.		*Min.*						
55	Nov. 24	61.0	58.2	65.7	95	10	10	------	1.0258	1.0261	15.5	15.8	7.3	Barre.
63	Dec. 4	125.8	113.0	108.7	90	5	10	------	1.0262	1.0267	17.3	17.0	-------	Do.
63B	Dec. 5	41.2	30.3	40.0	73	5	10	------	1.0260	1.0265	15.2	15.6	-------	Do.
64	---do----	66.0	73.0	80.7	111	5	10	------	1.0260	1.0264	16.2	16.6	-------	Do.
65C	Dec. 8	90.7	95.6	87.3	106	10	10	------	1.0268	1.0263	14.8	15.2	7.5	Pelto.
Average	----------	-------	-------	-------	95	-------	-------	------	-------	-------	-------	-------	-------	----------
54	Nov. 23	78.7	57.5	69.0	73	10	20	------	1.0255	1.0259	16.4	16.6	7.3	Barre.
64B	Dec. 6	77.5	80.2	82.5	103	5	20	------	1.0260	1.0257	16.2	16.6	-------	Do.
64C	---do----	95.0	74.8	96.3	79	10	20	------	1.0260	1.0258	17.1	17.3	-------	Do.
65D	Dec. 8	97.0	89.6	91.6	91	10	20	------	1.0268	1.0268	15.2	15.2	-------	Pelto.
Average	----------	-------	-------	-------	86.5	-------	-------	------	-------	-------	-------	-------	-------	----------
65	Dec. 7	74.2	70.2	89.0	94	10	33	------	1.0268	1.0302	15.0	15.0	7.3	Barre.
65B	Dec. 8	86.2	35.0	100.5	41	10	40	3	1.0268	1.0397	14.1	14.4	7.3	Do.
53	Nov. 21	71.2	55.0	68.0	77	10	33	------	1.02535	1.0379	12.8	13.2	7.3	Do.
53A	---do----	97.0	70.7	96.0	81	10	33	------	1.02535	1.0379	-------	15.9	-------	Do.
53B	Nov. 22	130.0	56.5	97.4	44	10	40	------	1.02559	1.0436	-------	16.6	7.7	Do.
Average	----------	-------	-------	-------	67.4	-------	-------	------	-------	-------	-------	-------	-------	----------
67A	Dec. 11	57.0	16.0	36.0	28	14	50	10	1.0267	1.0532	14.1	14.3	-------	Barre.
68A	Dec. 12	71.0	10.0	32.0	14	10	60	12	1.0267	1.0638	11.6	11.7	-------	Do.
68B	Dec. 13	91.0	21.5	18.0	24	10	80	29	1.0267	1.0851	12.0	12.0	7.5	Do.
69A	Dec. 15	84.0	4.5	24.5	5	10	100	120	1.0267	1.1064	14.4	15.4	7.5	Do.

EFFECT OF BLEED WATER ON THE RATE OF FEEDING

Eighteen experiments were made with "bleed water" or brine from the Barre and Pelto wells during November and December 1933, using the drop counting technique. An adjustment period of from 10 to 30 minutes preceded the beginning of the measurements. A summary of all the experiments is given in table 17. Column 3, "Before treatment," shows the rate of pumping in drops per minute, averaged by 5-minute intervals, from the time the kymograph was started until the test solution was turned on. The elapsed time for this period is usually 20 minutes.

Column 4, "During treatment", shows the average rate of flow in drops per minute while the test solution was flowing over the oyster, and for 10 minutes after the test solution was turned off, as this time is required to replace it with sea water. The test solution was on for 5 or 10 minutes in most cases (col. 7).

Column 5, "After treatment", shows the average rate of pumping in drops per minute for a period about 20 minutes immediately after treatment. The value is a measure of recovery occurring during this period. There was not always a sufficient time for the rate of flow to return to the level established before treatment, but a

study of recovery was not considered to be of sufficient importance to the problem to warrant additional time.

The effect of treatment obtained by dividing the average rate during treatment (col. 4) by the average rate before treatment (col. 3) multiplied by 100 is a measure of the toxicity of the test solution. However, this value sometimes masks the actual effects of the test solution, and for this reason each experiment is presented completely in table 18, in which the average rate of flow in drops per minute is shown for each 5-minute interval. The intervals in which the test solution was flowing are indicated in bold face type, the figure in the last column giving the actual number of minutes during which the bleed water was running into the experimental chamber.

An example of the masking of brine effects as shown in column 6, table 17, is experiment 55. In this table the reduction in rate of flow due to a 10-minute treatment with 10 percent bleed water solution is 5 percent. An examination of the actual figures in table 18, shows that during the first 5 minutes of treatment there was an accelerating effect of about 16 percent; during the second 5-minutes of treatment the rate fell to nearly normal; in the 5-minute period immediately succeeding treatment, the flow decreased 36 percent, and returned to normal in the next 5-minute interval. The effect of bleed water in experiment 55, therefore, consists of an initial acceleration in ciliary activity followed by a considerable inhibition.

Of the 5 experiments using approximately 10 percent bleed water solution, 3 (nos. 55, 63, and 63B) show a reduction in rate of flow during treatment, the other 2 having an increased rate of pumping. It was to be expected that similar to the action of various poisons the low concentrations of bleed water may have a stimulating effect at least in some of the individuals.

Owing to large individual differences in condition and resistance of oysters, it is impossible to establish an exact concentration level for bleed water solutions, above which the rate of pumping would always be reduced, and below which an increase in rate would occur. However, the rate of pumping in the 10 percent bleed water group is reduced an average of 5 percent, which seems to indicate that this concentration slightly exceeds the limit of tolerance.

Four experiments were made using 20 percent bleed water. These show a decidedly greater depressing effect, the average rate of flow during treatment for the group being only 86.5 percent of normal. This increase in depressing effect of the 20 percent bleed water probably is due to a greater proportion of ions affecting the gill cilia, for there was no increase in the specific gravity of the solution as compared with laboratory sea water. On the contrary it will be seen (table 17) that the specific gravity of the test solution in experiments with 20 percent bleed water is closer to that of the laboratory sea water than is the case in the experiments with 10 percent bleed water.

The effect of 33 percent bleed water solution is shown by three experiments (nos. 65, 53, and 53A). In two experiments (65B and 53B) 40-percent bleed water was used. The average reduction in rate of flow resulting from a 10-minute treatment with these concentrations of bleed water was 32.6 percent.

One experiment each was made with bleed water concentrations of 50, 60, 80, and 100 percent. There is comparatively little difference in the effects of these concentrations during treatment for 10 minutes. However, the length of time during which no water was pumped through the gills increases steadily, from 10 minutes in the case of 50 percent bleed water to more than 2 hours for 100 percent. The

exact extent of the nonflow period in the latter experiment is not known as the oyster began recovery sometime during the night.

TABLE 18.—*The effect of oil well bleed water on the rate of pumping of water by the gills of the oyster*

[Drop-counting method. Records of two experiments made in Beaufort, 1933]

Experiment No.	Date	Drops per minute, average by 5-minute intervals																Time treatment (minutes)
		Percent bleed water	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	
55	Nov. 24	10	65	59	57	63	71	63	39	62	66	70	61	66				10
63	Dec. 4	10	130	130	123	125	121	119	101	119	104	109	115	107				5
63B	Dec. 5	10	41	43	41	41	45	35	29	27	43	42	36	39				5
64	do	10	61	60	70	74	65	63	79	76	83	83	72	85				5
65C	Dec. 8	10	96	92	89	86	88	101	105	96	88	85	86	91				10
54	Nov. 23	20	74	81	77	83	84	54	25	67	71	68	68					10
64B	Dec. 6	20	74	76	82	78	89	93	78	71	78	91	77	84				5
64C	do	20	99	95	96	90	88	81	57	69	79	85	92	112				10
65D	Dec. 8	20	90	95	92	91	88	89	86	87	98	94	94	91				10
53	Nov. 21	33.3	67	76	73	69	64	59	38	59	60	70	70	71				10
53A	do	33.3	88	89	91	86	87	91	80	90	96	98	102	92	21	68	96	11
53B	Nov. 22	40	119	116	126	116	123	135	56	81	114	130	120	21	32	53	59	10
65	Dec. 7	33.3	69	75	76	77	77	65	62	77	85	87	90	94				10
65B	Dec. 8	40	89	88	80	88	84	37	1	18	86	99	111	106				10
67A	Dec. 11	50	52	61	56	59	58	19	20	0	2	18	34	39	41	47		14
68A	Dec. 12	60	52	69	77	81	76	38	2	0	0	9	26	31	37	37	38	10
68B	Dec. 13	80	93	89	77	8	1	0	0	0	0	0	0	0	11	19	22	10
69A	Dec. 15	100	79	89	85	9	7	2	0	0	0	0	0	0	0	0	0	10

Undiluted bleed water as it comes from the wells, has, as stated above, a specific gravity of about 1.1064 (17.5° C.). A 20-percent solution of brine has approximately the same specific gravity as the laboratory sea water during November and December. Higher concentrations of brine undoubtedly owe part of their inhibiting action on the gill cilia to an increase in density, but this effect is probably much less pronounced than that caused by its chemical composition. It has been found, for instance, that in sea water, the specific gravity of which was increased by the addition of salt to 1.0361, the reduction in rate of pumping was 2 percent, much less than the depression caused by a 20-percent solution of brine. Sea water having a specific gravity of 1.0422 (increased by adding NaCl) caused a decrease in the rate of flow by 20 percent, almost equal to that of the 20-percent solution of brine (specific gravity 1.0258). An inference from these observations is that the inhibitory effect is due to the chemical composition of brine rather than to the increased density of water.

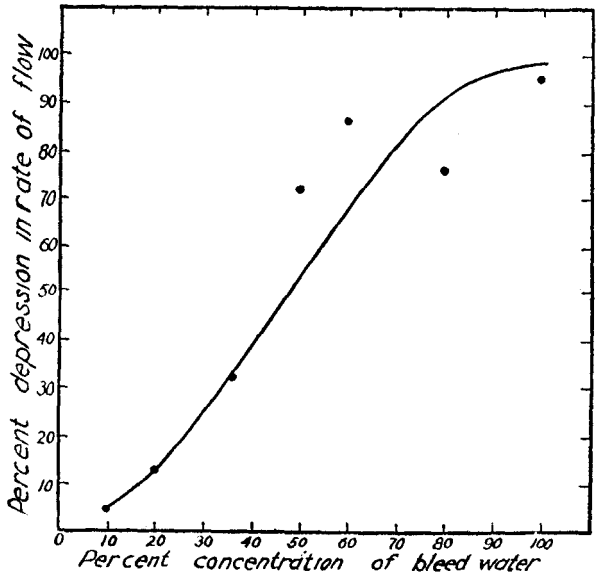

FIGURE 10.—Depression of the rate of pumping of the gills caused by various concentrations of "bleed water" (brine).

The percentage of brine in these experiments is beyond any possibility of occurrence in nature, except under most unusual conditions, and the oyster itself is unable to endure so high a salinity for more than a few hours, so that the results of the experi-

ments are not considered to be significant insofar as the oil pollution problem is concerned, and are included here only for the sake of completeness.

The experiments with bleed water show that it contains a substance or substances inhibiting the work of the ciliated epithelium. The action becomes apparent at a concentration of 10 percent brine in sea water. The toxicity increases in proportion to the increase in concentration. This is apparent from an examination of figure 10, in which the average depression in rate of flow of water through the gills, expressed in percentage of the normal, is plotted against the concentrations.

EFFECT OF CONSECUTIVE TREATMENTS

In the experiments described above the oysters were treated for a very short period of time lasting only a few minutes. The question arises as to whether or not as a result of a more prolonged exposure, they may become adapted or develop greater tolerance to the toxic substances present in crude oil and bleed water.

As stated previously, the drop counting technique is not adapted for experimentation over a period of more than 2 or 3 days. Several experiments were made in which the same oyster was treated with oil extract or bleed water several times within this period.

Five oysters were used in a total of 16 experiments. The results are summarized in table 19. Thirteen of these experiments have been analyzed to determine the effect of 2 or more treatments.

TABLE 19.—*The effect of consecutive treatments with soluble fraction of oil and bleed water on the rate of pumping by the gills of the oyster*

Experiment no.	Date	Test solution	Percent of solution	Effect of treatment	Length of treatment	Temperature
				Percent	*Minutes*	° *C.*
60	Nov. 28	Soluble fraction	100	119.6	5	13.6
60A	do	do	100	62.8	5	15.0
63	Dec. 4	Bleed water	10	90.0	5	17.3
63A	do	Soluble fraction	100	82.0	5	17.4
63B	Dec. 5	Bleed water	10	73.0	5	15.2
65	Dec. 7	do	33	94.0	10	15.0
65A	do	Soluble fraction	100	112.7	5	14.8
65B	Dec. 8	Bleed water	40	41.0	10	14.1
65C	do	do	10	106.0	10	17.1
65D	do	do	20	91.0	10	15.2
78	May 14	Soluble fraction	100	9.2	8	22.1
79	do	do	100	14.0	8	22.4
80	do	do	100	18.5	8	23.3
81	May 15	do	100	60.3	8	22.9
82	do	do	100	64.0	8	22.5
83	do	do	100	26.2	20	22.3

Oyster no. 60 was used in two experiments, 60 and 60A. The duration of treatment with soluble fraction from Barre oil was 5 minutes in both. Five hours elapsed between treatments. The difference in temperature at the beginning of the 2 experiments was 1.4° C. In experiment 60, the rate of pumping was accelerated almost 20 percent above normal, while in 60A there was a reduction in rate of about 37 percent.

Oyster no. 63 was used in experiments 63, 63A, and 63B. Bleed water was used in 63 and 63B, and soluble fraction from Barre crude oil in 63A. Two hours elapsed between 63 and 63A. 63B was made the following day, 18 hours after 63A. The duration of treatment was 5 minutes in each.

Comparing the effect of the two treatments with bleed water, it will be noted that the second treatment reduced the rate of flow 27 percent as compared with a 10-percent reduction for the first treatment. The interval between these treatments was more than 20 hours. The difference in temperature at the beginning of these experiments was 2.1° C.

Oyster no. 65 was used in 5 experiments, 4 with bleed water (65, 65B, 65C, and 65D), and 1 (65A) with soluble fraction from Pelto crude oil. Nos. 65 and 65A were made on December 7, with a 3-hour rest period between. The other three experiments were made the following day. The intervals between these experiments are 65A to 65B, 18 hours; 65B to 65C, 2.5 hours; 65C to 65D, 50 minutes. Comparison of the effects of several treatments in this case is difficult because a different concentration of bleed water was used in each. However, it will be observed that the final treatment (65D) with 20 percent bleed water was of the same order of effectiveness as the first treatment with 33 percent bleed water. The time of treatment was 10 minutes in both experiments, and the temperature at the beginning of each was practically the same.

Experiments 78, 79, and 80 were made with the same oyster, using the soluble fraction from Barre crude oil. The duration of treatment was 8 minutes for each and the temperature difference was negligible. Twenty minutes elapsed between 78 and 79; 3 hours elapsed between 79 and 80. The average reduction in rate of flow during treatment as shown in table 19 is 90.8 percent for experiment 78, 86 percent for experiment 79, and 81.5 for experiment 80. Thus it would appear that succeeding treatments were not so effective as the first. However, it will be remembered that the figures in this table are prepared to show only the average effect during the period of treatment, which is considered to be the actual interval during which the test solution flows over the oyster plus an additional 10 minutes for replacing the test solution with fresh sea water. A detailed analysis of the records shows that while the initial reduction in rate of flow is greater in the first experiment, and consequently the average reduction appears to be greater, yet the period of no current is 20 minutes in the second experiment and only 15 minutes in the first. Actually, the second treatment exerted a retarding action on the pumping activity of the cilia for a longer period than was the case in the first experiment. These remarks apply also to the third experiment, no. 80. The initial depressing effect is not so great, as in no. 78, and the period of no current is only 15 minutes, but this period begins after the test solution has been turned off, and subsequent recovery as evidenced by the average rate of flow will be seen to take place more slowly than in either of the preceding two experiments.

Experiments 81, 82, and 83 were made the same day with the soluble fraction from Barre crude oil. The interval between treatments is approximately 2 hours for experiments 81 and 82. Two and a half hours elapsed between treatments in 82 and 83. The duration of treatment was 8 minutes in the first two and 20 minutes in the third experiment. The latter, therefore, cannot be compared directly with the others.

Oyster no. 81 used in these experiments had the highest rate of pumping in the series and had a high resistance to treatment with soluble fraction. The reduction in rate of flow caused by the test solution was 39.7 percent in experiment 81 and 36 percent in 82. The average rate at 5-minute intervals as given in table 14 does not show an appreciable difference in effectiveness of the soluble fraction for the two experiments.

The results of 13 experiments may be summarized as follows:

1. Oysters subjected to several treatments of oil extract or bleed water do not develop higher tolerance to oil extract or bleed water in concentrations used, or within the time limits studied.

2. Particularly in the case of oil extract, the second and succeeding treatments have a less immediate but more prolonged retarding effect on the rate of pumping.

3. There is no evidence of permanent injury caused by this treatment. Recovery is usually complete.

EFFECT OF CRUDE OIL ON DIATOMS

By Paul S. Galtsoff and Vera Koehring

Since diatoms invariably appear to be constituents of the oyster diet, their rate of growth in the medium to which various polluting substances were added, may be taken as an index of the effect of pollutant upon the food supply of the oyster. In the regions where oysters grow, diatoms are usually distributed throughout the water, in the surface layers as well as on the bottom. Oil in water may affect their growth by forming a surface film which may interfere with the gaseous exchange between air and water or by the toxic action of water soluble constituents of the oil. It has been demonstrated by Lord Raileigh (1923) and Langmuir (1916, 1917) that the spreading of an oil upon water is due to the active carboxyl group of the oil molecule which because of its great affinity to water readily goes in solution, whereas the hydrocarbons having far greater attraction for one another than for the water, remain insoluble. By spreading into a monomolecular film the carboxyl groups combine with water without causing the separation of the hydrocarbon chains. Hence, a pure hydrocarbon oil, as has been demonstrated by Hardy (1912, 1919) for benzene and cymene, fails to spread. In case of oil in the natural waters the problem is more complex because we are usually dealing with mixed oils which, upon being exposed to air, change their chemical properties. Oxidized samples of oil, according to Hacker (1925), have an increased spreading power, and chemically inert hydrocarbons upon acquiring certain radicles, $-OH$, $-O$, $-COO$, and $-NH_2$, have an attraction for water. For a detailed discussion of this problem the reader must consult the original papers of the above-mentioned authors, whose findings are briefly mentioned here only as an illustration of the possible changes in the solubility and behavior of crude oil in water, which may account either for the formation of blobs or for the unchecked spread of oil film over a great area of the sea. A comprehensive investigation of the problem would require extensive chemical studies of the oil before and after its discharge into the sea, which the authors were not in a position to undertake although they fully realized the necessity of such a study for the solution of the oil pollution problem.

Oil discharged into the sea does not remain on the surface. Part of it is absorbed by the colloidal particles of clay present in the water and is gradually settled on the bottom. This can be seen in both the aquaria tanks in which oil-polluted sea water is kept and in many sections of the coastal waters affected by pollution. In a comparatively short period of time considerable quantities of oil floating in the water is found absorbed and deposited on the mud bottom from which it can be separated by squeezing and decanting. Mud contaminated with oil may be considered as a possible source from which water soluble constituents of the oil gradually go into solution even after a complete disappearance of oil from the surface.

Experiments carried out with diatom cultures and discussed in the present paper were devised to test the effect of oil (1) as a heavy layer covering the surface of the water; (2) absorbed by some neutral substance and held on the bottom of the culture flasks; and (3) as a soluble extract.

METHOD

Cultures of the single diatom species, *Nitzschia closterium*, E., were grown in the laboratory in solutions prepared according to the Miquel formula. (Solution A, potassium nitrate 20.2 g in 100 cc distilled water; Solution B, calcium chloride 4 g, sodium phosphate (secondary crystals) 4 g, ferric chloride 2 g, and 1 cc concentrated hydrochloric acid in 80 cc of water. Add 2 cc solution A and 1 cc solution B to one liter of carefully filtered sea water; sterilize by bringing just to the boilding point, then cool and filter.) Eighty cc of this solution were poured in round pyrex flasks of 150-cc capacity and inoculated by adding 2 or 5 cc of Nitzschia stock culture. Flasks covered with inverted small beakers were placed in front of the laboratory window where they were protected from direct sunlight. In some of the experiments instead of Miquel solution plain filtered sea water was used. Sea water used during winter experiments was received from Woods Hole, Mass., and stored in paraffined oak barrels. It contained noticeable amounts of hydrogen sulphide. Before using, the water was aerated for at least 24 hours and the precipitated sulphur filtered off. During the summer months the sea water from the laboratory supply was used. The salinity of the water varied between 31 and 32 parts per thousand. Twice a day temperature readings were made by means of a thermometer kept in one of the flasks filled with water. Fluctuations in the light and temperature conditions which were not controlled, are undoubtedly responsible for certain variations in the growth rates. To avoid this difficulty a comparison was always made between the experimental and the corresponding control flasks which stood by its side. The relative position of each pair of flasks was changed every other day to compensate for a possible difference in illumination.

Diatom counts were made by means of a photoelectric set-up (fig. 11) which consisted of Weston photronic cell (*Ph*) connected to a Weston D. C. microammeter (*A*) of 0–100 ranges, accurate within 0.5 percent of the full scale value at any part of it. For measuring the turbidity of a sample, 50 cc of it were poured in a cylindrical glass container *C*, having a diameter of 27 mm, 90 mm high, with fused bottom made of optical glass. The cylinder rested on a diaphragm, the opening of which was slightly smaller than the inside diameter of the cylinder. Both the diaphragm and the cylinder were placed directly over the photoelectric cell the surface of which was covered with thick black paper in such a manner as to cut all the light except that which passed through the column of water in the cylinder. A 21-candlepower, 6-volt Mazda bulb (*L*) fed by a 108 ampere-hour storage battery served as a source of light. The photoelectric cell was placed in a wooden box 4 by 4 by 12 inches. The bulb was mounted at the lower end of an adjustable arm which could be moved up and down and fixed in a desired position by a set screw. A piece of fine ground glass (*Gl*) separated the two compartments of the box. The front part of the box had a door through which the glass container could be placed in position. The box was painted inside with black paint. Great care was exercised in avoiding the fluctuations in the voltage and in insuring uniformity in the intensity of light. It was noticed that there was a drop in voltage during the first 10 minutes following the

turning on of the battery and small fluctuations occurred every time the current was turned off and on. To avoid this difficulty a second Mazda bulb (L) of the same candle power was introduced into the circuit. By means of a double switch (S) the current from the storage battery could be turned either through the bulb mounted in the box or through the second one located outside. During the observations the current was continuously passing through the spare bulb except during brief moments when measurements of the samples were made. By this arrangement the overheating of the box and difficulties due to the fluctuations in the voltage of the storage battery were overcome. The battery was kept well charged.

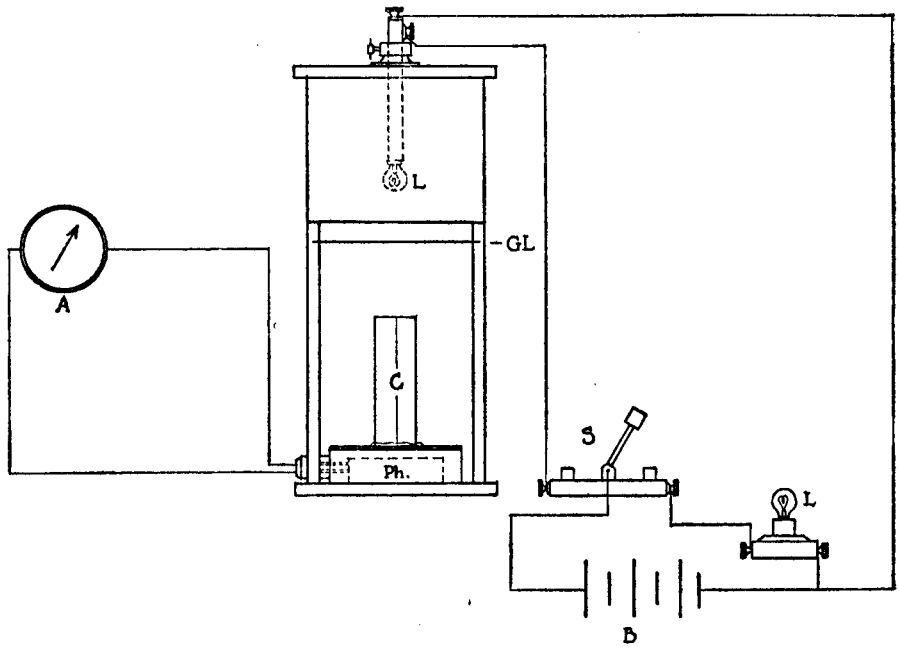

FIGURE 11.—Photoelectric set-up used for counting number of cells in Nitzschia culture. Ph, photoelectric cell; A, microammeter; C, glass container with fascil bottom made of optical glass; L and L_1, electric bulbs; Gl, ground glass; S, double key switch; and B, storage battery.

For the standardization of the apparatus the bulb was so adjusted that the light passing through the container filled with 50 cc of filtered sea water caused the needle deflection of the microammeter to stand at 30. This represented the zero point of the calibration curve. Other points were obtained by making readings with various concentrations of Nitzschia and counting by means of Sedgwick-Rafter chamber the corresponding number of cells. Altogether 35 samples were counted and from the data obtained, a curve was plotted which permitted the conversion of microammeter readings into number of diatoms per cubic centimeter.

Before withdrawing a sample for measurement each culture flask was thoroughly shaken for 2 minutes then 50 cc were taken by means of a certified volumetric pipette, and poured into container c. Care was taken to avoid air bubbles, the presence of which affected the ammeter readings. Upon measurement, which required about 30 seconds, the sample was returned to the same flask and both the container and pipette carefully washed in sterile distilled water and dried. Because of the simplicity and quickness of the operation it was possible to experiment with several dozens of flasks simultaneously.

An inconsiderable bacterial population was always present in the cultures. The bacteria were examined at intervals by plating them in agar medium prepared according to Waksmann's formula (1,000 cc sea water, 1 g peptone, 1 g glucose, 0.5 K_2HPO_4, 2–3 drops of 10 percent $FeCl_3$, and 15 g agar; sterilized in autoclave at 15 lbs. for 20 minutes).

When the diatoms and the surrounding medium are relatively free of bacteria the Nitzschia cells stay in suspension. When they tend to fall to the bottom and form loosely aggregated masses, microscopical examination shows them to be weighted with adherent bacteria. Plating under such conditions invariably shows a high bacterial count. All subcultures from the stocks were made, therefore, by carefully decanting only top portions containing diatoms in suspension.

At the beginning of each experiment all the flasks were inoculated with equal volumes of stock culture and 1 or 2 of them measured to determine the initial diatom population. Thereafter the cultures were measured every other day. At least 3 control and 3 experimental flasks were used in each test. In many experiments this number was doubled. All the figures given in tables or graphs are averages of three or more samples.

EFFECT OF HEAVY SURFACE LAYER OF OIL ON NITZSCHIA CULTURE

In this set of experiments Nitzschia was grown in 500 cc Erlenmeyer flasks containing 250 cc of culture covered by 25 cc of oil. The oil was sterilized in a boiling water bath for 1 hour.

There was no indication that the presence of oil kills the Nitzschia and no immediate effects on its growth were discernible even when the oil was thoroughly shaken up with the cultures several times a day. Microscopic examination showed no signs of oil sticking to the surface of the diatoms. For approximately a week the experimental cultures showed no significant difference in their growth as compared with the controls. Their further propagation was, however, markedly inhibited. Photoelectrical measurements of the cultures presented considerable difficulties as it was some times impossible to withdraw a portion of the sample free from oil globules. In two experiments, however, this difficulty was overcome. The first experiment, lasting 18 days, began on March 13 and was discontinued April 4, 1934. The second one, started on April 7, continued for 25 days until May 4. During the last experiment tests were made with purified mineral oil (Russian oil) and cod-liver oil. Cultures covered with cod-liver oil perished on the fourth day, those with mineral oil continued to the end of the experiment. The retarding effect of oil was noticeable in both groups, although in the cultures under Russian oil it was somewhat less pronounced than in those kept under crude Pelto oil (Fig. 12.) The adverse effect of oil can be measured by determining the percent of retardation of growth in the experimental flasks as compared with their growth in the controls. In the first experiment (March 13, Pelto oil) the retardation at the eighteenth day amounted to 35 percent. In the second experiment (lasting 25 days) retardation due to presence of Russian oil and Pelto oil was 37 and 42 percent, respectively.

An inhibitory effect of a heavy surface layer of oil on the diatom culture was quite visible in many other samples which could not be measured. This can be seen in the photographs (fig. 13) taken 30 days after the beginning of one of the experiments in February 1934. The control culture (left) had numerous diatoms and therefore

appears dark, whereas the flask on the right containing culture covered with oil had few diatoms, thus appearing much lighter.

All the experiments indicate that a heavy, unbroken surface layer of oil inhibits diatom growth when oil remains on the surface for a week and longer.

EFFECT OF OIL HELD ON THE BOTTOM

In attempting to devise a method whereby oil could be held at the bottom of the flask and would not interfere with the photoelectric measurements the following procedure was developed. Four grams of paraffin, melting point 52° to 55° C., was mixed with 6 drops of oil. The resulting mass, oily to the touch, and having a strong odor,

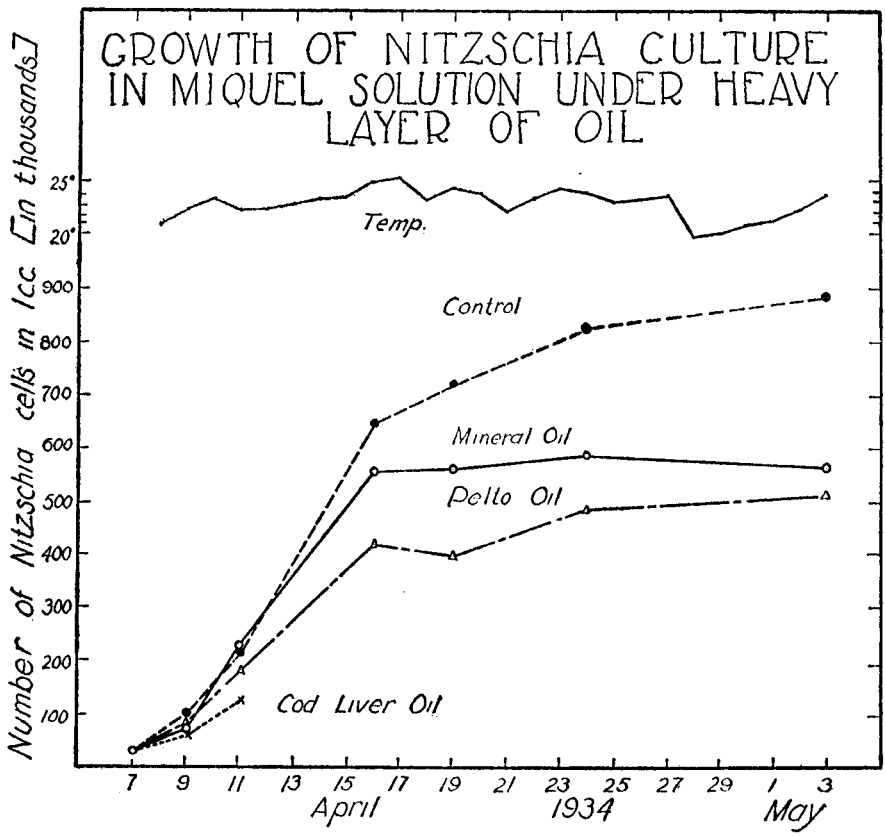

FIGURE 12.—Growth of Nitzschia culture under heavy layer of Pelto oil.

was sterilized at 150° C. and allowed to cool on the bottom of each flask and strongly adhering to it. Pure paraffin controls were prepared in the same manner. The flasks were filled with the standard Miquel medium, inoculated with Nitzschia and measured at regular intervals. The results of the experiments were, unfortunately, inconclusive. In three experiments the growth of Nitzschia in experimental flasks was retarded from 4 to 16 percent (fig. 14), as compared with their growth in pure sea water. In three other experiments there was a noticeable stimulating effect varying from 17 to 27 percent. Pure paraffin controls also produced inconsistent results. In one experiment in 13 days the number of diatoms reached exactly the same number as in the plain sea water. In other experiments the paraffin cultures

showed a retardation by 8–9 percent, while in one experiment the growth in pure paraffin and paraffin-oil cultures was increased by 17 percent (fig. 15).

Indefinite results of the experiments should probably be attributed to the action of bacteria which, as has been shown by Hopkins and Chinbal (1932), Buttner (1926), Tausson (1927), and Haas (1926), in the absence of more suitable material can grow on paraffin and utilize it as their only source of carbon. A great part of our paraffin and paraffin-oil cultures showed very abundant bacterial growth.

Other attempts to incorporate oil in some suitable substance at the bottom of culture flasks were unsuccessful.

EFFECT OF WATER SOLUBLE FRACTION OF OIL

Two different methods were used in preparing water soluble extracts of oil. The first method consisted in stirring together oil and filtered sea water and allowing the mixture to stand for various lengths of time. In the second method measured amounts of oil were poured in collodion bags suspended in flasks containing Nitzschia culture and the water soluble constituents of the oil gradually diffused through the membrane.

The proportions of oil and water used in preparation of the extracts according to the first method as well as the duration of stirring and standing are given in table 20.

TABLE 20.—*Preparation of oil extracts in sea water*

Proportions oil to water	Hours of stirring	Days of standing	Specific gravity of sea water (17.5° C./17.5° C.)	Specific gravity of extract (17.5° C./17.5° C.)
1:1	12	12	1.02433	1.02400
1:2	2	2	1.02461	1.02380
1:2	2	3	1.02435	1.02434
1:2	12	10	1.02463	1.02434
1:2	3	7	1.02445	1.02448

The oil was subsequently filtered off and the resulting clear aqueous extract was heated to boiling to allow for sterilization. Before sterilizing the specific gravity of the extract was determined. In most cases it was slightly lower than that of the sea water used.

The results of these experiments are summarized in table 21 which shows the percent of retardation (−) or stimulation (+) of growth caused by the addition of various concentrations of five different extracts. All the experiments were carried out with Lake Pelto oil. The figures are the averages of three or more samples.

TABLE 21.—*Effect of water soluble fraction of oil on the growth of Nitzschia culture*

[Figures in the body of the table represent percent of retardation (−) or stimulation (+)]

Extracts	1	2	3	4	5	*Extracts*	1	2	3	4	5
IN SEA WATER						IN MIQUEL					
12 percent	+48	+23	0	+11	−4	12 percent	−2	+27	−20	.....	−14
25 percent	+32	+10	−18	−17	−25	25 percent	−8	−7	−75	.....	−61
50 percent	.....	−36	−51	−100	−46	50 percent	.....	−62	−79	.....	−90

The figures given in table 21 represent the end results of experiments which ran from 9 to 21 days. Of the 25 experiments with various dilutions of oil extract 6

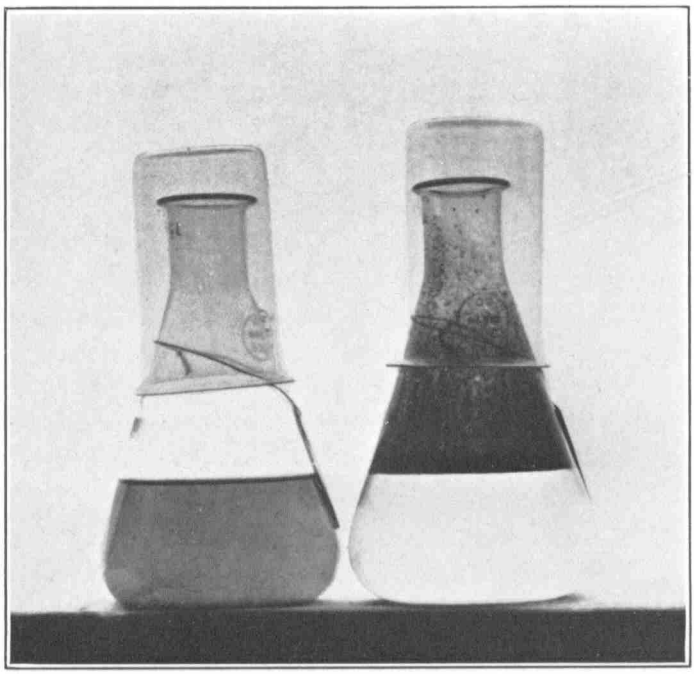

FIGURE 13.—30-DAY OLD NITSCHIA CULTURE IN SEA WATER (LEFT), AND IN SEA WATER UNDER HEAVY LAYER OF OIL (RIGHT).

(February 1934.)

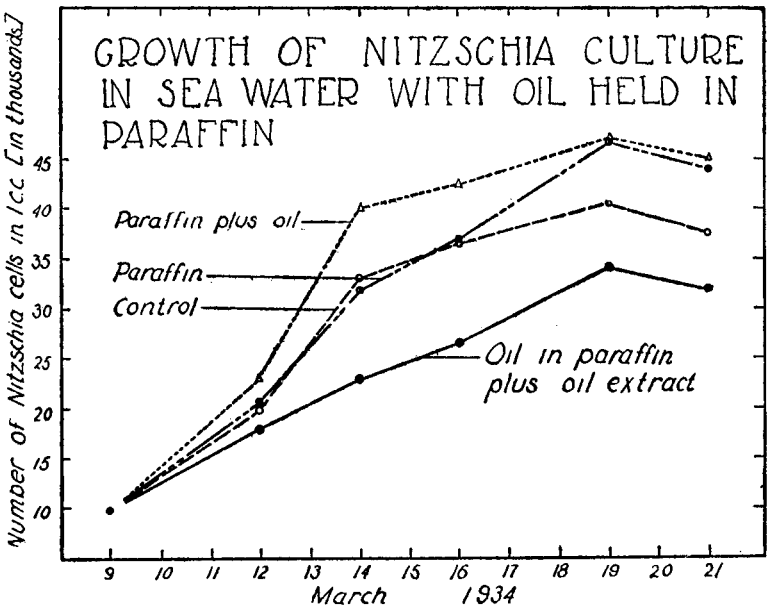

FIGURE 14.

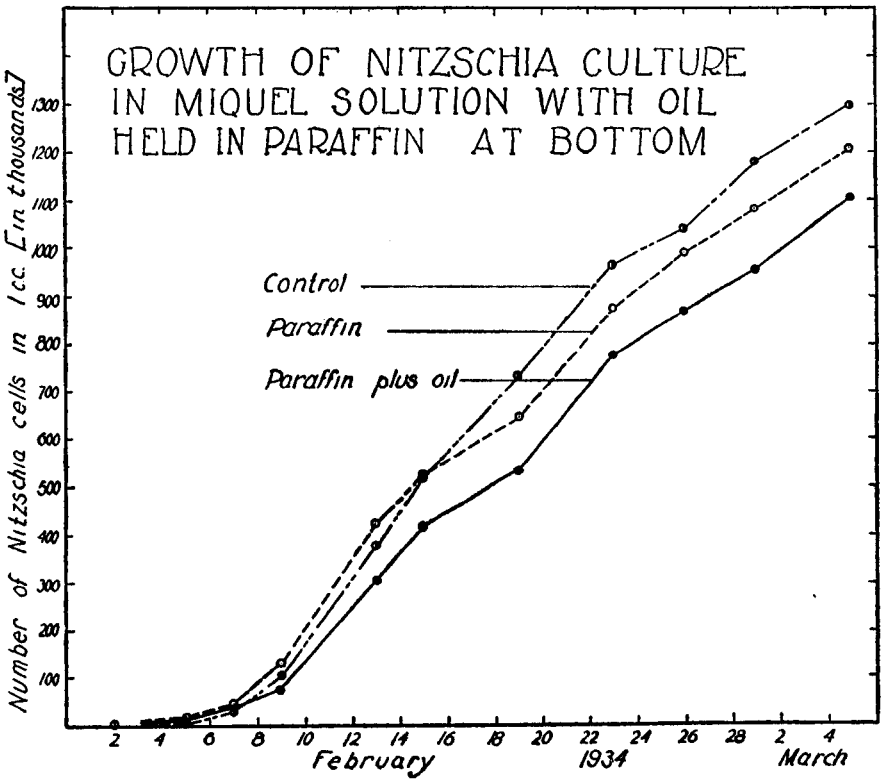

FIGURE 15.

showed increased growth as compared with the controls, while in 19 cases there was a retardation of the propagation or great mortality, accompanied by tremendous development of bacteria. In 14 experiments the population during some period of growth was greater than in the controls. These periods of increased rate of propagation occurred usually during the first few days of growth. Thereafter the controls continued to increase more rapidly and by the end of the experiment attained greater populations. These relationships may be noted by examining figure 16 representing the results of 3 experiments.

In all the experiments with oil extracts, the retarding effect of the latter is apparent in concentrations of 25 percent and higher and when the extract is permitted to act over a considerable period of time.

EFFECT OF OIL HELD IN COLLODION BAGS

The method used in these experiments consisted in suspending in a flask containing 80 cc of culture medium, a collodion bag with 2 cc of crude Pelto oil. Bags were made by dipping a test tube in a thin solution of collodion (Merck's reagent) and drying it for 45 seconds. Freshly made bags were sterilized by boiling in distilled water. Each bag remained suspended in a culture medium throughout the experiment. A more or less continuous dialysis through the collodion membrane was noticed, for water gradually collected in the bottom of the bag. The colorless and apparently somewhat volatile dialyzed substances have not been identified. Their presence was readily detected, however, by odor and irritating effect on the mucous membrane of the mouth while pipetting the sample for measurement. All the controls contained collodion bags filled with the Miquel solution or sea water. The end results of the experiments are given in table 22 the examination of which discloses that in all the cases there was a noticeable retardation in Nitzschia growth caused by oil held in collodion bags. Figure 17 presents a more complete record of one of the experiments.

TABLE 22.—*Retardation of growth of Nitzschia culture caused by oil held in collodion bags*

[Each figure is an average of measurements of 6 different flasks]

Beginning of experiment	Duration, days	Retardation of growth, percent	Medium
July 26	22	20	Miquel.
Aug. 6	12	24	Do.
Do	12	12	Sea water.
Aug. 22	14	32	Do.

EFFECT OF BRINE ON NITZSCHIA

Untreated brine (bleed water) separated from the oil as it comes out of the well was filtered from the heavy sediments accompanying it. The filtrate was carefully brought to the boiling point for sterilization. Sometimes this caused precipitation and the sample had to be discarded.

In a series of experiments lasting from 14 to 31 days tests were made with various concentrations of brine added to sea water or Miquel solution. As can be seen by examining figures 18 and 19 representing two typical experiments, the retardation

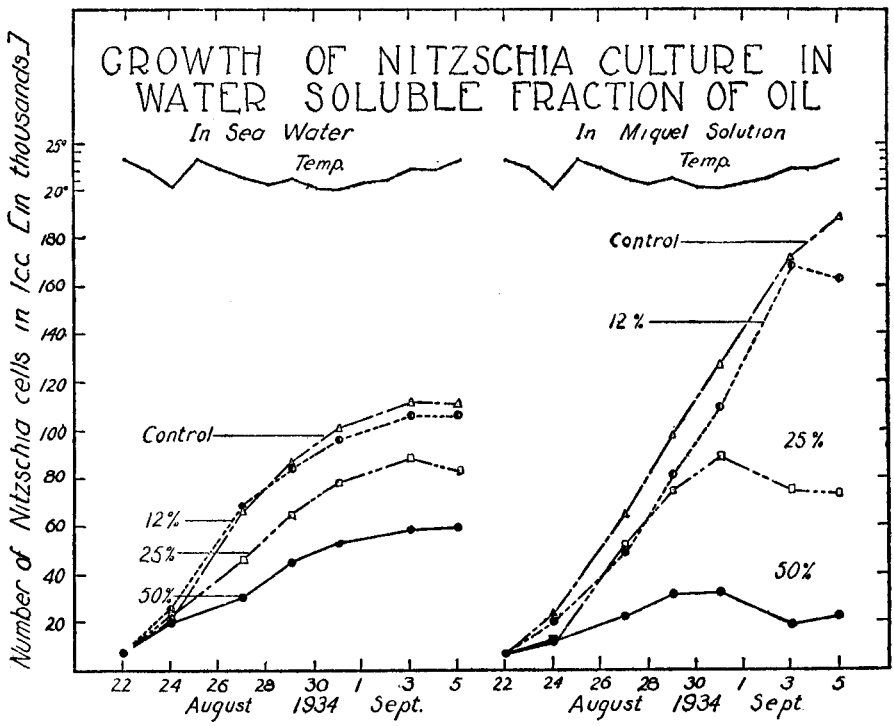

FIGURE 16.

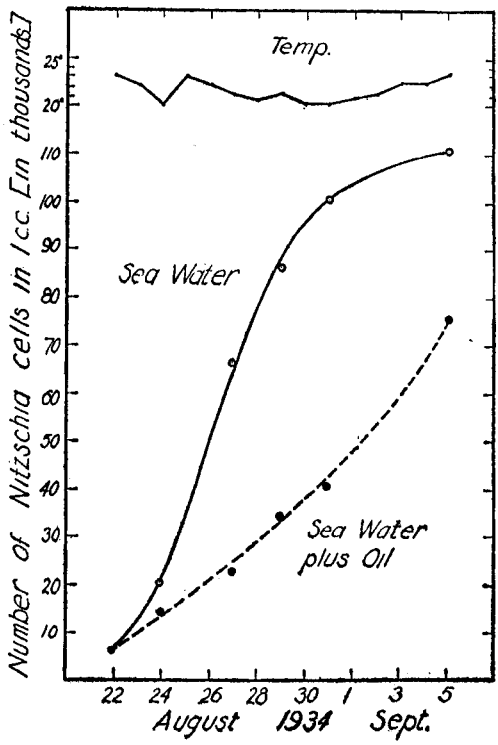

FIGURE 17.—Growth of Nitzschia in sea water with oil kept in collodion bag suspended in flask.

of Nitzschia growth is apparent in both media. An analysis of the results of all the experiments with brine summarized in table 23, shows that the retarding effect is more apparent in the sea water than in the Miquel solution. A 12-percent concentration of brine causes only 10 percent retardation of Nitzschia growth in the Miquel solution, whereas in the sea water retardation averages 41 percent.

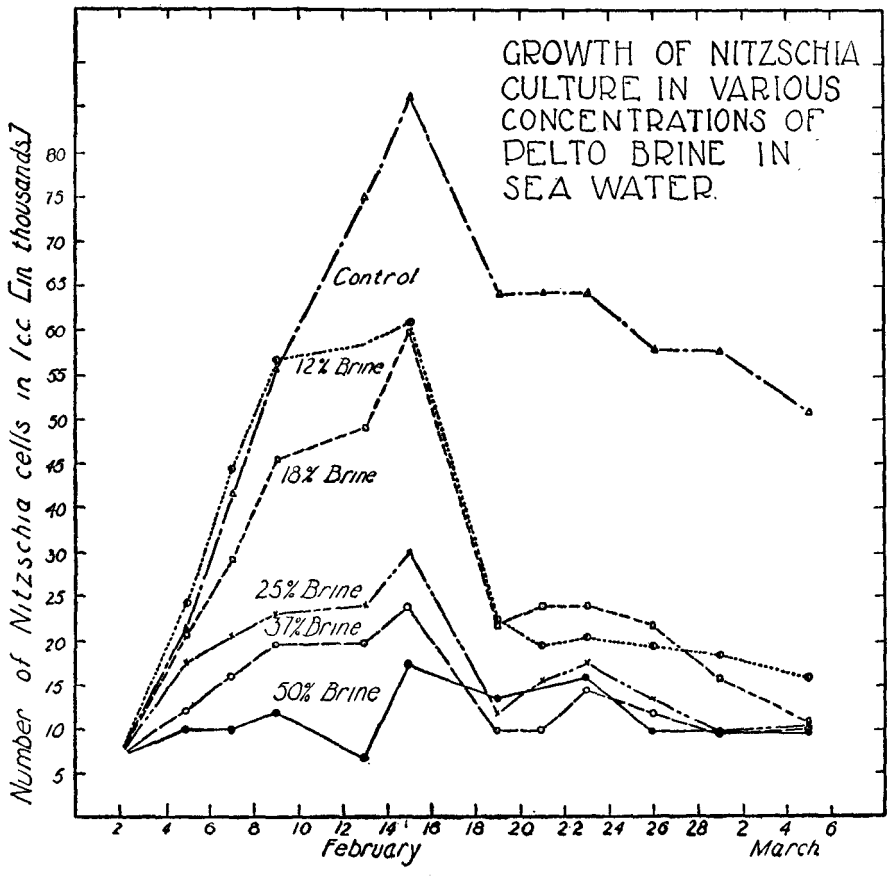

FIGURE 18.—Effect of brine on the growth of Nitzschia culture in sea water.

TABLE 23.—*Retarding effect of brine on the growth of Nitzschia culture*

[Figures in the body of the table indicate percent of retardation]

Concentration of brine	Dec. 23 (16 days)	Jan. 8 (22 days)	Feb. 2 (31 days)	Feb. 2 (31 days)	Apr. 2 (14 days)	Apr. 2 (14 days)	Average percent of retardation
Percent in Miquel solution:							
12	23	11	0	12	8	8	10
18.8	48	3	36	17			26
25	58	28	40	38	35	30	38
37.5			75	63			69
50			93	90			92
Percent in sea water:							
12		13	66	40		46	41
18		36	74	61			57
25		31	75	79		80	66
37			76	87			82
50			77	99			88

Both in the sea water and in Miquel solution the retarding effect is directly proportional to the concentration of brine (fig. 20).

From the results of the experiments it becomes apparent that brine contains substances which interfere with the growth and rate of propagation of the diatom.

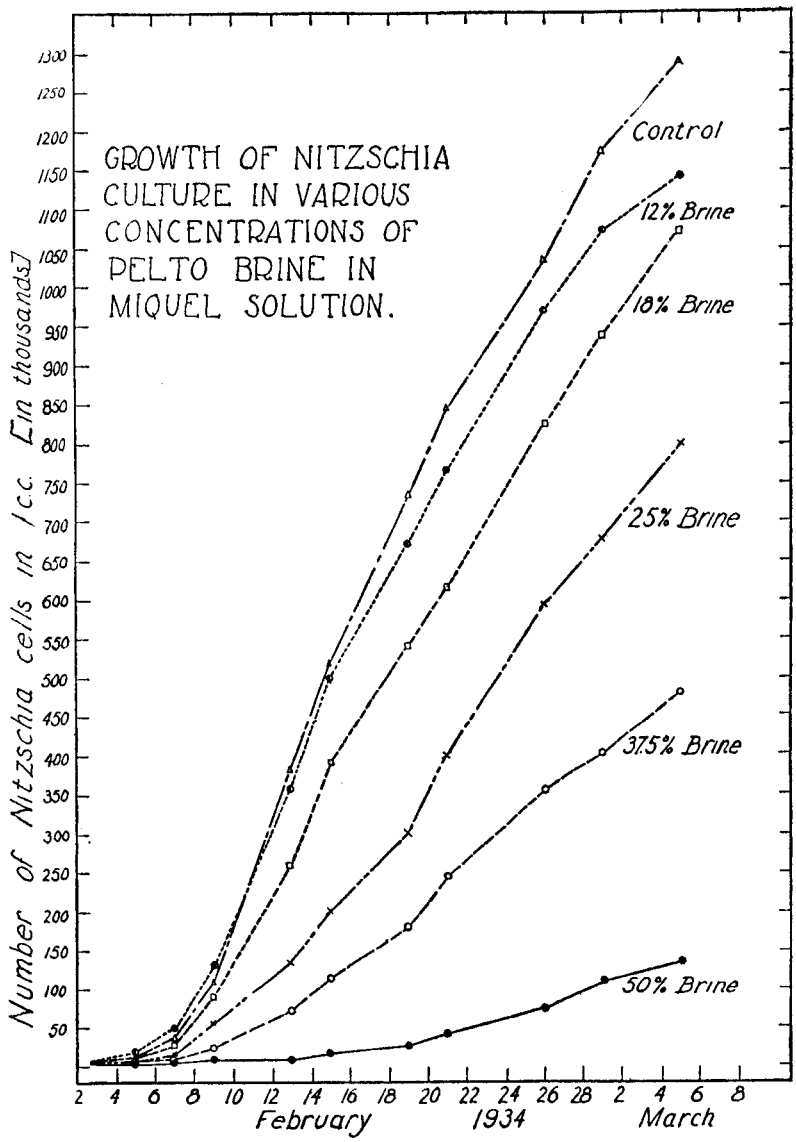

FIGURE 19.—Effect of brine on the growth of Nitzschia in Miquel solution.

The experimental work reported in this part of the report provides sufficient evidence of the possible adverse effect of crude oil and bleed water on the food supply of oysters and other plankton feeding animals of the sea. Probably the retarding effect of crude oil on the rate of diatom growth is primarily due to the toxic action of its water-soluble constituents. The extraction of this substance or substances is undoubtedly facilitated by the action of wind and current. Oil absorbed by mud

and deposited on the bottom may be therefore regarded as a source of potential danger to the microscopical algae. When the bottom is stirred by passing boats or by a strong wind action, a certain amount of oil may again become released and float in

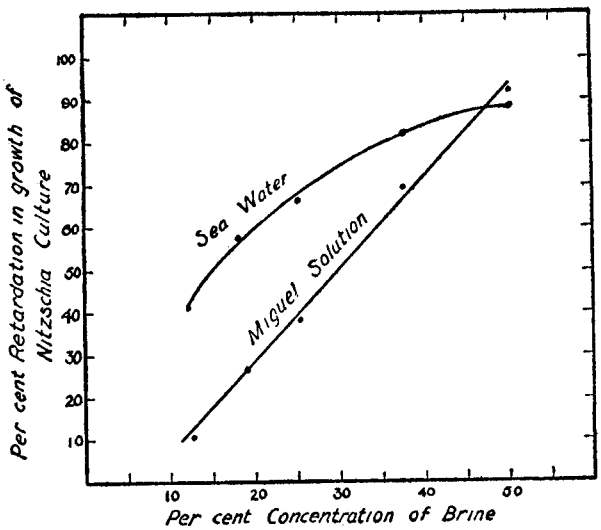

FIGURE 20.—Retardation in growth of Nitzschia culture in sea water and Miquel solution caused by various concentrations of brine.

the water giving off water-soluble toxic substances. The adverse effect of brine is even more pronounced than that of the oil.

DISCUSSION AND CONCLUSIONS

By PAUL S. GALTSOFF

Ecological and hydrographical observations presented in the first half of the report describe the conditions of the oyster bottoms affected by the oil-well pollution. Preliminary investigations carried out by Prytherch in 1933 failed to reveal the existence of a direct correlation between the intensity of mortality and the distance between the affected oyster bottoms and oil wells. This is evident from an examination of the chart (fig. 1), showing the intensity of mortality on various oyster beds (black circles) and the location of active oil wells. A number of oysters, barnacles, and green algae were found growing on the piling of oil wells, and no unusual mortality was observed among other organisms. The presence of small numbers of oysters on piling of oil wells was also observed in 1934 by Galtsoff and Smith. Examination of oysters and plankton showed that apparently there was no interference with the development of gonads, spawning, and setting of the larvae. The diseased condition of oysters was evidenced, however, by the loss of muscular tonus and the failure of the adductor muscle to maintain closure of the shell. It is known that if such a condition continues for a long time it results in a stunted growth and abnormal shape of the shell. No unusual changes in the salinity of water and other hydrographic conditions, which might account for a great mortality, were disclosed by these observations.

The oyster enemies, the borer, the boring clam, and the boring sponge, are rather abundant in Louisiana waters. Many dead oysters examined in 1933 showed heavy perforations caused by the boring clam and sponge, but on the other hand, at least

at one station (no. 6, fig. 1), 95 percent of dead shells were not infested by these pests. Oyster growers have not noticed an unusual increase in abundance of oyster enemies, and no evidence has been obtained which would indicate that such an outburst occurred at the time of the mortality in the winter of 1932–33. It is significant that in 1933 the mortality affected chiefly the larger and older oysters of marketable size and in several instances was especially severe among the recently transplanted oysters. Undoubtedly, the practice of overcrowding the beds by planting from 700 to 900 barrels of oysters per acre may be one of the contributing factors which aggravates the situation and in case of adverse environmental changes or the poor condition of the oysters, may materially increase their mortality.

A more detailed survey of the oyster bottoms, made by R. O. Smith in 1934, failed to assign the mortality to any known disturbance of the natural conditions on oyster beds, as for instance, temperature, salinity, current, and invasion of enemies. It has been noticed that in general mortality has been higher on soft, muddy bottoms than on hard ground. At the time this survey was carried out, pollution was noticeable at the mouth of Bayou Grey where the surface of the water was covered with oil for a distance of 3 miles below the wells and there was some mortality on the oyster beds of this section. All shells were covered with a brownish-black coating of tarry consistency and the meats were unpalatable because of the strong oily flavor. Considerable quantities of oil were held by mud, and oily patches appeared on the surface when the bottom was stirred. Light films of oil were observed also in the vicinity of the Lake Barre wells. In 1934 oysters on many beds throughout the region did not become fat until February or March, which points to a possible scarcity of food or to a disturbance in the functioning of the organs of feeding.

The shallowness of the water throughout the oyster-producing region in Louisiana must be regarded as a factor which tends to magnify the action of any polluting substance. Due to stirring by wind, the water carries much suspended matter which may absorb the pollutant, transport it over wide areas, and deposit it on the bottoms far from the source of pollution. Observations in the polluted areas show that on account of the absorption by suspended clay particles, oil quickly disappears from the surface and after being deposited on the bottom, remains there for a long time.

No information was obtained by the two surveys upon which to base an opinion as to the direct cause of mortality, but ample experimental evidence has been accumulated to show that the presence of crude oil in water produces conditions inimical to oysters.

The first series of experiments designed to determine whether oysters could be killed by the presence of oil in the water or by direct contact with oil, gave negative results. Unfortunately because of the circumstances over which the investigators had no control, these experiments were carried out not in Louisiana, but in a different environment at Beaufort, N. C., with uncultivated oysters taken from oyster reefs. Samples of crude oil collected by the State Conservation Department from Louisiana oil wells were shipped to Beaufort and used throughout the experiments. It is quite possible that the results might have been different had Louisiana oysters been used.

In a series of experiments lasting from 2 to 3 months, the mortality of oysters kept in running sea water under a surface layer of oil, and those kept in sea water that passed through oil was not greater than that in the controls. In the experiments carried out under similar but not identical conditions, Gowanlach (1934) observed considerable mortality among the oysters kept in oil-polluted water. The

discrepency between the two sets of experiments may be due to the difference in technique or to the better condition of North Carolina oysters used in Prytherch's experiments.

In another set of laboratory experiments no higher mortality than that in controls was observed among the oysters which, over a period of 6 to 8 weeks, were immersed at regular intervals in oil (table 3, p. 163). In some of the experiments the mortality among the controls was as high as 50 percent, indicating unfavorable laboratory conditions under which the animals were kept. It is possible that these conditions beclouded the effect of oil on oysters.

The fact that oysters survived the treatment with oil does not indicate that they were not affected by it. Analyses made by Galtsoff show slight decrease in glycogen content of oysters kept in the laboratory in the oil-polluted water (table 4). The result may be due either to the disturbance in the functioning of the feeding apparatus of the organism or to the decreased supply of food.

A regular operation of the muscular mechanism involved in closing and opening of the shell is prerequisite for the normal feeding of the oyster. Two sets of experiments, carried out by Prytherch in 1933 and Galtsoff and Smith in 1934, gave identical results showing that the presence of oil has no effect on the mechanism of the adductor muscle.

In the first set of experiments, continuous kymograph records were obtained of 5 oysters which were kept under observation for 3 months. The average number of hours per day the oysters were open was 11.2 for the controls and varied between 10.0 and 13.6 for the experimental oysters. In the second set of experiments, 6 control oysters kept under observation from 4 to 14 days, were open on the average of 10.5 hours daily, whereas the average figure for 10 experimental oysters kept under observation from 4 to 8 days, was 9.6 hours. In both cases the difference is insignificant.

Although the presence of oil in the sea water does not reduce the number of hours the oyster keeps its shell open, and therefore the duration of feeding of the mollusk is not decreased, the rate of feeding is easily affected by the presence of polluting substance. As the feeding of the oyster is primarily dependent upon the amount of water passed through the gills, the rate of pumping of water can be used as a measure of the rate of feeding. The results of the experiments in which the cone method, previously described by Galtsoff (1928) was used, and of those in which the drop counting technique was employed (fig. 5), show that crude oil contains substances soluble in the sea water which produces anaesthetic effect on the ciliated epithelium of the gills. The inhibiting action is not due to the mineral salts that may be leached out in preparing the water soluble fraction of the sample of oil by shaking it with sea water. It is apparent that certain organic compounds of oil are slightly soluble in sea water. This conclusion can be drawn from the observations that after 28 washings with water, the sample of oil did not lose its toxic property and yielded extract, the anaesthetic potency of which was equal to those obtained with the first washings. The inhibiting effect of the water-soluble fraction is proportional to its concentration (figs. 6, 7, 8, and 9). From a large number of experiments summarized in these figures and tables 11, 12, and 13, the inference can be drawn that a concentration between 20 and 30 percent of the soluble fraction will, on the average, reduce the rate of feeding of the oyster to one-half of its normal value (fig. 8).

Under the conditions of the experiments, the recovery of the ciliary motion following the removal of the oil extract, was almost complete. Inasmuch as the

experimental oysters were kept in the extract only for a limited period of time, the result of the prolonged exposure remains to be determined. There was no indication in the present experiments of an increased tolerance in oysters due to repeated treatment.

As it can be seen in tables 11, 12, 13, and 14, there was a large variation in the percentage of depression caused by a given concentration of the soluble fraction on individual oysters. Two explanations suggest themselves. First, there is a possibility that in spite of the precautions taken in preparing the soluble fraction, the toxicities of individual samples were different. Second, the oysters used in the experiments may have different sensitivity and tolerance. The second explanation seems to be more plausible, for the wild oysters used in the experiments at Beaufort, coming from exposed flats, greatly varied in appearance, glycogen content, and other characteristics.

From a large number of experiments with the water-soluble fraction the inference seems to be inevitable that crude oil discharged in the sea, regardless of whether it floats on the surface or, having been absorbed by mud particles, is deposited on the bottom, continuously yields water-soluble substances which narcotize the ciliated epithelium of the gills, thus reducing the rate of pumping of water and, therefore, materially decreasing the amount of food obtained by the organism. This should lead to gradual starvation and weakening of the oyster. The chemical nature of the substances and their concentration in the oil-polluted areas remains to be determined by future investigations.

The effect of brine or so-called "bleed water", which accompanies oil discharged by the wells and is usually dumped into the sea, has been studied by using the same technique as was employed in the experiments with oil. It has been found (table 6), that bleed waters of Lake Barre and Lake Pelto do not affect the muscular mechanism of the oyster in relatively high concentrations, provided the quantity present does not increase the salinity beyond the limits of tolerance. A 10-percent concentration of bleed water may exert a stimulating effect on the ciliated epithelium at least in some of the individuals. The depressing effect occurs at the concentration of 20 percent and higher. A 33–40 percent solution reduces the rate of pumping of water by the gills to 32.6 percent of its normal rate. The percentages of brine which cause this or greater depression are beyond any possibility of occurrence in nature.

Experiments reported in the last section of the paper attempt to throw light on the possible effect of oil and bleed water on the production of the food of the oyster. It has been assumed that the results of the laboratory experiments with Nitzschia, which occurs in the normal habitat of the oyster, and constitutes an important element in its diet, are applicable to other species of diatoms. It has been found that the presence of a heavy layer of oil on the surface of culture flasks inhibits the growth of Nitzschia (fig. 13) when oil remains on the surface for a week or longer. The soluble fraction of oil exerts a retarding effect on the growth of Nitzschia in concentration of 25 percent and higher and when the extract is permitted to act over a considerable period of time. Low concentration may have a slightly stimulating effect. In many instances the addition of the oil extract stimulated the growth of bacteria, small numbers of which were always present in cultures, and caused the death of diatoms.

Water-soluble substances obtained by dialysis through a collodion membrane also exerted a retarding effect on Nitzschia, both in natural sea water and in Miquel solution (table 22).

Bleed water retards the growth of Nitzschia, the inhibiting effect being pronounced in concentrations of 10 percent and higher. The retardation of growth is directly proportional to the concentration (fig. 20).

The experimental evidence presented in the report shows that the discharge of oil into the sea produces profound changes in the normal environment of the oyster. The substances which gradually dissolve from oil in the sea water irritate the delicate ciliated mechanism. In a very dilute solution they may act as stimulants, but in higher concentrations they inhibit the activity of the ciliated epithelium and may bring about complete stoppage of the current of water through the gills. The same substances which reduce the rate of feeding of the organism affect its food supply by retarding the rate of propagation of diatoms. Obviously the presence of oil creates adverse conditions.

In the light of the present investigation, it is easy to conceive that when the constitution of the organism is weakened by unfavorable meteorological conditions, natural changes in the environment or attacks of enemies, the pollution of water with oil may become a deciding factor which may cause irreparable injury and death of the oyster. It is obvious that from the point of view of conservation, the natural oyster resources of the sea must be protected from this danger.

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U. S. DEPARTMENT OF COMMERCE
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AGE AND GROWTH OF THE CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR), IN THE LAKES OF THE NORTHEASTERN HIGHLANDS, WISCONSIN

By RALPH HILE

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 19

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1936

For sale by the Superintendent of Documents, Washington, D. C. - Price 30 cents

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By RALPH HILE, Ph. D., *Assistant Aquatic Biologist, U. S. Bureau of Fisheries*

CONTENTS

	Page
Introduction	212
Acknowledgments	214
Materials	214
Methods	215
Gear used in collecting	215
Methods of fishing	215
Field data recorded for individual specimens	216
Treatment of preserved specimens and resulting shrinkage	217
Preparation and examination of scale material	217
Miscellaneous considerations	218
The scale method	218
Assessment of age and calculation of growth	218
Lee's phenomenon in the Silver Lake cisco	222
Possible causes of Lee's phenomenon in the Silver Lake cisco	224
Selection by gear	224
Selection due to dissimilar distribution within the lake of the various elements of the population	224
Selection due to differential mortality, correlated with growth rate	225
Other possible causes	225
General growth curves for the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake cisco populations	226
Growth in length	226
Growth in weight	230
Comparison of the growth of the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake cisco populations with that of cisco populations in other regions	232
Range of length in individual age groups; maximum length and weight	234
Condition and the relationship between length and weight	237
Length of growing season	249
Relationship between density of population and rate of growth	253
Age composition of the samples and the relative abundance of year classes	263
Age at maturity and sex ratio	267
Annual increments of growth	271
Variation in the amount of growth in different calendar years	271
Bimodality in the calculated growth for the first year of life	280
Growth compensation	282
Growth relationships in the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake cisco populations	286
Physical-chemical factors	287
Density of population	288
Length of the growing season	288
Parasitization	289
Condition	289
Sex ratio	292
General remarks	292
Fishes associated with the cisco	293
Selective action of gill nets	294
Review of previous investigations	294
Selective action of gill nets used in collecting samples of ciscoes from Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake	298
Trout Lake	298
Muskellunge Lake	300
Silver Lake	302
Clear Lake	304
Relative abundance of age groups in gill net samples	305
General conclusions	306
Summary	306
Bibliography	310
Appendix A. Growth of the cisco in Allequash and Tomahawk Lakes	316

[1] Bulletin No. 19. Approved for publication, July 31, 1935.

INTRODUCTION

In 1927 the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries instituted a cooperative study of the life histories of the fishes that inhabit the lakes of the highland district of northeastern Wisconsin. By the arrangements agreed upon, the survey furnished facilities for the conduct of field operations and staff members of the two organizations cooperated in the collecting and investigation of the research materials. The limnological laboratories of the survey at Trout Lake, Wis., served as headquarters for all field operations.

During the summer and early autumn of 1927 Dr. Stillman Wright of the Bureau, with the aid of an assistant made collections of fishes from several lakes of the region. In 1928, when it was impossible for Dr. Wright to be in direct supervision of the field work, the collections were made by Dr. Joseph Goldsmith and an assistant. A part of the collections for the years 1927 and 1928 served as a basis for a preliminary report on the growth of the rock bass in Trout and Muskellunge Lakes (Wright, 1929). In 1929 Dr. Wright found it necessary to devote his entire time to limnological investigations on Lake Erie and collecting operations were suspended during that year.

The collection of data for the investigation of the life histories of the fishes of the region was resumed in 1930. During this season the field work was carried on by Dr. Edward Schneberger of the survey and Dr. Ralph Hile of the Bureau. (In 1931 the collecting of materials was continued under the supervision of these 2 investigators with the aid of 2 assistants.) In 1932, when it was impossible for Dr. Hile to participate in the field operations, the collections were made by Dr. Schneberger, aided by one assistant.

Although the materials collected have afforded data on a number of species, the investigations have centered upon the life histories of three forms: The yellow perch, *Perca flavescens* Mitchill; the rock bass, *Ambloplites rupestris* Rafinesque; the cisco or lake herring, *Leucichthys artedi* (Le Sueur). Dr. Schneberger has given his attention to the study of the perch and Dr. Hile to the study of the rock bass and the cisco. The small collections of game fishes collected in the various years formed a part of the material used by Juday and Schneberger (1930, 1933) in their studies on the growth of game fishes in Wisconsin.

The ultimate aim of these studies of the fishes of northeastern Wisconsin is a more precise evaluation of the various environmental factors in their relation to the growth and abundance of the different fish forms. Since 1925 the survey has been conducting extensive limnological investigations on the lakes of the region.[2] The fish collections that were made for the growth studies have served also as material for study by survey staff members of food habits and parasitic infestation in the various species. The general consideration of the relationship between growth and environment awaits the termination of these several lines of investigation. In the present publication references will be made to relationship between growth and certain environmental factors, but no exhaustive discussion of the question will be undertaken.

In the investigation of the ciscoes an attempt was made to select the populations for study from "type" lakes. The selection of the four lakes with which this study is primarily concerned was based principally on the amount of fixed CO_2 present in

[2] For a history of the survey's operations consult Juday and Birge (1930). Annual summaries of the survey's activities appear in the Bureau's reports on Progress in Biological Inquiries (Rich, 1926; Higgins, 1928a, 1928b, 1930, 1931a, 1931b, 1932, and 1933).

the water. This factor was considered to be a fair index of the general productive capacity of the various waters. Size and form of basin were also taken into account in the selection of the lakes. Trout Lake is the second largest and the deepest lake of the region. In comparison with the surrounding bodies its water is relatively hard. Muskellunge is a lake intermediate as to size and as to the amount of fixed CO_2. Silver Lake is a small lake with intermediate conditions with respect to fixed CO_2. Clear Lake has an area approximately equal to that of Muskellunge Lake. Its water contains an unusually small amount of fixed CO_2.

Table 1 gives for each lake the details of location, area, depth, and also data relative to the physical and chemical nature of the waters. The two lakes, Allequash and Tomahawk, from which small samples of scales were obtained for growth study, are included in the table.

TABLE 1.—*Description of the 6 lakes of which cisco populations were studied*

[The characteristics, color, pH, conductivity, fixed CO_2, and organic content of plankton refer to average surface conditions. These data were furnished by the Wisconsin Geological and Natural History Survey]

Lake	Location	Length in kilometers	Width in kilometers	Surface area (hectares)	Maximum depth (meters)	Volume in 1,000 cubic meters	Secchi disk transparency (meters)	Color platinum cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO_2 in milligrams per litre	Organic matter of plankton in milligrams per litre
Clear	Town 39N, range VIIE	2.10	1.83	373	26.5		6.3	0	6.6	17	2.2	0.84
Muskellunge	Town 41E, range VIIE	3.30	1.18	375	19.3	26,172	4.0	4	7.3	40	10.0	1.16
Silver	Town 41N, range VIE	1.69	.64	87.3	19.5	9,884	5.5	4	7.5	62	15.0	.85
Trout:												
North basin	Town 41 and 42N, range VI and VIIE.	3.60	2.10	532	29.0	69,017	5.0	6	7.8	73	18.5	.66
South basin [1]		4.51	3.86	1,051	35.5	149,020	4.5	3	7.6	77	18.7	.92
Allequash	Town 41N, range VIIE	2.41	1.41	142	7.5		1.5	30	7.9	67	16.9	1.48
Tomahawk	Town 38 and 39N, range VI and VIIE.	7.24	3.00	1,476	22.5		4.2	8	7.6	69	16.7	.78

[1] All ciscoes collected from Trout Lake were taken in the south basin.

Juday and Birge (1930) published a general description of the northeastern highland lake district. Thwaites (1929) described the glacial geology of a part of Vilas County in which all but two (Clear Lake and Tomahawk Lake) of these lakes are located. Chemical, physical, and biological data concerning the various lakes have appeared from time to time in the publications of the limnological laboratory of the survey.

From time to time in the following discussion different species of fish will be mentioned by their common names. Because of the considerable local variation in the common names of fishes it is thought well to list the scientific names of the various species mentioned, along with their common names:

Bluegill, *Helioperca incisor* (Cuvier and Valenciennes).
Burbot, *Lota maculosa* Le Sueur.
Ciscoes or chubs, *Leucichthys spp.*
Cisco, lake herring, *Leucichthys artedi* (Le Sueur).
Lake trout, *Cristivomer namaycush* (Walbaum).
Largemouth black bass, *Aplites salmoides* (Lacépède).
Perch, yellow perch, *Perca flavescens* Mitchill.
Pike-perch, *Stizostedion vitreum* (Mitchill).
Rock bass, *Ambloplites rupestris* Rafinesque.
Sauger, *Stizostedion canadense* (Smith).
Smallmouth black bass, *Micropterus dolomieu* Lacépède.
Sucker, *Catostomus commersonnii* (Lacépède).
Whitefish, *Coregonus clupeaformis* (Mitchill).

ACKNOWLEDGMENTS

I wish to acknowledge the assistance and cooperation of the members of the staff of the Wisconsin Geological and Natural History Survey. Dr. Chancey Juday offered much valuable advice, particularly in the selection of lakes for study, and supplied needed limnological information. Dr. Edward Schneberger was completely in charge of the 1932 collecting operations.

Dr. John Van Oosten, in charge of the Great Lakes fishery investigations of the Bureau of Fisheries, gave much valuable advice (both as to field procedure and methods of analysis of data) during the execution of this work, and gave his assistance freely in the interpretation of difficult scales. Dr. Van Oosten also made a critical examination of the manuscript.

Dr. Carl L. Hubbs, curator of fishes in the Museum of Zoology of the University of Michigan, read the original manuscript and offered valuable suggestions for its improvement.

Harry C. Carver, professor of mathematics and insurance in the University of Michigan, read the section of the manuscript on the relationship between length and weight.

Dr. Peter Okkelberg, secretary of the Graduate School of the University of Michigan, checked the accuracy of my translation of portions of Huitfeldt-Kaas' (1917) publication. The reference to Olofsson's (1932) paper is based on an abstract prepared by R. W. Eschmeyer of the Michigan Institute for Fisheries Research.

The determination of age and the calculation of growth of the 1928 collection of the Trout Lake cisco are entirely the work of Dr. Stillman Wright, formerly of the Bureau of Fisheries.

MATERIALS

The investigation of age and growth has been based upon the determination of ages for 3,882 specimens and the calculation of growth for 3,694 specimens. Specimens other than those whose ages were determined have been used incidentally for other purposes such as the study of vertical distribution of the cisco and the density of population. Koelz (1931) described material from each of the six lakes whose populations are considered in this study. According to Koelz 3 subspecies of *Leucichthys artedi* are represented in these 6 populations. Clear Lake is the type locality for *L. artedi clarensis* Koelz. The same form is accredited to Muskellunge, Silver, and Allequash Lakes. Koelz described the Trout Lake cisco as *L. artedi clemensi* Koelz, and the form occurring in Tomahawk Lake as *L. artedi wagneri* Koelz. However, Hile (MS.) in a paper now in press has demonstrated that the ciscoes of these lakes at present are not susceptible of division into subspecies, but should be considered merely as populations of the species, *L. artedi.*

Table 2 lists the locality and year of capture of the ciscoes used in the life-history studies. The 1931 material includes 658 preserved specimens collected for a morphometric study to appear in a later publication, while all the 1932 Muskellunge Lake specimens and 95 of the 1932 Clear Lake specimens were preserved.

TABLE 2.—*Year of collection and number of specimens in the collections used in the study of age and growth of the cisco*

Lake	Year of collection				Total number
	1928	1930	1931	1932	
Trout	182	508	610		1,300
Muskellunge	281	245	616	188	1,330
Silver	135	118	378		631
Clear			249	191	440
Allequash	47	66			113
Tomahawk	68				68
Total	713	937	1,853	379	3,882

The relatively limited data from the small collections from Allequash and Tomahawk Lakes are not considered in the general discussions of this paper, but are treated in a special section (appendix A).

METHODS

GEAR USED IN COLLECTING

With the exception of a small number of 0-group individuals picked up on the beaches of Trout Lake all samples used in this investigation were collected by means of gill nets. The 1928 collections were made in nets of the following sizes of mesh: [3] 1⅜, 1½, 1¾, 2, 2½, and 3 inches, and in Trout Lake a 1¼ by 8-inch trammel. The trammel used in the capture of Trout Lake ciscoes would operate as a 1¼-inch gill net. In this year no net records were kept for individual specimens. It is unlikely, however, that in any of the three populations (Trout Lake, Muskellunge Lake, Silver Lake) ciscoes were taken either in the 2½-inch- or 3-inch-mesh nets.

The nets used in 1930 had also been used in 1928. However, the discarding of worn-out nets at the close of the 1928 season was so extensive that the only sizes of mesh available in 1930 for the capture of ciscoes in the three lakes named in the preceding paragraph were 1½ and 2 inches. These same nets were used in the early part of the 1931 collecting season. The depth of these nets varied from 3 to 4½ feet.

The gill nets used in 1930 and in the early part of the 1931 season were in a sorry state of repair. Not only were many of the meshes broken, but holes of considerable size were of frequent occurrence. The making of repairs was not feasible as the thread had deteriorated to the extent that even ordinary handling and use of the nets frequently produced new tears in the webbing.

The gear was completely replaced on July 22, 1931, after which date the following sizes of mesh were used: 1¼, 1½, 1¾, 2, 2¼, 2½, and 3 inches. Each net was 50 yards long and approximately 6 feet deep; 5-inch leads were used as a precaution against tangling of leads in the webbing. All Clear Lake samples (1931 and 1932) were taken in the new gear, but only a few lifts of the new gear were made in the other lakes.

The question of gill net selectivity, particularly with reference to the use of gill net samples for the study of age and growth, is considered in a special section (pp. 294–306).

METHODS OF FISHING

The new nets purchased in 1931 were fished in gangs containing 1 net of each of the 7 mesh sizes. In sets of the old nets the larger mesh sizes, known to be ineffective on the cisco populations that were being sampled, were occasionally

[3] Throughout this paper, sizes of mesh, unless otherwise indicated, are presented as stretched measure.

omitted. No attempt was made to arrange the nets in any definite order as to size of mesh. In general it was customary to intersperse the larger mesh sizes with the smaller. All sets were made on the bottom.

The nets were lifted and reset once each day. At least once each week they were removed from the water, stretched on a reel, and allowed to dry thoroughly. At intervals of about a month all the nets were treated with copper soap after a method suggested by Harry Hansen, formerly of the Bureau of Fisheries.

The 1928 data contain only scattered information as to the depth from which the various samples were taken. During 1930 observations were made regularly as to the general depth and the nature of the bottom in the region in which the nets were set. Later it was found desirable to possess more precise information on the matter of depth. Accordingly in 1931 and 1932 soundings were made to determine the depth at which each particular net was set. Routine records were kept as to the condition of the weather (cloudiness, precipitation, and strength and direction of the wind). Catches from the different sizes of mesh were placed separately in labeled pails. After the return to the field laboratory counts of the number of fish taken in each net were added to the field notes.

FIELD DATA RECORDED FOR INDIVIDUAL SPECIMENS

Scale samples were taken in the field from all specimens except those preserved for morphometric studies. (The treatment of preserved specimens will be discussed later.) The scale samples were removed whenever possible from the left side of the body dorsal to the lateral line and ventral to the dorsal fin. Scales were stored in standard Bureau of Fisheries scale envelops. On each serially numbered envelop were recorded date, locality, species, length, weight, sex, state of maturity,[4] and gear.[5] The field numbers included in the day's catch were cataloged.

The standard length (from the tip of the snout to the end of the vertebral column) was measured for each individual fish. Enough measurements of the total length (from the tip of the snout to the line connecting the tips of the extended caudal fin) were made to obtain a reliable figure for the ratio between standard and total length.[6] All lengths were measured with a steel tape in a straight line between the points indicated, not along the curvature of the body, and were recorded to the nearest millimeter. Throughout this paper the unit of length can be assumed to be the millimeter.

The smaller individuals were weighed on a Chatillon spring platform balance of 500-gram capacity with calibrations at 2-gram intervals. Weights of these fish were estimated to the nearest gram. Weight records above 500 grams were obtained by means of a Chatillon spring platform balance of 5-kilo capacity and with calibrations at 20-gram intervals. Weights of these larger fish were estimated to the nearest 5 grams. Toward the close of the 1931 collecting season the smaller balance developed a fluctuating error that was at no point greater than 2 grams. This balance was replaced by a new instrument at the beginning of the 1932 season.

[4] A fish whose sexual condition showed that it would spawn in the coming autumn was listed as mature, whether or not it may have spawned previously.

[5] Sex, maturity, and gear were not recorded for the 1928 samples.

[6] The ratio, total length in standard length, has the following values: Clear Lake, 0.84; Trout Lake, 0.84; Silver Lake, 0.85; Muskellunge Lake, 0.85; Allequash Lake, 0.84. The ratio was not determined for the Tomahawk Lake cisco.

TREATMENT OF PRESERVED SPECIMENS AND RESULTING SHRINKAGE

Part of the fish preserved for morphometric study were weighed and measured while fresh. These specimens were provided with individual, serially numbered tin tags. Other specimens to be preserved were divided into small groups which were wrapped in cheesecloth. Within each package was included a label bearing a record of date, locality, and usually of gear. The specimens were held in a 10-percent formalin solution until the close of the season. Upon removal from the formalin solution the fish were soaked in water about 4 days and then transferred permanently to a 70-percent solution of alcohol.

Since the preserved specimens—most of which were not weighed and measured in the field—constituted a part of the material used for a study of growth, it was of some importance to know the extent of the shrinkage brought about by the preserving fluids. Data on this question were obtained from 99 ciscoes from Clear Lake and from 105 ciscoes from Muskellunge Lake, all taken in 1932. These fish were weighed and their lengths measured at the time of capture. The dates of capture for the Clear Lake specimens were July 12 to July 19; for those from Muskellunge Lake, July 28 and July 29. The individuals of both collections were reweighed and remeasured October 10 and October 11, 1932. At this time they had been in alcohol about 5 weeks. The measurements and weighing of both the fresh and preserved material were made by the same method and by the same individual (Dr. Schneberger).

The ratio between preserved length and fresh length was 1.000 : 1.019 for the Muskellunge Lake cisco. This value of the shrinkage factor agrees closely with the figure, 1.016, determined by Van Oosten (1929) for the Lake Huron herring. Since the populations from Silver Lake and Trout Lake do not have greatly dissimilar length ranges (approximately 125–200 millimeters) the shrinkage factor based on the Muskellunge ciscoes has been used in correcting for shrinkage the lengths of the preserved specimens from these two lakes.

In the Clear Lake cisco, where the length range is much greater, the relative amount of shrinkage was found to vary at different lengths. The lengths of preserved specimens from this lake were corrected according to the following shrinkage factors:

Length interval:	*Shrinkage factor*	*Number of specimens*
350	1.005	16
250–349	1.010	65
150–249	1.028	18

The shrinkage factors for weight were 1.181 for the Muskellunge Lake ciscoes and 1.144 for the Clear Lake ciscoes. However, the individual shrinkage in weight varied so widely that it was not considered valid to employ a weight shrinkage factor for the purpose of making individual corrections. Only those preserved specimens that were weighed when fresh were used for the study of growth in weight.

PREPARATION AND EXAMINATION OF SCALE MATERIAL

Scales were soaked in water and cleaned by means of a dissecting needle and a small camel's-hair brush. Three scales from each fish were mounted on a microscope slide in a gelatin-glycerin medium prepared according to a formula presented by Van Oosten (1929). No regenerated scales or scales with abnormal or irregular shape

were mounted. On the label of each slide were recorded the field number, laboratory number, date and locality of collection, species, sex, maturity, length, weight, and gear. The scales were studied by means of the projection apparatus described by Van Oosten (1923). The magnifications used were X19 for scales of the Clear Lake ciscoes and X40.5 for scales of all other fish.

MISCELLANEOUS CONSIDERATIONS

It is the policy throughout this paper to apply toward the solution of each particular question all suitable data available. As a result of this procedure there appear certain discrepancies in the number of specimens listed in the tables pertaining to different phases of the general problem of the life history of the cisco. Since discrepancies of this sort, if unexplained, may prove a considerable annoyance to a reader, attention will be called to the causes for at least the most important of them.

Table 2 lists the fish upon which determinations of age were made. These specimens, with the exception of the 1932 Muskellunge Lake collections, separated into age groups and year classes, appear in the growth tables 3 to 7. The tables of general growth in length (10 to 14) are based on fewer specimens than tables 3 to 7 since certain indicated age groups were eliminated because of selection by gear. (The 17 0-group Trout Lake ciscoes were also omitted in the computation of the general growth curve.) The tables for growth in weight (15 to 18) are based on fewer specimens than those for growth in length since part of the preserved fish used in the growth study were not weighed before preservation. Of course, the study of the length-weight relationship and of condition was based only on specimens weighed in the field.

In the listing of catch per unit effort of gill nets (section on the relationship between density of population and rate of growth) it was, of course, valid to include fish that had not been aged. Similarly in the determination of the average length of all fish taken in a particular size of gill net (section on selective action of gill nets) it was also valid to include unaged fish. Further, the grand average length used for comparing the average length of an age group as determined from the combined catch of several different sizes of mesh with the average lengths of the same age group as based on the catch of individual sizes of mesh may include certain fish for which net records were not available. (Net records were lacking for a large part of the preserved fish.) The data of tables 40 and 73 are based in part on catches of Muskellunge Lake ciscoes taken in 1932 for morphometric investigations and included only incidentally in this study. None of the 1928 data is included in the analysis of net catches.

The 1928 data also lacked records of sex and maturity and hence could not be included in the sections on sex ratio and age at maturity.

Although some of these discrepancies are mentioned in the general discussions, a general statement of their origins was considered advisable.

THE SCALE METHOD

ASSESSMENT OF AGE AND CALCULATION OF GROWTH

The treatment here of the growth data of the cisco is based upon the use of the scale method. Van Oosten (1929) established the validity of the method for this species in his study of the life history of the Lake Huron herring. It is assumed that

the method is equally valid for the populations considered in this investigation. As will appear later, the results of the analysis of the growth material presented here seem to justify the assumption. Throughout this paper the individual ages are designated as the number of years of life that have been completed. Although the cisco spawns in late autumn or early winter, the life of the individual is assumed to begin the following spring when hatching takes place. During the first year of its life the individual is a member of the 0 group, during the second year it is a member of the I group, etc. Fish hatched in the same year belong to the same year class, regardless of their age at the time of capture.

Two examinations for age determination were made of the scales of each individual specimen. At the second examination either a definite assignment of age was made for the troublesome scales or the slides were marked as unreadable. At the time of the final examination one of the three scales on the slide was measured. This scale was selected on the basis of clearness of markings and symmetry of form. The diameters of the different growth areas were measured along the anteroposterior axis of the scale. For this measurement the ruler was placed in such a position that its edge passed through the focus of the scale and approximately bisected the posterior field (that portion of the scale which is exposed in its natural position on the fish). Scale measurements were made with a tested millimeter ruler and recorded to the nearest millimeter (occasionally the nearest half millimeter).

The assessment of age was based on the determination of the number of annuli or lines of discontinuity between growth areas of succeeding years. Two difficulties were encountered in the determination of individual ages. The later annuli of the older individuals (particularly those of the slower-growing populations) were sometimes so crowded together as to make their recognition difficult or even impossible. In the latter case the scales were discarded. Accessory annuli (summer checks) were not infrequent, but their characteristically indefinite appearance and their position with respect to the true annuli were such that they were ordinarily easily recognizable. Somewhat less than 5 percent of the total number of scales examined were discarded as unsatisfactory for the determination of age.

Accessory checks were found to occur regularly in all the samples of the scales of the Muskellunge Lake cisco. They could be separated from the true annuli quite easily in the growth fields of the earlier years, and consequently they presented no great difficulty in the age and growth analysis of the earlier (1928–31) collections which were composed almost entirely of I-, II-, and III-group fish. In 1932, however, IV-group fish were present in abundance for the first time. In this year's collection the presence of accessory annuli, along with the IV-group's excessively slow growth during the fourth year of life, made the separation of the III group and the IV group of that year's collection both difficult and uncertain. Because of these difficulties and because of the abundance of data from the preceding years, the 1932 collections were not used in the computation of a general growth curve for the Muskellunge Lake population. However, certain of the data from the 1932 Muskellunge Lake samples will be used from time to time for other purposes.

Van Oosten (1929) demonstrated that after the formation of the first annulus the ratio of the total scale length to body length is so nearly constant in the lake herring that the assumption of the absolute constancy of the ratio affords the most

satisfactory means for the calculation of growth during the various years of the individual's existence. The formula used in the calculation of growth was:

$$L_n = D_n \frac{L_T}{D_T}$$

where

L_T=length of fish at time of capture;
D_T=total diameter of scale;
L_n=length of fish at end of n^{th} year of life;
D_n=diameter of scale within the n^{th} annulus.

Tables 3 to 7 present the data for the calculated growth in length for the ciscoes of Trout, Muskellunge, Silver, and Clear Lakes. Since no difference in the growth of the two sexes was apparent in the fish of the first three lakes the data for these lakes as presented represent a combination of males and females. In the data for the Clear Lake cisco the sexes are treated separately.

TABLE 3.—*Calculated growth of Trout Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life											
					1	2	3	4	5	6	7	8	9	10	11	12
1919	1931	XII	1	226	80	104	117	130	148	169	180	190	199	211	218	224
1920	1931	XI	2	205	75	103	119	130	142	152	162	172	180	198	204	----
1922	1931	IX	2	200	83	112	127	140	154	168	180	190	198	----	----	----
1923	1931	VIII	5	192	87	115	134	145	156	169	179	190	----	----	----	----
1924	1928	IV	17	147	85	120	133	143	----	----	----	----	----	----	----	----
	1931	VII	4	175	80	113	128	141	153	162	174	----	----	----	----	----
1925	1928	III	61	143	84	123	137	----	----	----	----	----	----	----	----	----
	1930	V	9	167	82	116	135	148	160	----	----	----	----	----	----	----
	1931	VI	12	165	79	116	132	145	156	164	----	----	----	----	----	----
1926	1928	II	102	134	82	117	----	----	----	----	----	----	----	----	----	----
	1930	IV	99	156	82	118	137	147	----	----	----	----	----	----	----	----
	1931	V	79	156	81	118	135	145	154	----	----	----	----	----	----	----
1927	1928	*I	2	128	97	----	----	----	----	----	----	----	----	----	----	----
	1930	III	347	149	79	117	139	----	----	----	----	----	----	----	----	----
	1931	IV	269	148	78	115	135	146	----	----	----	----	----	----	----	----
1928	1930	*II	36	140	91	127	----	----	----	----	----	----	----	----	----	----
	1931	III	173	142	84	120	137	----	----	----	----	----	----	----	----	----
1929	1931	*II	61	136	87	127	----	----	----	----	----	----	----	----	----	----
1930	1930	0	17	66	----	----	----	----	----	----	----	----	----	----	----	----
	1931	*I	2	128	106	----	----	----	----	----	----	----	----	----	----	----

TABLE 4.—*Calculated growth of Muskellunge Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life			
					1	2	3	4
1925	1928	III	10	172	105	142	162	----
1926	1928	II	252	160	99	147	----	----
1927	1928	*I	19	137	97	----	----	----
	1930	III	14	166	85	132	157	----
	1931	IV	2	176	90	143	161	174
1928	1930	II	214	162	95	143	----	----
	1931	III	347	166	96	145	163	----
1929	1930	*I	17	148	103	----	----	----
	1931	II	258	149	98	138	----	----
1930	1931	*I	9	136	96	----	----	----

TABLE 5.—*Calculated growth of Silver Lake ciscoes to the end of each year of life for the different year classes at each age; sexes combined*

[Groups marked with asterisks unreliable because of selective action of gear]

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life						
					1	2	3	4	5	6	7
1923	1928	V	10	182	76	115	142	161	175		
1924	1928	IV	69	174	79	125	150	166			
	1930	VI	3	197	72	112	134	161	177	192	
	1931	VII	1	201	77	111	135	158	172	186	196
1925	1928	III	46	165	73	127	157				
	1930	V	25	193	74	120	145	165	185		
	1931	VI	21	194	78	119	142	158	177	189	
1926	1928	II	9	157	90	140					
	1930	IV	58	183	78	126	152	173			
	1931	V	108	188	80	126	150	168	182		
1927	1928	*I	1	133	95						
	1930	III	25	181	77	134	167				
	1931	IV	102	183	80	132	159	176			
1928	1930	II	7	173	99	151					
	1931	III	61	177	83	137	166				
1929	1931	II	19	171	104	151					
1930	1931	*I	66	141	105						

TABLE 6.—*Calculated growth of Clear Lake ciscoes (males) to the end of each year of life for the different year classes at each age*

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life								
					1	2	3	4	5	6	7	8	9
1923	1931	VIII	3	338	118	203	248	279	297	314	326	333	
	1932	IX	1	355	114	194	254	290	310	323	333	345	354
1924	1931	VII	8	331	110	198	249	279	298	312	324		
	1932	VIII	7	345	108	195	250	279	302	318	331	342	
1925	1931	VI	11	326	108	192	248	282	303	316			
	1932	VII	9	336	102	188	248	280	302	318	331		
1926	1931	V	4	325	110	189	247	290	312				
	1932	VI	2	320	98	183	251	283	299	315			
1927	1931	IV	10	317	104	190	258	292					
	1932	V	7	320	98	181	249	288	312				
1928	1931	III	26	285	104	188	255						
	1932	IV	11	314	105	191	260	302					
1929	1931	II	34	253	108	200							
	1932	III	23	290	110	198	268						
1930	1931	I	20	178	119								
	1932	II	20	254	113	218							
1931	1932	I	20	176	122								

TABLE 7.—*Calculated growth of Clear Lake ciscoes (females) to the end of each year of life for the different year classes at each age*

Year class	Year of capture	Age	Number of specimens	Length in millimeters	Year of life										
					1	2	3	4	5	6	7	8	9	10	11
1921	1931	X	2	376	111	211	264	288	308	328	341	353	362	370	
	1932	XI	1	378	110	214	265	294	313	332	342	351	361	369	376
1922	1931	IX	1	351	114	206	262	283	301	316	330	339	346		
	1932	X	1	379	113	235	278	301	312	326	340	353	370	377	
1923	1931	VIII	13	354	112	199	253	286	308	323	336	347			
	1932	IX	2	368	107	200	259	291	322	333	346	354	363		
1924	1931	VII	21	344	108	196	250	282	305	322	335				
	1932	VIII	8	356	105	194	246	278	304	324	339	351			
1925	1931	VI	12	339	105	183	241	283	311	327					
	1932	VII	12	362	108	190	252	294	322	339	357				
1926	1931	V	2	338	108	188	258	302	326						
	1932	VI	1	320	98	183	251	283	299	315					
1927	1931	IV	4	334	103	191	273	306							
	1932	V	7	342	98	177	251	297	329						
1928	1931	III	25	302	108	199	269								
	1932	IV	14	329	103	195	268	312							
1929	1931	II	35	264	108	207									
	1932	III	21	308	108	205	282								
1930	1931	I	18	186	119										
	1932	II	13	262	114	219									
1931	1932	I	11	176	123										

From an examination of the tables for Trout, Muskellunge, and Clear Lakes it will be noticed that "Lee's phenomenon" of "apparent decrease in the calculated growth" as it is determined from successively older groups of individuals, while possibly present, is not a source of any great discrepancies, especially where large numbers of individuals are involved. On the whole the calculated growths based on different age groups in the same year's collection or upon samples of the same year class taken at different ages, agree satisfactorily for corresponding years of life, with the exception of the large calculated growths obtained for the younger age groups (marked with asterisks in the tables) in the Trout Lake and Muskellunge Lake collections. These large growths can be explained as the result of the selective action of the gill nets used for their capture. (See section on gill net selectivity.) The small but fairly consistent discrepancies that appear in the corresponding calculated growths of older year groups of the Trout Lake fish may be partly the result of slight changes in the body scale ratio. It is probable that selective action of gear plays a role here also. At any rate the discrepancies are of such small magnitude that they affect but little any conclusions that might be drawn concerning the growth of the population as a whole.

LEE'S PHENOMENON IN THE SILVER LAKE CISCO

In the Silver Lake data (table 5) there appear much more pronounced disagreements among the corresponding calculated growths of different age groups than are present in the other three populations. Not only are these discrepancies relatively large, but the comparison of any two age groups shows that in general they tend to be cumulative with increased age. These discrepancies appear in the comparisons of calculated growths based on the same year class but taken in different seasons as well as in calculated growths based on the different age groups of a single year's collection. To illustrate these two points there may be examined (table 5) first the calculated growths of the III, V, and VI groups of the 1925 year class and second the calculated growths of the III, IV, V, and VI groups of the 1931 collection. With certain exceptions in the first year of life it will be noticed that each successively older age group tends to give smaller values for the calculated lengths for corresponding years of life. Thus it may be seen that the observed discrepancies in the calculated growths depend on the differences in the age of the groups studied.

It will be noticed further that the apparent change of growth rate as it appears in the fish older than the II group differs from Lee's phenomenon as it ordinarily occurs, in that it is the calculated growths of the later rather than the earlier years of life that are affected most.

The calculated lengths of the Silver Lake ciscoes at the end of the first year of life require some special consideration. If size of sample is taken into account, the calculated growths for the first year of life show fairly good agreement for all age groups older than II. The calculated growths for the first year of life as based on the II group are somewhat less than those based on the I group, but those of both groups are considerably greater than the growths based on the older-age groups. The high calculated growths for the first year of life as based on the I group can be explained in part by the selective action of the gill nets used in collecting the samples, for there is reason to believe that even the smallest mesh of these nets may have taken only the larger individuals of this group. Such an explanation, however, does not seem to hold for the fish of the II group, since on the basis of comparisons with samples from other lakes the range of size of the Silver Lake II group seems to be such that very little

selection by gear could have taken place. Some other explanation must be sought, therefore, for the high growth values of this age group.

Since disagreements in the calculated growth data of fish are generally attributed in part to changes with age in the growth relation between body and scale, it was deemed advisable to study this relationship in the Silver Lake cisco. The 1931 collection was selected as best suited for this purpose. As was mentioned previously (p. 216) the scale samples used in this entire investigation were all taken from the same region of the body. Selections of scales for mounting and for measuring were made on the basis of distinctness of the annuli and symmetry of form rather than on size. As a consequence of this procedure the relationship between the length of body and the diameters of the scales measured should be comparable in the different age groups of a single sample.

As may be seen in table 8 the average ratio between the body length and the magnified diameters of the scales does not vary greatly from one age group to another. The generally made assumption of a linear relationship between scale size and body size tends to the determination for the Silver Lake cisco of the equation:[7]

$$L = 10.7 \text{ mm} + 1.078\ D,$$

where L=length of body in millimeters,

and D=the (magnified) diameter of the scale in millimeters.

TABLE 8.—*The body-scale ratio for the different age groups of the Silver Lake cisco collected in 1931, and the average diameters of scales as measured at the magnification* $\times 40.5$

[D_T is total diameter. The diameters within the different growth areas of the scales are indicated by the subscript figure]

Age	Number of specimens	Body-scale ratio	D_T	D_1	D_2	D_3	D_4	D_5	D_6	D_7
VII	1	1.16	174.0	67.0	96.0	117.0	137.0	149.0	161.0	170.0
VI	21	1.16	168.3	67.5	104.0	123.7	139.5	153.6	164.5	----
V	108	1.13	167.9	70.9	112.6	133.8	150.5	162.6	----	----
IV	102	1.13	161.9	71.0	117.5	140.8	155.7	----	----	----
III	61	1.15	155.7	72.6	119.5	145.7	----	----	----	----
II	19	1.18	145.8	88.0	128.7	----	----	----	----	----
I	66	1.17	121.3	90.2	----	----	----	----	----	----

Table 9 gives a comparison of the calculated growths of the 1931 Silver Lake collection first as they were determined on the assumption of a constant body scale ratio at all ages and second as they appear after correction for the changing body-scale relationship indicated by the above equation. It will be noticed that while the "correction" produced changes in the actual values of the individual average calculated lengths, it did little toward the elimination of the discrepancies between the calculated growths of the different age groups. For example, it may be seen that the maximum discrepancy in the calculated growth for the first year of life (between the calculations for the I group and the VI group) was reduced from 28 millimeters in the uncorrected to 24 millimeters in the corrected data—an improvement in agreement of only 4 millimeters. Similarly, the improvements in the agreement in the calculated lengths for the later years of life are unimportant when they

[7] It is realized that a more precise evaluation of the body-scale relationship might have been obtained through the use of "key" scales selected from exactly the same location in each fish. However, the complete failure of the "correction" equation to eliminate the discrepancies in the calculated growths of the Silver Lake cisco together with the fact that no corrections are needed in the other three populations made any detailed study of the body-scale relationship in these cisco populations unnecessary.

are considered in relation to the total discrepancy. Thus it may be seen that the observed discrepancies in the calculated growth of the Silver Lake cisco did not originate in a change of the body-scale relationships with increasing age.

TABLE 9.—*Calculated growth of the Silver Lake cisco, collection of 1931*

Age	Length	Uncorrected calculated lengths							Corrected calculated lengths						
		L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_1	L_2	L_3	L_4	L_5	L_6	L_7
VII	201	77	111	135	158	172	186	196	84	116	138	160	173	187	196
VI	194	78	119	142	158	177	189	------	84	123	145	160	178	189	------
V	188	80	126	150	168	182	------	------	86	129	152	169	182	------	------
IV	183	80	132	159	176	------	------	------	86	135	160	176	------	------	------
III	177	83	137	166	------	------	------	------	89	139	167	------	------	------	------
II	171	104	151	------	------	------	------	------	108	152	------	------	------	------	------
I	141	105	------	------	------	------	------	------	108	------	------	------	------	------	------

Further light is thrown on the question by the examination of the actual average measurements of the growth areas of the scales upon which the Silver Lake growth calculations were based (table 8). The comparison of the diameter measurements of table 8 with the corresponding calculated lengths of table 9 shows clearly that the disagreements in the calculated growths of the different age groups appear also in the actual scale measurements upon which the growth calculations were made. Van Oosten (1929) also observed that Lee's phenomenon was to be found in actual scale measurements as well as in calculated growths.

The "apparent change in growth rate" in the Silver Lake cisco must, then, be considered a real change rather than an apparent change due to changing body-scale relationships. Since, as was pointed out previously, the phenomenon appears consistently both in comparisons between different age groups of the same year class and in comparisons between different age groups of different year classes taken in the same calendar year, it cannot be explained either on the basis of inherent differences in the capacity for growth in different year classes, or on the basis of varying environmental conditions affecting growth in different years. It must rather be considered the result of some selectional factor correlated with the length of time intervening between the years for which the computations and scale measurements were made and the year when the fish was captured. Attention will be called briefly to possible sources of selection.

POSSIBLE CAUSES OF LEE'S PHENOMENON IN THE SILVER LAKE CISCO

SELECTION BY GEAR

A more detailed consideration of the question of the selective action of the gear used will be presented later in this paper. (See section on selective action of gill nets.) It may be stated here, however, that this factor most probably does not operate on the Silver Lake ciscoes except in the I group and that therefore it cannot explain Lee's phenomenon in these fish.

SELECTION DUE TO DISSIMILAR DISTRIBUTION WITHIN THE LAKE OF THE VARIOUS ELEMENTS OF THE POPULATION

Since the gill nets used in collecting the cisco samples for these studies were set directly on the bottom they fished only the lower few feet of water. If it is assumed that the larger individuals of the population tend to lead a more pelagic existence

than the smaller ones, then the more rapidly growing fish within an age group would be less subject to capture by nets set on the bottom than the slower growing individuals within the same group. Further, the effect of such segregation would be greater as age increases. The above-mentioned assumption would serve well to explain decreasing growth as it has been observed in the Silver Lake cisco, but data for its verification are not available. The chief objection to such an explanation lies in the fact that it is the smaller fish not the larger that would normally be expected to lead the more pelagic existence.

SELECTION DUE TO DIFFERENTIAL MORTALITY, CORRELATED WITH GROWTH RATE

It has been observed repeatedly that poikilothermous organisms tend to grow more slowly and reach a greater age in northern latitudes. The phenomenon appears to depend on the relation of temperature to the rate of metabolism. It is not wholly unreasonable to assume that the individual rate of metabolism might affect the individual growth rate and the individual length of life. Were mortality greater among individuals of more rapid growth, those individuals that survived longest would be those that had actually grown most slowly. The early growth as calculated from these slow growing survivors of the older age groups would naturally be small. Further, the effect on calculated lengths of this selection through differential mortality would tend to be increased with greater age, and thus discrepancies of the type observed in the Silver Lake data would be explained.

The relation between individual growth rate and individual length of life has been studied experimentally by several investigators. Osborne et al. (1917) found that a temporary preliminary stunting delayed maturity and extended the life span of rats. Titcomb et al. (1928) and McCay et al. (1931) found that trout that did not grow lived longer than those which showed growth on a similar diet. Zabinski (1929) by effecting a retardation of growth was able to prolong life in the black beetle and the roach. McCay (1933) presented a brief discussion of the general problem of the relationship of rate of growth to longevity.

OTHER POSSIBLE CAUSES

It is recognized that the three possible causes of Lee's phenomenon in the Silver Lake cisco discussed in the preceding paragraphs are by no means the only possible explanations of the observed discrepancies in calculated growth as based on fish of different age. These three suggested explanations were emphasized because they appear to be the most plausible in the face of the available data. Other explanations should be mentioned briefly along with the reason for their rejection.

1. Growth may be better in some calendar years than in others. This explanation cannot be accepted as the growth discrepancies were found to occur between members of the same year class, captured at different ages.

2. Portions of the scale may be resorbed after being laid down. The examination of the scales offered no evidence for any kind of resorption.

3. The scale fields may contract after being laid down. The nature of the structure of scales makes this explanation totally unacceptable. (See Van Oosten, 1929.)

4. More than one annulus per year may be formed. The clarity of scale markings on the Silver Lake cisco was superior to that of the Trout Lake and Muskellunge Lake ciscoes; yet the measurements of the scales of the last two populations gave

quite consistent results in the calculation of growth. Accessory annuli were rare in the Silver Lake cisco scales. With the elimination of the more questionable scales it appears unreasonable to assume that the number of errors in the determination of ages was sufficient to account for the observed large discrepancies in the calculated growths. Certainly accessory annuli cannot account for the decrease with age in the diameter of the first growth field.

5. The individuals of the population may have segregated themselves on the basis of maturity with the result that the smaller, immature members of each age group may have been absent from the samples. This explanation lacks plausibility in the face of the strong evidence presented later (p. 268) that some if not most fish mature as members of the I group, while all II-group fish certainly can be considered mature. It should be mentioned further that segregation on basis of maturity would be expected to be most pronounced at the spawning time, not in midsummer when the cisco is confined in Silver Lake to a narrow stratum of water in the lower part of the thermocline and the upper part of the hypolimnion.

Regardless of the explanation or explanations accepted as to the cause of Lee's phenomenon in the Silver Lake cisco, it appears that the observed discrepancies do not affect the validity of the method used in this paper for the calculation of growth from scale measurements. Nevertheless, there remains the question as to why the phenomenon should be peculiar to the Silver Lake population.

GENERAL GROWTH CURVES FOR THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

GROWTH IN LENGTH

For each population considered here all collections were combined [8] to give a general growth curve (fig. 1). The indicated lengths at the end of the various years of life are in general the grand average of all calculated lengths for these years. In the Trout Lake and Clear Lake ciscoes, however, the irregularities in the later years, that result largely from the small samples, were smoothed in accordance with the observed data on the annual calculated growth increments.

The Silver Lake growth data raise a question as to the value and significance of any "general" growth curve in this population. The presentation of a general growth curve involves the tacit assumption that this curve can be taken to represent the course of growth of an individual that is typical of the population as a whole. However, the Silver Lake growth curve was derived from the combination of several age groups whose growth histories were fundamentally different. It appears characteristic of the Silver Lake cisco that individual growth history and individual life span are definitely correlated. Consequently the combining of all age groups to obtain a general growth curve involves the lumping together of a mass of heterogeneous growth material. The typical individual that such a curve is purported to represent is probably nonexistent. Nor can the growth curve obtained from a single age group be considered homogeneous. A sample of III-group fish, for example, can be expected to contain fish that would normally have died within the year of collection, and along with them others that would have survived to their fifth, sixth, or seventh year, or even longer. All these different groups within a single age group would have different types of growth.

[8] Certain age groups, however, were eliminated as unreliable because of selection by gear. These were: Trout Lake, all I groups and the II groups of 1930 and 1931; Muskellunge Lake, all I groups; Silver Lake, all I groups. For Clear Lake no groups needed to be eliminated.

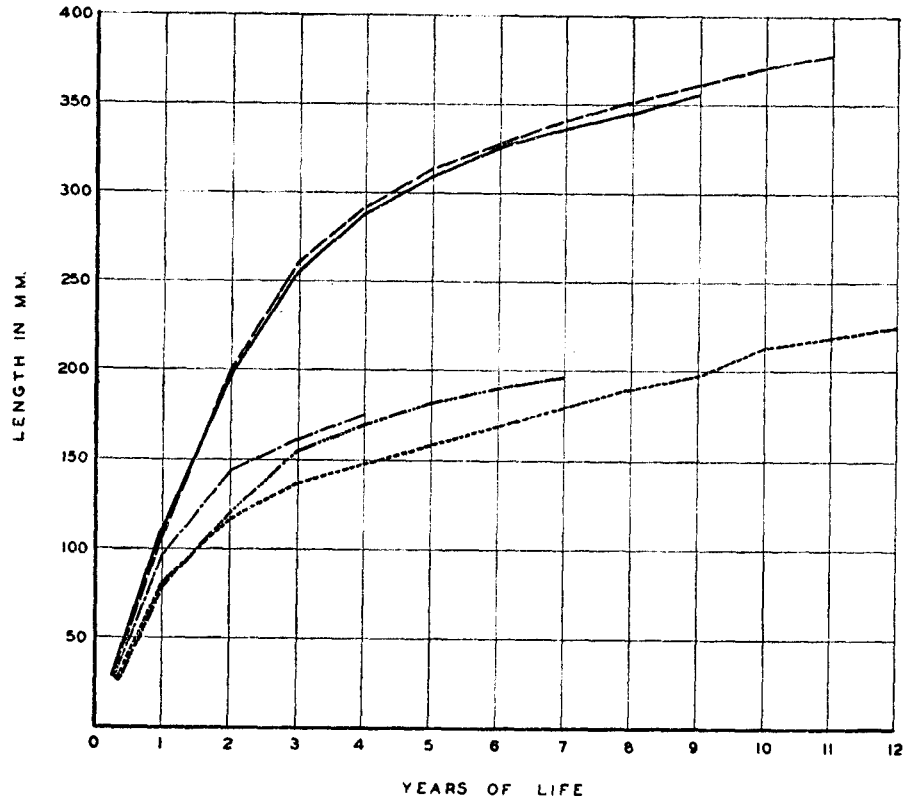

FIGURE 1.—General growth curves showing the average calculated standard length of the cisco (in millimeters) at the end of each year of life. Trout Lake, – – –; Muskellunge Lake, — . —; Silver Lake, — . . . —; Clear Lake (males), ——; Clear Lake (females), — — —.

Tables 10 to 14 give for each population the calculated length at the end of each year of life, and the increase, both absolute and percentile, during each year of life. These data are presented graphically in figures 1 to 3.

TABLE 10.—*Trout Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life*

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	12	225	6	2.7	26	6	168	10	6.3
3	11	219	6	2.8	114	5	158	10	6.8
3	10	213	16	8.1	499	4	148	11	8.0
5	9	197	8	4.2	1,080	3	137	20	17.1
10	8	189	10	5.6	1,182	2	117	36	44.4
14	7	179	11	6.5	1,182	1	81	81	----

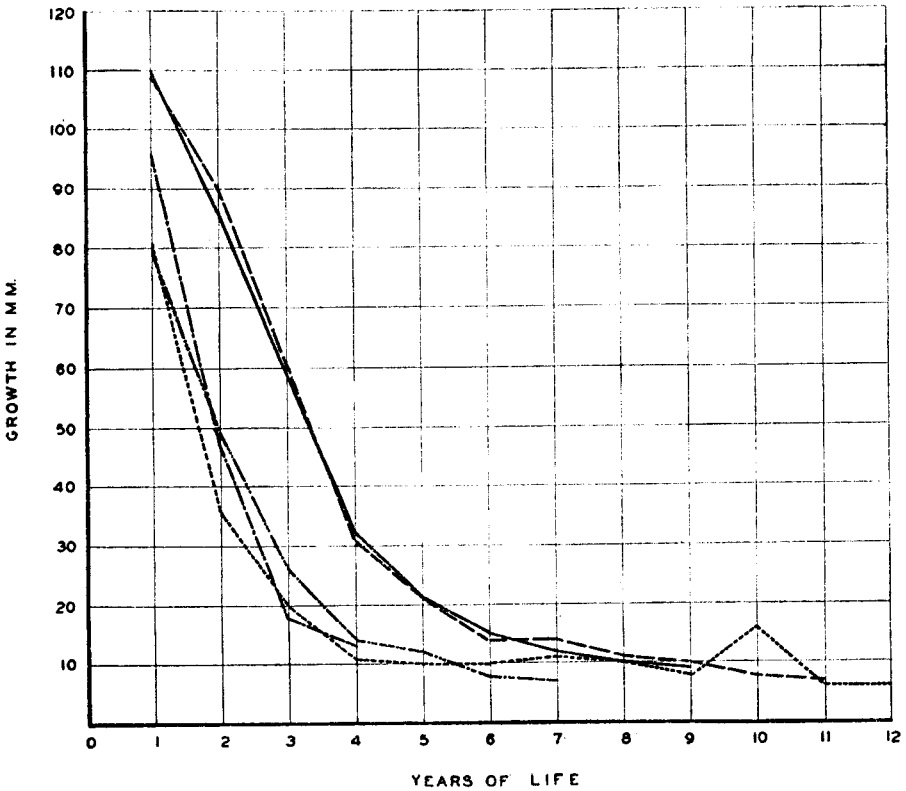

FIGURE 2.—Growth curves showing the increment of growth (in millimeters) in length of the cisco for each year of life. Trout Lake, – – –; Muskellunge Lake, — . —; Silver Lake, — . . . —; Clear Lake (males), ——; Clear Lake (females), — — —.

TABLE 11.—*Muskellunge Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life*

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
2	4	174	13	8.1	1,097	2	143	47	49.0
373	3	161	18	12.6	1,097	1	96	96	

TABLE 12.—*Silver Lake cisco—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life*

[All collections combined. Sexes combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	7	196	7	3.7	529	3	155	26	20.2
25	6	189	8	4.4	564	2	129	49	61.2
168	5	181	12	7.1	564	1	80	80	
397	4	169	14	9.0					

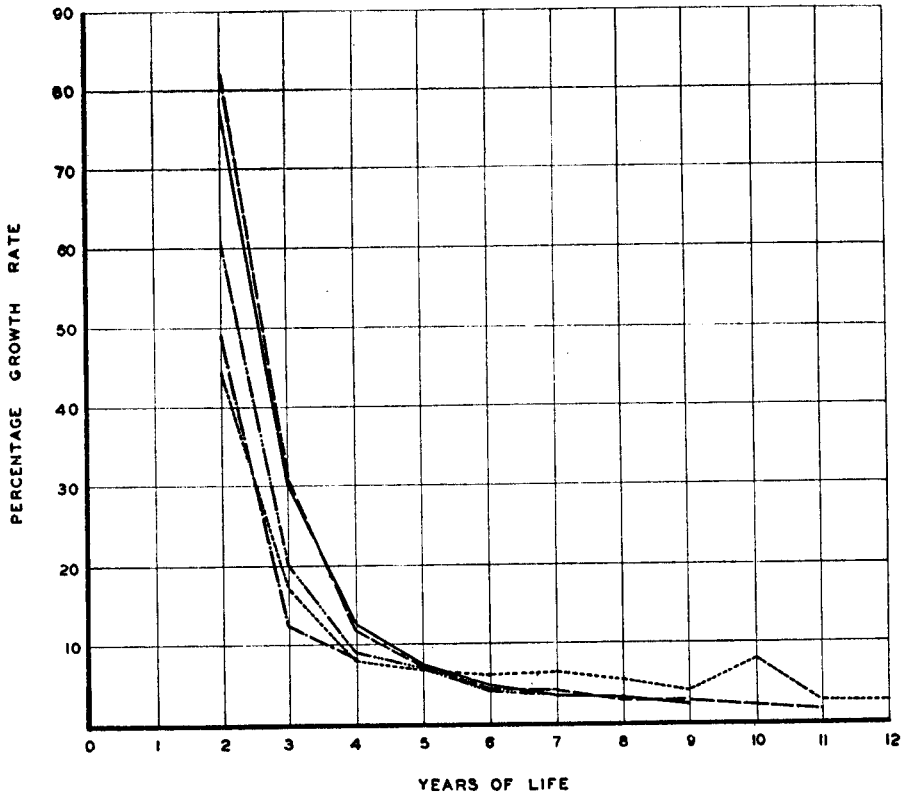

FIGURE 3.—General growth curves showing the percentage increase in length of the cisco in each year of life. Trout Lake, - - -; Muskellunge Lake, — . —; Silver Lake, — . . . —; Clear Lake (males), ——; Clear Lake (females), — — —.

TABLE 13.—*Clear Lake cisco—males—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life*

[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	9	354	9	2.6	73	4	287	32	12.5
11	8	345	10	3.4	122	3	255	59	30.1
28	7	335	12	3.7	176	2	196	86	78.2
41	6	323	15	4.9	216	1	110	110	
52	5	308	21	7.3					

TABLE 14.—*Clear Lake cisco—females—calculated length in millimeters at end of year, increase in length, and percentage increase in length for each year of life*

[All collections combined]

Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of specimens	Year of life	Length in millimeters	ΔL	$\frac{100\Delta L}{L}$
1	11	376	7	1.9	83	5	312	21	7.2
4	10	369	8	2.2	101	4	291	31	11.9
7	9	361	10	2.8	147	3	260	61	30.7
28	8	351	11	3.2	195	2	199	90	82.6
61	7	340	14	4.3	224	1	109	109	
74	6	326	14	4.5					

In the amount of growth the Clear Lake cisco stands far above the other three populations. The Trout Lake cisco shows the least amount of growth. The Silver Lake fish occupy a position intermediate between the Trout Lake and Muskellunge Lake populations. Examination of the curves showing annual increments and annual percentage increase throws further light on the nature of the growth of the four populations. If the percentage increase is considered to represent the rate of growth, it will be seen that beyond the fourth year of life the growth rates of the four populations show only small differences and that beyond the fifth year the Trout Lake fish, although the smallest in actual size, have consistently the highest rate of growth. The annual growth increments of the populations show no great differences beyond the fifth year of life. These facts indicate that the differences in the size of the adult fish in the four populations depend upon the nature of growth during the early years of life. There is a general convergence of growth rates at the fourth or fifth year of life, but at that time the characteristic nature of the size composition for each population is well established.

GROWTH IN WEIGHT

Tables 15 to 18 present the average weight in grams for each age group in each year's collection, together with summaries for the different years' collections combined, of average weight of each age group, the yearly increments based on the average weights, and the yearly percentage increase in weight. In the consideration of average growth in weight for the different populations the effect of gear selection should be kept in mind for the same age groups (marked with asterisks) that were eliminated in the calculation of the general growth in length (see footnote p. 226). It was found possible to combine the sexes in the Trout Lake and Muskellunge Lake samples, but not in the Clear Lake and Silver Lake collections. The females of the Clear Lake population grow in weight much more rapidly than do the males, while the males from Silver Lake tend toward a slightly better growth than do the females.

TABLE 15.—*Trout Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase*

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection; selection probably affected the II-group weight values only slightly. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	$\frac{100\ \Delta W}{W}$
	1928	1930	1931			
XII			172 (1)	172 (1)		
XI			119 (2)	119 (2)		
VII			111 (2)	111 (2)		
VI			50 (2)	50 (2)	3	6.4
V		54 (9)	45 (23)	47 (32)	6	14.6
IV	42 (17)	44 (99)	39 (139)	41 (255)	4	10.8
III	37 (61)	37 (347)	36 (129)	37 (537)	6	19.4
II	31 (102)	*32 (36)	*33 (50)	31 (102)		
I	*26 (2)		*27 (2)	*26 (4)		

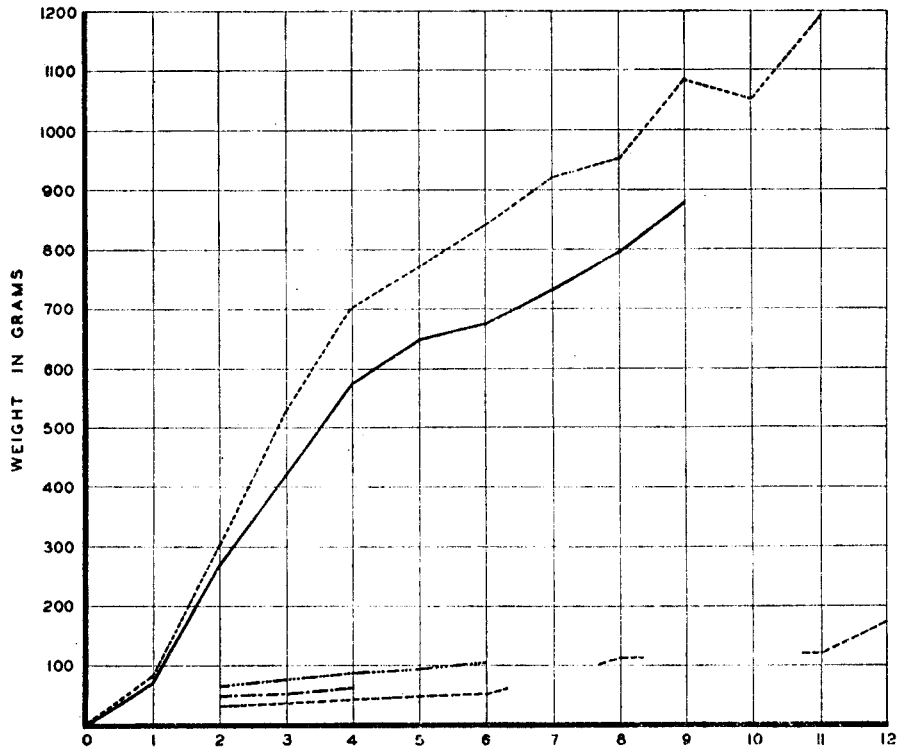

FIGURE 4.—General growth curves showing the average weight (in grams) of the different age groups of cisco at time of capture in summer. Trout Lake, - - -; Muskellunge Lake, — . —; Clear Lake, — . . . —; Clear Lake (males), ——; Clear Lake (females), — — —.

TABLE 16.—*Muskellunge Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, 1928, 1930, and 1931 collections combined, together with the annual increment and the percentage increase*

[Sexes combined. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture			Grand average	ΔW	$\frac{100\Delta W}{W}$
	1928	1930	1931			
IV			60 (2)	60 (2)	9	17.6
III	55 (10)	49 (14)	51 (266)	51 (290)	5	10.9
II	50 (252)	45 (214)	42 (229)	46 (695)	------	------
I	*33 (19)	*39 (17)	*31 (9)	*35 (45)	------	------

TABLE 17.—*Silver Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1930 and the 1931 collections combined, together with the annual increment and the percentage increase*

[Sexes separately. The average weights for the I-group fish are probably too high as the result of gear selection. Number of specimens in parentheses. Groups marked with asterisks unreliable because of selective action of gear]

Age	Year of capture					Grand average		ΔW		$\frac{100\Delta W}{W}$	
	1928	1930		1931							
	Male and female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
VI			106 (3)		104 (8)		104 (11)		11		11.6
V	81 (10)	98 (10)	99 (15)	95 (12)	92 (22)	96 (22)	95 (37)	10	11	11.6	13.1
IV	68 (69)	86 (23)	87 (35)	86 (13)	80 (22)	86 (36)	84 (57)	4	11	4.9	15.1
III	59 (46)	86 (13)	74 (12)	76 (10)	73 (13)	82 (23)	73 (25)	16	12	24.2	19.7
II	50 (9)	68 (3)	64 (4)	64 (4)	60 (8)	66 (7)	61 (12)	------	------	------	------
I	*28 (1)	------	------	*32 (24)	*35 (25)	*32 (24)	*35 (25)	------	------	------	------

TABLE 18.—*Clear Lake cisco—Average weight in grams of each age group in each year's collection, and grand average weight for each age group, for the 1931 and the 1932 collections combined, together with the annual increment and the percentage increase*

[Sexes separately. Number of specimens in parentheses]

Age	Year of capture				Grand average		ΔW		$\frac{100\Delta W}{W}$	
	1931		1932							
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
XI				1,190 (1)		1,190 (1)		128		12.1
X		1,035 (1)		1,090 (1)		1,062 (2)		−23		−2.1
IX		915 (1)	880 (1)	1,170 (2)	880 (1)	1,085 (3)	84	135	10.6	14.2
VIII	760 (3)	937 (11)	811 (7)	969 (8)	796 (10)	950 (19)	67	33	9.2	3.6
VII	718 (6)	859 (17)	737 (9)	1,000 (12)	729 (15)	917 (29)	56	76	8.3	9.0
VI	687 (7)	844 (8)	625 (2)	820 (1)	673 (9)	841 (9)	26	71	4.0	9.2
V	710 (2)	740 (1)	629 (7)	774 (7)	647 (9)	770 (8)	69	65	11.9	9.2
IV	603 (5)	756 (7)	567 (11)	680 (14)	578 (16)	705 (21)	160	175	38.3	33.0
III	413 (17)	525 (19)	422 (23)	534 (21)	418 (40)	530 (40)	151	230	56.6	77.7
II	272 (28)	303 (27)	259 (20)	295 (13)	267 (48)	306 (40)	196	220	276.1	275.0
I	75 (18)	88 (15)	68 (20)	70 (11)	71 (38)	80 (26)				

The weight data are based on fewer specimens than are the length data since most of the fish that were preserved for morphometric study were not weighed in the field and therefore were not used in these studies.

Examination of the data bearing on growth in weight reveals how sharply the growth of the Clear Lake cisco differs from that in the other three populations (fig. 4). The differences that exist among the populations depend upon differences in the length-weight relationships in the various populations as well as upon differences in the amount of growth in length. The questions of form and changes in form, and of the relationship between length and weight are considered in a separate section (pp. 237–247.)

COMPARISON OF THE GROWTH OF THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS WITH THAT OF CISCO POPULATIONS IN OTHER REGIONS

Data on the growth of the cisco or lake herring have been published for Lake Erie by Clemens (1922), for Oconomowoc and Pine Lakes in southern Wisconsin by Cahn (1927), for Lake Huron by Van Oosten (1929), for Lake Ontario by Pritchard (1931), for the Indian Village Lakes in northern Indiana by Hile (1931), and for Hudson Bay by Dymond (1933). Tables 19 and 20 present a comparison of the growth of these populations with that of the populations of the present investigation. The lengths (table 19) are expressed in millimeters, the weights (table 20) in grams, and the ages in both tables as the number of years of life completed. The methods of presentation of the various authors were altered to conform to this uniform method of expressing length, weight, and age. Dymond did not include data on growth in weight of the Hudson Bay cisco. The largest fish in his collection was a female, 383 millimeters long and weighed 793 grams.

TABLE 19.—*Comparison of growth in length, expressed in millimeters, of 11 cisco populations*

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout [1]	Muskellunge [1]	Silver [1]	Clear [1]		Huron [2]	Ontario [3]	Erie [3]	Indian Village [3]	Oconomowoc [4]	Pine [4]	Hudson Bay [3]
				Male	Female							
XII	225											
XI	219				376							
X	213				369		345			386	345	
IX	197			354	361		358			374	338	
VIII	189			345	351	292	303	285		362	330	336
VII	179		196	335	340	274	297	275	374	336	314	324
VI	168		189	323	326	258	270	255	336	315	283	308
V	158		181	308	312	244	253	235	342	282	246	290
IV	148	174	169	287	291	235	233	215	316	223	195	284
III	137	161	155	255	260	218	226	190	301	174	162	214
II	117	143	129	196	199	185	196	160	260	135	125	184
I	81	96	80	110	109	127	129	125				

[1] Calculated lengths at the end of the year of life indicated.
[2] A combination of calculated lengths and actual lengths measured in November.
[3] Actual measured lengths at time of capture during the growing season. The ages of the fish are really greater than indicated here.
[4] Actual measured lengths in midwinter after the completion of the growing season.

TABLE 20.—*Comparison of growth in weight, expressed in grams, of 10 cisco populations*

[The data for the 6 lakes at the right were adapted from various authors as indicated in the text]

Age	Trout	Muskellunge	Silver		Clear		Huron	Ontario	Erie	Indian Village	Oconomowoc	Pine
			Male	Female	Male	Female						
XII	172											
XI	119					1,190						
X						1,062		666			696	436
IX					880	1,085		751			623	406
VIII	111				796	950		454	354		611	343
VII					729	917		488	269	810	527	262
VI	50			106	673	841	221	303	213	782	445	190
V	47		96	95	647	770	175	216	156	648	366	120
IV	41	60	86	84	578	705	159	181	128	523	257	85
III	37	51	82	73	418	530	143	159	85	462	166	60
II	31	46	66	61	267	306	100	105		278	105	45
I					71	80		31				

It should be mentioned that the length data of table 19 are not in all cases strictly comparable from one population to another. The data for Trout, Muskellunge, Silver and Clear Lakes are all calculated lengths; the data for Lake Huron are a combination of calculated lengths and actual lengths measured in November; the data for Lake Ontario, Lake Erie, the Indian Village Lakes, and Hudson Bay represent actual measurements of fish caught during the growing season; and the data of Oconomowoc Lake and Pine Lake are actual average measurements of fish taken in the winter after the close of the growing season. These small differences in the manner of presentation should not affect the value of the data for purposes of comparison.

Though growth in length of the cisco varies widely in different localities, certain consistent likenesses as to the manner of growth are apparent. The greatest growth in length occurs in the first year of life. The growth of the second year is large but less than that of the first. Growth decreases markedly in the third year of life. Throughout the later years the annual increment of growth in length tends to remain fairly constant. Growth in weight is too greatly complicated by the questions of differences in form and of change of form to permit a general description of the style of growth with respect to this character.

Willer (1929) called attention to the fact that certain fishes can be said to possess a typical species growth curve that retains a characteristic form regardless of the extent to which external factors influence the actual amount of growth. With respect to growth in length the cisco seems to possess such a species growth curve.

It will be noticed in table 19 that the populations showing the greatest (Clear Lake, Indian Village Lakes) and the least (Trout Lake) amount of growth are found in small, inland lakes. Such a situation might be expected in view of the greater diversity of habitat furnished by the smaller bodies of water. The growth in the different populations cannot be classified according to latitude or region, but rather, the differences in growth seem to depend upon purely local conditions within the individual lake or possibly upon the genetic make-up of the local stock.

A population showing a greater amount of growth in length than another does not necessarily show a greater amount of growth in weight. Two examples will illustrate this situation. (See tables 19 and 20.) At all ages beyond the seventh year the Oconomowoc Lake cisco is longer than either the males or females of the Clear Lake cisco, and yet at all ages the weights of the Oconomowoc fish are less than those of the Clear Lake fish of corresponding age. Secondly, at the age of 7 years the weights of the Clear Lake and the Indian Village Lakes ciscoes are approximately equivalent. At the same time the length of the Indian Village Lakes fish at the age of 7 years is greater than that attained by the Clear Lake [9] males in the ninth year and equal to the length reached by the Clear Lake females in the tenth or eleventh year. These discrepancies between growth in length and growth in weight find their origin in the different length-weight relationships in the various populations. Populations may differ both as to general body form itself and as to the manner of change of form with increase in length.

RANGE OF LENGTH IN INDIVIDUAL AGE GROUPS; MAXIMUM LENGTH AND WEIGHT

Tables 21 to 25 show for the four lakes under consideration here the length distribution of the different age groups in each year's collection. On the whole, length is a poor index of age. The amount of overlap between consecutive age groups is so great that in most instances a fish of a given length might have any of several different ages. This is particularly evident in the Trout Lake data of table 21. In the rapidly growing Clear Lake population, however, the positions of both sexes of the first three age groups (I, II, and III) stand out clearly in the length frequencies. In the 1931 Silver Lake collection the I group is well separated from the remainder of the sample. The Muskellunge Lake collection of 1931 shows a fairly distinct separation of the II and III groups, but a greater abundance of other age groups in the collections of this year might have obscured this division.

[9] The average lengths of the Clear Lake fish measured at the time of capture were: IX group, male, 355 millimeters; X group, female, 377 millimeters; XI group, female, 378 millimeters.

TABLE 21.—*Length frequencies (5-millimeter intervals) of each age group of the Trout Lake cisco in each year's collection*

Length	I		II			III			IV			V		VI	VII	VIII	IX	XI	XII
	1928	1930	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931	1931	1931	1931	1931	1931	1931
225 to 229																			1
220 to 224																			
215 to 219																			
210 to 214																		1	
205 to 209																			
200 to 204																1	1		
195 to 199															1	1	1		
190 to 194																2		1	
185 to 189												1				1			
180 to 184																1			
175 to 179										1		1		3					
170 to 174										2		1		1	1				
165 to 169							1			8			6	2					
160 to 164							6			14	6	4	12	3	2				
155 to 159							42	1	2	28	26	2	29	1					
150 to 154				2		3	120	9	4	20	74		21	1					
145 to 149			2	13	2	15	94	41	5	15	98		8	1					
140 to 144			9	6	18	30	70	67	5	2	46		3						
135 to 139			30	6	18	12	12	42	1		16								
130 to 134		1	43	4	15	1	2	12			3								
125 to 129	2		16	4	8			1											
120 to 124		1	2	1															
Average	128	128	134	140	136	143	149	142	147	156	148	167	156	165	175	192	200	205	226

TABLE 22.—*Length frequencies (5-millimeter intervals) of each age group of the Muskellunge Lake cisco in each year's collection*

[The 1932 III and IV groups are not included because of the high degree of uncertainty in their separation]

Length	I				II				III			IV
	1928	1930	1931	1932	1928	1930	1931	1932	1928	1930	1931	1931
180 to 184					1				2		3	
175 to 179					3	4			1		13	2
170 to 174					14	14			2	4	73	
165 to 169					28	46	3	1	2	5	126	
160 to 164		2		1	88	92	20	8	3	4	111	
155 to 159	4	2			78	35	24	6		1	20	
150 to 154	1	2			27	18	60	7			1	
145 to 149		4		2	12	5	93	1				
140 to 144		6	1	3	1		50	1				
135 to 139	1		4	5			5					
130 to 134	5		4	4			3					
125 to 129	8	1										
Average	137	148	136	140	160	162	149	156	172	166	166	176

TABLE 23.—*Length frequencies (5-millimeter intervals) of each age group of the Silver Lake cisco in each year's collection*

Length	I		II			III			IV			V			VI		VII
	1928	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1928	1930	1931	1930	1931	1931
205 to 209													2				
200 to 204										1			1	6	1	5	1
195 to 199						1	1			1	1		5	13	2	4	
190 to 194							2	1	1	13	13	1	8	26		8	
185 to 189							6	6	3	12	22	2	7	28		4	
180 to 184				1	1		7	6	6	19	37	4	2	21			
175 to 179				1	6	1	5	20	19	6	17	1		14			
170 to 174				2	6	9	2	19	24	6	10	2					
165 to 169			2	3	2	12	1	8	12		2						
160 to 164			2		3	15		1	4								
155 to 159		2	1		1	8											
150 to 154		3	3				1										
145 to 149		14															
140 to 144		21	1														
135 to 139		17															
130 to 134	1	5															
125 to 129																	
120 to 124		1															
Average	133	141	157	173	171	165	181	177	174	183	183	182	193	188	197	194	201

TABLE 24.—*Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (males) in each year's collection*

Length	I		II		III		IV		V		VI		VII		VIII		IX
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1932
360 to 369																2	
350 to 359									1							1	1
340 to 349											3		1	5	1	1	
330 to 339							2	1		2	1		5	1	2	1	
320 to 329								3	1	3	2	2	2	2		2	
310 to 319					1	2	6	4	1	1	5			1			
300 to 309					1	2	2	2	1								
290 to 299					10	10											
280 to 289					8	4				1							
270 to 279			5	1	3	4		1									
260 to 269			5	8	3												
250 to 259			14	4		1											
240 to 249			5	5													
230 to 239			3	1													
220 to 229			1														
210 to 219	1		1	1													
200 to 209	1																
190 to 199	1																
180 to 189	4	5															
170 to 179	8	10															
160 to 169	5	5															
Average	178	176	253	254	285	290	317	314	325	320	326	320	331	336	338	345	355

TABLE 25.—*Length frequencies (10-millimeter intervals) of each age group of the Clear Lake cisco (females) in each year's collection*

Length	I		II		III		IV		V		VI		VII		VIII		IX		X		XI
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1932
380 to 389														2					1		
370 to 379														2	1			1		1	1
360 to 369													3	2	3	2			1		
350 to 359									1	1			3	3	7	5	1	1			
340 to 349							1	2	1	4	4		7	3	1						
330 to 339							2	6		2	3		4		1	1					
320 to 329					2		1	3	1		2	1	3								
310 to 319					5	9		3			2		1								
300 to 309					8	10															
290 to 299			1		6	1															
280 to 289			3		4																
270 to 279			6	4																	
260 to 269			11	2		1															
250 to 259			10	7																	
240 to 249			3																		
230 to 239			1																		
220 to 229																					
210 to 219																					
200 to 209	4																				
190 to 199	1	1																			
180 to 189	8	2																			
170 to 179	5	7																			
160 to 169																					
150 to 159		1																			
Average	186	176	264	262	302	308	334	329	338	342	339	320	344	362	354	356	351	368	376	379	378

There are some disagreements between the length distributions of fish of the same age, but taken in different seasons. Some of these differences, particularly in the younger age groups, are due to the variation in the time of the collection of the sample within the growing season. The I groups of Clear Lake will serve as an example. (See tables 24 and 25.) In 1932 these ciscoes were collected from July 12 to July 19, while in 1931 they were taken during two periods, July 22 to July 28 and September 3 to September 5. Since the September samples averaged more in length (the average length of the September fish was about 200 millimeters) than the July samples, their presence accounts for the greater upward extension of the length distribution of the 1931 I-group Clear Lake ciscoes. However, at least some

of the other differences between the length distributions of fish of the same age may be accounted for by the actual differences in the growth histories of the year classes they represent. This appears to be true, for example, in the II groups from Muskellunge Lake (table 22). The 1931 II-group fish from this lake were much smaller in average size than those of the preceding 2 years. The examination of the tabulation of calculated lengths for these various groups (table 4) likewise shows that the 1931 II group (1929 year class) actually grew less during the first and second years of life than did the 1929 and 1930 II groups (year classes of 1927 and 1928).

In table 26 are given the data relative to the longest and the heaviest fish taken from each population. (Data concerning the lengths and weights of the oldest fish taken may be obtained from tables 3 to 7.) There is sufficient variation in individual growth that the largest individual need not necessarily be the oldest. In the Silver Lake collections and for both sexes of the Clear Lake samples the largest fish are from 1 to 4 years below the observed maximum age. It is true further that the largest fish with respect to length is not always the heaviest (for example, see the data on the longest and the heaviest fish from Silver Lake). The differences among the maximum sizes attained in the different populations are more striking if size is considered in terms of weight. The Clear Lake fish reach a weight approximately 17 times as great as those from Muskellunge Lake, 10 times as great as those from Silver Lake, and 7 times as great as those from Trout Lake.

TABLE 26.—*Data concerning the longest and the heaviest cisco in each of the 4 lakes*

Lake	Year of capture	Age	Length in millimeters	Weight in grams	Sex
Trout	1931	XII	226	172	Female.
	1932	IV	180	70	Do.
Muskellunge	1932		[1] 188		Male.
	1930	V	206	110	Female.
Silver	1930	VI	204	120	Do.
	1932	VIII	368	910	Male.
Clear	1931	X	[1] 388		Female.
	1932	VII	383	1,210	Do.

[1] This fish was not weighed before it was preserved. The length recorded includes a correction for shrinkage.

The maximum size attained depends both upon rate of growth and upon the maximum age of survival. The Trout Lake cisco is the slowest growing of the four populations, yet a few individuals survive to such an age as to reach a size greater than is attained by the fish in either Silver or Muskellunge Lakes. It is probable that further collections might change the order of arrangements of the lake with respect to the maximum size reached by the cisco, as well as the absolute maximum values for length and weight.

CONDITION AND THE RELATIONSHIP BETWEEN LENGTH AND WEIGHT

Weight in fishes may be considered a function of the length. If form and specific gravity [10] were constant throughout life the relationship could be expressed by the equation,

$$W=cL^3, \tag{1}$$

where W=weight,

L=length,

and c=constant.

The above equation is a statement of the well-known cube law. Actually, in nature, the value of c is not constant for a species or population but is subject to a

[10] Reibisch (1908) could find no appreciable seasonal variation in the specific gravity of the plaice. Keys (1928) pointed out that the hydrostatic equilibrium that exists between the fish and its environment renders great fluctuations in specific gravity unlikely.

wide range of variation. The values of c under various definitions (coefficient of condition, condition factor, length-weight factor) have been used widely by fisheries investigators as measures of individual or average seasonal and regional differences in the condition or "degree of well-being" of fishes. Some investigators have used the coefficient as a measure of the state of sexual development. Others have considered condition to apply only to the state of nourishment and have removed the gonads before taking the weight for the calculation of the coefficient. Yet others have used the coefficient merely as a measure of relative heaviness and have recognized the effect of both the state of sexual development and of the state of nourishment on the determination of its value.

In addition to its use as a means of estimating condition, the equation (1) has been employed also to describe the general length-weight relationship in populations of fishes, and thus serve as the basis for the calculation of unknown weights of fish of known length or of unknown lengths of fish of known weight. The use of the equation in this latter capacity has met with indifferent success, due to the failure of the cube law to describe accurately the relationship of length to weight in many forms of fishes. Fulton (1904) who applied the law to the relationship of length to weight in several marine species stated:

> The law in regard to the increase in weight according to the cube of the length, although broadly true, does not accurately apply in the case of the fishes examined. With scarcely an exception, the weight at a given length is greater than the weight calculated from the law, so that if the specific gravity of the fishes remains constant they must increase somewhat more in other dimensions than in length

Although the cube law does appear to apply to the length-weight relationship in some species (Crozier and Hecht, 1914; Hecht, 1916), these instances appear to be the exceptions, for the observations of Fulton in regard to the inadequacy of the cube law in describing the length-weight relationship in fishes have been repeated by numerous investigators and on many forms of fishes. In recent years a much more satisfactory method of describing the length-weight relationship in fishes has been developed through the use of the more general equation:

$$W=CL^n, \tag{2}$$

where W=weight,

L=length,

and c=constant.

In this equation the values of both C and n are determined empirically.

Such a relationship has been determined by Järvi (1920), Tjurin (1927), Clark (1928), Keys (1928), Fraser (1931), Hart (1931, 1932), Tester (1932), Walford (1932), and Schultz (1933).

Some of the above authors have, however, confused the two entirely distinct issues of describing condition and expressing the length-weight relationship, and have abandoned the use of coefficients of condition based on the cube relationship in favor of those based on an empirically determined exponent (C in $W=CL^n$). That coefficients calculated from the cube relationship and from empirically determined exponents are in no sense of parallel significance as measures of condition appears from the following simple illustration.

A fish with a length of 1 foot and a weight of 1 pound will show on the basis of the cube relationship a coefficient of condition of 1.00. In conformity with a rather general usage this quantity may be designated as K. If this fish doubles its length without change of form or of specific gravity its weight at the length of 2 feet will be 8 pounds, and the value of K will continue to be 1.00. If, however, the weight at 2 feet is 10 pounds instead of 8 the value of K at this greater length will be 1.25, and it will be known that a change of form [11] has occurred along with growth in length. It may be considered that 2 pounds of the weight of this 10-pound fish represent its change of form; this change is measured directly in the increased value of K. The 10-pound fish is 25 percent heavier than the 8-pound fish and is 25 percent *relatively* heavier than the 1-pound fish (that is, the 10-pound fish corresponds in form to a fish that would have a weight of 1.25 pounds at the length of 1 foot). Thus it may be seen that values of K, by reason of their calculation from the cube relationship are direct and quantitative measures of form or relative heaviness, and in this sense are directly comparable between fishes of any length.

Now if the weights of 1 pound at the length of 1 foot and of 10 pounds at 2 feet were to represent actual average conditions within a population, the corresponding length-weight equation would be:

$$W=1.00L^{3.32193}$$

The coefficients of condition calculated from this higher empirical exponent are 1.00 both for the fish at the length of 1 foot and weight of 1 pound and for the fish at the length of 2 feet and weight of 10 pounds. Thus it may be seen that the coefficient C fails entirely to measure in any way the change of form that occurred with increase in length. Further, the value of C for a fish that weighs 8 pounds at the length of 2 feet is 0.80, and from this value it would appear that a fish that doubles its length without change of form actually suffers a loss of condition. Since the assumption is hardly tenable that a fish can suffer such a great loss of condition without undergoing any change of form or relative heaviness it must be concluded that values of C calculated from empirically determined exponents fail to serve as satisfactory measures of condition. Questions concerning the use of C as a coefficient of condition will receive further consideration in connection with the presentation of the data of this investigation on condition and the length-weight relationship in the cisco populations of Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake. At the present time, however, a brief review will be presented of the observations and opinions of authors who have used or suggested the use of C in equation (2) as a coefficient of condition.

The observations of Järvi (1920) should be included in this review, although in justice to that author it should be emphasized that he was concerned primarily with the calculation of unknown lengths and weights from a general length-weight relationship rather than with the measure of condition. Järvi's data are of particular interest here since he included a comparison of coefficients based on the cube relationship and as determined from equations of the type, $W=CL^n$, with empirically determined exponents. His coefficients for the males, the ripe females, and the spent females of the kleine Maräne (*Coregonus albula*) were, on the basis of the cube relationship,

[11] The term "form" as employed throughout this section carries with it no implications as to details of shape, but refers only to relative heaviness of stature.

0.00848, 0.00989, and 0.00830, respectively.[12] The coefficients as calculated from formulas with empirically determined exponents were, for the males, ripe females, and spent females, 0.0050, 0.0020, and 0.0056, respectively. The exponents in these last three formulas were 3.2 for the males, 3.64 for the ripe females, and 3.16 for the spent females. The comparison of the coefficients derived by the two methods shows clearly that those based on empirical exponents fail completely to reflect the relative heaviness of the fish groups to which they pertain. While the values of K based on the cube relationship show that the ripe females are on the average the relatively heaviest group, followed in order by the males and the spent females, the values of the coefficients calculated from equations with empirical exponents follow exactly the reverse order. Thus on the basis of the values of C of equation (2) the relatively heaviest group of fish would appear to be in the poorest condition. If the values of the two types of coefficients are compared in relation to the values of the exponents, n, it appears that while the values based on the cube relationship depend on the relative heaviness of the fish upon which they are based, the values of the coefficients calculated from equations with empirical exponents depend primarily not on the heaviness of the fish but rather on the value of the exponents. A large value of n is associated with a small value of the coefficient—and the reverse.

Clark (1928) appears definitely to have confused the two problems of describing condition and expressing the length-weight relationship. From her study of condition and the length-weight relationship in the California sardine (*Sardina caerulea*) Clark concluded: "The weight of sardines increases at a rate slightly greater than the cube of the length. For the data studied the correct formula for the weight-length factor was found to be $F=\frac{1000\,W}{L^{3.15}}$. But for the purpose of the present study the formula $F=\frac{1000\,W}{L^3}$ was sufficiently accurate."

Clark evidently believed that the coefficient of condition (weight-length factor), to be accurate, should tend to hold a constant value at all lengths of the fish, for she stated: "The more a species departs from this general weight-length relationship [cube relationship], the greater the error involved in the factor." Concerning the changes in the value of the factor with increasing length she observed further: "Due to the error introduced from calculating F on the basis of the cube of the length, the curve resulting from the equation $F=\frac{1000\,W}{L^3}$ rises consistently throughout the range of sizes represented in the commercial catch at San Pedro."

Clark's conclusion that the failure of the cube law to describe the length-weight relationship makes inaccurate the use of coefficients of condition (weight-length factors) based on the cube relationship is scarcely justifiable, particularly in view of the fact that coefficients based on empirical exponents fail to reflect differences in form or relative heaviness while those based on the cube relationship offer a direct measure of relative heaviness independent of general length-weight relationships and comparable as measures of relative heaviness between fish of any length. Clark actually studied variations in the weight-length factor on the basis of values calculated from the cube relationship, but did so only because she considered that the use of these values introduced "only a minor error into the work."

[12] In the data from which these coefficients were determined weights were recorded in grams and lengths in centimeters.

Clark's data on the correlation between weight-length factors (calculated from the cube relationship) and the fat content of the sardine offers convincing evidence that measures of condition should be calculated from the cube relationship. Her data show conclusively that variations with length in the value of the weight-length factor are reflected closely in corresponding variations with length in the fat content of the sardine. Inasmuch as relative heaviness is thus showed to be dependent on fatness (condition), changes with length in relative heaviness must be considered also to represent changes of condition. In view of this fact it does not appear valid to measure condition in terms of a quantity that tends to be constant for fish of all lengths regardless of actual changes that may occur in relative heaviness of form with change in length. Since the quantity C in the equation $W=CL^n$ tends toward this constancy and fails to measure relative heaviness it must fail also to measure the differences of fatness (condition) upon which differences in relative heaviness depend.

Tester (1932) likewise appears to have confused the two problems of measuring condition and describing the general length-weight relationship. Concerning his method of determining the general length-weight relationship in the smallmouth black bass (*Micropterus dolomieu*) he stated:

> Following the method used by Hart (1931) and others the relationship between length and weight for bass from Perch Lake [Ontario] was obtained by plotting average lengths against average weights on double logarithmic paper and deriving the natural slope of the resultant straight line drawn through the points. It was found that the weight increased by the power 3.1(7) of the length. * * *

Tester assumed, however, that the failure of the cube law to describe the length-weight relationship made the use of coefficients of condition based on the cube relationship invalid. Concerning the equation, $K=\frac{100\,W}{L^3}$, employed by Hile (1931) to describe condition in several species of Indiana lake fish, Tester stated:

> This equation is only approximate and might be better expressed—
>
> $$K=\frac{100\,W}{L^x}$$
>
> In the case of the Perch Lake bass the power x would have a value 3.1(7). If the power $x=3$ is used, the value of K tends to increase with the length of the fish whereas it should remain constant.

Tester used the value $x=3.1(7)$ as determined from the Perch Lake bass to compute coefficients of condition for his smaller samples from Phantom Lake, Lake Nipissing, and Georgian Bay, but observed that, "To be strictly accurate, the value x should be determined separately for each of the latter three bodies of water. * * *"

Had Tester actually determined the value of the exponent for each of the bass populations he studied he would probably have become aware of the difficulties involved in the use of coefficients of condition based on empirical exponents.

Schultz (1933) expressed the relationship of length to weight in the bay smelt (*Atherinops affinis oregonia*) by the equation $W=FL^{2.59}$. He also employed the quantity F as a measure of seasonal changes in weight, dependent on the state of development of the gonads. That Schultz considered the length-weight factor, F, identical in significance with factors calculated from the cube relationship is apparent from the following statement: "The length-weight factor, F, was used to estimate the state of development of the gonads, as has been done by D'Arcy Thompson (1917),

Van Oosten (1929), Clark (1928b), Weymouth (1918 and 1923), Reibisch (1911), Crozier and Hecht (1915), and others.[13]

Of the above authors some employed the cube relationship in the study of the length-weight relationship (Thompson, Van Oosten, Weymouth (1918), Crozier and Hecht), while others used empirical exponents (Clark, Weymouth (1923)).

Because of the serious objections to the use of coefficients of condition based on empirical exponents, condition in this investigation has been measured by coefficients calculated from the cube relationship. The comparison of the equations $W=KL^3$ and $W=CL^n$ reveals an interesting connection between condition and length in populations that deviate from the cube relationship. The equation, $W=CL^n$, may be written in the form:

$$W=f(L).\phi(L), \tag{3}$$

where

$$f(L)=CL^m,$$
$$\phi(L)=L^3,$$

and

$$m=n-3.$$

Thus it may be seen that where weight can be expressed as a parabolic function of the type $W=CL^n$ condition can be expressed by a similar function of length. While this definition of condition as a function of length is valid only insofar as the equation (3) actually describes the length-weight relationship, the failure of equation (3) has no effect on the value of coefficients calculated from the cube relationshie as measures of relative heaviness. Where the coefficient of condition does behavp as a parabolic function of length (hyperbolic if $m<o$), the value of $m=n-3$ measures the rate of change of form or condition.[14]

In order to have the most complete data for the study of condition the value of $f(L)=\frac{W}{L^3}$ was calculated for each individual specimen. Since lengths were recorded

[13] This statement of Dr. Schultz as it pertains to the studies of other investigators is in some points inaccurate. Van Oosten made no use of the coefficient of condition to study the state of sexual development but was interested primarily in deriving a general length-weight equation; he did, however, quote Thompson (1917) as to the effect of sexual state on the value of the coefficient. Clark used the weight-length factor chiefly as a measure of the state of nourishment or fatness as the following statement shows: "The monthly and yearly fluctuations in the weight-length factors of sardines were due, therefore, to some changes in the composition of the body tissue of the fish, presumably an increase or decrease in the fat content, and not to the amount of food in the alimentary tract, or to the growth of the sex organs." Weymouth (1918 and 1923) was concerned with the general length-weight relationship and not with any individual or seasonal fluctuations in the length-weight factor. Reibisch's coefficient was calculated neither from $W=KL^3$ nor $W=CL^n$, but was a "Dickenkoeffizient" with the formula $\delta=\sqrt{\frac{40000}{\pi}\cdot\frac{G}{L^3}}$, ($G$=weight in grams, L=length in centimeters). Reibisch discussed the effect of sexual state on the state of nourishment, but, in order to make δ describe only the state of nourishment, removed the gonads before weighing. Crozier and Hecht were concerned with the determination of a general length-weight equation. They stated: "All the fish examined (over 400) were either spent or unripe; so we are sure that none of the weights recorded are influenced by the ripening of the gonads." (The date of issue of Crozier and Hecht's paper was 1914, not 1915.)

[14] The differential equations corresponding to the equations $W=CL^n$, and $f(L)=K=CL^m$ are:

$$\frac{dW}{W}=n\frac{dL}{L},$$

and

$$\frac{dK}{K}=m\frac{dL}{L}.$$

Now $\frac{dW}{dt}\cdot\frac{1}{W}$, $\frac{dL}{dt}\cdot\frac{1}{L}$, and $\frac{dK}{dt}\cdot\frac{1}{K}$, where t=*time*, are the relative rates of change in weight, length, and condition, respectively. The exponent n describes the ratio of the relative rates of change of weight and length, while m describes the ratio of the relative rates of change of condition (form) and length. If $n=3$, $m=0$, and growth proceeds without change of form. If $n\pm3$, then $m\pm0$, and the values of the exponents measure the rate of change of form.

in millimeters and weights in grams, the actual values of $f(L)$ were quite small. To avoid the use of such small decimals the coefficient of condition K as actually used was defined:

$$K=f(L)\times 10^5 \tag{4}$$

In the Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake populations the variation of condition with length, and of weight with length conforms closely over certain length intervals with the conditions defined by equation (3). Consequently it was possible to determine equations describing condition and weight as functions of length by fitting parabolic equations to the observed average values of K at different lengths.

The assumed relationship between K and L indicates a linear relationship between the logarithms of their values:

$$\log K=a+m \log L, \tag{5}$$

where

$$a=\log C+5.$$

It is possible to determine the values of C and m by fitting a straight line to the logarithms of corresponding values of K and L. The determined values of C and m can be used in writing not only the equation for K as a function of length but also for writing the equation for weight as a function of length.[15]

Table 27 contains the equations obtained for $K=C\times 10^5\ L^m$ and $W=CL^n$. The data from which the equations were determined are found in tables 28 to 31. The tables mentioned last contain also a comparison of actual weights with theoretical weights calculated from the length-weight equations of table 27.

TABLE 27.—*Equations for* $K=C\times 10^5 L^m$ *and* $W=CL^n$ *as determined for the various cisco collections*

Lake	Year of collection	Sex	Number of specimens	Range of L	$K=C\times 10^5\ L^m$	$W=CL^n$
Trout	1928	♂, ♀	138	125–154	$K=6.5232\ L^{-0.33741}$	$W=6.5232\times 10^{-5}\ L^{3.07339}$
	1930	♂, ♀	483	125–169	$K=4.8834\ L^{-0.25967}$	$W=4.8834\times 10^{-5}\ L^{3.71035}$
	1931	♂, ♀	338	125–164	$K=38.7640\ L^{-0.69345}$	$W=38.7640\times 10^{-5}\ L^{3.30758}$
Muskellunge	1928	♂, ♀	263	145–179	$K=4,568.9\ L^{-1.63290}$	$W=4,568.9\times 10^{-5}\ L^{1.37710}$
	1930	♂, ♀	244	140–179	$K=567.36\ L^{-1.23469}$	$W=567.36\times 10^{-5}\ L^{1.76538}$
	1931	♂, ♀	505	130–179	$K=141.92\ L^{-0.94933}$	$W=141.924\times 10^{-5}\ L^{3.05068}$
	1932	♂, ♀	93	145–179	$K=182.87\ L^{-0.99615}$	$W=182.87\times 10^{-5}\ L^{3.00385}$
Silver	1930–31	♂	110	130–199	$K=0.25532\ L^{0.82370}$	$W=0.25532\times 10^{-5}\ L^{3.82370}$
	1930–31	♀	160	135–204	$K=0.12322\ L^{0.45373}$	$W=0.12322\times 10^{-5}\ L^{3.45373}$
Clear	1931	♂	85	160–359	$K=0.10104\ L^{0.80330}$	$W=0.10104\times 10^{-5}\ L^{3.80330}$
	1931	♀	105	170–379	$K=0.04555\ L^{0.64991}$	$W=0.04555\times 10^{-5}\ L^{3.64991}$
	1932	♂	100	160–379	$K=0.04954\ L^{0.69476}$	$W=0.04954\times 10^{-5}\ L^{3.69476}$
	1932	♀	85	150–389	$K=0.03652\ L^{0.68489}$	$W=0.03652\times 10^{-5}\ L^{3.68489}$

[15] For the purpose of fitting the equations the specimens were divided into length groups (10 millimeters in the Clear Lake cisco, 5 millimeters in the other populations) and the average values of K and L determined for each interval. A straight line was fitted to the logarithms of these values by the equating of moments. Combinations of the sexes and of different years' collections were made wherever the data justified the procedure. In Trout Lake and Muskellunge Lake the sexes were combined in each year's collection. In Silver Lake the sexes were treated separately, but the 1930 and 1931 collections were combined. In Clear Lake each sex and each year's collection received separate treatment. The data upon which the equations were based include only the size ranges for which adequate numbers of specimens were available.

TABLE 28.—*Trout Lake ciscoes.—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals*

[Sexes combined]

1928				1930				1931			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
128	29	28	1.33	127	25	26	1.22	128	28	29	1.38
132	31	30	1.31	132	27	27	1.18	133	31	31	1.32
137	33	34	1.31	137	31	31	1.17	137	33	32	1.25
142	37	36	1.28	143	34	33	1.14	142	36	35	1.24
147	40	40	1.27	147	36	36	1.15	147	39	39	1.21
150	43	44	1.28	152	40	40	1.13	152	42	42	1.21
				157	43	43	1.12	156	45	45	1.18
				162	48	48	1.14	162	49	49	1.15
				166	51	51	1.11				

TABLE 29.—*Muskellunge Lake ciscoes—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals*

[Sexes combined]

1928				1930				1931				1932			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
147	44	45	1.40	142	36	36	1.24	134	33	32	1.34	145	38	39	1.24
152	46	45	1.28	147	38	37	1.18	137	34	33	1.28	153	46	44	1.27
157	48	48	1.25	153	41	42	1.16	142	37	37	1.30	157	47	46	1.22
162	50	51	1.21	157	43	43	1.11	147	40	41	1.28	162	50	49	1.18
166	52	53	1.16	162	45	46	1.08	152	42	44	1.26	167	52	52	1.12
172	55	58	1.13	166	47	48	1.04	157	45	46	1.19	172	55	55	1.08
176	57	54	.98	172	50	49	.97	162	48	49	1.15	176	57	58	1.05
				177	53	52	.94	166	51	49	1.08				
								172	55	55	1.09				
								176	57	54	.99				

TABLE 30.—*Silver Lake ciscoes—Values of length, theoretical weight, actual weight, and K at 5-millimeter length intervals*

1930–31, male				1930–31, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
132	29	30	1.28	138	30	30	1.15
137	32	32	1.24	142	34	35	1.19
143	37	36	1.23	147	38	37	1.16
172	69	70	1.36	167	58	55	1.19
177	76	77	1.37	172	65	67	1.32
182	83	84	1.39	177	72	74	1.32
187	91	91	1.39	182	79	81	1.33
191	98	99	1.42	187	87	89	1.34
197	108	106	1.38	192	95	95	1.35
				196	102	102	1.34
				201	111	108	1.33

TABLE 31.—*Clear Lake ciscoes—Values of length, theoretical weight, actual weight, and K at 10-millimeter length intervals*

1931, male				1931, female				1932, male				1932, female			
Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K	Length	Calculated weight	Actual weight	K
167	62	68	1.47	177	73	76	1.38	168	57	59	1.26	155	42	43	1.13
174	72	70	1.37	183	83	85	1.36	176	69	68	1.24	175	68	68	1.26
182	84	80	1.34	197	108	106	1.39	183	79	79	1.29	180	76	75	1.29
203	124	124	1.48	201	116	122	1.51	215	141	138	1.39	195	106	100	1.43
234	204	195	1.53	231	193	184	1.49	234	192	182	1.42	255	268	268	1.62
246	241	240	1.62	244	237	226	1.54	245	227	226	1.53	265	314	309	1.69
253	268	272	1.67	256	280	284	1.69	255	262	244	1.47	274	338	351	1.64
265	316	316	1.70	266	321	312	1.68	264	297	292	1.53	290	394	433	1.62
273	351	330	1.62	275	365	352	1.69	273	335	370	1.82	306	520	529	1.81
282	392	385	1.71	283	406	385	1.69	288	407	434	1.75	315	594	588	1.90
293	448	445	1.77	296	480	462	1.77	294	437	443	1.85	324	695	650	2.05
301	493	465	1.71	303	522	546	1.96	302	484	508	1.80	334	704	724	1.90
316	582	595	1.89	314	589	570	1.84	315	565	563	1.90	345	812	821	1.98
322	624	663	1.99	327	686	712	2.05	326	634	657	1.90	356	984	923	2.18
333	700	708	1.92	335	752	766	2.04	334	695	708	1.91	365	1,002	1,012	2.06
343	777	803	2.00	345	833	866	2.07	343	767	773	1.92	373	1,107	1,091	2.12
350	834	850	1.98	353	905	933	2.12	352	847	840	1.82	384	1,198	1,212	2.12
				362	997	1,036	2.18	365	960	885	1.79				
				371	1,088	1,048	2.05								

The comparisons of theoretical and actual weights show that the equations of table 27 fit the observed data in a quite satisfactory manner, for in general the agreement between actual and calculated weights is good. The discrepancies between actual and calculated weights are greater in the Clear Lake samples (table 31) than in those of the other three lakes. This might be expected not only because of the smaller numbers of fish in the Clear Lake collections but also because of the much greater size range shown by the ciscoes of this lake.

The equations themselves (table 27) contribute interesting information relative to the problem discussed previously (pp. 238–242) concerning the use of C as a coefficient of condition. The examination of the values taken by $C \times 10^5$ shows how widely this quantity can vary not only within different populations of the same species but also in different sexes and in different years' collections of the same population. Certainly the value 0.03652 (Clear Lake females, 1932) cannot be compared directly as a measure of condition with the value 4,568.9 (Muskellunge Lake, 1928), particularly in view of the fact that the higher value of C pertains to the slenderer form. Nor can the higher values of C shown by the males in the Clear Lake equations be interpreted as showing the males of this population to be in better condition than the females. The actual values of K and of weight for length show that the reverse is true. The table shows yet other examples that demonstrate clearly that values of C cannot be compared either between the sexes or between different years' collections of the same population, much less between different populations.

If the variations in the value of C are examined in relation to variations in the values of the exponents, m and n, it may be seen again that the values taken by C depend on the values taken by n. If n is high, C is small—and the reverse. Thus it may be seen that here as in Järvi's data the values of C do not depend on relative heaviness but on the rate of change in relative heaviness as measured by the exponents, m and n.

The examination of the values taken by n show further that this quantity is not fixed either for a species or a population. The values of the exponent not only vary tremendously from lake to lake but also vary considerably from year to year in the

samples of a single population. It will now be shown that not only does n vary from population to population and from year to year in the same population but further that in two populations, at least, the values of n determined for a single year's sample apply only to the length intervals for which the equations were fitted and do not hold for fish whose lengths lie outside these length ranges.

If the equation, $K=C\times10^5L^m$, for each year's collection of the Muskellunge Lake cisco is solved for $L=100$ millimeters the following values of K are obtained: 1928, $K=2.59$; 1930, $K=1.93$; 1931, $K=1.80$; 1932, $K=1.86$. These values of the coefficient of condition indicate a fairly robust body form. Ciscoes of such heavy build are indeed found among the larger fish of the Clear Lake population (table 31), but it is very unlikely that such heavily built individuals may be found at the length of 100 millimeters in the Muskellunge Lake cisco population, or in any population of the same species. This view is supported by the comparison of the K values upon which the 1928 length-weight relationship was determined (table 29) with those of the 15 fish that were less than 145 millimeters long. Eight of these 15 fell in the 125–129 millimeter length interval and had an average value of 1.23 for the coefficient of condition, K; the 5 individuals in the 130–134 millimeter interval had an average K value of 1.25; while 2 single individuals whose lengths were 138 and 144 millimeters had K values of 1.29 and 1.34, respectively. These data show that in 1928 the values of K in Muskellunge Lake ciscoes less than 145 millimeters long were much lower than the theoretical length-weight equation (based on specimens more than 145 millimeters long) indicated they should be.

The 1931 data for Trout Lake furnish another example of the failure of a length-weight equation to describe the length-weight relationship for fish outside the length range for which the equation was determined. The length-weight equation for 1931 (see table 27) was based on specimens whose lengths ranged from 125 to 164 millimeters. The same collections contained five large fish (189 to 225 millimeters long). Since the 1931 length-weight equation for Trout Lake indicates a continuous decrease of K with increase in length, these large fish would be expected to show small values for the coefficient of condition. Table 32 which contains a comparison of actual and theoretical values of weight and K for these five fish shows that they fail completely to fulfill this expectation, for the actual values of weight and K are far above the theoretical values calculated from the length-weight equation.

TABLE 32.—*Values of length, weight, and K for the 5 longest individuals of the 1931 Trout Lake cisco collection*

Age	Length	Calculated weight	Actual weight	Calculated value of K	Actual value of K
VIII	189	69	100	1.03	1.48
XI	192	72	90	1.02	1.27
VIII	203	82	122	.98	1.46
XI	218	97	148	.93	1.43
XII	226	105	172	.91	1.49

Observations on the failure of a single value of n to hold for all lengths of fish within a population have been made previously by Clark (1928), Walford (1932), and Schultz (1933).

Materials for the comparison of condition in the different populations and in different years are to be found in tables 28 to 31 and 33. The last-named table

shows the variation in K according to age, while the earlier tables show the variation of K with length. On the whole the changes of K with age depend on differences in the average length of the various age groups. In Clear Lake in particular large differences in average lengths of age groups are associated with large differences in the average value of K, while smaller differences in average length are associated with smaller differences in the average value of K.

TABLE 33.—*Value of K according to age groups*

[Number of specimens in parentheses]

Age	Trout Lake			Muskellunge Lake			Silver Lake		
	1928	1930	1931	1928	1930	1931	1928	1930	
								Male	Female
XII			1.49 (1)						
XI			1.35 (2)						
X									
IX									
VIII			1.47 (2)						
VII									
VI			1.14 (2)						1.39 (3)
V		1.17 (9)	1.18 (23)				1.34 (10)	1.38 (10)	1.37 (15)
IV	1.32 (17)	1.15 (99)	1.21 (139)			1.10 (2)	1.29 (69)	1.42 (23)	1.37 (35)
III	1.28 (61)	1.13 (347)	1.24 (129)	1.11 (10)	1.06 (14)	1.13 (266)	1.30 (46)	1.38 (13)	1.34 (12)
II	1.30 (102)	1.16 (36)	1.30 (50)	1.23 (252)	1.07 (214)	1.26 (229)	1.29 (9)	1.28 (3)	1.26 (4)
I	1.24 (2)		1.28 (2)	1.24 (19)	1.18 (17)	1.28 (9)	1.19 (1)		

Age	Silver Lake, 1931		Clear Lake			
			1931		1932	
	Male	Female	Male	Female	Male	Female
XII						2.20 (1)
XI						2.00 (1)
X				2.15 (1)		
IX				2.12 (1)	1.97 (1)	2.36 (2)
VIII			1.97 (3)	2.13 (11)	1.99 (7)	2.16 (8)
VII			2.00 (6)	2.12 (17)	1.95 (9)	2.09 (12)
VI		1.36 (8)	1.96 (7)	2.06 (8)	1.82 (2)	2.50 (1)
V	1.40 (12)	1.34 (22)	1.88 (2)	2.10 (1)	1.93 (7)	1.93 (7)
IV	1.41 (13)	1.28 (22)	1.86 (5)	2.03 (7)	1.83 (11)	1.90 (14)
III	1.31 (10)	1.29 (13)	1.73 (17)	1.86 (19)	1.70 (23)	1.82 (21)
II	1.30 (4)	1.25 (8)	1.66 (28)	1.66 (27)	1.56 (20)	1.64 (13)
I	1.22 (24)	1.18 (25)	1.38 (18)	1.39 (15)	1.25 (20)	1.27 (11)

The analysis of the data was made to include the examination of variation of K with size in fish of the same age and the variation of K with age in fish of the same size. Without presentation of the extensive tabular material that would be necessary to show the detailed results of these analyses it may be stated that the variation of K with length within an age group proceeds in the same direction as the variation of K with length in the population as a whole, and that, on the whole, the value of K appears to be independent of age in fish of the same length.

The tables 28, 29, 30, 31, and 33 show further that condition varies from year to year in the same population. In both Trout Lake and Muskellunge Lake the ciscoes were slenderer in 1930 than in 1928 or 1931. In Silver Lake the lack of sex records for 1928 makes a comparison of that year with later years difficult. There is some indication, however, that in 1928 the Silver Lake cisco may have been in poorer condition than in 1930. In Clear Lake there do not appear to be any notable differences in the condition of the cisco in 1931 and 1932.

With respect to average condition, from poorest to best, the populations fall in the following order: Muskellunge Lake (sexes combined), Trout Lake (sexes combined), Silver Lake females, Silver Lake males, Clear Lake males, and Clear Lake females.

The order of the four populations of this investigation with respect to average condition is the same as their order with respect to average duration of life (p. 267). The indicated association between condition and longevity finds support in the observation (table 32, p. 246) that in Trout Lake survival to an advanced age appears to be accompanied by, if not contingent upon, a departure from the general tendency for condition to become poorer with increased length.

The study of condition and of the length-weight relationship in these four cisco populations may well be concluded with an illustration of how progressive change of condition is reflected in a progressive change in body proportions. In order to determine the intensity of the excess vertical and lateral growth that produced the heavy body form in the older and larger Clear Lake ciscoes the relationship of length to depth and width was studied in 95 preserved specimens collected in 1932. Since the relationship of length to weight in the Clear Lake cisco can be expressed satisfactorily by a parabolic equation it was assumed that a similar relationship may hold between length and width and length and depth. On the basis of this assumption the following equations were derived:

Male—46 specimens:

$$\text{Depth}=5.052\times10^{-2}\ L^{1.2939}$$
$$\text{Width}=0.656\times10^{-2}\ L^{1.5502}$$

Female—49 specimens:

$$\text{Depth}=5.230\times10^{-2}\ L^{1.2899}$$
$$\text{Width}=0.173\times10^{-2}\ L^{1.7879}$$

L=length in millimeters.

TABLE 34.—*Clear Lake ciscoes, 1932—Comparison of theoretical and actual values of body depth and body width*

Males					Females				
Length	Calculated depth	Actual depth	Calculated width	Actual width	Length	Calculated depth	Actual depth	Calculated width	Actual width
165	37	36	18	19	150	34	34	13	13
175	40	38	20	19	165	38	37	16	20
181	42	44	21	21	172	40	40	17	19
206	50	49	25	26	190	46	48	20	24
235	59	62	31	31	265	69	68	37	36
255	66	68	35	35	274	73	72	39	35
266	69	69	37	36	295	80	80	45	41
284	76	79	42	41	305	84	85	48	47
292	78	81	44	43	314	87	87	50	49
302	82	81	46	47	324	90	86	53	45
316	86	87	49	43	334	94	92	56	54
326	90	89	51	51	345	98	99	59	64
334	93	91	54	56	355	102	105	63	67
345	97	92	56	63	362	105	111	65	69
					376	110	111	69	65
					383	113	109	72	59

Table 34 shows the lengths, depths, and widths from which the above equations were calculated. The data of the same table also make possible the comparison of actual measured depths and widths with theoretical values calculated from the equations. If due consideration is given the small number of specimens the agreement between the actual and theoretical values of depth and width is, in general, good.

The equations show that both the males and females of the Clear Lake cisco grow more rapidly in depth and width than in length. The differential growth of the dimension, width, proceeds more rapidly than the differential growth of the dimension, depth, that is, the change to a heavier stature proceeds more rapidly along the lateral than along the vertical axis. The comparison of the equations for the two sexes shows further that the differential growth in depth proceeds at approximately the same rate in the males and the females, while the differential growth in width proceeds more rapidly in the females than in the males. It is this higher differential growth in width that accounts for the higher K values in the Clear Lake females.

Values of K for cisco populations have been presented by Van Oosten (1929) and by Hile (1931). The former author found K to have an average value of 1.13 for the Lake Huron herring (0.01126 in his method of presentation). The sexes showed no consistent differences, and there was only a slight tendency for the value of K to increase with increase in length. Hile's data on the cisco of the Indian Village Lakes (Indiana) were too scanty to afford any information on the change in the value of K with change in length. The largest value of K which he found for any age group was 1.79, the smallest, 1.56. Since both Van Oosten and Hile employed the cube relationship for the calculation of K values, their results can be compared directly with those of this study.

A comparison of the values of K in the Lake Huron herring and the Indian Village Lakes cisco with those of the populations of this study shows that the Lake Huron herring is a very slender fish of approximately the same relative heaviness as the Muskellunge Lake cisco, while the Indian Village Lakes cisco is more heavily built than the Trout Lake, Muskellunge Lake, and Silver Lake ciscoes, but slighter in form than the Clear Lake cisco.

LENGTH OF GROWING SEASON

It was not possible in this investigation to follow the course of the season's growth in the different populations by means of a systematic collection of specimens at different times throughout the spring, summer, and autumn. Since all collections were made in July, August, and early September, and the single year's collections within a single lake were frequently made within a period of only a few days, any estimate of the course of growth during the growing season or of the length of the growing season in the different lakes must depend largely upon an indirect approach. However, the fact that the growth materials from each lake represent collections in 2 or more years makes possible at least a rough estimate of the length of the growing season in each lake. The following example will illustrate the method by which these estimates may be made:

The 1928 collection of the Trout Lake cisco contained 102 specimens of the II group (1926 year class). These fish had an average length of 134 millimeters at the time of capture (July 21, 28, and 29). The calculation of their earlier growth from scale measurements indicated that their average length at the beginning of the 1928 growing season (end of second year of life) was 117 millimeters. Thus it may be seen that these II-group fish of 1928 had grown 17 millimeters between the beginning of the growing season and the time of their capture in late July. The question now arises as to what part of the total 1928 growth of the II group this 17-millimeter increment may represent. The presence of this same (1926) year class in the 1930 collections as the IV group and in the 1931 collections as the V group makes a quite reliable answer to this question available, for it is possible to calculate the total

1928 growth from the scale measurements of each of these later collections of the year class. The 1930 IV-group samples indicated that the 1926 year class had a total growth of 19 millimeters in 1928, while the 1931 V group gave an average calculated growth of 17 millimeters for the same year. The combination of the 1930 and 1931 data gives a calculated total growth of 18 millimeters for the 1926 year class in the calendar year 1928. Since the 1928 specimens themselves had grown 17 millimeters at the time of their capture in late July it is apparent that the 1928 II group had practically completed its season's growth at the time of capture of the samples.

It is obvious that comparisons of the sort given above, to be most dependable, should be based on different years' collections of the same year class. By such a procedure errors that might arise from unequal growth of the same age fish in different calendar years are completely avoided. The confining of comparisons to different years' collections of the same year class of course limits this type of analysis to those year classes that are well represented in more than 1 year's collection. However, for the question at hand dependability is more important than a diversity of material.

Since data of the above type throw light only on the probable time at which growth ends, the presentation of the available data on the amount of the season's growth already made by the different populations at the time of capture of the samples should be preceded by a brief consideration of probable time at which the season's growth begins. Juday and Birge (1930) stated that in the lakes of this region "The ice disappears about the 1st of May; the shallower lakes usually lose their covering of ice a few days before the larger and deeper lakes." From these facts it may be considered valid to assume that in general growth does not occur in any of the four populations of this study before early May, and that the time at which growth begins does not differ by more than 1 or 2 weeks from one lake to another.

Table 35 shows a comparison of the amount of calculated growth made by three age groups of the Trout Lake cisco between the beginning of the growing season and the time of capture of the samples, with the total calculated growth for the season as determined from later years, collections of the same year class. The data for the 1928 II group which were used to illustrate the method of comparison have already been discussed. It may be seen at once that the 1930 III and IV groups agree with the 1928 II group in indicating that the season's growth of the Trout Lake cisco is practically if not entirely complete by the end of July. The growing season for the Trout Lake cisco is not longer than 3 months and, since growth may not start at once upon the disappearance of the ice, may actually be somewhat less than 3 months.

TABLE 35.—*Calculated growth of 3 age groups of the Trout Lake cisco up to the time of capture in the summer, compared with the growth for the entire summer calculated from collections of the same year class in later years*

[Number of specimens in parentheses]

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on later collections of	
				1930	1931
1926	July 21, 28, 29, 1928	II	17 (102)	19 (99)	17 (79)
1926	July 29, 30, 31, 1930	IV	9 (99)		9 (79)
1927	Do	III	10 (347)		11 (269)

Only one year class (1928) occurred in sufficient numbers in more than 1 year's collection of the Muskellunge Lake cisco to make possible a comparison of growth up to time of capture with the total season's growth. The 1930 II group (see table 4) had an average calculated growth of 19 millimeters for the 1930 season up to the time of capture, August 28 and 29. The 337 specimens of this same year class taken as the III group of 1931 showed an average calculated growth of 18 millimeters for the entire 1930 season. Although these data can scarcely be taken to demonstrate a shrinkage of 1 millimeter in the average size of the 1930 II group between the time of capture of the samples and the time of the formation of the third annulus, they do indicate that the season's growth of the Muskellunge Lake cisco is complete at the end of August.

It is, of course, possible that growth in the Muskellunge Lake cisco may be complete several weeks before the end of August. The 1928 and 1931 collections were taken earlier in the summer but, unfortunately, no comparisons are possible between the data of any age groups of the samples of these 2 years and data based on collections of the same year class in other years. In the 1928 collections (made July 1 to July 4) only the II group was well represented and none of the 1926 year class individuals was taken in any of the later collections. The 1931 collections (made July 14 to 28—over 80 percent of the former date alone) cannot be compared with the 1932 collections since for reasons discussed previously (p. 219) the 1932 catches were not included in the Muskellunge Lake growth data. It is possible, however, to compare the season's growth before capture of the 1928 and 1931 II groups with the grand average of 18 millimeters calculated growth in the third year of life, based on the combination of all age groups above the II group and all years' collection. These comparisons show that the 1928 II group which had grown 13 millimeters at the time of capture in early July was still 5 millimeters short of the average growth of fish in the third year of life, while the 1931 II-group fish which had grown 11 millimeters up to the middle of July still lacked 7 millimeters of having attained the average for third-year growth. These two comparisons, particularly the latter, indicate that the Muskellunge cisco is growing actively throughout July and that in all probability this growth extends at least into early August. Consequently the Muskellunge Lake cisco may be accredited with a slightly longer growing season than the Trout Lake cisco.

Since it was felt that the prominence of Lee's phenomenon in the growth data of the Silver Lake cisco made the comparison of age groups separated by more than 1 year of life inadvisable, none of the 1928 material was used in the study of length of the growing season in that lake. Table 36 shows the comparison of the 1930 calculated growth of three age groups of the Silver Lake cisco up to the time of capture in the middle of August with the total 1930 growth of these age groups calculated from 1931 collections of the same year classes. It may be seen that at the time of capture of the 1930 samples, August 9 to 15, the season's growth of the Silver Lake cisco was approximately two-thirds to three-quarters complete. From this fact it may be concluded that the Silver Lake cisco is still growing throughout the month of August and that the growing season probably extends on into early September. It may be concluded, therefore, that the growing season of the Silver Lake cisco is longer than that of either the Trout Lake or the Muskellunge Lake cisco.

TABLE 36.—*Calculated growth of 3 age groups of the 1930 Silver Lake cisco collections up to the time of capture in the summer, compared with the growth for the entire summer of 1930 calculated from collections of the same year classes in 1931*

[Number of specimens in parentheses]

Year class	Date of capture	Age at time of capture	Growth in summer up to time of capture	Growth in entire summer based on 1931 collections
1925	Aug. 9, 10, 15, 1930	V	8 (25)	12 (21)
1926	Do	IV	10 (58)	14 (108)
1927	Do	III	14 (25)	17 (102)

The 1931 Clear Lake cisco samples were collected in two groups, the first from July 22 to 28, and the second from September 2 to 5. Tables 37 and 38 show the calculated growth during 1931 up to these 2 periods of capture for 7 age groups (sexes considered separately) and also the entire 1931 growth for these age groups as calculated from 1932 collections of the same year classes. Although there are several irregularities in the tables it can be seen at once that much of the season's growth occurred after the latter part of July and that growth was by no means entirely completed in early September. If all age groups are considered together, the males taken in late July had completed 64 percent of their 1931 growth while those taken in early September had completed 81 percent of the season's growth; the same data for the females are 68 percent for the July samples and 76 percent for the September samples. From these facts it may be concluded that the growth of the Clear Lake cisco probably continues through September and possibly into October, and further that the growing season of the Clear Lake cisco is longer than in any of the other three lakes.

TABLE 37.—*Calculated growth of 7 age groups of the Clear Lake cisco (males) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections*

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22–28	1931 growth up to Sept. 2–5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22–28	1931 growth up to Sept. 2–5	Total 1931 growth based on 1932 collections
1924	VII	8 (7)	5 (1)	11 (7)	1928	III	27 (16)	33 (10)	42 (11)
1925	VI	9 (6)	10 (5)	13 (9)	1929	II	51 (27)	61 (7)	70 (23)
1926	V	13 (2)	14 (2)	16 (2)	1930	I	55 (16)	77 (4)	105 (20)
1927	IV	18 (6)	22 (4)	24 (7)					

TABLE 38.—*Calculated growth of 7 age groups of the Clear Lake cisco (females) up to the time of capture in the summer of 1931, compared with the entire 1931 growth calculated from the same year classes in the 1932 collections*

[Number of specimens in parentheses]

Year class	Age at time of capture in 1931	1931 growth up to July 22–28	1931 growth up to Sept. 2–5	Total 1931 growth based on 1932 collections	Year class	Age at time of capture in 1931	1931 growth up to July 22–28	1931 growth up to Sept. 2–5	Total 1931 growth based on 1932 collections
1924	VII	9 (16)	7 (5)	12 (8)	1928	III	31 (18)	36 (7)	44 (14)
1925	VI	12 (6)	12 (6)	18 (12)	1929	II	55 (27)	60 (8)	77 (21)
1926	V	12 (1)	13 (1)	16 (1)	1930	I	63 (14)	78 (4)	105 (13)
1927	IV	26 (2)	26 (2)	32 (7)					

While the Clear Lake cisco undoubtedly has an advantage over the other three populations in the length of the growing season, this advantage may not be as great as might at first be suspected. The autumn of 1931, in which year the length of the growing season of the Clear Lake cisco was estimated, was abnormally warm. The records [16] of the United States Weather Bureau station at Minocqua, about 6 kilometers west of Clear Lake, show that the air temperature in September 1931, was 4.5° F. above the normal, while in October and November it was 3.0° F. and 6.5° F. above normal, respectively. This warm autumn may have extended the growing season of the Clear Lake cisco beyond its normal limit. If this is true the growth beyond early September in normal years may not be as much as 20 percent or more of the season's growth as tables 37 and 38 would indicate.

If the length of the growing season in the different lakes is considered in relation to the growth rates of the various populations, it may be seen that poorest growth occurs in the lake with the shortest growing season (Trout Lake) while the best growth occurs in the lake with the longest growing season (Clear Lake). The two lakes (Muskellunge and Silver Lakes) in which the growth rate was intermediate also have growing seasons of intermediate length. Thus it appears that differences in the length of the growing season are important contributing factors toward differences in growth rates. However, these differences in the length of the growing season can by no means explain entirely the observed differences in the amount of growth in the four populations. The growth of the Clear Lake cisco up to July, for example (tables 37 and 38), is well in excess of that found in Trout Lake cisco (table 35) or the Silver Lake cisco (table 36) of corresponding ages at any time in the growing season or for the entire growing season.

RELATIONSHIP BETWEEN DENSITY OF POPULATION AND RATE OF GROWTH

It was stated in the introduction that these studies on the growth of the cisco have been made on populations from "type" lakes that were selected on the basis of their biologically productive capacities as estimated chiefly from the amounts of fixed carbon dioxide in their waters. It was hoped that the comparison of the growth of the various populations might yield information as to the extent and nature of the effect of the natural richness of the waters upon the growth rates of the fish populations that live in them. The investigators who collaborated in planning and initiating the studies of which the present one is a part harbored no delusions to the effect that the relationship between the growth of fishes and the environment is in any sense simple. It was nevertheless surprising to find early in the investigation of the growth of the cisco that the growth rates of the populations did not fall at all in the order of the estimated productive capacities of the lakes in which they occurred, but rather that the reverse was true. Trout Lake with 18.7 parts per million of fixed CO_2 contains the slowest growing cisco of the four populations, while the cisco of Clear Lake, in which body there occur only 2.2 parts per million of fixed CO_2, stands out by far as the fastest growing of the four stocks. In Silver Lake and Muskellunge Lake where the amounts of fixed CO_2 are intermediate in value (Silver, 15.5 parts per million; Muskellunge, 10.0 parts per million) the growths of the cisco populations are also intermediate.

It can hardly be concluded that an inverse causal relationship exists between the growth rate of the cisco and the fixed CO_2 content of the lake it inhabits. Rather

[16] Climatological Data of the United States by Sections, vol. 18, 1931.

it would appear that the growth rate of the cisco in these lakes depends primarily on some factor other than that of the productive capacity of the lake as that capacity is estimated from the concentration of bound CO_2 in its waters. If it is assumed that the various stocks do not differ greatly in their hereditary capacities for growth and that environmental conditions are in general comparable, then it may be expected that the amount of growth in the various populations will depend in large measure upon the availability of food. The determining factor is then the amount of food available to each individual fish. If the poorest growth occurs in the lake that produces the greatest amount of food, it may be assumed that here in all probability the number of feeding individuals is so great and the competition for food so strong that these individuals cannot secure a sufficient amount of food to maintain their normal rate of growth. On the other hand, if a relatively rapid growth occurs in a lake with a scanty basic supply of food it may be assumed that the feeding population in that lake is so small that in spite of the scarcity of food the individuals are still able to secure sufficient nourishment to maintain rapid growth.

This conception of a dependence of growth upon density of population is based primarily upon the assumption that there exists a competition for food. If food is present in a quantity greater than the maximum which the population can utilize for purposes of maintenance and growth, then an increase in the density of the population should not affect its growth rate until that point is passed where the food available becomes less than the maximum quantity which the population can use. From this point on a continued increase in the density of population involves a decrease in the ration of the individual fish and reduces the amount of individual growth. If the density of the population becomes sufficiently great, there is finally reached the point at which the food supply suffices only for purposes of maintenance and there is no excess for growth.

The evidence that investigators have presented to show a relationship between density of population and rate of growth in fishes has been of two sorts: (1) Change in rate of growth accompanying transfer from a thickly populated to a sparsely populated region, and (2) change in rate of growth accompanying changes in the density of the population within the same region.

European investigators have conducted numerous experiments that show the effect on growth rate of transplanting young plaice from the overcrowded coastal nursery grounds to less densely populated areas with more abundant food. The classic of all such experiments is the Danish work of transplanting young plaice from the overcrowded nursery grounds at the entrance of the Limfjord to the thinly populated areas of the inner broads. Although three-fourths of the fish are retaken within the year following the time of their liberation, their increase in size is so great that a continuation of these transplantation operations, which were begun in 1892, has proved profitable up to the present time.[17]

Borley (1912) gave the results of experimental transplantation of plaice from the English coastal waters to the Dogger Bank. He believed that there was "at least a doubling of the growth" (in length). In the same paper Borley reviewed the results of similar experiments by Dutch and Danish investigators. Lee and Atkinson (1912) also reviewed the results of earlier transplantation experiments. A good general review of European plaice transplantation experiments may be found in Blegvad's paper published in 1933.

[17] There was no transplantation in 1917. Johansen (1928) summarized the results of the transplantation operations in the Limfjord up to that time.

The study of the relationship between the density of population in marine fishes and their rate of growth received considerable stimulation from the observation of the conditions that resulted from the almost complete suspension of fishing operations in the North Sea during the World War. During the war there occurred an accumulation of the stock of plaice. Large fish became more plentiful but the average rate of growth decreased. With the resumption of fishing on a large scale the accumulated population was largely fished out. Large fish became relatively scarce and the average rate of growth increased. Further investigations disclosed the fact that in general in regions with a dense population of plaice the rate of growth tended to be low and vice versa.[18]

Bückmann (1932) expressed the relationship between growth in weight and the density of population as being inversely proportional and referred to it as a "Vereinfachtes Wachstumgesetz" which he defined: "Die Gewichtzunahme verhält sich umgekehrt proportional zur Bestandsdichte." Bückmann expressed this law by the equation,

$$w^1 = w\frac{n}{n^1},$$

where w is the weight increase per individual in a population of n individuals and w^1 is the increase in weight that would occur if the number of individuals were changed from n to n^1. Bückmann recognized the law to be inexact and mentioned certain disturbing influences. He pointed out that it is incorrect to assume that all the food consumed is applied toward increase in size. A certain definite amount is utilized to maintain individual metabolism. The percentage of the food that is so used varies according to the total amount of food available to each individual. Further, the efficiency with which a fish makes use of its food varies according to the abundance of food at hand.[19] Yet another complicating factor is the competitive action of other species. Bückmann developed a growth formula that contained correcting factors for these sources of error.

Russell (1932) made a somewhat similar analysis of the relationship between growth and population density in fishes.

In some species fluctuations in the density of the population appear to have no effect on the rate of growth. Concerning the haddock Bowman (1932) stated:

> It cannot be inferred from the results of the extensive and continuous investigations that, in comparable areas, the average growth rates of successive broods in their first year of life vary with differences in brood densities.

Hjort (1932) pointed out that growth in the Norwegian cod and herring stocks is remarkably uniform from year to year and quite independent of the density of the stock. He contended that growth was determined by specific conditions in the sea rather than by the numbers of fish in the population.

Marine populations, particularly round fishes, can wander freely over extensive areas. It is possible for them to seek out those regions with the most suitable food conditions, and in some instances it is probable that the role of food as a limiting factor for growth is insignificant as compared to other environmental influences. Within the restricted limits of a small inland lake a closer dependence of the growth

[18] The following papers listed in the bibliography touch upon the question of the relationship between density of population in marine fishes (largely the plaice) and their rates of growth: Strodtmann and Langhammer (1925), Heincke and Bückmann (1926), Garstang (1926), Jensen (1928) and (1932), Bückmann (1932), Bowman (1932), Hjort (1932), and Russell (1932). These papers are only representative of the rather voluminous literature of the subject.

[19] Bückmann referred to Dawes' (1930, 1931) feeding experiments with plaice.

rate upon the density of the population might be expected. Here ordinarily it is impossible for underfed fish to move to an area with more abundant food; they must subsist as best they can upon the food supply available within the lake. If the lake contains a "natural" population, a population not disturbed by any extensive removal of individuals through a fishery, then it may be assumed that in all probability a competition for food exists, and that this competition may in some lakes be quite severe. Several examples of the dependence of fish growth upon the density of the population have been observed in fresh-water lakes.

The Norwegian farmers have long recognized the disadvantages of an overcrowded stock in trout lakes. The appearance of emaciated and undersized individuals is taken as an indication that a more intensive fishery is desirable. Through the regulation of the intensity of the fishery they "keep the trout under discipline" (Huitfeldt-Kaas reviewed by Rugde (1923) in the Salmon and Trout Magazine). In another paper Huitfeldt-Kaas (1927) stated, "Very great rapidity of growth is shown by fish [trout] in lakes with quite small stock * * * This type of growth I think can suitably be termed '*slender stock type*'."

Surbeck (1921) stated that the decrease in numbers in the stock of the "Balchen" (*Coregonus schintzii helveticus* Fatio) in Vierwaldstättersee following 1900 was accompanied by a significant increase in individual size.

Järvi (1920 and 1924) was able to show that in the "kleine Maräne" (*Coregonus albula*) of the Finnish lakes the poorest growth occurred when the fish were most plentiful and the best growth occurred when the fish were scarce. The fishermen consider the presence of large young fish in the early catches of the fishing season as an indication that the year will be bad.

Pirognikoff (1927) stated that the decline of the intensity of the fishery for the rudd (*Rutilus rutilus lacustris* Pallas) in Lake Chani and the consequent increase in the abundance of that form was accompanied by a distinct decline in the rate of growth.

Hart (1931) found that whitefish taken in different parts of Lake Ontario showed different rates of growth, which he was able to explain in part by the selective action of the gear used in collecting the samples, but stated with reference to the slow growth of the fish taken at Pleasant Point, "An explanation on the grounds of detrimentally keen competition for food in the first years in the neighborhood of a much frequented spawning ground is a tempting one."

In his studies of the trout (*Salmo kamloops* Jordan) of the Kamloops district, British Columbia, Mottley (1932) observed that the opening of a lake to intensive fishing was followed not only by a decrease in the abundance of trout but also by an increase in their "size for age." He advocated that an annual determination of growth rates be included in the data upon which stocking policies for the lakes of the region are based.

Juday and Schneberger (1933) reported the discovery of abundant populations of undersized smallmouth black bass in two small lakes in Vilas County, Wis. They considered the inferior growth of these bass as the results of a too great density of the populations in relation to the amount of available food.

On the basis of experimental studies on young trout Willer (1929) asserted that crowding operates as an inhibitor to growth in a manner over and above the effect it may have in producing competition for food. He considered this "Raumfaktor" to account for the irregularities found by him (Willer, 1924), and by Järvi (1920) in

the growth of the kleine Maräne and stated that he had found the same situation in the smelt (Willer, 1926).

In view of the numerous demonstrations by other investigators of a relationship between density of population and growth rate in fishes it was considered advisable in this study to investigate the relative densities of the four cisco populations with particular reference to a possible relationship between these densities and the observed differences in the growth rates of the various stocks.[20]

An important source of difficulty in the study of the relationship between population density and growth rate lies in the fact that the estimation of the density of a fish population, either absolute or relative, is at its best difficult and in a large measure uncertain. Ordinarily the chief sources of information are the results of experimental fishing and the statistics of the commercial yield. In the present investigation dependence must be placed entirely upon the size of the catch per unit of effort as based on the action of experimental gear (gill nets). In this connection some of the chief difficulties and sources of error in the gathering and the interpretation of data on the gill-net catches should be mentioned.

Gill nets fish from a fixed position, and their effectiveness is dependent upon the movements of the fish. If the amount of movement varies according to time, locality, or population, such variations will be reflected in the catch of the net. The effect of the movements of the cisco is complicated by a tendency for the fish to shoal or move in groups. Group movements cause a great variation in the catch from day to day from nets set in exactly the same location.

Further difficulty lies in the fact that the catches of the same net or the same group of nets in different lakes are not always directly comparable.[21] For example, the seven mesh sizes of the "new" gear employed in collecting the samples for the later part of this investigation failed to take equally adequate samples of all the age groups in the different populations. The Clear Lake catches probably represent reliable samples of the I group and all older groups as well. In Silver Lake and Muskellunge Lake, however, the I groups cannot be considered adequately represented, while in Trout Lake the representation of the II group as well as the I group are to be considered too small. The comparison of the Clear Lake catches with those in which the I and II groups are absent or poorly represented would of course lead to a too high estimate of the relative density of the Clear Lake population.

It must be recognized also that the fishing effort represented by a series of nets varies from one lake to another, for obviously no effort can be accredited to a net that is wholly ineffective for the capture of the members of a particular population. On the other hand, in a population with a wide length range two or three sizes of mesh may be necessary to capture a sample directly comparable to the catch of a single mesh size in a population with a more compact size range. Because of these difficulties it is not possible on the basis of gill-net catches to derive "index numbers" that can be taken directly as reliable measures of relative densities in populations of greatly dissimilar size ranges. In general, however, the examination of the catch of each size of mesh in each lake will, in spite of these aforementioned difficulties, give a fairly good idea of relative population densities in different lakes.

[20] It is realized that competition for food is not at all confined to competition among individuals of the same species. With the possible exception of the Muskellunge Lake cisco population, however, the competition of other species is probably of insignificant importance in this study. At present there are available few data on the degree of competition between the Muskellunge Lake cisco and the perch that occur abundantly in the same regions of the lake. (See the section, Fishes Associated with the Cisco.)

[21] For a more detailed discussion of the action of gill nets see the section, "The selective action of gill nets."

In the comparision of net catches from different lakes it is important further to know whether observed differences in net catches result from real differences in population densities or whether they depend merely upon the actual positions in which the nets were set within the lakes. For this purpose it is necessary to have some knowledge of the vertical distribution of the cisco in each of the lakes whose populations are to be compared. The importance of such information will appear from the following discussion of the vertical distribution of the cisco in Trout, Muskellunge, Silver, and Clear Lakes. Particular attention will be given the question of the relationship between the vertical distribution of the cisco and the temperature and oxygen concentration in the different lakes. The data on the vertical distribution of temperature and O_2 in Silver Lake were taken from Juday and Birge (1932, table VI) and those for Trout Lake, Muskellunge Lake, and Clear Lake were supplied by Dr. Chancey Juday from the records of the Wisconsin Geological and Natural History Survey.

The cisco collections from Trout Lake were taken during July, both in 1930 and 1931, and in nets set on the bottom [22] at depths of from 15 to 33.5 meters. Nets set anywhere within this region always took good catches of ciscoes while nets set in shallow water (less than 7.5 meters) for the capture of other species caught ciscoes only rarely. The few that were taken in the shallow water nets can be considered stragglers. From the examination of the data of table 39 it can be seen that in Trout Lake in middle and late summer there lies below the depth of 10 or 12 meters a large body of cold water with a good supply of oxygen. It is in this region that the cisco lives during this season of the year, and it is in this region that the samples used for study of density were collected.

TABLE 39.—*Trout Lake, July 1, 1931, and Aug. 27, 1931. Relationship of temperature and dissolved oxygen to depth*

[O_2 in milligrams per liter]

July 1, 1931			Aug. 27, 1931		
Depth in meters	Temperature in °C.	O_2	Depth in meters	Temperature in °C.	O_2
0	25.4	7.77	0	19.9	8.60
5	19.4	8.75	5	19.9	8.80
10	13.5	9.71	10	16.8	8.45
15	9.5	8.89	15	9.8	7.00
20	8.3	8.31	20	8.4	5.40
25	7.6	7.20	25	7.8	3.80
28	7.5	7.07	28	7.6	2.00
31	7.3	5.71	31	7.3	.56

It is in Muskellunge Lake that the late-summer habitat shows the most marked restriction to a limited stratum. The record of the first three lifts in the 1930 collecting season shows how closely the number of specimens taken depends upon the depth at which the nets are set. On August 27, 1930, nets were lifted in Muskellunge Lake from a depth of 17.5 meters. The total catch was a single sucker. The nets were then reset at a depth of from 7 to 11.75 meters. The catch on August 28 was: 38 perch, 17 suckers, 3 smallmouth black bass, 1 rock bass, and 226 ciscoes. Most of the ciscoes were taken in the nets set at a depth greater than 9 meters. The position

[22] It should be remembered throughout these discussions for all lakes that the nets were always set on the bottom at the recorded depths. They actually fished the stratum of water, 3.5 to 6 feet thick, immediately above the bottom.

of the nets was again shifted, this time to depths of 7 meters and shallower. The catch on August 29 was: 60 perch, 13 suckers, 8 smallmouth black bass, 3 rock bass, and only 13 ciscoes. Thus it may be seen that at the end of August 1930, ciscoes occurred on the bottom in abundance only within a rather limited region. They were not plentiful in depths less than 9 meters and were absent in the deeper portion of the hypolimnion.

Most of the ciscoes collected from Muskellunge Lake in 1931 were taken in a single set made July 14 at a depth of 9.5 to 10 meters. Although there are no 1931 data that may be used to set the upper and lower limits of the vertical range of the Muskellunge Lake cisco in that year, nets set at depths less than 8 meters for the capture of other species failed to take ciscoes.

The results of the rather extensive fishing of the 1932 collecting season (table 40) give the most complete information concerning the vertical distribution of the cisco in Muskellunge Lake. From these samples which were taken at different times in July and early August it appears that approximately two-thirds of the fish were captured in nets set at depths between 11 and 13 meters (the fish were taken in the stratum of water 6 feet thick immediately above the bottom). Data on the O_2 and temperature conditions in Muskellunge Lake in the late summer of 1932 based on the results of a vertical series of temperature and O_2 concentration determinations made August 25 (table 41) offer an explanation of the concentration of the cisco into such a narrow stratum and suggest that such a concentration most probably occurs every year. The data of table 41 indicate that in Muskellunge Lake in late summer, oxygen is almost completely lacking in the hypolimnion and may be abundant in the upper part only of the thermocline. As a result of this deficiency of oxygen in the deeper strata the ciscoes are forced out of the cooler strata and by reason of their preference for cool water and their need of oxygen become concentrated in that stratum of water that has the lowest temperature available and yet contains sufficient oxygen to support life.

TABLE 40.—*Muskellunge Lake cisco, 1932—Vertical distribution of the cisco*

[The data show the catch per day's fishing of 100 square yards of gill net, set at different depths. In parentheses are given the number of lifts upon which each average lift was based]

Depth in meters	Size of mesh (in inches)			Depth in meters	Size of mesh (in inches)		
	1¼	1½	1¾		1¼	1½	1¾
Less than 5	0.0 (1)	0.1 (10)	0.1 (9)	11 to 13	42.0 (1)	93.4 (5)	0.5 (2)
5 to 7	.0 (1)	.1 (9)	.0 (10)	13 to 15	1.5 (2)	17.0 (1)	
7 to 9	.8 (5)	11.2 (4)	.5 (4)	No depth record	21.5 (2)	26.3 (3)	.0 (2)
9 to 11	10.3 (6)	29.0 (6)	1.5 (10)				

TABLE 41.—*Muskellunge Lake, Aug. 25, 1932—Relationship of temperature and dissolved oxygen to depth*

[O_2 in milligrams per litre]

Depth in meters	Temperature in ° C.	O_2	Depth in meters	Temperature in ° C.	O_2	Depth in meters	Temperature in ° C.	O_2
0	21.3	8.02	10	14.5	5.33	15	10.5	0.56
5	21.3	8.70	11	13.8	2.67	19	10.1	.24
8	20.7	8.25	12	12.0	.43			

Because of the heavy concentration of the Muskellunge Lake ciscoes within a narrow stratum in late summer, it is apparent that the catch of ciscoes in a particular net will vary greatly according to the depth at which the net was set. To obviate this difficulty the estimate of the relative density of the population of the Muskellunge Lake cisco was based only on catches of nets set in the depths at which the cisco is most abundant. These depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

The conditions of life that the Muskellunge Lake cisco finds in middle and late summer in the upper strata of the thermocline are probably far from the optimum for the species. Not only is the water temperature higher than they would normally be expected to select but the crowding itself and the probable competition with the perch that inhabit the same region in large numbers (p. 293) may be expected to make for quite unsatisfactory feeding conditions. In view of these unsatisfactory conditions of life the poor condition (p. 248) of the individuals of this population in contrast to those of other lakes in which chemical conditions are better, and their short life span are not surprising.

That the existence of conditions that force the cisco into unsuitable strata of water may have damaging effects on the population was pointed out by Cahn (1927), who stated that when "the cisco is forced into water far warmer than it ordinarily selects * * * the result is often disastrous", and a high mortality occurs. Scott (1931) showed that where there is formed a "thermoclinal notch" in the oxygen curve the disappearance of the oxygen from the hypolimnion may force a sudden movement of the ciscoes from the hypolimnion to the upper strata of water. His observations on the cisco of Snow Lake, northeastern Indiana, showed that no great mortality results from this sudden move, but rather that the fish are only temporarily incapacitated. After floating for a short time at the surface they make a recovery and remain in the epilimnion for the remainder of the season. Such a forced removal into an undesirable habitat, either sudden or gradual, doubtless entails considerable shock to the individual fish. It is readily conceivable that a temporary stoppage of growth might occur, and that the occurrence of accessory annuli such as appear in the Muskellunge Lake cisco scales can be thus explained.

The Silver Lake cisco agrees with the Muskellunge Lake cisco in showing a rather sharply delimited vertical distribution. In the summers of both 1930 and 1931 ciscoes were taken only in nets set in depths between 10.5 and 15.5 meters. The dates of collection in 1930 were August 9, 10, and 15; in 1931, July 17 and August 22. The reason for this concentration within a 5-meter stratum appears from the examination of the data of table 42, which shows the relationship between depth and the temperature and O_2 concentration in Silver Lake on August 28, 1931. If the data of table 42 are considered in relation to the known vertical distribution of the cisco in Silver Lake, it would appear that a preference for cool water keeps the ciscoes from entering the warmer strata less than 10 meters deep, while a deficiency of oxygen prevents them from occupying the lower portions of the hypolimnion. Thus in late summer the Silver Lake cisco is confined to a narrow stratum in the upper part of the hypolimnion and the lower part of the thermocline. The catch of nets set between the depths of 10.5 and 15.5 meters can be taken to represent the relative abundance of the Silver Lake cisco at that time.

TABLE 42.—*Silver Lake, Aug. 28, 1931—Relationship of temperature and dissolved oxygen to depth*

[O_2 in milligrams per litre. From Juday and Birge (1932)]

Depth in meters	Temperature in °C.	O_2	Depth in meters	Temperature in °C.	O_2	Depth in meters	Temperature in °C.	O_2
7	20.2	9.20	11	9.4	9.80	14	7.7	1.60
8	18.8	9.90	12	8.6	7.50	15	7.2	.60
9	14.7	13.20	13	8.2	4.40	18	6.8	.00
10	11.4	11.70						

The field records of lifts of ciscoes in Clear Lake indicate that in this lake the cisco occurs in all parts of the hypolimnion from midsummer to early autumn. (The dates of collection were July 22 to 28, 1931, Sept. 3 to 5, 1931, and July 12 to 19, 1932.) This distribution of the cisco in Clear Lake suggests that it may at all times find a plentiful supply of oxygen throughout the hypolimnion. Such an assumption is supported by the data on the temperature and dissolved oxygen conditions in this lake based on a vertical series taken August 19, 1932 (table 43). These data show that at this time of the year there is in Clear Lake a plentiful supply of oxygen at all depths. Thus it is valid to assume that the net samples captured at different depths in the hypolimnion may be taken to represent the relative abundance of the cisco in Clear Lake.

TABLE 43.—*Clear Lake, Aug. 19, 1932.—Relationship of temperature and dissolved oxygen to depth*

[O_2 in milligrams per litre]

Depth in meters	Temperature in °C.	O_2	Depth in meters	Temperature in °C.	O_2	Depth in meters	Temperature in °C.	O_2
0	20.9	8.07	12	12.4	9.46	23	8.4	4.51
5	20.9	7.91	15	9.9	7.93	26	8.0	3.25
10	18.5	8.07	20	8.6	6.03			

The data for the comparison of the relative density of the four cisco populations (table 44) represent the catch of 100 square yards of gill net fished over a period of 24 hours. The lifts upon which the data are based were all made from depths at which the cisco occurred in abundance at the time of capture. These depths include the entire hypolimnions of Trout Lake and Clear Lake and the 10.5–15.5 meter stratum of Silver Lake, while in Muskellunge Lake the depths were 9 to 11 meters in 1930, 9.5 to 10 meters in 1931, and 11 to 13 meters in 1932.

TABLE 44.—*Catch in number of ciscoes per 100 square yards of gill net per 24 hours' fishing*

[Data arranged according to lake, year of capture, and mesh of net]

Lake	Year of capture	Size of mesh						
		1¼	1½	1¾	2	2¼	2½	3
Trout	1930		104.8					
	1931	[1] 61.0	73.0	[1] 1.0	2.8			
Muskellunge [2]	1930		106.1					
	1931		143.9					
	1932	[1] 42.0	93.4	[1] .5				
Silver	1930		31.6		50.0			
	1931	[1] 62.0	30.0	[1] 76.0	45.0			
Clear	1931	.1	1.4	2.3	3.5	3.7	5.5	7.5
	1932	.2	.9	1.9	.7	2.4	4.3	3.8

[1] This size of mesh was not represented in the gear of the preceding years.
[2] The data for the 1932 Muskellunge Lake collections are presented in detail in table 40.

From the examination of the data of table 44 it may be seen that the various populations show considerable differences in their relative densities at the time of capture in the depths from which the samples were taken. The Muskellunge Lake fish appear to be the most abundant although Trout Lake is not far behind. The Silver Lake data show a relative abundance slightly less than that in Trout Lake or Muskellunge, while the Clear Lake cisco population may be considered relatively sparse.

The estimate of the relative densities of the four cisco populations at the time of capture is not, however, of primary importance in this investigation. Since this section is concerned chiefly with the relationship between density of population and rate of growth the most significant comparison of population densities must include a comparison of densities throughout the entire growing season rather than at some particular time within the growing season. It was pointed out in the section on the length of the growing season that growth of the Trout Lake cisco is practically complete at the end of July; the Muskellunge cisco completes its growth by the end of August, possibly sooner; the season's growth of the Silver Lake fish is two-thirds to three-quarters complete in mid August; and the Clear Lake cisco has completed well over half its season's growth by late July. From these facts it is apparent that the relative density of the four populations in late spring and the first half of the summer is more significant than their relative densities at the time the samples were collected. There is strong evidence that in Muskellunge Lake and Silver Lake at least the densities of the cisco populations earlier in the growing season were less than at the time of capture in late summer. The concentration of these populations in late summer within a narrow stratum may be considered the result of the temperature and oxygen condition at that time. It is most probable that in late spring and early summer no such concentration existed, since in the early season oxygen would be expected to occur at all depths in the hypolimnion. Consequently the relative densities for the Muskellunge Lake and Silver Lake fish in table 44 must be considered too high as compared to those from Trout Lake and Clear Lake.

If attention is given to the relative densities during the entire growing season the most probable arrangement of the lakes from the most dense to the least dense population is: Trout, Muskellunge, Silver, Clear. This is the same order these lakes show with respect to growth rate in weight (with slowest growth in Trout Lake and fastest growth in Clear Lake). The growth rates of the four populations are approximately in the reverse order of the productive capacities of the lakes as estimated from the amount of bound CO_2 in their waters (Clear Lake was estimated as the least productive, followed in order by Muskellunge, Silver, and Trout). Thus it appears that the growth rates of these populations are determined primarily by their relative densities rather than by the basic productive capacities of the waters they inhabit. Although it is recognized that crowding itself may possibly impede growth to a certain extent independently of its effect in creating competition for food, and that various physical-chemical factors may affect growth rate directly, it is believed that the differences in growth rate in these four populations depend in large measure on the varying degrees of competition for food in the different lakes. It is further probable that variation in the intensity of competition for food from lake to lake may be related to the observed differences in the length of the growing season of the different stocks. (See preceding section.)

AGE COMPOSITION OF THE SAMPLES AND THE RELATIVE ABUNDANCE OF YEAR CLASSES

Because of its importance in the study of commercial fisheries the question of age composition of the stock and of the existence of dominant year classes has in recent years received a great amount of attention. It is now well known that the success of different years' hatches as measured in terms of the number of young produced is subject to a wide range of variation from one year to another. The hatches of some years may be so successful that that particular year class may dominate in the fishery over a period of 1 or several years. Yet other hatches may be so unsuccessful as to make only minor contributions to the stock. The common occurrence of relatively successful and unsuccessful year classes has been demonstrated in many species of fish of commercial importance. The study of the age composition of the commercial catch over a period of years has served as a most valuable tool in the investigation of fluctuations in abundance. In both Europe and America the known age composition of the commercial stock, together with the observed rate of falling off of a year group from year to year, has been used by fisheries investigators as a basis of prediction of the probable yield of the fishery for the approaching season.

In spite of the extensive researches that have been made on the subject of fluctuations little is known as to the causes that make a year class good or bad. Hjort (1914) stated that while the basic causes of fluctuations in abundance are unknown, it appears that fluctuations "have their origin in certain conditions prevailing at a very early period in the life of the fish." He repeated this opinion in 1926. Storrow (1932) pointed out that not only are the factors that determine the success or failure of a year class complex, but also that the difficulty of observing the fish in its natural environment is great. He called attention further to the failure of attempts to simulate natural conditions in the laboratory, a convincing proof of inadequate knowledge of optimum conditions.

The most thorough-going studies on the question of fluctuations in abundance in coregonids and their causes are those of Järvi (1920, 1924, 1930). He was able to show not only a great variation in the abundance of different year classes of the "kleine Maräne" (*Coregonus albula*) but also a distinct connection between such variations in abundance and weather conditions in the spring just after the time of hatching. If there are strong winds at this critical period many of the delicate newly hatched young are destroyed by the wave action. Järvi found, however, that strong winds at the time of spawning are less harmful.

Huitfeldt-Kaas (1917) found that in some years in Lake Mjøsen almost all the spawning run individuals of *Coregonus albula* are taken in the commercial fishery before they have had an opportunity to spawn, and that poor year classes may result.

Because of the manner (collecting with gill nets) in which the samples were obtained in the present investigation the study of the relative abundance of the various age groups in the four cisco populations and along with it the consideration of the relative abundance of the different year classes must be approached with great caution. (The limitations of gill net samples in the study of relative abundance of age groups and year classes are discussed in the section on the selective action of gill nets.) The age composition of a gill-net sample must in general be considered as descriptive of the sample rather than of the population as a whole. Exceptionally, however, the representatives of some particular year class may appear so prominently or be so scarce at all of the ages at which that year class appears in different

collecting years that it may be possible to designate the year class as good or poor. The examination of the age composition of the different years' collections in each of the four lakes (tables 45 to 48) does indicate the presence of certain year classes that can be termed relatively good or relatively poor.

In the Trout Lake collections (table 45) the year classes of 1926 and 1927 appear to represent good years for the production of young. The former year class as the II group of 1928 made up more than half of that year's collection, and 3 years later as the V group of 1931 it was still relatively abundant, comprising 13 percent of the total collection in this latter year. By reason of gear selection the 1927 year class (I group of 1928) was almost entirely lacking in the 1928 collections. This year class was, however, dominant in the collections of the later years, first as the III group of 1930 and then as the IV group of 1931. These conclusions as to the "goodness" of the 1926 and 1927 year classes are supported by the comparison of the relative abundance of corresponding age groups in the different years' collections. The 1926 year class furnished the greatest relative abundance of any II group in any year [23] (56.0 percent of 1928 collection) and also of any V group (13.0 percent of the 1931 collection). Similarly the 1927 year class furnished the greatest relative abundance of any III group (1930) and of any IV group (1931). It should be mentioned further that the presence of these two relatively successful groups contributed toward the progressive increase from year to year in the average age and average size of the fish in the collections obtained from Trout Lake.

TABLE 45.—*Age composition of the samples of the Trout Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1928	2 (1.1)	102 (56.0)	61 (33.5)	17 (9.3)								
1929												
1930		36 (9.2)	247 (63.2)	99 (25.3)	9 (2.3)							
1931	2 (0.3)	61 (10.0)	173 (28.4)	269 (44.1)	79 (13.0)	12 (2.0)	4 (0.7)	5 (0.8)	2 (0.3)		2 (0.3)	1 (0.2)

In the Muskellunge Lake collections (table 46) the year class of 1928 (II group of 1930, III group of 1931) may be considered relatively successful. This year class, as the III group composed 55.6 percent of the 1931 collections, whereas in preceding years the III group composed a negligible portion of the total collection. The similarity of the age composition of the 1928 and the 1930 collections suggests the possibility that the 1926 year class may have been exceptionally abundant and that a collection in 1929 would have shown a high percentage of III-group individuals. However, the almost total absence of all age groups above the II group in the 1928 and 1930 collections suggests also the possibility that heavy mortality may regularly reduce the numbers of Muskellunge ciscoes early in life, and that the great relative abundance of the III group in 1931 may depend not only on the great relative abundance of the 1928 year class but also in part on the failure of this year class to suffer this customary great mortality. The scarcity of I-group individuals in all Muskellunge Lake collections may be considered the result of selectivity by gear.

[23] The great abundance of II-group fish in 1928 may depend in part on the smaller mesh gill nets used in that year.

TABLE 46.—*Age composition of the samples of the Muskellunge Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age			
	I	II	III	IV
1928	19 (6.8)	252 (89.7)	10 (3.6)	
1929				
1930	17 (6.9)	214 (87.3)	14 (5.7)	
1931	9 (1.5)	258 (41.9)	347 (55.3)	2 (0 3)

The study of the age composition of the Silver Lake collections (table 47) reveals the presence of one year class (1926) which may be considered good and of one year class (1929) which may be considered poor. The 1926 year class was dominant in the collections of 2 of the 3 years, as the IV group of 1930 and as the V group of 1931. The scarcity of 1926 year class individuals as the II group in the 1928 collection can be explained on the basis of gear selectivity. The 1929 year class must be considered relatively poor because of its relative scarcity as the II group of the 1931 collections. This scarcity can hardly be the result of selection by gear as the individuals of the age groups on either side are more than three times as numerous. The great abundance of I-group fish in 1931 as compared with 1930 is the result of the introduction of smaller meshed nets in the first-named year. The lack of individual net records makes it impossible to determine the reason for the scarcity of I-group fish in 1928. However, the 1930 year class can safely be considered more abundant than the 1929 year class. The 1924 year class which was dominant as the 1928 IV group may possibly represent a good production year.

TABLE 47.—*Age composition of the samples of the Silver Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age						
	I	II	III	IV	V	VI	VII
1928	1 (0.7)	9 (6.7)	46 (34.1)	69 (51.1)	10 (7.4)		
1929							
1930		7 (5.9)	25 (21.2)	58 (49.2)	25 (21.2)	3 (2.5)	
1931	66 (17.5)	19 (5.0)	61 (16.1)	102 (27.0)	108 (28.6)	21 (5.6)	1 (0.3)

The Clear Lake samples (table 48) present much more definite and consistent indications of the presence of successful and unsuccessful year classes than were found in the other three lakes. Figure 5 shows graphically the year class composition for the 1931 and 1932 collections. The agreement between the 2 years in the relative abundance of the different year classes is close. Since the individuals of each year class were a year older in 1932 than in 1931, and consequently of a different size range, this close agreement between the year class composition of the 2 years' collections may be taken as strong evidence for a high degree of reliability of the Clear Lake samples both as to year class and as to age composition.

TABLE 48.—*Age composition of the samples of the Clear Lake cisco*

[The percentages are given in parentheses]

Year of capture	Age										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1931	38 (15.3)	69 (24.5)	51 (20.5)	14 (5.6)	6 (2.4)	23 (9.2)	29 (11.6)	16 (6.4)	1 (0.4)	2 (0.8)	------
1932	31 (16.2)	33 (17.3)	44 (23.0)	25 (13.1)	14 (7.3)	3 (1.6)	21 (11.0)	15 (7.9)	3 (1.6)	1 (0.5)	1 (0.5)

It can be seen at once from the examination of table 48 and figure 5 that in Clear Lake the 1926 year class (V group of 1931, VI group of 1932) was very unsuccessful,

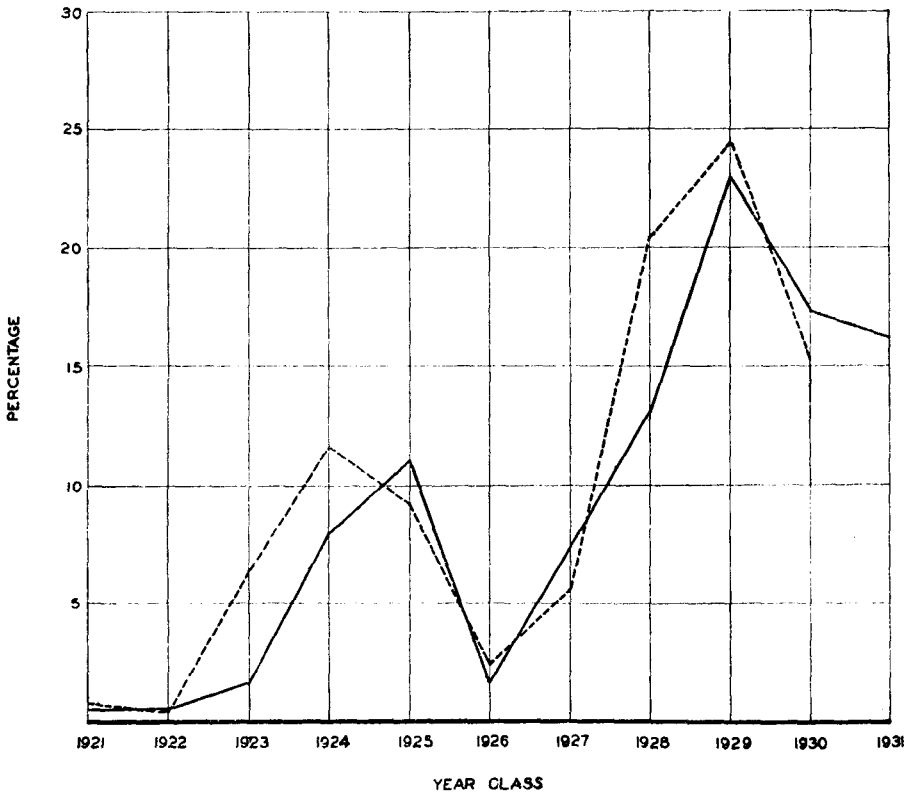

FIGURE 5.—Percentage representation of the different year classes in the Clear Lake cisco collections. 1931, broken line; 1932, solid line.

while the 1929 year class (II group of 1931, III group of 1932) which was dominant in the collections of both years may be termed good. It can be considered valid to state further that the 1924 and 1925 year classes (VII and VI groups of 1931) and probably the 1928 year class (III group of 1931) were more successful than those of 1926 and 1927 (V and IV groups of 1931), and that the 1929 year class (II group of 1931) was more successful than either that of 1930 (I group of 1931) or 1931 (I group of 1932).[24]

In the comparison of the relative abundance of different year classes in Clear Lake some consideration should be given the matter of the age of the samples upon

[24] In contrast to the other 3 populations the I-group samples of Clear Lake can be considered representative. (See the section on "The selective action of gill nets.")

which the estimations are based. For example, the 1927 year class which as the IV group composed 5.6 percent of the 1931 collection and as the V group composed 7.3 percent of the 1932 collection must be considered to represent a much less successful year than the 1924 year class which as the VII group of 1931 composed 11.6 percent of that year's collection and a year later as the VIII group made up 7.9 percent of the 1932 collection. Although the 1924 year class individuals in both years' collections combined were only about one and one-half times as numerous as those of the 1927 year class, the former year class, by reason of its 3 years greater age, had suffered the reducing effect of natural mortality over a longer period of time. Consequently the 1924 year class as compared with the 1927 year class may be considered much more successful than the comparison of the representation of the two groups in the collections would indicate. A similar line of reasoning leads to the conclusion that the 1925 year class (VI group of 1931) also represents a very successful year. The same conclusion may possibly apply to the 1923 year class which was well represented as the VIII group of 1931.

In the preceding discussion it was shown that in each population there existed a considerable variation in the numerical abundance or successfulness of the various year classes. The years that appear to have had a production of relatively successful year classes were: Trout Lake—1926, 1927; Muskellunge Lake—1928; Silver Lake—1926; Clear Lake—1924, 1925, 1929. In Silver Lake the 1929 year class was poor, and in Clear Lake the 1926 and 1927 year classes must be considered relatively unsuccessful.

Since the four populations show no agreement in the matter of goodness or poorness of the various year classes, it may be concluded that in each population the success of the individual year classes depends on the purely local conditions within the lake. This conclusion is of particular interest in view of the rather general opinion that fluctuations in the relative abundance of year classes have their origin in differences in weather conditions from one year to another. Inasmuch as these four lakes are grouped closely together (the maximum distance between any two of them is about 18 kilometers) they must all be subjected to approximately the same weather conditions.

It must be remembered that relative abundance is not a wholly reliable index of absolute abundance. A poor year class may appear quite numerous in comparison to a yet poorer one. Järvi (1920) gave an excellent illustration of this fact when he pointed out that the great relative abundance of third year fish in some years' catches of the "kleine Maräne" depended not upon the actual abundance of that particular age group but was rather the result of the scarcity of fish in their second year of life.

The data of tables 45 to 48 make possible a comparison of longevity in the four populations. The Muskellunge Lake cisco has definitely the shortest average life span. The Trout Lake cisco falls second and the Silver Lake cisco third, while the average life span of the Clear Lake cisco is quite long. A possible explanation of these differences among the four populations as to the average length of life was mentioned in the section on condition in the different populations.

AGE AT MATURITY AND SEX RATIO

Although the collections of the cisco were made in July, August, and early September, several months before the time of spawning in November, the development of the gonads was such as to leave little doubt as to the sexual maturity of the

individual. Fish that would have spawned the following autumn could be distinguished easily from those which would not have spawned at that time. The former were considered here as matured fish even though they may not have spawned previously.

Sexual maturity occurs at an early age in each of the four populations. All the Clear Lake fish with the exception of a few I-group individuals were mature or maturing. Since there is good reason to believe that the I-group samples from Clear Lake are representative, it may be concluded that in this population the first spawning occurs in the autumn of the second year of life. Practically all the I-group individuals in the samples from Trout, Muskellunge, and Silver Lakes would have spawned the following autumn. There is reason to believe, however, that in these populations the nets used for collecting the samples took only the larger I-group individuals. The smaller members of the age group may have been immature. In all three populations, however, all II-group individuals indicated that they would spawn in the autumn.

The ciscoes of the four populations considered in this investigation attain sexual maturity at an earlier age than has been found by some investigators of this species. Clemens (1922), referring to *L. artedi* in Lake Erie, stated that first spawning is "probably at the end of the third summer." The ciscoes of the inland lakes of southern Wisconsin spawn at the age of 3 years (Cahn 1927). Van Oosten (1929) found that in the Saginaw Bay herring only a few fish matured in the second year, and that the majority matured in the third and fourth years of life. Van Oosten's data were based on the examination of individuals from the spawning run. In the Lake Ontario cisco Pritchard (1931) found a few females but no males mature at 2+years. He stated further that several individuals of both sexes were mature at 3+years, while spawning was general at 4+years. Dymond (1933) found that in Hudson Bay the cisco does not mature "until the fourth and probably the fifth year."

The sex ratio expressed as the number of females per 100 males was determined by age groups for each of the four populations. These data are presented in table 49.

TABLE 49.—*Sex ratio according to age in each of the four populations*

[The ratio is expressed as the number of females per 100 males. The numbers of specimens are shown in parentheses. The age groups which were composed entirely of one sex are indicated by the sex symbols. The Clear Lake data were obtained by combining the 1931 and 1932 collections. The data for the remaining three lakes are based on the combination of the 1930 and 1931 collections]

Lake	Age					
	I	II	III	IV	V	VI
Trout	100 (2)	162 (97)	204 (520)	354 (368)	1,367 (88)	1,100 (12)
Muskellunge	100 (26)	130 (472)	151 (361)	♂ (2)		
Silver	110 (66)	160 (26)	126 (86)	111 (160)	129 (133)	200 (24)
Clear	72 (69)	89 (102)	94 (95)	86 (39)	82 (20)	100 (26)

Lake	Age						Average
	VII	VIII	IX	X	XI	XII	
Trout	♀ (4)	400 (5)	♀ (2)		♂ (2)	♀ (1)	267 (1,101)
Muskellunge							137 (861)
Silver	♀ (1)						124 (496)
Clear	194 (50)	210 (31)	300 (4)	♀ (3)	♀ (1)		104 (440)

With the exception of the irregular data of Silver Lake, the females tend to become relatively more abundant as age increases. The tendency toward a progressively greater preponderance of females finds an extreme condition in Trout Lake where male individuals are rare beyond the IV group. The Clear Lake fish differ from those of the other three lakes in that the males outnumber the females in the first five age groups. In the VI group the numbers are equal while in the age groups above 6 years the females are much more numerous than the males. Differences among the populations in the rate of change of the sex ratio with increased age are reflected in the average sex ratio for each population as based on the combination of all age groups.

It is believed that the data of table 49 are a reliable index of the sex composition of the four populations. Cahn (1927) and Van Oosten (1929) pointed out that males arrive at the spawning ground earlier than the females. European investigators of coregonids have observed frequently that not only do males arrive at the spawning grounds earlier than females but that they remain there longer. As a consequence, if samples are taken from the spawning run the conclusions concerning the sex ratio would not only be affected by the time within the spawning period of the taking of the sample but also would tend to contain a too high percentage of males. The collections used in this investigation are not open to such a criticism. All samples were taken during the summer, several months before the spawning time, and there is no evidence pointing toward a segregation of the sexes at this period of the year.

The data relative to the sex ratio in the four populations differ from those given by Cahn (1927) for the lakes, Mendota and Oconomowoc, in southern Wisconsin and by Van Oosten (1929) for the Lake Huron herring. Cahn found 101 males and 62 females in his collections from Lake Mendota and 429 males as against 315 females in his samples from Oconomowoc Lake. He combined the collections from the two lakes to obtain a ratio of 100 males to 71.2 females. Cahn attributed the greater abundance of males to the relatively higher mortality of the females during the warm weather of late summer. His data on sex ratio were not correlated with age.

Van Oosten (1929) found males and females approximately equally abundant (49.5 percent males) in his samples of the Lake Huron herring taken at Bay City, Mich. He did, however, find differences in the sex ratio in the different age groups. Females were the more numerous in the younger age groups (I and II in the method of age designation used in this paper) while the males were the more abundant in the older age groups. Van Oosten attributed the shifting sex ratio to an earlier attainment of sexual maturity on the part of the females and a consequent tendency for them to appear in the commercial catch at an earlier age.

The change with age in the sex ratio of the four cisco populations of this study must be explained on the basis of a differential mortality of the two sexes. Since there is no fishery for the cisco in these lakes, there can be no disturbance of the natural relationship through the catching of more individuals of the one sex than of the other. The reason for the observed differences in differential mortality in the four lakes presents a problem difficult of explanation. Attention should be called to the fact that with respect to the relative abundance of males in the entire samples the lakes fall in the same order that they show with respect to the amount of growth in weight, that is the population with the slowest growth (Trout Lake) has relatively fewest males. The possible significance of this parallelism will be considered later.

Willer (1929) suggested that selective destruction by carnivorous forms might affect the sex ratio in the kleine Maräne (*Coregonus albula*). In the younger groups the heavier, less agile female would fall prey to predators more readily than the males. In the older groups the heavier females would be protected by virtue of their size as the predatory fish would select the slenderer males as prey of more suitable proportions. Such an assumption does not serve to explain the change with increase in age in the sex ratio of the four populations of the present investigation. Though the Trout Lake stock shows the most rapid shift toward a preponderance of females, the growth of the two sexes in this lake is the same both with respect to length and weight. Furthermore, the greatest changes in sex ratio occur between age groups that show only slight differences in average length and weight. The situation in Muskellunge Lake is similar to that in Trout Lake. In Silver Lake the males tend to be slightly heavier than females of the same age while in Clear Lake the females are distinctly heavier than the males. Yet in both populations, particularly in the Clear Lake cisco, females are relatively more abundant than males in the older age groups.

In view of the fact that the greatest progressive change in the sex ratio with increase in age occurs in the population in which there is least reason to expect selection on the basis of sex by the carnivorous forms which prey on that population, it must be concluded that the differential mortality upon which the changing sex ratios depend is not the result of selection by predators. The differential mortality of the two sexes is probably the result of basic differences in their innate physiological mechanisms, differences that vary in their manifestations from one population to another, and whose effects appear to be associated to some extent with the growth rate of each particular population.

The above suggestion of an explanation of the differential mortality of the sexes of the cisco is in agreement with the conclusions of Geiser (1923, 1924, a, b,) [25] who held that females are inherently better fitted than males to survive adverse environmental conditions. The explanation of the sex ratio on these grounds assumes particular interest when it is considered in relationship to the correspondence between sex ratio and growth rates in the four cisco populations of this study. It was pointed out (p. 269) that in these populations slow growth is associated with a relative paucity of males. It appears logical to assume that the environmental factors that doubtless contributed to the observed differences in growth rate may at the same time have produced corresponding differences in the sex ratios of these same populations. Thus the very slow growth of the Trout Lake cisco may be associated with very adverse environmental conditions that also produce an exceptionally high mortality among the less viable males. This excessive mortality of males as compared to females would produce the observed rapid change with increased age in the sex ratio and the relatively high abundance of females in the population as a whole. Similarly, the better growth in Muskellunge Lake and Silver Lake may be taken to represent conditions less adverse than those in Trout Lake. In these less adverse environments of Muskellunge and Silver Lakes the mortality of males as compared to females is less than in Trout Lake, and females are relatively less abundant in the populations as a whole. Finally, the favorable conditions that permit such excellent growth in the Clear Lake cisco are reflected in the slowly changing sex ratio and the almost equal representation of the two sexes in that population.

[25] In these papers Geiser included comprehensive reviews of the literature on the subjects of sex ratios and differential mortality of sexes, not only in the fishes but in other animal groups as well.

ANNUAL INCREMENTS OF GROWTH

VARIATION IN THE AMOUNT OF GROWTH IN DIFFERENT CALENDAR YEARS

Tables 50 to 54 show the calculated annual growth increments for each of the best represented age groups in the collections of each cisco population. (In Clear Lake all age groups below the IX group were included.) The arrangement of the tables is such that each horizontal row shows the growths in different calendar years of fish of the same age and in the same year of life. The vertical columns show growth increments for the same calendar year but for fish that are either of different age or in different years of life, sometimes both. Each diagonal row shows the growth increments in the different calendar years of a single age group in a single year's collection. The calendar year corresponding to the first year of life of any particular age group is the year of birth, while the year of capture of each age group is one year later than the calendar year of the last growth increment shown in the table for that age group.

TABLE 50.—*Annual calculated growth increments in millimeters of the Trout Lake cisco, ages III to V, according to calendar year and year of life*

Age	Year of life	1924	1925	1926	1927	1928	1929	1930	Average
V	5						12	9	10.5
	4					13	10		11.5
	3				19	17			18.0
	2			34	37				35.5
	1		82	81					81.5
IV	4				10		10	11	10.3
	3			13		19	20		17.3
	2		35		36	37			36.0
	1	85		82	78				81.7
III	3				14		22	17	17.7
	2			39		38	36		37.7
	1		84		79	84			82.3

TABLE 51.—*Annual calculated growth increments in millimeters of the Muskellunge Lake cisco, ages II and III, according to calendar year and year of life*

Age	Year of life	1925	1926	1927	1928	1929	1930	Average
III	3			20		25	18	21.0
	2		37		47	49		44.3
	1	105		85	96			95.3
II	2			48		48	40	45.3
	1		99		95	98		97.3

TABLE 52.—*Annual calculated growth increments in millimeters of the Silver Lake cisco, ages II to VI, according to calendar year and year of life*

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	Average
VI	6							15	12	13.5
	5						16	19		17.5
	4					27	16			21.5
	3				22	23				22.5
	2			40	41					40.5
	1		72	78						75.0
V	5					14		20	14	16.0
	4				19		20	18		19.0
	3			27		25	24			25.3
	2		39		46	46				43.7
	1	76		74	80					76.7
IV	4					16		21	17	18.0
	3				25		26	27		26.0
	2			46		48	52			48.7
	1		79		78	80				79.0
III	3					30		33	29	30.7
	2				54		57	54		55.0
	1			73		77	83			77.7
II	2					50		52	47	49.7
	1				90		99	104		97.7

TABLE 53.—*Annual calculated growth increments in millimeters of the Clear Lake cisco (males), age groups I to VIII, according to calendar year and year of life*

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII	8								7	11	9.0
	7							12	13		12.5
	6						17	16			16.5
	5					18	23				20.5
	4				31	29					30.0
	3			45	55						50.0
	2		85	87							86.0
	1	118	108								113.0
VII	7								12	13	12.5
	6							14	16		15.0
	5						19	22			20.5
	4					30	32				31.0
	3				51	60					55.5
	2			88	86						87.0
	1		110	102							106.0
VI	6								13	16	14.5
	5							21	16		18.5
	4						34	32			33.0
	3					56	68				62.0
	2				84	85					84.5
	1			108	98						103.0
V	5								22	24	23.0
	4							43	39		41.0
	3						58	68			63.0
	2					79	83				81.0
	1				110	98					104.0
IV	4								34	42	38.0
	3							68	69		68.5
	2						86	86			86.0
	1					104	105				104.5
III	3								67	70	68.5
	2							84	88		86.0
	1						104	110			107.0
II	2								92	105	98.5
	1							108	113		110.5

TABLE 54.—*Annual calculated growth increments in millimeters of the Clear Lake cisco (females), age groups I to VIII, according to calendar year and year of life*

Age	Year of life	1923	1924	1925	1926	1927	1928	1929	1930	1931	Average
VIII	8								11	12	11.5
	7							13	15		14.0
	6						15	20			17.5
	5					22	26				24.0
	4				33	32					32.5
	3			54	52						53.0
	2		87	89							88.0
	1	112	105								108.5
VII	7								13	18	15.5
	6							17	17		17.0
	5						23	28			25.5
	4					32	42				37.0
	3				54	62					58.0
	2			88	82						85.0
	1		108	108							108.0
VI	6								16	16	16.0
	5							28	16		22.0
	4						42	32			37.0
	3					58	68				63.0
	2				78	85					81.5
	1			105	98						101.5
V	5								24	32	28.0
	4							44	46		45.0
	3						70	74			72.0
	2					80	79				79.5
	1				108	98					103.0
IV	4								33	44	38.5
	3							82	73		77.5
	2						88	92			90.0
	1					103	103				103.0
III	3								70	77	73.5
	2							91	97		94.0
	1						108	108			108.0
II	2								99	105	102.0
	1							108	114		111.0

The examination of tables 50 to 54 shows that the amount of growth made by fish of the same age and in the same year of life varies considerably from one calendar year to another. This variation is doubtless to a certain extent random and of no particular significance. In each population, however, there may be detected certain calendar years that by reason of the consistently good or poor growth made in them may be considered good or poor growth years. For example, the growth of the Silver Lake cisco and the Muskellunge Lake cisco (possibly that of the Trout Lake cisco also) appears to have been better than average in the year 1929 while the Clear Lake cisco shows excellent growth for 1931. On the other hand, growth in the first three of the above populations appears to have been relatively poor in 1930, while the Clear Lake cisco shows poor growth for 1926 and 1927 at least.

The relative positions of the different calendar years with respect to goodness or poorness of growth may be brought out more clearly by simple methods of analysis. In the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations the relative position of each calendar year was determined on the basis of the percentage deviation from average growth in that particular year. As an illustration of the method of determining the deviation from average growth consider the growth of the Silver Lake cisco in the calendar year 1924 (table 52). The calculated first year growth of 72 millimeters of the VI group (year class of 1924) represents a −4.0 percent deviation from the average of 75-millimeter growth for VI-group fish in the first year of life; the 39-millimeter growth of the V group (1923 year class) in its second year of life represents a −10.8 percent deviation from the average growth of 43.7 millimeters for V-group fish in the second year; and finally the 79-millimeter first year's growth of the III group (year class of 1924) represents a 0.0 percent deviation from the average of 79-millimeter growth for III-group fish in the first year of life. The mean of these three deviations is −4.9, and it may be considered that the growth of the Silver Lake cisco in 1924 was 4.9 percent below average. The deviations from average growth for each calendar year calculated by the above method are shown in table 55 for Trout, Muskellunge, and Silver Lakes.

TABLE 55.—*Percentage deviation from average growth in the different calendar years*

Lake	Calendar year								
	1923	1924	1925	1926	1927	1928	1929	1930	1931
Trout	----------	4.0	0.0	−5.2	−3.2	3.8	5.6	−4.2	----------
Muskellunge	----------	----------	10.2	−7.4	−3.2	1.4	9.1	−13.0	----------
Silver	−0.9	−4.9	−0.9	−0.7	−0.5	−1.7	7.7	−8.0	----------
Clear	3.3	−4.1	−5.1	−8.5	−8.5	−0.4	3.2	3.1	17.1

In criticism of the above method of determining the relative position of the different calendar years as to the amount of growth, it should be mentioned that the evaluation of the different years depends on comparisons that are based on different combinations of year classes and age groups, and that the evaluation of a single calendar year is based not upon a single comparison with all other calendar years involved but rather is the average of a group of comparisons no one of which involves more than 3 calendar years. If one of these single comparisons should happen to involve, for example, 3 poor-growth years the resultant percentage deviations would give too high an estimate of the relative goodness of these growth years as compared to calendar years not involved in the comparison. Similarly, a comparison that involves 3 good-growth

years will give too low an estimate of the goodness of growth in these years as compared with years not involved in this particular comparison. The possible distorting effect of examples such as those just given is obviated in large measure, however, by the fact that the evaluation of the goodness of growth of a single year involves comparisons with so many other calendar years that the effect of a single distorted comparison will tend to be greatly reduced.

In Silver Lake (table 52), for example, the evaluation of the year 1927 is based on comparisons that involve all other years from 1924 to 1930, inclusive. At the best, however, the evaluation of growth in different calendar years shows only their relative positions, and a general shifting of values might be expected to follow the

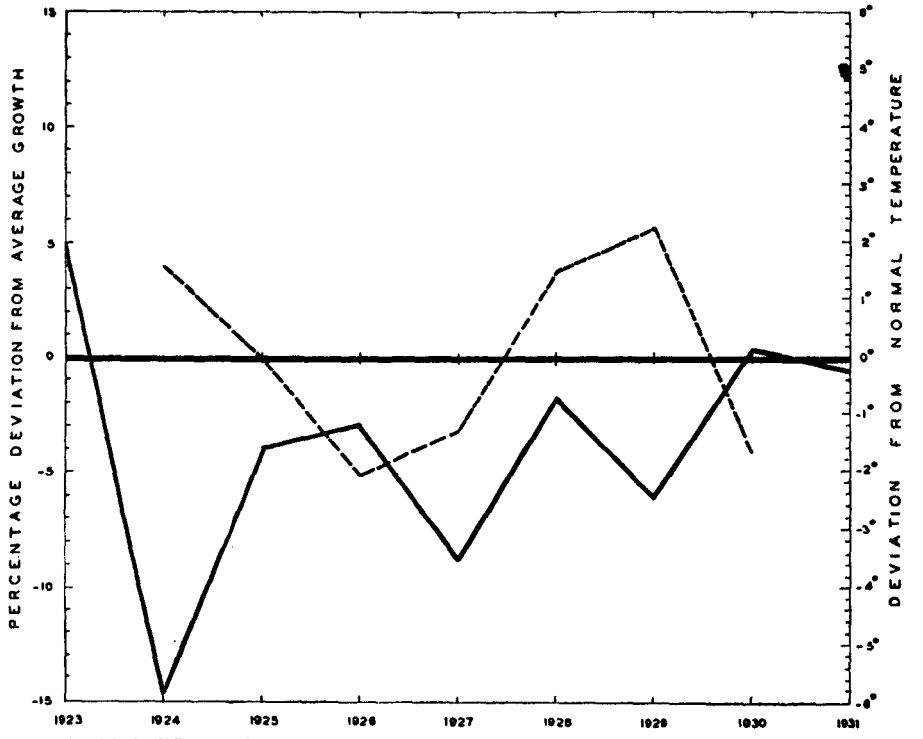

FIGURE 6.—Relationship in different calendar years between the deviation of the growth of the Trout Lake cisco from the average and the deviation of the air temperature from the normal during the cisco's growing season. Deviation from the average growth, broken line; deviation from normal temperature, solid line.

elimination or addition of another calendar year in the comparisons. The method of comparing goodness of growth in Trout, Muskellunge, and Silver Lakes in different calendar years has the advantage that all the single comparisons are based on fish of the same age, and that any possibility of a distortion through Lee's phenomenon is thereby eliminated.

The fact that collections of the Clear Lake cisco were made in only 2 consecutive calendar years makes necessary a slightly different procedure in the comparison of growth in that lake in different calendar years. In Clear Lake the evaluation of the goodness of growth by the method employed in the other three populations would mean that the estimate of the relative position of a single calendar year would be based not on comparisons with several other calendar years but on comparisons with only the single years immediately preceding and immediately following the year in

question. Since, as will be brought out presently, the calendar years 1924 to 1927, inclusive, were all below average as to goodness of growth, while the years 1929, 1930, and 1931 were all above average, the limitation of the estimate for a poor year, as for example 1926, to comparisons with two other poor years, 1925 and 1927, or of a good year as 1930 to comparisons with other good years, 1929 and 1931, would lead inevitably to erroneous conclusions concerning the goodness of growth in these years. To avoid this difficulty the evaluation of the different years was based on the comparison of total growth in each calendar year with that of the preceding year.

An illustration will be given of the method used in the evaluation of goodness of growth of the Clear Lake cisco in different calendar years. (See table 53.) In 1924

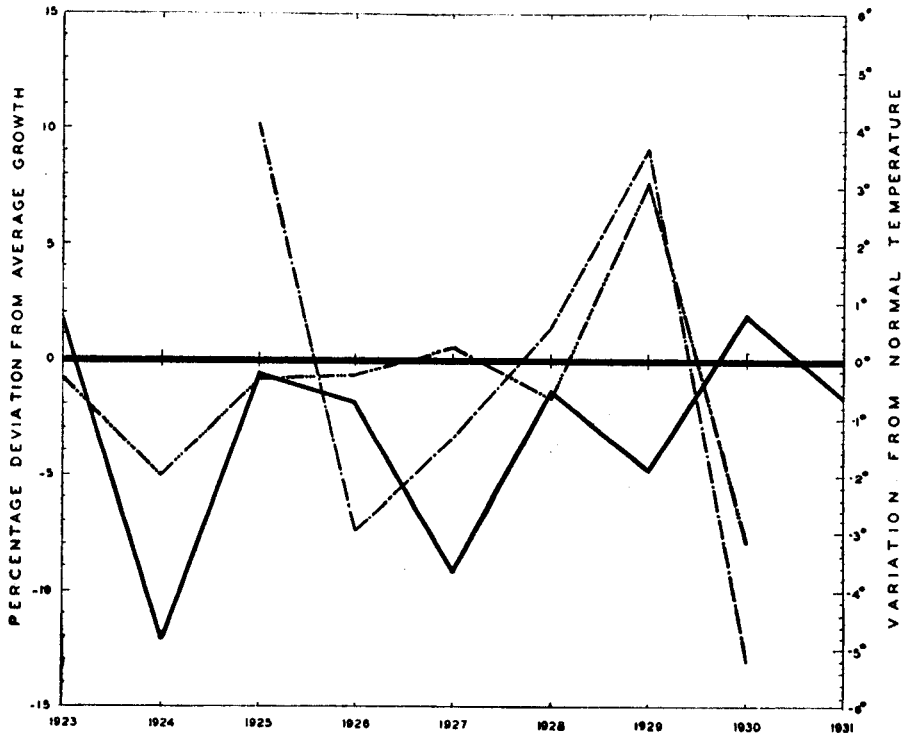

FIGURE 7.—Relationship in different calendar years between deviation of growth of Muskellunge Lake cisco and of Silver Lake cisco from average, and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, Muskellunge Lake cisco — . —; Silver Lake cisco — . . . —; deviation from normal temperature, ———.

the first year's growth of the VIII-group fish was 108 millimeters. This growth was 10 millimeters or 8.5 percent less than the first year's growth of the preceding year (118 millimeters in 1923). Thus the calendar year 1924 shows a −8.5-percent deviation from 1923 as to goodness of growth. Similarly the 1925 growths of 87 (VIII group, second year of life) and 102 (VII group, first year of life) show a total of 189 or a deviation of −3.1 percent from the total corresponding growth of 195 millimeters in 1924. The position of 1925 with respect to 1923 is the sum of the deviations, −8.5 and −3.1 or −11.6 percent. A continuation of this procedure shows the position of each calendar year with respect to the year, 1923. In order to make the relative positions of the different years describe their deviations from average growth rather than from 1923 growth, the mean value of all the deviations as computed from 1923 as the starting point was subtracted from the individual devia-

tion of each year. The final figures after a combination of the sexes (table 55) indicate that growth in 1923 was 3.3 percent above average. Although the Clear Lake data of table 55 were obtained by a different method from the data pertaining to the other three lakes, the fact that all these "deviations from average growth" are used only to show relative positions of the different calendar years makes a comparison of the data of all four lakes valid.

The data of table 55 are presented graphically in figures 6 to 8. The examination of the curves reveals a certain degree of correspondence as to goodness or poor-

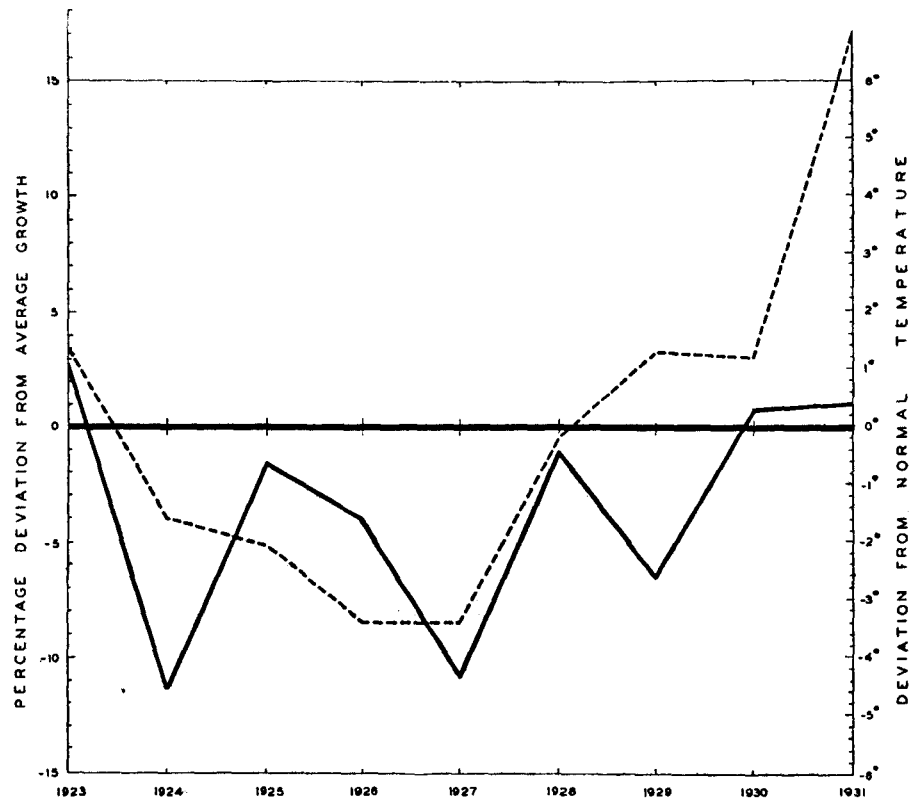

FIGURE 8.—Relationship in different calendar years between the deviation of growth of Clear Lake cisco from average and deviation of air temperature from normal during cisco's growing season. Deviation from average growth, broken line; deviation from temperature, solid line.

ness of growth for certain populations and over certain periods of years. For example, Trout, Silver, and Muskellunge Lakes agree in showing improvement in growth from 1928 to the relatively good year 1929, followed by a distinct drop to the relatively poor year of 1930. Similarly Trout, Muskellunge, and Clear Lakes agree in showing poor growth in 1926 and 1927.

Agreements of the sort just pointed out suggest that the amount of growth in different calendar years may possibly be determined in part by factors that affect all four lakes. The failure of any general agreement of the growth deviation curves indicates, however, that local conditions that exist within a single lake also exert a powerful influence on the amount of growth in different calendar years.

The most apparent influence that might affect growth similarly in all lakes is the average temperature during the growing season, while growth within a single

lake might be expected to vary somewhat with annual fluctuations in the abundance of the population within that particular lake. References to the literature on the question of the change in growth rate that accompanies change in the density of population have been made previously (pp. 254–257). Some mention should be made of the much less numerous observations on the relationship between annual fluctuations in average temperature and annual fluctuations in growth, particularly as these observations have been made with reference to coregonids.[26]

Huitfedlt-Kaas (1917) demonstrated a close correlation between first-year growth and average annual temperature in the lagesild or pollan (*Coregonus albula*) of Mjøsen and Storsjø. At the same time he recognized the possible effect on growth rate of changes in the density of population from one year to another.

In a later paper (Huitfedlt-Kaas, 1927) he was able to show a relationship between the amount of growth and summer temperature in the gwiniad (*Coregonus lavaretus*) and the pollan (*C. albula*). (He noted a similar situation in several tribes of the trout (*Salmo eriox*).)

Olofsson (1932) compared the growth of three species of *Coregonus* (*C. wartmanni borealis, C. wartmanni generosus,* and *C. lavaretus*) of Norrland in the warm summer of 1930 with that in the cold summer of 1931. In all three forms there was large growth in the warm summer and slow growth in the cold. Olofsson called attention particularly to the fact that occasionally growth during a cold season may be so small that the year ring formed on the scales might easily be overlooked. Some scales may even fail to form a distinct year band. The differences observed between growth of the years 1930 and 1931 were exhibited by fish of different sizes and ages.

Krogius (1933) found that the curve of the deviation from average growth in different calendar years for *Coregonus lavaretus* of Lake Baikal followed closely the corresponding curves for deviation from average annual temperature and average annual precipitation.

Van Oosten (1929) found no relation between annual fluctuations in the air temperatures during the growing season and the annual fluctuations in the first year's growth in the Saginaw Bay herring (*L. artedi*).

There are no records of water temperature available upon which to base a comparison of annual deviation from normal temperature during the growing season and annual deviation from average growth in the cisco populations of this study. It is possible, however, to make a comparison between annual deviation from average growth and annual deviation from normal air temperature [27] in the region. For this purpose the records of the meteorological stations at Big St. Germaine Dam and Rest Lake Dam were taken as representative for Trout, Muskellunge, and Silver Lakes, while the records of the Minocqua station were taken as representative for Clear Lake.[28]

Since the lengths of the growing seasons (pp. 249–253) are not the same in the different lakes the annual deviations from normal summer temperature were calculated

[26] Although his work does not deal with the coregonids, mention should be made of Segerstrale's (1932, 1933) observations on the relationship between summer temperature and the growth of fishes in southern Finland. This work dealt with the perch (*Perca fluviatilis*) and several species of cyprinids. Segerstrale found that the amount of growth during the summer is a quantity highly sensitive to the average summer temperature.

[27] Climatological Data for the United States, U. S. Department of Agriculture, Weather Bureau, vols. X–XVIII, 1923–31.

[28] Muskellunge Lake lies about 3 kilometers east of Trout Lake, and Silver Lake lies about 1 kilometer off the southwest corner of Trout Lake. The St. Germaine weather station is about 13 kilometers southeast of Trout Lake while the Rest Lake station lies at an approximately equal distance to the northwest of Trout Lake. The town of Minocqua is about 6 kilometers due west of Clear Lake.

from different combinations of months. The St. Germaine and Rest Lake data were used to determine the annual deviation from normal temperature for the periods May to July and May to August, both inclusive. The former period of time may be taken to correspond approximately to the growing season of the Trout Lake cisco, and the latter to the growing seasons of the Silver Lake and Muskellunge Lake ciscoes. The annual deviation from normal temperature for the longer Clear Lake growing season (May to September, inclusive) were determined from the Minocqua station data. In these calculations of deviations from normal temperature, records for a single month were found to be occasionally lacking in the data for a station. For these few gaps in the data the corresponding records of the nearest neighboring station were substituted. This substitution is justifiable for the corresponding deviations from normal temperature at the different stations were almost always close to each other in value.

Table 56 shows the annual deviations from normal air temperatures as based on the different combinations of months and for the weather stations mentioned in the preceding paragraph. These data are presented graphically in figures 6 to 8 along with the corresponding curves of deviation from average growth. The examination of these curves shows that there is little evidence of a connection between annual deviation from average growth and annual deviation of the air temperature from the normal during the growing season. In the Trout Lake data (fig. 6) the years (1924, 1928, and 1929) with better than average growth were years with subnormal temperature for the period, May to July. On the other hand, 1930 with a temperature slightly above normal was a poor growth year. The year 1929 was a good growth year in both Muskellunge Lake and Silver Lake (fig. 7), while 1930 was a year of poor growth. Yet the air temperature for the period, May to August, was below normal in 1929 and above normal in 1930. Certain other years, however, show both subnormal temperature and growth below average (for example, Silver Lake, 1924). There is some indication that in Clear Lake (fig. 8) there may be some slight connection between annual variations in growth and annual variations in average air temperature over the period May to September. It may be seen that in Clear Lake all the calendar years with poorer than average growth (1924 to 1928, inclusive) showed subnormal temperatures during the growing season while 3 of the 4 years with better than average growth (1923, 1929, 1930, 1931) had temperatures above normal during the growing season. The year 1929 showed growth slightly above average, but temperature below normal. In general, however, the Clear Lake curves for annual deviation of the cisco's growth from the average and the annual deviation of the air temperature during the growing season from normal show a rather conspicuous lack of parallelism.

TABLE 56.—*Average deviation of air temperatures from normal during the growing season of the cisco*

[Deviations are in degrees Fahrenheit; 1.8° F.=1.0° C.]

Stations	Months	1923	1924	1925	1926	1927	1928	1929	1930	1931
St. Germain Rest Lake	May, June, July	2.0	−5.8	−1.6	−1.2	−3.5	−0.7	−2.4	0.2	−0.2
Do	May, June, July, August	.8	−4.8	−0.2	−0.7	−3.6	−0.5	−1.9	.8	−0.6
Minocqua	May, June, July, August, September	1.1	−4.5	−0.6	−1.6	−4.3	−0.4	−2.6	.3	.4

The failure of the data discussed in the preceding paragraph to show any clear dependence of growth in different calendar years on the temperature of the air during

the growing season should not be taken to show that in these four cisco populations the amount of growth in a particular summer does not depend in part on the temperature of the lakes' waters during the growing seasons of the several stocks. It must be recognized first that fluctuations in air temperature may not offer a perfect index of fluctuations in water temperature. A more probable explanation of the failure of annual fluctuations in temperature and in growth to show correspondence is that annual differences in growth are so closely dependent on some other factor or factors that the effect of annual differences in temperature are almost completely obscured. There is reason to believe that in the populations of this investigation the annual fluctuations in the goodness of growth may show some dependence on annual fluctuations in the densities of the different populations.

It has been shown previously (p. 262) that the growth rates (in weight) of these four populations follow the inverse order of the relative densities of their populations. In view of this demonstrated relationship between growth rate and density of population it might well be expected that within a single population changes in the density of the cisco may be accompanied by changes in its growth rate.

In the study of the age composition of the cisco samples from Trout Lake (table 45, p. 264) it was pointed out that the years 1926 and 1927 saw the production of abundant year classes, and that as the result of the abundance of these two groups the 1930 Trout Lake cisco samples were on the average composed of older fish than the 1928 samples while the 1931 samples were composed of older fish than either the 1928 or 1930 collections. This accumulation of old fish together with the contributions of young in the years later than 1927 probably caused the density of the population to be rather high in 1930. This increase in the density of the population may account in part for the drop in growth from 1929 to 1930.

The data for the Muskellunge Lake cisco also afford evidence for a dependence of growth variations on variations in population density. While the 1928 and 1930 collections contained only a few individuals more than 2 years old, a large number of the 1928 year class individuals were present as the III group in 1931. (See p. 264.) The great abundance of the III group in 1931 suggests that an accumulation of the stock may have been occurring in Muskellunge Lake in 1929 and 1930. This accumulation may possibly account for the drop in the amount of growth from 1929 to 1930.

The age and year class composition data for the Silver Lake cisco (table 47, p. 265) show that here as in Trout Lake there was probably an accumulation of the stock in 1930. In the examination of the data of table 47 it should be remembered that the large number of 1931 I–group fish causes the representation of the older age groups of the 1931 samples to appear relatively too low; the gear used in 1928 and 1930 captured few I–group individuals. If due consideration is given to the absence of the I–group fish in the 1928 and 1930 collections the relative abundance of the older age groups in the 1931 Silver Lake collections must be recognized to be higher than in 1930, while the 1930 collection in turn shows a greater abundance of old fish than the 1928 collection. In Silver Lake as in Trout Lake and Muskellunge Lake the accumulation of older fish was accompanied by a decrease in growth from 1929 to 1930.

It should be mentioned that the data upon which a suggested explanation of the drop in growth from 1929 to 1930 in Trout, Silver, and Muskellunge Lakes was based fail to offer any logical explanation for the improvement of growth from 1928

to 1929. Unfortunately there are no 1929 collections upon which to base a comparison of the age composition of that year with the years 1928, 1930, and 1931.

In the Clear Lake cisco the evidence for a dependence of annual fluctuations in the amount of growth on annual fluctuations in the density of the population is somewhat stronger than in the Trout, Muskellunge, and Silver Lake populations. The years 1923, 1924, and 1925 (p. 265, table 48, fig. 5) were undoubtedly excellent years for the production of young. The presence of three successive good hatches must have led to a considerable accumulation of the cisco stock. Corresponding with this accumulation the amount of growth per year decreased from 1923 to 1927 (fig. 8). The production of young was poor in 1926 and 1927. The occurrence of 2 poor production years combined with natural mortality could be expected to lessen the crowding of the population. The growth improved from 1927 to 1929, fell back a little in 1930, and improved again in 1931.[29]

The relationship indicated in the Trout Lake, Muskellunge Lake, Silver Lake ciscoes, and especially in the Clear Lake cisco, between annual fluctuations in population density and annual fluctuations in growth is in agreement with Järvi's observations (1920, 1924) on the kleine Maräne (*Coregonus albula*).

The failure of variations in the amount of growth in different calendar years to show any close general dependence on either annual variations in temperature or annual variations in population density suggests that possibly these variations in growth depend closely on both factors, and that the failure of these factors to operate in the same direction in the same year tends to obscure the effect of each of them.

BIMODALITY IN THE CALCULATED GROWTH FOR THE FIRST YEAR OF LIFE

The examination of the frequency distributions of the calculated growth for the first year of life in the best represented age groups (tables 57 to 60) shows that some of these distributions have a distinct bimodality, which appears to be characteristic for a year class and present regardless of the age of the fish upon which the calculated growths were based.

TABLE 57.—*Trout Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life*

Length	Year class							
	1926			1927		1928		1929
	II	IV	V	III	IV	II	III	II
	1928	1930	1931	1930	1931	1930	1931	1931
110	1				1	1		
105	1			1	1	1	1	1
100	4	1	1	7	4	5	6	2
95	6	2		14	4	8	15	6
90	7	8	5	17	16	6	34	13
85	9	21	15	32	24	7	31	20
80	15	30	23	74	48	5	26	12
75	30	20	27	85	78	3	31	6
70	26	11	6	83	72		26	1
65	3	6	2	30	18		3	
60				5	3			
55				1				

[29] The good growth in 1931 may have been in part due to the climatic conditions of that year as well as to the reduced number of ciscoes in the stock. The temperature over the period, May to September, inclusive, was only slightly above normal (table 56) but the autumn temperatures were exceptionally high (p. 253). It is probable that the warm autumn of 1931 gave the Clear Lake cisco a longer growing season in that year than it usually enjoys.

TABLE 58.—*Muskellunge Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life*

Length	Year class				Length	Year class			
	1926	1928		1929		1926	1928		1929
	II	II	III	II		II	II	III	II
	1928	1930	1931	1931		1928	1930	1931	1931
125	2		2		90	20	39	28	56
120	6	2	7		85	35	41	64	22
115	28	8	16	3	80	29	26	60	4
110	24	20	46	7	75	17	12	17	1
105	35	21	39	33	70	1	2	5	
100	27	17	37	60	65	2			
95	16	21	26	72					

TABLE 59.—*Silver Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life*

Length	Year class							
	1924	1925			1926		1927	1928
	IV	III	V	VI	IV	V	IV	III
	1928	1928	1930	1931	1930	1931	1931	1931
120								
115								
110								
105							1	2
100							4	5
95					1	2	8	4
90	5		1		1	7	5	4
85	8		3	3	9	11	8	7
80	17	6	2	4	10	36	20	9
75	22	11	9	7	16	29	21	16
70	12	17	2	4	11	16	26	9
65	3	7	6	1	7	6	5	3
60	2	5	2	1	2	1	4	2
55					1			

TABLE 60.—*Clear Lake cisco—Frequency distribution by 5-millimeter intervals of the calculated growth in length during the first year of life*

Length	Year class										
	1924		1925		1928		1929		1930		1931
	VII	VIII	VI	VII	III	IV	II	III	I	II	I
	1931	1932	1931	1932	1931	1932	1931	1932	1931	1932	1932
140								1			
135									2	3	4
130		1			1			1	3	1	6
125	2						1	1	5		6
120	3	1		2	1	1	4	3	7	3	5
115	1	2	1	1	5	3	11	4	13	5	4
110	8	1	5	2	10	5	11	8	6	9	1
105	5	3	8	6	11	3	24	10	4	7	2
100	9	1	7	7	12	4	12	8		1	2
95	3	4	1	2	7	4	7	7		4	1
90		1	1	1	5	2	1	1			
85		1				3					

This bimodality of the length frequencies of the calculated growth for the first year of life may be found in the 1928 year class from Trout Lake and in the 1926 and 1928 year classes from Muskellunge Lake. All the other year classes from these two lakes, and all year classes from Silver Lake and Clear Lake, where the samples are large enough to give reliable results show unimodal distributions for the calculated growth of the first year of life. The fact that bimodality in the first year's growth occurs only in two populations and in only one or two year classes of these populations suggests that the occurrence of the phenomenon depends on the nature of the local conditions within each lake and that these conditions vary from year to year.

The most reasonable explanation for bimodality in the first year's growth lies in the assumption that in certain years there are two hatchings rather than a single one. In early spring a period of warm weather with brilliant sunshine and no strong winds can warm the waters of the shallow littoral region to a temperature several degrees above that of the main body of the lake. At such a time the development of the eggs of the cisco would be accelerated and some might hatch. If, however, there occurred before the completion of hatching season a period of cold, windy weather the temperature of the water of the littoral region would undergo a sudden drop of several degrees.[30] The development of the unhatched eggs would be retarded, and their hatching might be delayed for several days or even weeks. Such a situation would explain the observed cases of bimodality in the amount of growth during the first year of life. Eggs that develop in more exposed regions of a lake or in a lake more swept by winds would be less affected by fluctuations in weather conditions.

GROWTH COMPENSATION

The phenomenon of "growth compensation"—the tendency for individuals that grow relatively slowly in the early years of life to grow relatively rapidly during the later years—has been observed by numerous investigators and in several species of fish. The only study of growth compensation in the cisco was made by Van Oosten (1929) on the Saginaw Bay herring of Lake Huron. He concluded that "the large fish of an age group were the large fish in each preceding year of life * * * but that the differences between the small and large yearlings diminished each year of age—that is, the small yearlings were rapid growers and the large yearlings slow growers." Thus he found that compensation did occur, but that it was not sufficient to overcome completely any advantage in length which a large individual might hold at the end of the first year of life.

A comparison of growth compensation in age groups with unimodal and bimodal length distributions at the end of the first year of life should yield information as to the effect of the dispersion of the length frequency in early life upon the manner of growth in later life. In the 1931 collection from Muskellunge Lake (table 58) the distribution of the calculated lengths at the end of the first year is unimodal in the II group and bimodal in the III group. Both age groups are represented by large samples (258 for the II group and 347 for the III group). For these reasons they were selected as the basis for a study of growth compensation.

Table 58 shows the frequency distributions of the calculated lengths for both age groups at the end of the first year of life. The calculated length distributions of the

[30] Forel (1892) pointed out that the development of high temperatures in the littoral region depends on days of great calm and brilliant sunshine, and that this warming process proceeds slowly. The negative changes in temperature proceed much more rapidly. Forel observed that with a strong south wind the temperature of the littoral waters at the port of Geneva at times dropped as much as 6° C. to 8° C. or more from one day to another.

same groups at the end of the second year of life appear in table 61. Table 62 shows the frequency distribution of the increments of growth during the second year of life. All of these data are presented graphically as percentage frequencies in figure 9.

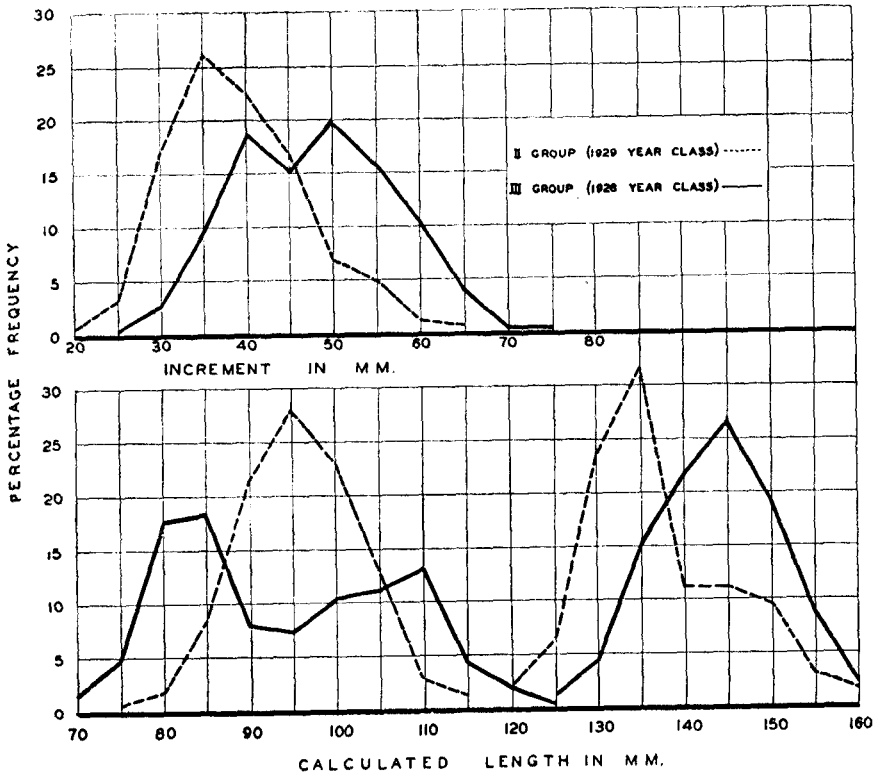

FIGURE 9.—Percentage frequency distribution of the 1931 samples of 1928 and 1929 year classes of Muskellunge Lake cisco with respect to calculated lengths at end of first year of life (below at left), the calculated lengths at end of second year of life (below at right), and calculated increments of growth during second year of life (above).

TABLE 61.—*Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated length at the end of the second year of life as based on the II group and the III group*

Age group	Length interval									Total number
	120–124	125–129	130–134	135–139	140–144	145–149	150–154	155–159	160–164	
II	5	16	61	82	28	29	25	8	4	258
III	----	4	16	53	76	92	67	31	8	347

TABLE 62.—*Muskellunge Lake cisco, 1931—Frequency distribution by 5-millimeter intervals of the calculated growth during the second year of life as based on the II group and the III group*

Age group	Length interval											Total number
	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–59	60–64	65–69	70–74	75–79	
II	1	8	44	68	58	44	18	13	3	1	----	----	258
III	----	1	16	35	65	53	69	55	37	14	1	1	347

Examination of the data shows that during the second year of life of the III-group fish there occurred sufficient growth compensation to change the length distribution of the group from the bimodal to the unimodal condition. The existence of intense compensatory growth is indicated in the bimodal character of the curve for the second-year growth increments of the III group.

A more adequate conception is given of the growth compensation in these two age groups by the study of the correlations between the lengths attained at different times in the individual life histories, and the amounts of growth made by the individuals during different years of life. The correlation was computed for each age group for the following combinations of characters: (1) Calculated length at the end of the first year of life and calculated length at the end of the second year of life; (2) calculated growth in length during the first year of life and calculated increment of growth in length during the second year of life; (3) calculated length at the end of the first year of life and actual length at the time of capture. The results of these computations are given in table 63. Here L_1 is the calculated length at the end of the first year; L_2 is the calculated length at the end of the second year; ΔL_1 is the calculated growth during the second year; and L_T is the actual measured length at the time of capture.

TABLE 63.—*Muskellunge Lake cisco, II and III groups of 1931—Correlations between calculated length at the end of the first year and calculated length at the end of the second year, between the amount of growth during the first year and during the second year, and between the calculated length at the end of the first year and total length at the time of capture*

Data upon which the correlation is based	Coefficient of correlation and its probable error	
	II	III
L_1 and L_2	0.513±.046	0.708±.027
L_1 and ΔL_1	−0.311±.056	−0.826±.017
L_1 and L_T	.404±.052	.399±.045

Tables 64 to 67 show the data from which the correlations between L_1 and L_2 and between L_1 and ΔL_1 were calculated. The examination of tables 64 and 65 shows clearly that in both the II group and the III group the smaller fish at the end of the first year of life tend to be the smaller fish at the end of the second year of life, and that this tendency is the greater in the III group. Tables 66 and 67 show that in both age groups the individuals that grew least in the first year of life tend to grow most in the second, and that here again the tendency is more pronounced in the III group than in the II group.

TABLE 64.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, II group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life									Total
	75–79	80–84	85–89	90–94	95–99	100–104	105–109	110–114	115–119	
160 to 164							2	2		4
155 to 159					1	2		2	3	8
150 to 154			1	2	5	7	10			25
145 to 149			3	7	4	7	8			29
140 to 144		1		2	13	6	3	3		28
135 to 139			4	15	28	28	7			82
130 to 134		3	7	22	16	10	3			61
125 to 129	1		4	6	5					16
120 to 124			3	2						5
Total	1	4	22	56	72	60	33	7	3	258

TABLE 65.—*Relationship between calculated length in millimeters at the end of the first and second years of life in the Muskellunge Lake cisco, III group of 1931*

Calculated length at end of second year of life	Calculated length at end of first year of life												Total
	70–74	75–79	80–84	85–89	90–94	95–99	100–104	105–109	110–114	115–119	120–124	125–129	
160 to 164								1	1	2	3	1	8
155 to 159				1			4	5	10	8	2	1	31
150 to 154			2	4	5	5	9	16	20	4	2		67
145 to 149	1	3	11	18	14	7	12	11	13	2			92
140 to 144		1	20	22	6	10	10	5	2				76
135 to 139	1	8	19	15	3	4	2	1					53
130 to 134	2	4	6	4									16
125 to 129	1	1	2										4
Total	5	17	60	64	28	26	37	39	46	16	7	2	347

TABLE 66.—*Relationship between amount of growth in millimeters during the first year of life and the amount of growth during the second year of life in the Muskellunge Lake cisco, II group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life									Total
	75–79	80–84	85–89	90–94	95–99	100–104	105–109	110–114	115–119	
65 to 69			1							1
60 to 64			1	2						3
55 to 59		1	2	4	4	2				13
50 to 54	1	2	1	5	3	3	2	1		18
45 to 49		1	7	9	9	9	6	3		44
40 to 44			6	17	18	5	10		2	58
35 to 39			4	15	27	17	4		1	68
30 to 34				3	8	23	7	3		44
25 to 29				1	3	1	3			8
20 to 24							1			1
Total	1	4	22	56	72	60	33	7	3	258

TABLE 67.—*Relationship between amount of growth in millimeters during first year of life and amount of growth during the second year of life in the Muskellunge Lake cisco, III group of 1931*

Calculated growth during second year of life	Calculated growth during first year of life												Total
	70–74	75–79	80–84	85–89	90–94	95–99	100–104	105–109	110–114	115–119	120–124	125–129	
75 to 79	1												1
70 to 74		1											1
65 to 69	1	3	6	4									14
60 to 64	2	5	19	9	2								37
55 to 59	1	4	17	23	8	1		1					55
50 to 54		3	15	20	14	7	8	1	1				69
45 to 49		1	2	7	2	10	10	12	8	1			53
40 to 44			1	1	2	8	16	14	17	5	1		65
35 to 39							3	9	15	5	2	1	35
30 to 34								1	5	5	4	1	16
25 to 29								1					1
Total	5	17	60	64	28	26	37	39	46	16	7	2	347

On the basis of the data that have been presented it is possible to draw the following conclusions concerning growth compensation as it is indicated in the two age groups considered here:

(1) Growth compensation occurs in both the group with a unimodal distribution of calculated lengths at the end of the first year of life and the group with a bimodal distribution of these lengths (negative correlation of L_1 and ΔL_1).

(2) Growth compensation is more intense in the group with the greater dispersion of the calculated lengths at the end of the first year of life (higher negative correlation between L_1 and ΔL_1 in the III group). The tendency toward compensation can lead to a bimodal distribution of the growth increments for the second

year, and can within a single season change the length distribution of the group from a bimodal to a unimodal condition.

(3) When the length distribution at the end of the first year of life is unimodal and the dispersion small, individual length at the end of the first year of life exerts more effect on individual length at the end of the second year of life, than the amount of growth during the first year of life exerts on the amount of growth during the second year of life. (In the II group the positive correlation of L_1 and L_2 is greater than the negative correlation between L_1 and ΔL_1.) In the group with the greater dispersion and the bimodal distribution of lengths at the end of the first year of life the situation is reversed, that is, there is a closer connection between the amount of growth during the first year of life and the amount of growth during the second year of life than there exists between the length at the end of the first year and the length at the end of the second year. (In the III group the negative correlation between L_1 and ΔL_1 is greater than the positive correlation between L_1 and L_2.)

(4) In spite of the growth compensation that occurs there is a tendency for the individual to hold throughout life a part of any advantage in length which it may hold at the end of the first year of existence. Compensation reduces individual advantage in length, but does not obliterate it (positive correlation in both groups between L_1 and L_T).

GROWTH RELATIONSHIPS IN THE TROUT LAKE, MUSKELLUNGE LAKE, SILVER LAKE, AND CLEAR LAKE CISCO POPULATIONS

Throughout the preceding sections attention has been called repeatedly to the order in which the cisco populations of the four lakes arrange themselves with respect to certain characteristics such as growth rate, sex ratio, condition, and the like. In view of the apparent high degree of correspondence among certain of these orders of arrangement it is considered advisable to present the data concerning them in a summarized form, together with a brief discussion and review of the possible significance of the observed correlations. Table 68 shows that arrangement of the lakes with respect to the amount of bound carbon dioxide in their waters and to the amount of organic matter in the plankton, and also with respect to certain phases of the life history of the cisco. Although these data demonstrate a close dependence of certain phases in the life history of the cisco on the conditions of its animate and inanimate environment, as will appear in the following discussion, any attempt to describe these relationships in precise terms of cause and effect meets with serious difficulty.

TABLE 68.—*Order of the 4 lakes with respect to the concentration of bound CO_2 and the abundance of organic matter in the surface plankton, and also with respect to certain phases of the life history of the cisco*

Item	Lakes			
	Clear	Muskellunge	Silver	Trout
Growth in length	1	2	3	4
Growth in weight	1	3	2	4
Bound CO_2 in water	4	3	2	1
Density of population	4	2	3	1
Length of growing season	1	3	2	4
Sex ratio (females per 100 males)	4	2	3	1
Organic matter in plankton	4	1	3	2
Condition (K)	1	4	2	3
Average length of life	1	4	2	3

Before entering into the discussion of the relationship between growth rate and the environmental factors that may affect it, attention should be called to the fact that the order of the four lakes with respect to growth in length is not the same as their order with respect to growth in weight. Although the Muskellunge Lake cisco shows better growth in length than the Silver Lake cisco, its growth in weight is inferior to that of the Silver Lake population. The reason for this reversal of order lies in the very poor condition of the Muskellunge Lake fish. Weight unquestionably furnishes a better measure of increase in living matter than does length, but for the purposes of the present discussion it will probably be sufficient to consider both populations merely as intermediate between the extreme conditions represented by the Trout Lake cisco and the Clear Lake cisco.

PHYSICAL-CHEMICAL FACTORS

Certain factors may be ruled out immediately as inadequate for the observed differences in the growth rates of the four populations.

Temperature fails to account for the observed differences in growth rate. Since all four lakes are located within a short distance of each other the climatic conditions that affect each of them are essentially the same. Differences in the size and form of the various basins may lead to differences in average water temperature during the summer, but here it should be pointed out that while the cisco finds its coldest summer habitat in Trout Lake and Clear Lake, the populations of these two lakes represent the extremes in growth rate.

Oxygen conditions also fail to explain the differences in the growth rates of the four populations. Here, as was the case with temperature, Trout Lake and Clear Lake resemble each other most closely. Each possesses large masses of well oxygenated water in the hypolimnion, the favorite habitat of the cisco.

The abundance of bound CO_2 and the closely related hydrogen-ion concentration and conductivity are the only physical-chemical characteristics known to show any correlation with growth rate. Growth rate in length and the abundance of bound carbon dioxide stand in an inverse relationship to each other. It is hardly reasonable to assume that an abundance of bound CO_2 impedes growth directly or that a scarcity of bound CO_2 accelerates it. The effect of the abundance of CO_2 on growth rate is probably indirect and operative through its modification of the biological nature of the cisco's environment.

In general, the amount of bound CO_2 in a lake's waters is roughly indicative of the biological productive capacity of that lake. In view of this fact it would hardly be expected that the poorest growth of the cisco would occur in the lake with the greatest concentration of bound CO_2. This apparently paradoxical situation is explained, however, if it is assumed that an abundance of bound CO_2 makes not only for a greater production of food organisms, but also makes for a much greater abundance of the ciscoes themselves, and that the abundance of the ciscoes in turn determines their growth rates. Such an assumption has the support of the observed fact that the cisco population is most dense in Trout Lake with the greatest amount of bound CO_2 and sparsest in Clear Lake with the least amount of bound CO_2, while Muskellunge Lake and Silver Lake with intermediate concentration of bound CO_2 have populations of intermediate densities.

DENSITY OF POPULATION

The section on the relationship between density of population and growth rate inclined toward the opinion that differences in the severity of competition for food related to differences in the densities of the various populations are largely responsible for differences in the growth rates of the four cisco stocks. This opinion was presented as the most logical, even in the face of the facts, first that the actual existence of any competition for food in any one of the four populations remains to be demonstrated, and second that there exists a strong possibility that crowding may impede growth independently of competition for food (Willer's "Raumfaktor").

As to the causes of the observed differences in the densities of the four populations it may be seen, as was mentioned previously, that the greatest density of the cisco population occurs in the lake with the heaviest concentration of bound CO_2 (Trout Lake) while the least density occurs in the lake with the lightest concentration of bound CO_2 (Clear Lake). The positions of Silver Lake and Muskellunge Lake are reversed with respect to the concentration of bound CO_2 and the density of population, but both are intermediate to the conditions found in Trout Lake and Clear Lake.

Since it is generally held that the success or failure of a hatching of fish depends primarily on conditions that determine the survival of the young at a very early stage, it does not appear unreasonable to hold that differences, traceable to the concentration of bound CO_2, in the amount and kind of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four populations. A study of the plankton cycle in each lake should throw light on the subject.

There does not appear to be any complete correlation between the amount of organic matter in surface samples of plankton taken during the summer and the density of the cisco populations. Although Clear Lake with the least amount of organic matter in the surface plankton has the sparsest cisco population, Trout Lake, with the densest cisco population does not have the greatest amount of organic matter in the surface plankton.

It is possible further that these differences in the densities of the cisco populations may depend on yet other factors such as the availability of suitable spawning areas or the destruction of eggs and young by predators.

Regardless of whether it is held that differences in growth rate depend directly on differences in population density or that both are dependent on yet other factors, it must be admitted that growth rate and density of population show a very close correlation.

LENGTH OF THE GROWING SEASON

In the general section under this title it was pointed out that differences in the growth rates of the four cisco populations can be explained in part by actual differences in the length of the cisco's growing season in the various lakes. The Trout Lake cisco has definitely the shortest growing season, followed by the Muskellunge Lake cisco, the Silver Lake cisco, and the Clear Lake cisco in the order named. Thus it may be seen that in the four populations the length of the growing season follows the same order as their growth rates (in weight) and the inverse order of their densities of population.

These differences in the length of the growing season cannot be accounted for on the basis of temperature and oxygen conditions for the same reasons that temperature and oxygen conditions fail to account for the differences in growth rate. (See p. 287.)

It is possible that an explanation of the differences in the lengths of the growing season may be found in the study of the plankton cycles in the four lakes. Particular attention should be given to the abundance at all times of the season, and in the strata actually inhabited by the cisco, of the plankton forms most commonly taken by that species.

A second possible explanation of the differences in the length of the cisco's growing season in the various lakes is suggested by the fact that in fishes in general the termination of the season's growth in adult fish is coincident with the onset of the development of the gonads preliminary to spawning. (The determination of the length of the growing season in the four cisco populations was based almost entirely on mature and maturing individuals.) Since the average size (weight) of the spawning individuals of the four populations follows the same order as their growth rates and the lengths of their growing season, it is suggested that the development of the gonads in small spawners may begin earlier in the season than in large spawners, and that the slowness of growth of a slow-growing population may be thereby accentuated.

PARASITIZATION

The only published data on the incidence and severity of parasitization in the cisco populations of Trout, Muskellunge, Silver, and Clear Lakes are those presented by Dr. Chancey Juday in the Bureau of Fisheries' report on Progress in Biological Inquiries 1931 (Higgins, 1932). Juday summarized the data then available as follows:

> Thirty ciscoes from Silver Lake were examined for parasites, and cestodes were found in the intestines of all of them; 80 percent of them also had Acanthocephala. In Muskellunge Lake 80 percent of the ciscoes contained cestodes and 20 percent were free of visceral parasites. In Trout Lake 16 percent were negative, 82 percent had cestodes in their intestines, and 10 percent also had Acanthocephala. The ciscoes from Clear Lake, on the other hand, were 96 percent negative; only 2 specimens out of 60 examined yielded any parasites. These fish were found to be feeding almost exclusively on Daphnia, and this may be partly responsible for the very small parasite infestation. Clear Lake also has very soft water, and the snail population, as a result, is relatively small, so that the danger of parasite infestation from this source is correspondingly small.

Although the above data show that the Clear Lake cisco with the fastest growth rate has the lightest parasite infestation, the relationship between parasite infestation and growth rate in the remaining three populations is not clear. The solution of the problem concerning the relationship between growth rate and parasite infestation in the cisco awaits the examination, within each population, of the effect of individual parasitization on individual growth rate.

CONDITION

In the section that dealt with condition and the relationship between length and weight it was pointed out that the order of the four lakes with respect to the average condition of their cisco populations, from poorest to best, is: Muskellunge, Trout, Silver, Clear. While this arrangement does describe the order of the lakes with respect to condition as based on the samples taken, it is open to the criticism that because of the variation of K with length, additional samples taken in yet other years and showing different length distributions of the fish might possibly bring about a change in the arrangement. The determination of an average value of K within a population depends, first, on the manner of change of K with length and, second, on the length distribution of the fish used.

It is quite possible that the most significant phase of the study of condition in these four cisco populations does not lie in the determination of average values of K for the different stocks but lies rather in the study of the change of condition with increasing length. This is particularly true since the separation of the lakes with respect to the manner of change of K with increased length is much sharper than it is with respect to the average value of K in the entire population. The significance of the changes of K with length will become more apparent with the examination of

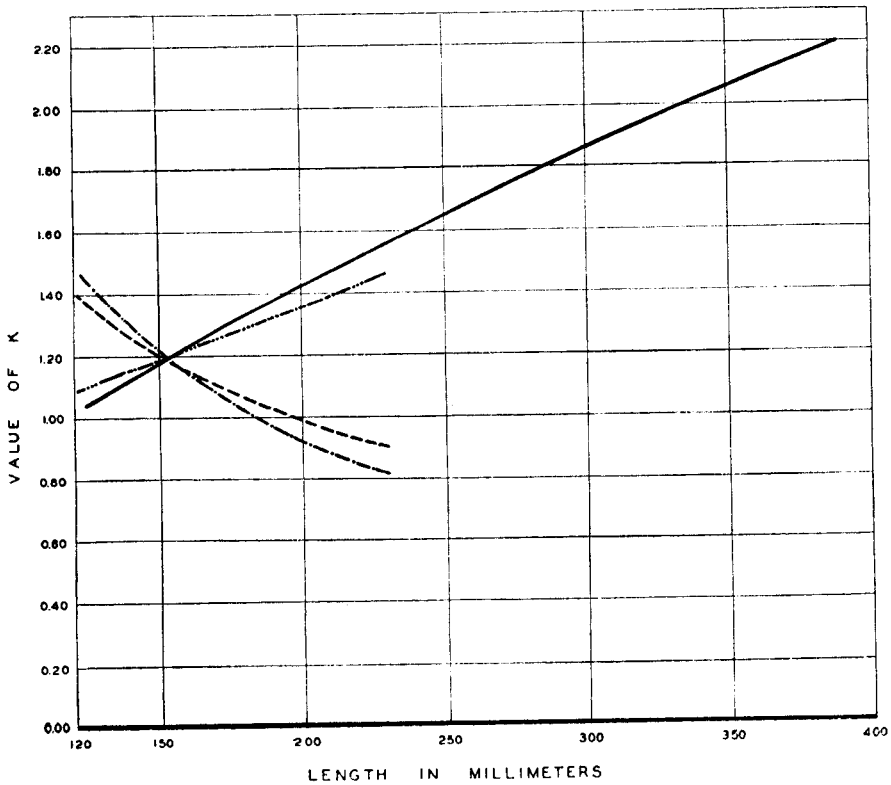

FIGURE 10.—Theoretical values (in 1931) of the coefficient of condition (K) at different lengths, calculated from equations of the type $K=C\times10^{4}L^{m}$. Trout Lake, - - -; Muskellunge Lake, — . —; Silver Lake (females), — ... —; Clear Lake (females), ———.

the equations that describe K as functions of length. These equations for 1931 (the only year in which samples were taken from all four lakes) are: [31]

Muskellunge Lake:

$$K=141.924\ L^{-0.94932}$$

Trout Lake:

$$K=38.7640\ L^{-0.69245}$$

Silver Lake (females):

$$K=0.12322\ L^{0.45372}$$

Clear Lake (females):

$$K=0.04555\ L^{0.64991}$$

The theoretical values of K at different lengths, calculated from the above equations appear in table 69 and are presented graphically in figure 10.

[31] For the purposes of this discussion one equation from each lake is sufficient. The equations for the males of Silver and Clear Lakes may be found in table 27.

TABLE 69.—*Theoretical values of the coefficient of condition (K) at different body lengths, calculated from equations based on 1931 collections*

Lake	Length in millimeters																	
	130	140	150	160	170	180	190	200	210	220	230	250	270	290	310	330	350	370	390
Trout	1.332	1.266	1.207	1.154	1.107	1.064	1.025	0.989	0.956	0.926	0.898	-----	-----	-----	-----	-----	-----	-----	-----
Muskellunge	1.397	1.302	1.220	1.147	1.083	1.026	.975	.928	.886	.848	.813	-----	-----	-----	-----	-----	-----	-----	-----
Silver (females)	1.122	1.160	1.197	1.232	1.267	1.300	1.332	1.357	1.394	1.424	1.453	-----	-----	-----	-----	-----	-----	-----	-----
Clear (females)	1.077	1.131	1.182	1.233	1.283	1.331	1.379	1.426	1.471	1.517	1.561	1.648	1.733	1.815	1.895	1.974	2.051	2.126	2.200

The remarks, made previously (p. 246), concerning the validity of using length-weight equations for the calculation of unknown lengths or weights outside the range of the empirical data apply likewise to the calculation of unknown values of K for lengths outside the range of empirical data. However, it may be pointed out further, on purely mathematical grounds, that the K equations cannot possibly be used for the calculation of K values in very small fish, since as length approaches zero the values of K increase without limit in the equations with negative exponents and approach zero in the equations with positive exponents.

In the 1931 K equations it may be seen that the order of the four populations with respect to the value of the exponent, m, which describes the rate of change of K with change of length, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake. The differences in these rates of change are reflected in the forms of the curves of figure 10. Here it may be seen that the Muskellunge Lake cisco loses condition rapidly with increase in length. The Trout Lake cisco also loses condition with increase in length, but at a slower rate than does the Muskellunge Lake cisco. In Silver Lake the condition of the cisco improves with increase in length, although this improvement is not as rapid as it is in the Clear Lake cisco. The courses of the curves indicate further that at a length of between 150 and 160 millimeters the conditions of all four populations are closely similar.

If the above facts are examined in relation to the growth rates of the four populations it may be seen that, while the Clear Lake cisco with the most rapid growth shows the most rapid progressive improvement in condition, the Trout Lake cisco with the least rapid growth does not show the most rapid loss of condition. Although the Muskellunge Lake cisco shows better growth than the Trout Lake cisco with respect to both length and weight, the loss of condition with increase in length proceeds considerably more rapidly in the former population. This fact demonstrates at least a partial independence between the factors that determine growth rate and the factors that determine condition. Further, the fact that the factors which bring about a rapid loss of condition in one population may fail to reduce the growth rate of this population below that of a second stock with a less rapid loss of condition may be construed as a strong argument for the operation of the "space factor" in the determination of growth rate.

The data of table 68 show that the arrangement of the four lakes with respect to average condition and the rate of change of condition follows the reverse order of their arrangement with respect to the average abundance of the organic matter in the surface samples of plankton. (The greater number of these plankton samples were taken during the summer months.) Although the abundance of organic matter in surface samples of plankton may not serve as a wholly reliable index of the abundance of plankton forms most commonly taken by the ciscoes and in the strata of

water inhabited by that species, the data do show that the cisco suffers the most rapid loss of condition with increase in length and shows the poorest average condition in the lake (Muskellunge) with the most eutrophic environment, while the most rapid gain in condition and the best average condition are found in Clear Lake with the most oligotrophic environment. While it is hardly to be inferred that a mere abundance of food causes loss of condition in the cisco or that a scarcity of food makes for better condition, it is quite probable that the cisco does not thrive in the physical and chemical conditions most conducive to a large production of food organisms. The eutrophic environment of Muskellunge Lake may, for example, force the cisco to live under such undesirable conditions of temperature and dissolved oxygen that it fails to thrive even in the presence of abundant food, while in Clear Lake favorable physical and chemical conditions may make it possible for the cisco to reach the best of condition on a substantially smaller basic abundance of food.

Average longevity and condition appear to be more closely correlated than average longevity and growth, for the four populations follow exactly the same order with respect to the two first-named characteristics. Such a relationship is logical. With particular reference to the populations whose K equations show negative exponents, it appears probable that the progressive loss of condition with increase in length may bring the cisco to a point of emaciation beyond which survival is impossible. Since length is a function of age the imposition of a limit on the length that can be attained places also a limit on age. It has been pointed out previously (p. 246) that in the Trout Lake cisco the few very old individuals taken had not followed the same length-weight relationship that held for the main body of the population.

The relationship between individual condition and individual parasite infestation is not known. The Clear Lake cisco with the lightest parasite infestation of any of the four populations is the population with the best condition.

SEX RATIO

The cisco population of the four lakes follow the same order with respect to growth in weight and the average relative abundance of males. In the section on sex ratio it was pointed out that the less viable males probably suffer greater mortality under adverse conditions that produce slow growth, and hence that the correlation between growth rate and sex ratio may be considered to result from the dependence of these two characteristics on the same environmental factors.

GENERAL REMARKS

The failure of certain of the growth relationships of the cisco to conform to generally accepted principles and theories suggests that, on the basis of our present knowledge, generalizations concerning these relationships are scarcely safe. A satisfactory understanding of the growth relationships of the cisco can be attained only after exhaustive studies into the biology of this form. Further, the great plasticity and adaptability of the cisco makes advisable the study of its biology in the greatest possible diversity of habitats.

An illustration of the dangers of making generalizations concerning the growth and biology of the cisco is offered by the examination of the relationship between

condition (K) and environmental factors. The data of this study indicate that the cisco is in the best condition in the most oligotrophic environment and in the poorest condition in the most eutrophic environment. However, the situation found in the Indian Village Lake (Indiana) shows that such a relationship cannot be considered general for this plastic species. Although the lakes of northeastern Indiana are of the extreme eutrophic type and the Indian Village Lake cisco lives under what are apparently the most undesirable conditions with respect to temperature and oxygen conditions (Scott, 1931), the Indian Village Lake cisco shows excellent growth and is in better condition than any but the Clear Lake population of this study (p. 249).

FISHES ASSOCIATED WITH THE CISCO

There is little resemblance among the fish associations of which the four cisco populations are parts. In table 70 are recorded the numbers of individuals of all species taken in the nets used for the cisco. Fish are considered to have been taken along with the cisco if they were taken in a net of any mesh set at the same time and approximately the same depth as the nets that caught ciscoes.

TABLE 70.—*Numbers of individuals of other species of fish taken in the net catches along with the cisco samples*

Species	Lakes			
	Trout	Muskellunge	Silver	Clear
Cisco	1,197	1,863	524	465
Perch		1,543	1	5
Pike-perch				37
Rock bass		8		1
Sucker		130		
Lake trout	32			
Whitefish	32			
Burbot	1			
Smallmouth black bass		14		

In Trout Lake the fish taken with the cisco were all typical deep-water forms. There is no evidence that the deeper regions of the lake are invaded by individuals of the shallow-water forms. The trout were mostly large individuals that were caught and held by the teeth in small mesh nets.

The situation in Muskellunge Lake is unusual. The close association of the cisco with shallow-water forms is the result of the deficiency in oxygen that drives the ciscoes up from the lower, cooler strata of the lake.

In Silver Lake the cisco is practically isolated, at least during the late summer. The single perch taken at a depth of 14.5 meters may be considered a straggler.

In Clear Lake the pike-perch that were taken regularly along with ciscoes appear to be distributed generally throughout the region occupied by the cisco in this lake. The five perch were taken at depths between 19.5 and 24.5 meters. The rock bass was captured at a depth of 15.5 meters. Since both rock bass and perch are known to be plentiful in the shallow water of this lake their presence in the hypolimnion may be considered more or less as accidental.

In all the lakes the nature of the associations of which the ciscoes are part probably undergoes considerable change according to the time of year.

SELECTIVE ACTION OF GILL NETS

REVIEW OF PREVIOUS INVESTIGATIONS

Since the collections upon which the present investigation is based were made by means of gill nets, it is of importance to have some measure of the selective action of the nets used upon the various populations sampled. Several investigators have presented observations on the selective action of gill nets, and some of these observations have been made with specific reference to the problem of securing samples for the study of age, growth, and length distributions within a population.

Much of the published material on the selective action of gill nets has been included incidentally in growth and life history studies. Other data have been presented in routine fishery reports. Because of the generally scattered nature of these data on gill-net selectivity and because of the importance to fisheries biologists of having a more adequate idea of the reliability of the samples that they take with gill nets, the presentation of the data of this investigation on the question of gill-net selectivity will be preceded by a brief review of the literature [32] on the subject.

The problem presented by the selective action of gill nets in the collection of materials for scientific investigations has been known for several decades. The Report on the Sea and Inland Fisheries of Ireland for 1902 and 1903 [33]; Part II—Scientific Investigations, contained in the report of the scientific adviser the statement that the investigation of herring shoals met a great difficulty in the selective action of the nets used in the commercial fishery. It was stated further, however, that the results of fishing nets of different meshes together (these experiments were made in another connection) indicated "that the selection is much less in practice than it would seem to be in theory. * * *"

Delsman (1914) in his study of the age and growth of the North Sea and Zuider Zee herrings presented data to show that the selective action of the gear used in obtaining samples can exert an important effect on the nature of the results obtained from the study of those samples. He compared samples of drift nets and of seines of different sizes of mesh. From his observations he concluded:

> Fänge an derselben Stelle mit Netzen verschiedener Maschenweite gemacht, werden verschieden sein und die Zusammensetzung des Fanges nach Grösse und Alter wird von der Maschenweite abhangen. Fischt man dagegen mit demselben Netz an verschiedenen Stellen * * * so werden auch die Fänge verschieden sein, und die Verschiedenheiten in ihrer Zusammensetzung werden durch die Zusammensetzung der Heringsschwärme im Meer bedingt werden.

Bjerkan (1917) disagreed with Delsman as to the great importance of selectivity of gear in determining the nature of herring samples from drift nets. From the comparison of trawl and drift-net catches he concluded that selection through the failure of drift nets to take smaller fish "cannot be very material." He pointed out further that "drift caught samples may point to the presence of rich year classes of very different ages." As to the effect of mesh size on the composition of drift net catches he stated further that "the size of mesh in the nets used affects the composition of the catches, but not to such an extent as might have been expected."

Further data on the action of drift nets were presented by Borley and Russell (1922). In connection with the study of the herring trawl fishery they measured the

[32] No claims are made as to the completeness of this review; it should, however, bring together a sufficient mass of the miscellaneous data on the subject to furnish a good general conception of the nature of the problem of gill-net selectivity.

[33] Published in 1905.

catches of herring in drift nets of three sizes of mesh.[34] They summarized their results as follows:

> According to these samples the finer-meshed nets caught the larger fish. The conclusion to be drawn is that the size distribution of the drift-net catch is probably not determined to any great extent by the selective action of the net.

Buchanan-Wollaston (1927) included with his discussion of the selective action of a trawl net certain observations as to the method of selection in drift nets. He called attention to the fact that drift nets do not capture all fish in the same manner. He pointed out that certain large individuals are retained by the maxillary barbs; some small individuals are held only because of the gill covers; while the majority are held between the gill covers and the dorsal fin. The different types of net action may lead to discontinuity in the length distribution of the catch.

Hodgson (1927) presented the analysis of data from the catch of herrings in three drift nets of different-size mesh.[35] Although the number of specimens was not great his results showed clearly that selective net action can lead to erroneous conclusions concerning the size and age composition of a population and also lead to inaccurate determinations of average lengths for the various age groups. Later the same author (Hodgson, 1933) presented the results of further experiments on the selective action of drift nets. These experiments were conducted with particular reference to the effect on the herring stock of the size of mesh in the drift nets employed in the commercial fishery. On the basis of two separate experiments Hodgson concluded:

> that there is a very definite and subtle gradation in the length of the herrings caught by nets of even slightly different meshes, and it is also plain that the whole character of a fishery can be changed by the use of different nets.

These investigations were all concerned with a single marine fishery—the drift-net fishery for herring. The opinions of the different investigators, however, show considerable disagreement.

Of greater interest with respect to the present study are the data concerning the selective action of gill nets as they are fished in fresh water. In the following paragraphs certain of the available data with respect to the selective action of gill nets are mentioned briefly. The various investigations are treated in general in the chronological order of their appearance without any attempt at grouping according to variety or kind of fish concerned.

Järvi (1920) compared the catches of the kleine Maräne (*Coregonus albula*) taken by seine with those taken by a series of seven nets having meshes ranging from 10 to 15 millimeters (bar measurement). The length compositions of the samples from the two sources agreed well.

Järnefelt (1921) noticed that his growth curves for several species of fish showed irregularities that could be traced to the selective action of the nets that he used in obtaining his samples. Concerning these irregularities Järnefelt stated: "* * * dass es ebenso viel Senkungen der Kurve gibt wie Netze verschiedener Maschenweite benutzt werden." However, Segerstråle (1933) held that the irregularities observed by Järnefelt and others in growth curves resulted to a large extent from inaccurate methods of calculating growth from scale measurements, and that

[34] The sizes were 30, 31, and 33 meshes to the yard (bar measurement).

[35] The nets used had 35, 38, and 48 meshes to the yard (bar measurement).

irregularities in growth curves resulting from the selective action of nets are on the whole small.

Creaser (1926) in connection with his study of the growth of the sunfish (*Eupomotis gibbosus*) observed that gill nets are "particularly selective in their collecting" and advocated the use of a wide range of mesh size in gathering material for biological investigation, but included no data on the selective action of gill nets.

Koelz (1926) pointed out that in the Lake Ontario chub (*Leucichthys* spp.) fishery an increase of a quarter inch in the stretched measure of the mesh (from 2½ to 2¾ inches) reduced the number of fish taken by more than half.

Pritchard (1928) presented data on the selective action of six different sizes of mesh as that action affected the individual weight of Lake Ontario chubs (*Leucichthys* spp.). (The mesh size of his gill nets ranged from 1½ to 3 inches, stretched measure.) On the basis of his observations he stated, "The difference of one-quarter of an inch in the size of mesh may mean to the fishermen either a profitable or a 'starvation' industry." In a later paper (Pritchard, 1931) he presented the numbers of chubs of all species taken in nets of 12 different sizes of mesh (1¼ to 5 inches). Some data were included on the average lengths of the fish taken in different mesh nets. The data of Pritchard's 1931 paper agree with his earlier findings in indicating that a very small increase in the size of mesh may produce a great decrease in the number of fish taken.

Hart (1928) published detailed data on the length distribution of pike-perch and saugers of Lake Nipigon and Lake Abitibi taken in 6 different sizes of mesh ranging from 1½ to 4½ inches, stretched measure. Although Hart confined his discussion to the question of the proper legal mesh size in the commercial fishery, his data on the length distribution of the catches in different mesh size show clearly that a single size of mesh can take these spiny-rayed fish over a considerable length range. In a later paper (Hart, 1931) the same author pointed out that observed differences in the growth rate of the whitefish (*Coregonus clupeaformis*) in different parts of Lake Ontario could be explained in part by the tendency for the gill nets used in collecting samples from some localities to take only the larger fish of the younger age groups while pound-net samples were largely free from such selection. A more detailed consideration of the selective action of gill nets on whitefish appeared in Hart's (1932) study of the population statistics of Shakespeare Island Lake. (His experimental gear included 11 sizes of mesh, 1½ to 5 inches.) Hart found a correlation of 0.84 ± 0.01 between size of mesh and size of fish in Shakespeare Island Lake, while in Nipigon the correlation between the same variables was 0.51 ± 0.02. He pointed out further that "large fish may be taken in small meshed nets although small fish are practically never taken in nets of coarse mesh."

Lechler (1929), referring to the selectivity of gill nets used in the fishery for the Reinanke (*Coregonus fera*) held that the selective action of the net is quite sharp. He stated: "Die Zusammensetzung der Fänge nach den Jahresklassen und damit die Grösse der Fische ist eine Funktion des Umfangs und direkt von der Netzmaschenweite abhängig." Further experiences caused him to modify this view slightly, for in a later publication (Lechler, 1930) he observed, "Die Fängigkeit der Netze ändert sich je nach der Beschaffenheit eines Bestandes."

Wright (1929) eliminated the younger age groups from his growth data on the rock bass (*Ambloplites rupestris*) as the selective action of the nets caused these early groups to have too high average values for length.

Haakh (1929) in his study of the age and growth of several species of fish in the Bodensee found that net selection led to inaccurate determinations of the average length of some age groups.

Wagler (1927, 1930a, 1930b, 1932, 1934) in his investigations of the coregonids of Bodensee and other north alpine lakes mentioned repeatedly the distorting effect of the selective action of the gill nets used in taking his samples for the study of age and growth. The effects of the selection were noticeable particularly in the high average lengths determined for the younger, smaller age groups and in the great variation in the relative abundance of the different year classes as determined from the various gill nets used. Wagler held that a close relationship exists between net selection and maximum girth of the individual fish (cf. Lechler, 1929). Elster (1934) in his study of the Blaufelchen (*Coregonus wartmanni*) expressed opinions similar to those of Wagler.

Van Oosten (1929b) in his discussion of the problems of the commercial fisheries of the Great Lakes pointed out the complex nature of the question of selectivity in the gill nets of the commercial fishery and included a small amount of data on the number and size of small trout (*Cristovomer namaycush*) and several species of chubs (*Leucichthys* spp.) taken in 2½- and 2¾-inch mesh nets.

In a later paper Van Oosten (1933) published a preliminary report of experimental chub net investigations conducted by the United States Bureau of Fisheries in Lake Michigan waters, 1930–32. The data presented included average catch per net, expressed in pounds and number of fish, for the lake trout and the chub in five different sizes of mesh. The meshes used were all of commercial fishery size, and varied from 2⅜ to 3 inches, stretched measure. The variation in the catch of chubs in nets of different size mesh was striking. In lower Lake Michigan nets of 2⅜-inch mesh caught more than twice as many chubs as did nets of 2½-inch mesh, and eight times as many as nets of 3-inch mesh.

In view of the marked disagreement that the preceding review shows to exist among some authors as to the nature and scope of the selective action of gill nets, it appears probable that each species and each locality offers its own special problem of gear selection.

The selective action of gear as size of mesh affects the amount of total catch (with respect both to numbers and weight) is particularly noteworthy. The existence of an intensive commercial fishery employing a more or less standard size mesh can, however, exaggerate the differences of catch between two different sizes of mesh. Ordinarily all the commercial gear of the same type used in a region for the capture of a species or group of species of similar size will meet approximately the same specifications particularly with reference to the size of mesh. Consequently there tends to be a great reduction in numbers in that portion of the population most liable to capture by the standard commercial gear. The withdrawal of large quantities of commercial size fish produces an abnormal condition in size distribution of the population as a whole. The introduction of nets of other, noncommercial sizes of mesh may then lead to comparisons that do not describe accurately the fishing action of the nets in question. Data based on catches from a population unaffected by commercial fishing might be expected to show somewhat less sharp selectivity than those from a population subjected to heavy fishing. It will be seen that the data of the present investigation tend to support this view.

SELECTIVE ACTION OF GILL NETS USED IN COLLECTING SAMPLES OF CISCOES FROM TROUT, MUSKELLUNGE, SILVER, AND CLEAR LAKES

In this investigation, although other phases of selectivity will be considered briefly, the study of the selective action of gill nets will be concerned primarily with the effect of selection upon the determination of growth in the various populations. The analysis will involve particularly the comparison of average lengths as determined for a single age group from samples taken in nets of different sizes of mesh. The analyses will show the basis for the elimination of certain selected groups in the computation of general growth curves (see footnote, p. 226) and will furnish a better idea of the validity of the use of gill-net samples in the study of growth. Such analysis is of especial importance here since different ranges of mesh sizes were employed in taking the different years' collections.

Attention should be called to certain criteria that are of general value in determining the reliability of gill-net samples for growth study. It may be pointed out that in general a sparse representation in a sample of a young age group whose average length is near the lower limit of effectiveness of the nets used, is a source of suspicion as to the reliability of the sample of that particular group. If this same sparsely represented group gives calculated growths that are in serious disagreement with those of the older age groups it should be eliminated from the data used for the study of growth in the population as a whole. A further check on the reliability of the material that represents a particular age group lies in the comparison of the average lengths for the group as determined from samples in different sizes of mesh and as determined from the different combinations of such samples. The examination of the length distributions of the catch of nets of different size mesh may also give an idea as to the adequacy of the sampling with respect to particular age groups.

As was mentioned in the introduction the 1928 data do not include records of gear for individual fish. For this reason the 1928 data cannot be used in the study of gill-net selectivity.

For purposes of convenience the gear used in 1928, 1930, and the early part of the 1931 season will be designated throughout this section as "old",[36] and the gear used during the latter part of the 1931 season and through the 1932 season will be known as "new." Descriptions of the two groups of nets were included in the section on methods.

Tables 71, 72, 74, 75, 76, and 77 show the effect of size of mesh on the determination of average size of the different age groups in the populations of Trout, Muskellunge, Silver, and Clear Lakes. Because of the generally small number of specimens upon which the average of lengths of the various age groups depend, attention must be given to the general trend of the differences that result from differences in gear rather than to the actual amount of the difference in any specific case. Since each population represents a distinct and separate problem in the study of selectivity, the data for each lake will be discussed separately.

TROUT LAKE

With the exception of a single specimen all the ciscoes collected in Trout Lake in 1930 were obtained from 1½-inch mesh nets, while the 1928 samples were probably taken in nets of 1¼-inch (trammel), 1⅜-inch, 1½-inch, and perhaps a few in 1¾- and

[36] Although the "old" gear as fished in 1930 and in the early part of 1931 included 5 different sizes of mesh, only the 1½-inch and 2-inch nets caught ciscoes. All collections from Clear Lake were made with the new gear. The date of change in gear was July 22, 1931.

2-inch mesh nets. In 1928 the average length of 182 ciscoes was 138 millimeters, and in 1930 the average length of 490 individuals was 150 millimeters. The smaller average size of the fish of the 1928 collection may be accounted for by the use of mesh sizes smaller than 1½ inches and by the relatively greater abundance of young fish in that year's samples. The relative abundance of the different age groups as well as the average lengths of these age groups in the samples of the 2 years may be found in table 3.

TABLE 71.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Trout Lake cisco, 1931 collection*

[The first 2 rows show the average lengths of 5 age groups as based on samples taken July 22 in 1¼- and 1½-inch mesh gill nets. The third row shows the average of the 2. The fourth row shows the average lengths of the various age groups based on all fish taken in 1½-inch mesh gill nets in 1931. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
1¼ inches	124 (1)	134 (22)	139 (14)	147 (18)	155 (2)	140 (61)
1½ inches		137 (16)	143 (20)	149 (15)	158 (4)	145 (58)
Averages combined	124 (1)	135 (38)	141 (34)	148 (33)	157 (6)	
Average of all 1931 1½-inch samples	132 (1)	137 (39)	142 (159)	148 (246)	156 (77)	147 (522)

A single set of the "new" gear lifted July 22, 1931, provides the only data for Trout Lake for the comparison of growth as based on samples taken in nets with different size mesh. These data appear in table 71. In the first row appear the average lengths for the various age groups as based on fish taken in the 1¼-inch mesh net. The second row gives the same information for the sample from the 1½-inch mesh net. It will be seen that while the average length of all ciscoes taken in the 1½-inch mesh net was 5 millimeters greater than that of the ciscoes from the 1¼-inch mesh net, the differences between samples of the same age group varied from 2 to 4 millimeters and averaged only about 3 millimeters. The third row shows the average lengths of the different age groups as based on the combination of the July 22 samples taken in the 1¼- and 1½-inch mesh nets while the bottom row shows for comparison the average lengths of the various age groups as based on all the ciscoes taken in Trout Lake in the 1931 season in 1½-inch mesh nets. It may be seen that with the exception of the I group the averages based on the 1½-inch mesh net samples for the entire season differ but little from those based on the combined catches from 1¼- and 1½-inch mesh nets. While the necessity for the elimination of the I group from the Trout Lake growth data is at once apparent, the problem presented by the II group requires further consideration. In spite of the rather close agreement between the average length of the II-group fish as determined from samples from nets of 1¼- and 1½-inch mesh, the sparse representation of this age group in both the 1930 and 1931 collections (table 3) throws suspicion on the reliability of the samples. This suspicion is supported by the high calculated lengths at the end of the first and second years of life as based on both the 1930 and 1931 II groups. Consequently both of the groups were eliminated from the Trout Lake growth data. The II group of 1928, for which year no individual net records are available, was, however, retained, first because of its abundant representation in that year's collection, second because of the good agreement between its calculated growth and the corresponding calculated growth both of older age groups of the same year's collection and of samples of the same (1926) year class taken in the later years, 1930 and 1931, and finally because of the

knowledge that smaller mesh sizes were used in 1928 than in 1930 and the early part of 1931.

The relationship of net size to fish size (new nets, 1931) in the Trout Lake cisco is shown in figure 11.

MUSKELLUNGE LAKE

The old gear was used in the collection of ciscoes from Muskellunge Lake in 1928, 1930, and 1931. In the last 2 years all the fish were taken in the 1½-inch mesh net. In 1928 the gear used included the following sizes of mesh: 1⅜-, 1½-, 1¾-, and 2-inch. The 2-inch mesh was probably not effective. Data on the average lengths of the various age groups in these years' collections will be found in table 4. In 1932

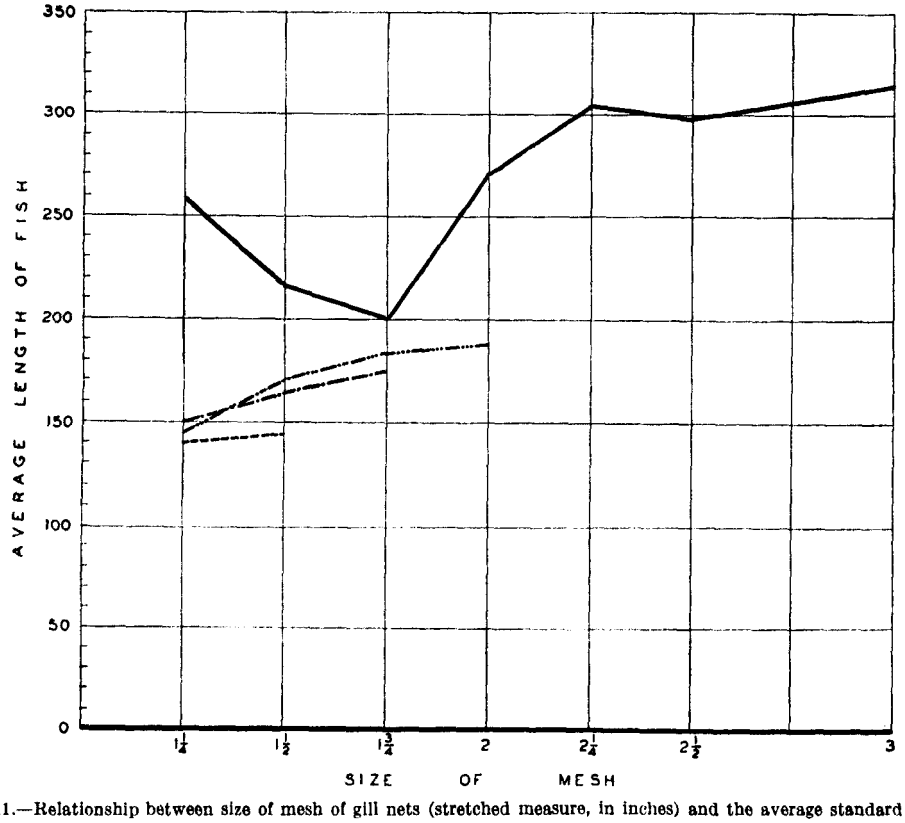

FIGURE 11.—Relationship between size of mesh of gill nets (stretched measure, in inches) and the average standard length in millimeters of the ciscoes taken. Trout Lake, - - -; Muskellunge Lake, — . —; Silver Lake, — . . . —; Clear Lake, ———.

all the specimens were taken in three (1¼-, 1½-, and 1¾-inch) of the seven sizes of mesh used in the new gear.

The 1932 material provides the only data for the study of the effect of mesh size on the average size of fish taken and for the comparison of the average lengths of the various age groups as based on samples from nets of different sizes of mesh. Scale examinations were made for 201 specimens of the 1932 collection, but ages could be estimated for only 189 of this number. The results of these determinations appear in table 72.[37] The table shows considerable differences between the nets of

[37] These data represent all the fish taken in the 1¾-inch mesh net in 1932 and lifts of the 1¼- and 1½-inch mesh nets on July 28, 29, and 30, and Aug. 3, 1932. The numerical representations of the 1¼- and 1½-inch mesh nets are comparable, while that for the 1¾-inch net is by comparison too high. This high representation of the 1¾-inch net samples has probably caused the grand average length for the IV group to be too high, but it had little effect on the grand average length for the III group.

different mesh size both in the average size of the fish and in the relative abundance of the different age groups.[38] Selectivity according to length appears to be greater in the Muskellunge Lake cisco, where the 1½-inch mesh net caught fish 14 millimeters longer than the 1¼-inch mesh sample, than in the Trout Lake cisco (table 71) where the fish from the 1½-inch mesh net were only 5 millimeters longer than those from the 1¼-inch mesh net. It will be noticed further that nets of the same size mesh caught larger fish in Muskellunge Lake than in Trout Lake (fig. 11).

TABLE 72.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Muskellunge Lake cisco, 1932 collection*

[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	I	II	III	IV	V	
1¼ inches	137 (12)	152 (7)	159 (11)	168 (3)	----------	150 (33)
1½ inches	150 (3)	158 (12)	162 (59)	168 (59)	172 (1)	164 (150)
1¾ inches	----------	----------	166 (5)	177 (12)	----------	174 (18)
Average	139 (15)	156 (24)	162 (75)	170 (74)	172 (1)	----------

The question of the reliability of the 1930 and 1931 collections is largely a question of the reliability of samples from 1½-inch mesh nets, for the collections of these 2 years were taken in nets of this size mesh. The 1928 samples may be considered as reliable as the 1932 samples. The data of table 72 show that in spite of the selection that does occur the 1½-inch mesh net samples, with the exception of the I group, give averages for the lengths of the different age groups that differ insignificantly from the corresponding averages based on the catch of nets of three different sizes of mesh. It is, therefore, a safe conclusion that with the elimination of the I groups the length data obtained from 1½-inch nets in the preceding seasons are accurate within the range of a very few millimeters.

TABLE 73.—*Length frequencies of Muskellunge Lake ciscoes taken in 1932 in nets of different mesh size*

[Sexes combined. The frequencies represent 18 lifts for the 1¼-inch mesh net, 38 for the 1½-inch mesh net, and 37 for the 1¾-inch mesh net]

Length	1¼-inch net	1½-inch net	1¾-inch net	Total	Length	1¼-inch net	1½-inch net	1¾-inch net	Total
185 to 189	----------	2	1	3	145 to 149	18	48	----------	66
180 to 184	----------	6	3	9	140 to 144	24	20	----------	44
175 to 179	----------	27	4	31	135 to 139	40	4	----------	44
170 to 174	2	102	6	110	130 to 134	7	----------	----------	7
165 to 169	5	157	2	164					
160 to 164	13	186	1	200	Total	154	813	18	985
155 to 159	24	170	1	195					
150 to 154	21	91	----------	112	Average length	146	160	174	----------

The above conclusion is supported by the examination of the length frequencies of the total catch of Muskellunge Lake ciscoes in each mesh size in the entire 1932 season (table 73). In the length frequencies of the 1¼-inch net samples there occurs at the 145 to 149 millimeter interval a depression that marks the separation of the I

[38] It was pointed out previously (p. 219), that because of slow growth in the later years and the common occurrence of accessory annuli the separation of the later age groups above the II group in the 1932 Muskellunge Lake samples was difficult. As a consequence, the average lengths listed for the III-group and the IV-group samples may be slightly in error. Any error that exists should not, however, impair greatly the general usefulness of the data for the purpose of studying the effect of net selection on the determination of the average lengths of age groups.

group from fish of greater age. Since the bulk of the II-group fish must lie above this depression it can be seen that their length distribution lies well within the range of efficiency of the 1½-inch mesh net. The fish taken in the 1¾-inch net are so few in number that they would have little effect in the determination of growth.

SILVER LAKE

The "old" gear was used in the collection of all the 1928 and 1930 samples of ciscoes from Silver Lake and for the first sample taken in 1931 (July 17). A gang of the "new" nets was used in taking the only other sample of this year in this lake (Aug. 22, 1931). In the sets of the old gear in 1930 and 1931 ciscoes were taken in 1½- and 2-inch mesh nets only; in 1928 they were probably taken in the 1⅜- and 1¾-inch meshes also. In the new gear they occurred in the 1¼-, 1½-, 1¾-, and 2-inch mesh nets.

Table 74 shows the average length of fish taken in different mesh sizes and the effect of net selectivity on the determination of the average length of the various age groups of the 1930 collection (5 lifts of 1½-inch nets, 3 of 2-inch nets) while table 75 gives similar information for the 2 lifts made in 1931.

TABLE 74.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1930 collection*

[Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group					Average length
	II	III	IV	V	VI	
1½	173 (7)	178 (16)	182 (34)	190 (4)	198 (1)	186 (66)
2 inches	----------	186 (9)	188 (24)	193 (20)	196 (2)	190 (64)
Average	173 (7)	181 (25)	183 (58)	193 (25)	197 (3)	----------

TABLE 75.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Silver Lake cisco, 1931 collection*

[The data in the upper part of the table are based on a lift of the "old" nets, July 17. The data in the lower part are based on a lift of the "new" gear, Aug. 22. The grand average for the year includes a number of preserved fish for which no net records were available. Sexes combined. Number of specimens in parentheses]

Size of mesh	Age group							Average length
	I	II	III	IV	V	VI	VII	
1½ inches	143 (6)	168 (5)	174 (3)	173 (3)	----------	----------	----------	163 (18)
2 inches	----------	----------	189 (3)	187 (5)	192 (14)	198 (5)	----------	191 (29)
Average	143 (6)	168 (5)	182 (6)	182 (8)	192 (14)	198 (5)	----------	----------
1¼ inches	141 (51)	172 (3)	175 (3)	172 (1)	195 (2)	----------	----------	146 (60)
1½ inches	146 (6)	170 (6)	176 (4)	173 (6)	187 (7)	----------	----------	171 (30)
1¾ inches	----------	174 (2)	178 (22)	182 (25)	186 (23)	193 (4)	----------	183 (83)
2 inches	----------	----------	174 (1)	184 (12)	190 (18)	192 (2)	201 (1)	188 (37)
Average	142 (57)	171 (11)	177 (30)	181 (44)	188 (50)	193 (6)	201 (1)	----------
Grand average for 1931	142 (66)	171 (19)	177 (61)	183 (102)	188 (108)	194 (21)	201 (1)	----------

The data in tables 74 and 75 show rather large differences in the average size of fish taken in nets of different sizes of mesh. Although the fish taken in the 2-inch-mesh net of the old gear in 1930 were only 4 millimeters longer than those taken in the 1½-inch net, the 1931 samples taken in the same gear showed a difference of 28 millimeters, while the 2-inch-mesh net fish of the 1931 collection in the new gear had an average length 17 millimeters above the average for those from the 1½-inch net. A comparison with the Trout Lake and Muskellunge Lake data (tables 71 and 72, fig. 11) shows that the selection of the nets is sharper in the Silver Lake cisco than

in either of the former populations. The difference in average length between fish taken in 1¼- and 1½-inch-mesh nets was for example 5 millimeters in Trout Lake, 14 millimeters in Muskellunge Lake, and 25 millimeters in Silver Lake. Further, the difference in average length between fish taken in 1½- and 1¾-inch-mesh nets in Muskellunge Lake was 10 millimeters while in the Silver Lake cisco this difference was 12 millimeters.

Tables 74 and 75 show also that the average length for a particular age group varies considerably in samples taken by nets of different size mesh. Although certain irregularities occur (as might be expected from the small size of the samples) there is a general tendency for the samples from larger mesh nets to show distinctly higher average lengths for a given age group than do the samples from nets of smaller mesh. Further examination shows, however, that this tendency does not in general affect the validity of the averages of age groups based on the combination of the samples of several nets.

In the analysis of the data of tables 74 and 75 to establish the validity of the growth data for the Silver Lake cisco, it should be pointed out first that all ages above the II group in the 1931 sample taken in the new nets must be considered to have adequate representation throughout their entire length range. This is apparent from the fact that these older age groups are relatively scarce in the 1¼-inch-net catch, while at the other extreme a 2¼-inch-mesh net that was fished in the string failed to take any ciscoes at all. Since these average lengths of the older age groups from the new net sample can be considered reliable they can be used as a basis for the estimation of the reliability of the corresponding average lengths as determined from the old net samples. The fact that the average lengths for corresponding age groups of the 1930 and 1931 old net collections resemble each other on the whole more than either of them resembles the average lengths based on the 1931 new net collection suggests that the addition of the 1¼- and 1¾-inch nets may have increased the reliability of the Silver Lake samples. The differences between the corresponding average lengths of the older age groups of the old and new net samples are not, however, of sufficient magnitude to invalidate the use of the earlier materials collected by the old gear.

The II-group samples present a more difficult problem. The general scarcity of II-group individuals in the collections of the old gear would indicate that its length range may lie just below the range of efficiency of the 1½-inch net, even though this size mesh was very efficient in Trout and Muskellunge Lakes in the taking of fish whose lengths were well below the observed average length (about 170 millimeters) for the Silver Lake II group. The 1931 sample with the new gear shows, however, that it is very unlikely that the Silver Lake II group has suffered serious selection by gear, as that selection affects average length, in any of the samples. The scarcity of the II-group fish in this sample taken in the new gear must be considered to show that this group in 1931 actually was less abundant than the neighboring age groups, for there is no reason to hold that the same nets that took 57 I-group and 30 III-group fish should fail to take II-group individuals in equal numbers provided they were equally abundant in the population. These facts together with the good agreement between the average lengths of the II-group samples as based on old and new gear samples make the retention of the II-group fish in the growth data advisable.

Since there is no means of demonstrating the reliability of any of the I-group samples they must be considered, at the best, questionable. They were accordingly eliminated from the growth data.

CLEAR LAKE

All Clear Lake specimens were collected with the "new" nets. Tables 76 and 77 show the average lengths of the different age groups according to the gear by which they were captured. Because of differences in growth rate the sexes are treated separately. Table 78 and figure 11 present the length frequencies and the average lengtn of the catch according to mesh size for the total 1931 and 1932 catch of ciscoes from Clear Lake. The Clear Lake data differ from those of the three populations just considered in two important respects. First, the relationship that increase in size of mesh is correlated with an increase in the average size of the fish taken does not hold for Clear Lake as it did in the other three lakes; while the differences in the average size of the fish taken in different meshes are great, the larger mesh does not always take the larger fish (table 78, fig. 11). Second, in Clear Lake, fish were taken in all seven of the sizes of mesh used, and were most abundant in nets that were totally ineffective in all the other three populations, that is, nets whose mesh size was greater than 2 inches. The circumstance that the largest mesh (3 inches) took the greatest number of fish indicates that in making these collections it would have been desirable to use additional nets of mesh size greater than 3 inches. There is, however, reason to believe that the selection resulting from failure to fish with larger mesh nets affects chiefly the relative abundance of the larger fish in the sample. The increase in size of mesh from 2¼ to 3 inches had little effect on the average length of the individuals captured. If this trend were to continue, nets of a mesh size greater than 3 inches would be expected to add to the number of large fish without producing any important upward extension of the size range of the sample.

TABLE 76.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931–32 collections*

[(Males) Number of specimens in parentheses]

Size of mesh	Age group									Average length
	I	II	III	IV	V	VI	VII	VIII	IX	
1½ inches	173 (12)			311 (1)			336 (3)			212 (16)
1¾ inches	176 (24)	236 (3)	254 (1)							185 (28)
2 inches	190 (2)	245 (3)	291 (4)		307 (3)	310 (1)		341 (1)		275 (14)
2¼ inches		250 (12)	286 (5)	314 (4)	328 (4)	326 (2)	333 (5)	347 (3)		296 (35)
2½ inches		256 (25)	289 (12)	319 (6)		328 (2)	329 (1)	334 (2)	355 (1)	281 (49)
3 inches		267 (5)	291 (18)	324 (4)	338 (2)	324 (3)	334 (6)	344 (4)		307 (42)
Average	176 (38)	254 (48)	289 (40)	318 (15)	323 (9)	324 (8)	334 (15)	343 (10)	355 (1)	

TABLE 77.—*Effect of size of mesh of gill nets on the determination of the average lengths of the age groups of the Clear Lake cisco, 1931–32 collections*

[(Females) Number of specimens in parentheses]

Size of mesh	Age group											Average length
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
1¼ inches	155 (1)							336 (1)				246 (2)
1½ inches	179 (5)							350 (1)	351 (1)	364 (1)		245 (8)
1¾ inches	180 (12)	279 (1)					356 (3)	357 (1)				227 (17)
2 inches	186 (7)	263 (7)	301 (1)	325 (1)	338 (1)		336 (1)	360 (3)	376 (1)			268 (22)
2¼ inches	201 (1)	259 (4)	300 (9)	323 (3)		371 (1)	351 (9)	360 (2)				316 (29)
2½ inches		265 (14)	308 (14)	332 (5)	335 (3)	342 (4)	357 (6)	351 (7)			378 (1)	315 (54)
3 inches		260 (14)	310 (15)	332 (8)	347 (4)	334 (4)	350 (11)	358 (7)	352 (1)	379 (1)		319 (65)
Average	181 (26)	263 (40)	307 (39)	330 (17)	341 (8)	342 (9)	352 (30)	355 (22)	360 (3)	372 (2)	378 (1)	

TABLE 78.—*Length frequencies of Clear Lake ciscoes taken in nets of different mesh size*

[The 1931 and 1932 collections and the sexes are combined]

Length	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	Total
150 to 159	1							1
160 to 169		4	6					10
170 to 179		10	17	3				30
180 to 189		3	12	3				18
190 to 199				2				2
200 to 209			1	1	1			3
210 to 219			1					1
220 to 229					1			1
230 to 239				2	3			5
240 to 249			2		1	8		11
250 to 259			1	4	7	12	8	32
260 to 269				2	5	11	8	26
270 to 279				3	1	9	4	17
280 to 289	1			2	2	4	7	16
290 to 299					4	8	10	22
300 to 309				2	8	6	6	22
310 to 319		1		3	4	12	13	33
320 to 329				2	7	6	11	26
330 to 339	1	2		2	6	7	12	30
340 to 349		1	1	1	4	10	12	29
350 to 359		2	2	2	3	6	10	25
360 to 369		1	1		5	1	5	13
370 to 379				1	2	2	1	6
380 to 389						1	1	2
Total	3	24	44	35	64	103	108	382
Average length	259	217	201	271	306	299	315	

The Clear Lake samples with the exception of the I groups do not show as close dependence between the determination of the average length of individual age groups and the size of mesh by which the sample was taken (tables 76 and 77) as was observed in the other three populations. The proof of the reliability of the Clear Lake growth data must be based, therefore, on a demonstration that the population was adequately sampled throughout its length range rather than on a comparison of the average lengths of age groups as determined from samples from nets of different mesh size. It was pointed out in the preceding paragraph that the sampling of the larger fish was probably adequate. The scarcity of fish in the 1¼-inch net can be taken to show that the younger age groups were also adequately sampled. Accordingly, no age groups were eliminated from the Clear Lake samples.

RELATIVE ABUNDANCE OF AGE GROUPS IN GILL NET SAMPLES

The examination of tables 71, 72, 74, 75, 76, and 77 shows that on the whole the selectivity of nets is much more sharp in its effect on the number of fish in a given age group than in its effect on the determination of the average length of that age group. The following examples will illustrate this point. In Muskellunge Lake (table 72) the average lengths of the III-group fish in the 1¼- and 1½-inch-mesh nets were 159 millimeters and 162 millimeters, respectively; however, the 1¼-inch net took only 11 fish of this age group while the 1½-inch net took 59. In Silver Lake (table 75, data on lift of new nets) the III-group sample of the 1½-inch mesh had an average length only 2 millimeters less than the III-group sample from the 1¾-inch net, but was nevertheless represented by only 4 fish as compared with the 22 fish from the 1¾-inch-mesh net. In the same day's collection the V-group samples from the same two sizes of mesh had practically identical average lengths, but were more than three times as numerous in the 1¾-inch-mesh net as in the 1½-inch net. In Clear Lake (tables 76 and 77) the fish of the older age groups were more abundant in the samples of the 2½- and 3-inch-mesh nets, but the average lengths of these older age groups as determined from 2¼- and

3-inch-net samples failed to be consistently higher than the average lengths determined for the same age groups from samples that were taken in smaller meshes.

From the above examples it may be concluded that selection by numbers is much sharper than selection by length. Apparently nets of different mesh size, which in their operation upon a population take samples that disagree only slightly as to average length, may take their samples with unequal degreees of facility, with the result that while their catches agree closely in average length they may differ markedly as to the actual number of fish taken. Table 78 (catch of 2¼-, 2½-, and 3-inch nets) shows such a situation. If small differences in the sizes of mesh are accompanied by large differences in the number of fish captured from a certain size range, then small differences in the average sizes of different groups of fish may be expected to produce large differences in their numerical abundance in the catch of a particular size mesh.

From the above conclusions it can be seen that a series of nets that may take quite reliable samples of particular age groups, as average length is concerned, may at the same time fail to capture the members of these age groups in numbers corresponding to their actual relative abundance in the population of which they are part. Consequently gill-net samples must be employed with extreme caution in the study of the relative abundance of age groups and year classes.

GENERAL CONCLUSIONS

If the collections from the four lakes are considered as a whole it may be stated that the action of a gill net of specified mesh is predictable only with reference to the specific nature of the population to be sampled. The action of a net of specified mesh depends first upon the range of length and abundance of the fish within the population and second upon those morphological characteristics that determine in what manner the fish is held captive. A demonstration of the reliability of a sample obtained by use of gill nets from one population does not indicate that the same gear will obtain an equally reliable sample from a second, different population.

On the question of the use of gill-net samples for growth studies it was demonstrated that the analysis of growth data with respect to size of mesh of the gear in which samples are taken aids in the detection of age groups whose appearance in the sample is by reason of selection not representative. These age groups should be eliminated completely from the data. Such selected age groups were detected in three of the four populations considered here. It was demonstrated further that if these selected groups are eliminated the remaining growth data can be considered accurate and trustworthy within very narrow limits. No such high degree of reliability can be claimed for gill-net samples in the study of the relative abundance of the different age groups.

SUMMARY

1. This study of the growth of the cisco was based on the determination of age of 3,882 specimens and the calculation of growth from scale measurements of 3,694 specimens. The data for Trout, Muskellunge, Silver, and Clear Lakes are presented in the general paper while the smaller samples from Allequash and Tomahawk Lakes are treated separately in an appendix.

2. It was assumed that Van Oosten's (1929) demonstration of the validity of the scale method in *Leucichthys artedi* can be considered to apply to the four cisco popu-

lations of the present investigation. The consistent results obtained appear to justify the assumption.

3. The calculation of growth from scale measurements was based on the assumption that body length and scale diameter show a constant ratio at all lengths beyond that at which the first annulus is laid down. In the Silver Lake cisco alone were there any discrepancies between growth as calculated from fish of different age and as determined empirically that might throw doubt on the validity of the assumption.

4. It was demonstrated that Lee's phenomenon in the Silver Lake cisco does not depend on changing body-scale relationships with increase in length and age, but rather that the growth discrepancies are reflected in the actual scale measurements upon which the calculated growths were based.

5. Among the suggestions for the explanation of Lee's phenomenon in the Silver Lake cisco were: (1) Selection by gear, (2) selection due to dissimilar distribution within the lake of the various elements of the population, and (3) selection due to differential mortality correlated with individual growth rate (greater mortality among individuals with more rapid growth).

6. The four populations (Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake ciscoes) show wide differences in the amount and rate of growth both in length and weight. Their order with respect to growth rate in length, from minimum to maximum, is: Trout Lake, Silver Lake, Muskellunge Lake, Clear Lake; the order with respect to growth in weight is: Trout Lake, Muskellunge Lake, Silver Lake, Clear Lake.

7. On the basis of data on the growth of the cisco in this and other publications a "cisco-type" of growth was described.

8. On the whole the high degree of overlap of the length distributions of consecutive age groups of the cisco makes length alone a poor index of age.

9. Because of individual variation in growth rate the largest fish within a population is frequently not the oldest.

10. Condition was described in terms of the quantity K in the equation, $W=K\times10^{-5}L^3$ (W=weight in grams; L=length in millimeters). It was pointed out that coefficients of condition calculated from the cube relationship describe relative heaviness independently of the general length-weight relationship, and are more satisfactory measures of condition than the quantity C in the equation $W=CL^n$ where the value of n is determined empirically.

11. The four cisco populations show wide differences with respect both to average condition and the manner of change of condition with change in length. The Muskellunge Lake cisco and the Trout Lake cisco show a loss of condition with increase in length (the rate of loss of condition is the more rapid in the former population). The Silver Lake cisco and the Clear Lake cisco, on the other hand, show improvement of condition with increase in length (the rate of improvement in condition is the greater in the Clear Lake cisco). The order of the four lakes with respect to the average condition of the fish in the samples, from minimum to maximum, is: Muskellunge Lake, Trout Lake, Silver Lake, Clear Lake.

12. In all four populations the relationship between length and weight may be described over certain length intervals by equations of the type, $W=CL^n$, where W=weight, L=length, and C=a constant. In some of the populations, at least, these equations cannot be extended to lengths outside the range of the empirical data.

13. The approximate date at which the season's growth of the cisco is completed in each of the lakes is: Trout Lake, end of July; Muskellunge Lake, late August; Silver Lake, early September; Clear Lake, late September or early October. Growth probably begins in all four populations shortly after the disappearance of the ice at about the 1st of May. The data show that the length of the cisco's growing season depends on the local conditions within each lake and not on the climatic conditions that are approximately the same for all four lakes.

14. The bathymetric distribution of the cisco in middle and late summer is highly sensitive to conditions of temperature and dissolved oxygen concentration. A knowledge of the vertical distribution of the cisco is important in the comparison of the densities of the populations of different lakes.

15. The order of the four lakes with respect to the density of their cisco populations, from the minimum to the maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake.

16. The large differences observed in the relative abundance of the various year classes show that the degree of success of the hatch of the cisco in different calendar years is subject to a wide range of variation. Since the years that saw relatively successful or unsuccessful hatches of the cisco are not the same in different lakes, it must be concluded that the relative abundance of a particular year class depends (as does the length of the growing season) on the local conditions within each individual lake, and not on general climatic conditions that would affect all lakes in the same manner.

17. In the Clear Lake cisco sexual maturity appears to be general at the end of the second year of life. In the other populations the cisco is known to be mature at the end of the third year of life, while some, at least, mature in the second year.

18. The order of the four lakes with respect to the sex ratio of the cisco populations (expressed as the number of females per 100 males), from minimum to maximum, is: Clear Lake, Silver Lake, Muskellunge Lake, Trout Lake. The differences among the populations with respect to the sex ratio depend on differences in the differential rates of mortality of the two sexes.

19. The available data indicate a close connection between certain phases of the life history of the cisco and the nature of its animate and inanimate environment.

20. The order of the four lakes with respect to the rate of growth of their cisco populations (in weight) is the same as their order with respect to the length of the cisco's growing season, and the reverse of their order with respect to the density of their cisco populations.

21. The observed differences in the length of the cisco's growing season in different lakes cannot account entirely for the observed differences in growth rate, but probably serve only to accentuate differences that already exist.

22. Suggested explanations of differences in the length of the cisco's growing season in different lakes were: (1) That they may depend on differences from lake to lake in the nature of the plankton cycle, and (2) that the smaller spawners of slow-growing populations may begin the development of the gonads, preliminary to autumn spawning, earlier in the season than do the larger spawners of the rapidly growing populations. (The four lakes follow the same order with respect to growth rate, length of the growing season, and the average size of mature fish.)

23. The correlation between density of population and growth rate may depend on differences in the severity of the competition for food, or upon the operation of a

"space-factor", whereby crowding alone impedes growth independently of the abundance of food.

24. Since, with the exception of a reversal of the positions of the closely similar Muskellunge Lake and Silver Lake populations, the four lakes arrange themselves in the same order with respect to the density of their cisco populations and with respect to the concentration of bound CO_2 in their waters, it was suggested that differences (traceable to the concentration of bound CO_2) in the kind and abundance of plankton available to newly hatched ciscoes may account for the observed differences in the densities of the four cisco populations.

25. Although the relationship between parasite infestation and growth rate has not been thoroughly investigated in the cisco it is known that the Clear Lake cisco, which has by far the best growth of any of the four populations, is practically free of parasites (96 percent negative), while the slower-growing populations from Silver, Muskellunge, and Trout Lakes have a heavy infestation of intestinal parasites (80 percent, or more, positive).

26. The best growth of the cisco occurs in Clear Lake with the smallest amount of organic matter in the surface plankton, but Muskellunge Lake, with the greatest amount of organic matter in the surface plankton does not have the slowest-growing cisco population.

27. The order of the four lakes with respect to the value of the sex ratio (females per 100 males) is the reverse of their order with respect to the rate of growth (in weight). It was suggested that the same factors that determine the rates of growth may cause the differential mortality rate of the less viable males to be greater in the slower-growing populations.

28. The Clear Lake cisco with the most rapid growth is in the best average condition (highest average value of K) and shows the most rapid improvement of condition with increase in length, but the Muskellunge Lake cisco with the poorest average condition and the most rapid loss of condition with increase in length is not the population with the slowest growth.

29. The at least partial independence of the factors that determine growth rate and the factors that determine condition may be construed as a strong argument for the operation of the "space-factor" in the determination of growth rate.

30. The order of the four lakes with respect to the average condition of their cisco populations and the rate of change of condition with increase in length is the reverse of their order with respect to the abundance of organic matter in the surface plankton. Thus it appears that the poorest condition is found in the most eutrophic environment and the best condition in the most oligotrophic environment.

31. Longevity and condition appear to be correlated. The average life span of the cisco is shortest in Muskellunge Lake where the average condition (K) is poorest and increase in length is accompanied by a rapid loss of condition, and the longest in Clear Lake where the average condition is best and condition improves as length increases.

32. In a general review and summary of the growth relationships of the cisco, it was brought out that some of these relationships fail to conform to generally accepted theories. The need was mentioned for a broader knowledge of the biology of the cisco based on observations in a great diversity of habitats. Attention was called to the danger of premature generalizations concerning the growth relationships and the biology of this very plastic species.

33. In each cisco population the amount of growth made by fish in the same year of life but in different calendar years was found to vary considerably. There is no apparent correlation between these variations in the amount of growth in different calendar years and annual variations in the average air temperature during the growing season. There is some indication that annual fluctuations in the density of each individual population may affect the amount of growth made in different calendar years, but with the possible exception of Clear Lake the data in support of such a relationship are not convincing.

34. The 1928 year class of Trout Lake and the 1926 and 1928 year classes of Muskellunge Lake show a bimodal distribution of the calculated lengths at the end of the first year of life. It was suggested that the reason for these bimodal distributions lies in exceptional weather conditions that bring about two hatchings in the spring. However, the effectiveness of weather conditions in bringing about two hatchings appears to depend on local conditions within each lake.

35. The 1928 year class in Muskellunge Lake which has a bimodal distribution of the calculated lengths at the end of the first year of life, and the 1929 Muskellunge Lake year class, which has an unimodal distribution of the calculated lengths at the end of the first year of life, were used as the basis of a study of the effect of the distribution of lengths at an early stage in the life history on the phenomenon of growth compensation in later years. It was found that growth compensation is much more intense in the group with the greater dispersion of the length distribution at the end of the first growing season. In both groups the larger fish at the end of the first year of life tend to be the larger fish at the end of the second year of life and at the time of capture in the third or fourth summer. Growth compensation in later years reduces the advantage of the large first year fish but fails to eliminate it completely.

36. The fish associations of which the ciscoes are part vary from lake to lake. In midsummer the cisco is taken in Trout Lake only with the typical deep water forms, the whitefish, the lake trout, and the burbot; in Muskellunge Lake large numbers of perch and other shallow-water fish are taken with the cisco; in Silver Lake the cisco spends the summer in practical isolation; and in Clear Lake the pike-perch is relatively abundant in the strata inhabited by the cisco.

37. Because of the scattered nature of the available published data, a review was made of earlier investigations concerning the selective action of gill nets.

38. The examination of the size and age composition of the gill-net samples showed that the action of a net or group of nets in taking samples of a cisco population cannot be predicted on the basis of experiences with other populations of the same species, but that each population presents its own problem of gill-net selectivity. Although gill nets are very selective in their operation, the judicious elimination of selected age groups can make gill-net samples highly reliable for the determination of growth curves. Extreme caution must be employed, however, in the use of gill-net samples for the study of age and year class composition.

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APPENDIX A. GROWTH OF THE CISCO IN ALLEQUASH AND TOMAHAWK LAKES

Small collections of ciscoes were obtained from Allequash Lake in 1928 and in 1930 and from Tomahawk Lake in 1928. Since it is unlikely that any further collections of ciscoes will be made in either of these lakes in the near future, the available growth data for each of the populations are being presented at this time.

Tables 1 and 2 show the average length, average weight, average value of K, and the calculated length at the end of each year of life in each age group for each of the three collections. The most noteworthy features of the growth in these two populations are the slow growth during the first year of life in the Allequash fish, the generally excellent growth of the Tomahawk Lake cisco, and the indication that in the Allequash Lake cisco the year 1929 was one above the average in the amount of growth. (It should be pointed out that 1929 was a good growth year in the Trout Lake, Muskellunge Lake, and Silver Lake cisco populations.) The I group of the 1930 Allequash collection shows a particularly high growth for the 1929 season. It is, of course, true that the selective action of gear would be expected to cause a too high calculated growth for this group in any year but selection can hardly explain such a great growth as that which is present here in 1929, for it may be seen that in 1929 the calculated growth for the first year of life is 29 millimeters greater than that calculated for 1927 from the 1928 I group.

TABLE 1.—*Allequash Lake cisco*

[Length, weight, value of K, and calculated length at the end of each year of life. Division of data is according to year class and year of capture. Sexes combined]

Year class	Year of capture	Age	Number of specimens	Weight in grams	K	Length in millimeters	Year of life			
							1	2	3	4
1925	1928	III	3	54	1.50	155	54	101	127	
1926	1928	II	17	45	1.51	144	59	107		
	1930	IV	1	140	1.67	203	49	98	138	175
1927	1928	I	27	25	1.36	123	64			
	1930	III	12	108	1.56	190	58	115	165	
1928	1930	II	11	71	1.54	167	54	133		
1929	1930	I	42	42	1.43	143	93			

TABLE 2.—*Tomahawk Lake cisco, 1928*

[Length, weight, value of K, and calculated length at the end of each year of life for each age group. Sexes combined]

Year class	Age	Number of specimens	Weight in grams	K	Length in millimeters	Year of life				
						1	2	3	4	5
1923	V	1	156	1.53	217	81	138	172	193	210
1924	IV	16	146	1.59	209	78	141	174	198	
1925	III	39	125	1.58	199	76	140	182		
1926	II	11	99	1.61	183	81	155			
1927	I	1	35	1.42	135	83				

Because of the poor growth in the first year of life the general growth of the Allequash Lake cisco differs from that of all four populations considered in the main body of this study. The closest resemblance is probably with the Silver Lake cisco. The growth of the Tomahawk Lake cisco although poorer than that of the Clear Lake cisco is distinctly better than that found in Trout, Muskellunge, and Silver Lakes.

In both Allequash and Tomahawk Lakes the high values of K indicate good condition.

The exceptional conditions under which the Allequash cisco lives should be mentioned. (See table 1 of general paper.) Formerly there existed a rather general belief that the coregonids as a stenothermic form adapted to a cold-water habitat were limited in their distribution to the larger, deeper, lakes. Willer (1924) showed that such a generalization did not apply to the distribution of the kleine Maräne, *Coregonus albula*, in the lakes of East Prussia. Scott (1931) called attention to the exceptional conditions under which the cisco lives in Indian Village Lake (Indiana). This lake is small and shallow (6.4 meters) and in midsummer there is "only a trace" of oxygen below 4 meters. Allequash Lake is another example of a shallow-water habitat for the cisco. The cisco here must not only adjust itself to a wide annual range of temperature variation but also to unusual associates in the form of other species of fish. Along with the 70 ciscoes captured in 1930 were taken 1 blue gill, 15 suckers, 22 pike-perch, 32 rock bass, and 182 perch.

U. S. DEPARTMENT OF COMMERCE
Daniel C. Roper, Secretary
BUREAU OF FISHERIES
Frank T. Bell, Commissioner

SUPPLEMENTAL NOTES ON FISHES OF THE GULF OF MAINE

By HENRY B. BIGELOW and WILLIAM C. SCHROEDER

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 20

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1936

For sale by the Superintendent of Documents, Washington, D. C. - Price 10 cents

SUPPLEMENTAL NOTES ON FISHES OF THE GULF OF MAINE[a]

By HENRY B. BIGELOW and WILLIAM C. SCHROEDER, *Woods Hole Oceanographic Institution*

CONTENTS

	Page
Introduction	320
Hagfish, *Myxine glutinosa* Linnaeus	321
Sea lamprey, *Petromyzon marinus* Linnaeus	321
Smooth dogfish, *Mustelus mustelus* (Linnaeus)	321
Great blue shark, *Prionace glauca* (Linnaeus)	321
Dusky shark, *Carcharhinus obscurus* (LeSueur)	321
Shovel-head shark, *Cestracion tiburo* (Linnaeus)	322
Hammerhead shark, *Cestracion zygaena* (Linnaeus)	322
Thresher, *Alopias vulpinus* (Bonnaterre)	322
Mackerel shark, *Isurus nasus* (Bonnaterre)	322
Sharp-nosed mackerel shark, *Isurus tigris* (Atwood)	322
White shark, *Carcharodon carcharias* (Linnaeus)	322
Spiny dogfish, *Squalus acanthias* Linnaeus	323
Greenland shark, *Somniosus microcephalus* (Bloch and Schneider)	323
Key to skates and rays	324
Little skate, *Raja erinacea* Mitchill	324
Big skate, *Raja diaphanes* Mitchill	325
Prickly skate, *Raja scabrata* Garman	325
Brier skate, *Raja eglanteria* Bosc	325
Smooth skate, *Raja senta* Garman	325
Barn-door skate, *Raja stabuliforis* Garman	325
Torpedo, *Narcacion nobilianus* (Bonaparte)	326
Chimaera, *Chimaera affinis* Capello	326
Common sturgeon, *Acipenser sturio* Linnaeus	326
Short-nosed sturgeon, *Acipenser brevirostris* LeSueur	326
Eel, *Anguilla rostrata* (LeSueur)	326
American conger, *Conger oceanica* (Mitchill)	326
Snake eel, *Pisodonophis cruentifer* Goode and Bean	326
Herring, *Clupea harengus* Linnaeus	327
Alewife, *Pomolobus pseudoharengus* (Wilson)	327
Blueback, *Pomolobus aestivalis* (Mitchill)	327
Thread herring, *Opisthonema oglinum* (LeSueur)	327
Round herring, *Etrumeus sadina* (Mitchill)	327
Anchovy, *Anchoviella mitchilli* (Cuvier and Valenciennes)	327
Striped anchovy, *Anchoviella epsetus* (Bonnaterre)	328
Argentine, *Argentina silus* Ascanius	328
Pearlsides, *Maurolicus pennanti* (Walbaum)	328
Viperfish, *Chauliodus sloanei* Bloch and Schneider	328
Lancetfish, *Alepisaurus ferox* Lowe	328
Needlefish, *Scomberesox saurus* (Walbaum)	328
Trumpetfish, *Fistularia tabacaria* Linnaeus	328
Pelagic pipefish, *Syngnathus pelagicus* Linnaeus	329
Common pipefish, *Syngnathus fuscus* Storer	329
Northern barracuda, *Sphyraena borealis* DeKay	329
Mackerel, *Scomber scombrus* Linnaeus	329
Tuna, *Thunnus thynnus* (Linnaeus)	329
Common bonito, *Sarda sarda* (Bloch)	330
Spearfish, marlin, *Makaira albida* (Poey)	330
Swordfish, *Xiphias gladius* Linnaeus	330
Pilotfish, *Naucrates ductor* (Linnaeus)	331
Rudderfish, *Seriola zonata* (Mitchill)	331
Mackerel scad, *Decapterus macarellus* (Cuvier and Valenciennes)	331

[a] Bulletin No. 20, approved for publication May 18, 1936. Contribution No. 119 of the Woods Hole Oceanographic Institution.

80054—36

	Page
Saurel, *Trachurus trachurus* (Linnaeus)	331
Big-eyed scad, *Trachurops crumenopthalma* (Bloch)	331
Hardtail, *Caranx hippos* (Linnaeus)	331
Hardtail, *Caranx crysos* (Mitchill)	331
Lookdown, *Selene vomer* (Linnaeus)	332
Leatherjacket, *Oligoplites saurus* (Bloch and Schneider)	332
Bluefish, *Pomatomus saltatrix* (Linnaeus)	332
Common dolphin, *Coryphaena hippurus* Linnaeus	332
Opah, *Lampris regius* (Bonnaterre)	332
Johnson's sea bream, *Taractes princeps* Johnson	332
Butterfish, *Poronotus triacanthus* (Peck)	332
Harvestfish, *Peprilus alepidotus* (Linnaeus)	333
Striped bass, *Roccus lineatus* (Bloch)	333
Sea bass, *Centropristes striatus* (Linnaeus)	333
Triggerfish, *Balistes carolinensis* Gmelin	333
Filefish, *Monacanthus hispidus* (Linnaeus)	334
Filefish, *Monacanthus ciliatus* (Mitchill)	334
Unicornfish, *Alutera scripta* (Osbeck)	334
Puffer, *Spheroides maculatus* (Bloch and Schneider)	334
Rosefish, *Sebastes marinus* (Linnaeus)	334
Black-bellied rosefish, *Helicolenus dactylopterus* (De la Roche)	334
Hook-eared sculpin, *Artediellus uncinatus* (Reinhardt)	335
Mailed sculpin, *Triglops ommatistius* Gilbert	335
Longhorn sculpin, *Myoxocephalus octodecimspinosus* (Mitchill)	335
Deep-sea sculpin, *Cottunculus microps* Collett	335
Sea raven, *Hemitripterus americanus* (Gmelin)	335
Sea snail, *Neoliparis atlanticus* Jordan and Evermann	336
Striped sea snail, *Liparis liparis* (Linnaeus)	336
Red-winged sea robin, *Prionotus strigatus* (Cuvier)	336
Remora, *Remora remora* (Linnaeus)	336
Rock eel, *Pholis gunnellus* (Linnaeus)	336
Snake blenny, *Lumpenus lampetraeformis* (Walbaum)	336
Shanny, *Leptoclinus maculatus* (Fries)	337
Arctic shanny, *Stichaeus punctatus* (Fabricius)	337
Radiated shanny, *Ulvaria subbifurcata* (Storer)	337
Wrymouth, *Cryptacanthodes maculatus* Storer	337
Spotted wolffish, *Anarrhichas minor* Olafsen	337
Eelpout, *Zoarces anguillaris* (Peck)	337
Wolf eel, *Lycenchelys verrillii* (Goode and Bean)	338
Silver hake, *Merluccius bilinearis* (Mitchill)	338
Pollock, *Pollachius virens* (Linnaeus)	338
Cod, *Gadus callarias* Linnaeus	338
Haddock, *Melanogrammus aeglefinus* (Linnaeus)	339
Long-finned hake, *Urophycis chesteri* (Goode and Bean)	339
Spotted hake, *Urophycis regius* (Walbaum)	339
Four-bearded rockling, *Enchelyopus cimbrius* (Linnaeus)	339
Cusk, *Brosme brosme* (Müller)	339
Common grenadier, *Macrourus bairdii* Goode and Bean	340
American plaice, *Hippoglossoides platessoides* (Fabricius)	340
Four-spotted flounder, *Paralichthys oblongus* (Mitchill)	340
Rusty dab, *Limanda ferruginea* (Storer)	340
Winter flounder, *Pseudopleuronectes americanus* (Walbaum)	340
Georges Bank flounder, *Pseudopleuronectes dignabilis* Kendall	341
Witch flounder, *Glyptocephalus cynoglossus* (Linnaeus)	341
Gulf Stream flounder, *Citharichthys arctifrons* Goode	341
American goosefish, *Lophius americanus* Cuvier and Valenciennes	341
Sargassum fish, *Histrio histrio* (Linnaeus)	341
Deep-sea angler, *Mancalias uranoscopus* (Murray)	342
Bibliography	342

Introduction

Since the publication by the Bureau of Fisheries of "Fishes of the Gulf of Maine" (Document No. 965, U. S. Bureau of Fisheries, Bigelow and Welsh, 1925) enough new information of general interest has come to hand regarding abundance, distribution, migrations, breeding habits, and food habits to warrant the issuance of a supplement to that publication. Many of these data have been obtained during the investigations carried on by the Bureau; part have been collected from correspondence, while part have been gleaned from published material. Brief notes

and records of distribution have been taken from the Bulletin of the Boston Society of Natural History (see Firth (1931), Kendall (1931), MacCoy (1929, 1931a, 1931b, 1933), Schroeder (1931)); from Reports of the Newfoundland Fishery Research Commission (1932–1933); and from the Proceedings and Transactions of the Nova Scotian Institute of Science (Leim 1930). For the distribution of certain New England sharks in South African waters, not referred to in this paper, the reader is referred to Barnard (1925). For allowing us the use of unpublished notes we wish to thank F. E. Firth, Dr. G. W. Jeffers, Dr. A. H. Leim, Walter H. Rich, and O. E. Sette.

The nomenclature used in this supplement is as in "Fishes of the Gulf of Maine."

Hagfish, *Myxine glutinosa* Linnaeus

Recent detailed studies of the sex organs make it certain that the hag is not functionally hermaphroditic as was formerly supposed, but that in each individual either the male portion of the common sex organ matures, with the female organ remaining rudimentary, or vice versa (Conel, 1931). The fact that a 60 cm specimen from Georges Bank contained 30 eggs, 20–25 mm long, shows that large females may produce somewhat more and slightly larger eggs than previously recorded.

Sea lamprey, *Petromyzon marinus* Linnaeus

The known range of the sea lamprey in the western Atlantic has been extended northward to the west coast of Greenland (Jensen, 1926).

Smooth dogfish, *Mustelus mustelus* (Linnaeus)

The genus Mustelus is established for this species by an opinion rendered by the International Commission on Zoological Nomenclature (Smithsonian Institution, 1926, p. 8).

Smooth dogfish are taken so seldom in winter that capture of three by a trawler off Bodie Island, N. C., in 34–45 fathoms, February 1931, is of interest.

Great blue shark, *Prionace glauca* (Linnaeus)

The International Commission on Zoological Nomenclature (Smithsonian Institution, 1925, p. 27) has rejected Valmont's name, Galeus; consequently the correct generic name of the species is Prionace Linnaeus.

The blue shark has recently been recorded from the southwest part of the Grand Bank (Rept., Nfld. Fish. Res. Lab., 1935, p. 79). Although formerly considered a stray in the Gulf of Maine, recent observations have shown the blue shark to be common there in August and September, with occasional records for July. While most often seen offshore, a number were observed and several caught by J. W. Lowes during the summer of 1935 in Massachusetts Bay.

Young ones are seldom seen along our shores, but Robert Goffin reports one only 20 inches long from Menemsha Bight, near Woods Hole, Mass., August 31, 1925; while F. E. Firth records another, 38 inches long, taken 65 miles southeast of Highland Light, Cape Cod, on October 23, 1930.

Dusky shark, *Carcharhinus obscurus* (LeSueur)

The capture of an 11-foot fish on the northeast peak of Georges Bank, August 10, 1931, extends the known range to the offshore banks (Firth, 1931, p. 9).

Shovel-head shark, *Cestracion tiburo* (Linnaeus)

One specimen of this southern species was recorded by Garman (1913, p. 160) from Massachusetts Bay.

This record was omitted from "Fishes of the Gulf of Maine" (Bigelow and Welsh, 1925).

Hammerhead shark, *Cestracion zygaena* (Linnaeus)

Captures of a 12-foot fish, in August 1928, by the swordfishing schooner *Doris M. Hawes*, between Browns and Georges Banks, and of a small one in Halifax Harbor, September 1932 (Vladykov, 1935, p. 8), extend the known range to the northward and eastward.

Thresher, *Alopias vulpinus* (Bonnaterre)

The International Commission on Zoological Nomenclature rejects Valmont's name, *Vulpecula marina*, consequently the next oldest name, *Alopias vulpinus*, must be substituted (Smithsonian Institution, 1925, p. 27).

Mackerel shark, *Isurus nasus* (Bonnaterre)

The fact that *Isurus punctatus* (Storer) is identical with *I. nasus* (Bonnaterre) has been pointed out by Bigelow and Schroeder (1927).

The range of the mackerel shark in the western side of the Atlantic is now known to extend as far north as the Grand Bank of Newfoundland (Rept., Nfld. Fish. Res. Lab., 1935, p. 79).

Sharp-nosed mackerel shark, *Isurus tigris* (Atwood)

The many recent fishery investigations in the Gulf of Maine have indicated that this species is much less common there than *I. nasus*, for whereas many of the latter have been observed and captured since 1923, only one record of the sharp-nosed mackerel shark has come to our attention within that time, a fish 8½ feet long taken 10 miles northeast of Nantucket Lightship, June 22, 1930, by the schooner *Linta* (Firth, 1931, p. 8).

White shark, *Carcharodon carcharias* (Linnaeus)

To the few existing Gulf of Maine records of this ferocious shark are added that of a 13-foot fish taken off Portland in a gill net during October 1931 (identified by Dr. W. C. Kendall); one (identified from a tooth) which attacked a fishing boat off Digby Gut, Bay of Fundy, July 2, 1932;[1] a somewhat doubtful record from off Halifax, June 27, 1930;[2] and another, 15 feet long, apparently of this species, caught off Monomoy Point, Cape Cod, in the fall of 1928.

Spiny dogfish, *Squalus acanthias* Linnaeus

The spiny dogfish is now known along the American coast as far northward as the Straits of Belle Isle. It has also been taken off the west coast of Greenland at Sukkertoppen and in the vicinity of Holsteinborg (Jensen, 1914, p. 7).

[1] Harry Piers, Proc., Nova Scotian Institute of Science, vol. XVIII, pt. 3, p. 198, 1934.
[2] Ibid., p. 196.

The winter home of the spiny dogfish off the American coast has long been a subject of uncertainty, hence it is of interest to record that the schooner *Victor* found them plentiful about 90 miles southeast of Ambrose Channel Lightship on the tilefish grounds the middle of January 1928, and that the *Albatross II* trawled many specimens in February 1931, between Cape Hatteras, N. C., and Cape Henry, Va., in 16 to 70 fathoms of water. It appears probable, therefore, that the continental slope to the southward of New England is the chief wintering ground of this species on this side of the Atlantic.

Analysis of the sizes and of the stages of development of embryos in females taken at various dates and localities along the coast, and of recent captures of new born dogfish, also adds to our knowledge (previously scanty) of the breeding habits.

Up until 1925 we had no record of new born dogfish within the Gulf of Maine. This, together with the facts that females containing large embryos had been often taken there in early autumn, that dogfish depart entirely from the gulf over the winter, and that new born young had been reported off Long Island in summer suggested that the area of reproduction of this species is confined to waters west and south from Cape Cod.

This is not the case, however, for during the past few years, when special watch has been kept for new born dogfish, we have learned of their presence in considerable numbers on Nantucket Shoals and at various localities in the Gulf of Maine from June to August. Evidently, then, the gulf, as well as the waters off southern New England, is an important nursery. The tact that embryos, sometimes with yolk sac nearly absorbed, have repeatedly been found in females off New York in autumn and on the wintering grounds off Virginia and North Carolina in January and February might suggest that the coastal waters of the Middle Atlantic States also so serve. As no new born "dogs" have yet been reported to the southward of New York at any season, this question remains open, however.

If it should prove that young are born in the southern wintering as well as in the northern summering grounds, the sizes of the embryos, at different localities and dates, would suggest that some are set free as early as January or February; in other words, that the season extends from midwinter right through the spring and summer.

Greenland shark, *Somniosus microcephalus* (Bloch and Schneider)

So seldom is the Greenland shark captured in the Gulf of Maine that it is of interest to record a large one taken off Portland Lightship the summer of 1926, and four others, 4 to 5 feet long, taken in the offing of Portland from 1927 to 1933. A large one was also taken somewhere in the gulf and brought into Gloucester in January 1929, and another, about 15 feet long, caught in an otter trawl on Jeffreys Ledge 27 miles northeast of Thatchers Island, off Cape Ann, February 16, 1931.

KEY TO SKATES AND RAYS

Experience has shown that existing keys are not adequate for the identification of Gulf of Maine skates and rays. The following revision is therefore offered:

1. No long dorsal spine on the tail 2
   Tail with long dorsal spines (sting rays) 11
2. Two small dorsal fins, but no distinct caudal fin (includes all our common skates) 3
   There is a large triangular caudal fin as well as the two dorsals ..... Torpedo
3. Ventral surface with minute rounded tubercles ..... *Raja granulata*,[8]
   Ventral surface smooth 4

[8] Although *Raja granulata* is not known from the Gulf of Maine it can be expected there as it has been recorded from La Have Bank and from the continental edge off Halifax, Nova Scotia, from 200 fathoms.

4. No thorns along mid-zone of disc between eyes and ventrals.
Barn-door skate, *Raja stabuliforis*
With one or more rows of thorns along mid-dorsal zone of disc behind eyes 5
5. Posterior third of tail without any large thorns ..... Smooth skate, *Raja senta*
Posterior third of tail with one or more rows of large thorns 6
6. Tail with only one row of large thorns ..... Young *Raja scabrata*
Tail with three or more rows of thorns 7
7. Mid-row of tail thorns very much larger than any other thorns on tail.
Prickly skate, *Raja scabrata*
Mid-row of tail thorns absent or if present not much larger than other thorns on tail 8
8. Three rows of thorns on tail ..... Brier skate, *Raja eglanteria*
Four or more rows of thorns on tail 9
9. Length of fish more than 2½ feet ..... Big skate, *Raja diaphanes*
Length of fish less than 2½ feet 10
10. Teeth in 70 to 104 rows in each jaw; usually an eye-spot present on each pectoral.
Big skate, *Raja diaphanes*
Teeth in 38 to 60 rows in each jaw; eye-spot rarely present ..... Little skate, *Raja erinacea*
11. No dorsal fins on tail ..... Sting ray, *Dasybatus marinus*
Tail with a dorsal fin in front of spine ..... Cow-nosed ray, *Rhinoptera quadriloba*

With regard to the relative abundance of different species of skates on the offshore fishing banks of the Gulf of Maine, it is of interest that on a trip to Georges Bank (chiefly the northeastern part) in September 1929, aboard the otter trawler *Kingfisher*, 37 hauls yielded from 0 to 105 skates per haul (total 495), as follows: *Raja senta*, 57; *R. scabrata*, 325; *R. stabuliforis*, 42; and *R. diaphanes*, 71.

Little skate, *Raja erinacea* Mitchill

This skate has been described as lacking thorns along the midline; but small specimens 3½ to 9½ inches long and one half-grown specimen of 13½ inches, recently examined by us, have this row well developed.

Big skate, *Raja diaphanes* Mitchill

Recent investigations have shown that the range of this skate extends northward not only to the Gulf of St. Lawrence, as long known, but to the Grand Banks as well, and southward to Virginia.

The big skate rarely has a median row of thorns except in the very young, so it is of interest to record a female 18 inches long taken near Jeffreys Ledge, November 1, 1927, which bears a row of large spines along the midline, from the shoulder girdle to the origin of dorsal on the tail.

Young specimens of *R. diaphanes* and *R. erinacea*, especially the females, are not easily separated from each other by a casual glance, hence the number of rows of teeth which they possess has been an important means of identification. Investigators have given various tooth counts ranging from 80 to 110 rows for *diaphanes* and around 50 rows for *erinacea*. Several specimens in the Museum of Comparative Zoology, from New England waters, show 70 to 100 rows of teeth on the jaw of *diaphanes* and from 46 to about 60 rows in *erinacea*.

Prickly skate, *Raja scabrata* Garman

At the time of publication of "Fishes of the Gulf of Maine" the northern boundary of this skate (widespread in the Gulf of St. Lawrence) was unknown in the open Atlantic. Since then it has been found plentifully on the Grand Banks and reported from the east and north coasts of Newfoundland.

Examination of a large number of prickly skates, ranging in size from young, recently hatched, to the largest recorded, allows us to add the following to previous descriptions:

The pavementlike teeth are in 41 or 42 rows in the upper jaw, 40 to 44 rows in lower jaw (4 specimens) and in the male, at least, there are rather sharp cusps on those teeth situated toward the angles of the jaw. The number of large curved thorns along the midline of the tail and body was as follows on 23 specimens: 12 (2), 13 (10), 14 (8), 15 (3), with no correlation between the number of thorns and the size of the specimen. The brownish back is usually marked with small white spots. The young are more spotted than the adults and have six or seven dark cross bars on the upper surface of the tail.

This skate grows to 3 feet in length, or slightly larger; a 32-inch fish is about 23 inches wide. The smallest nearly mature male found was 26 inches long.

Since nothing was known of the breeding habits of the prickly skate, it is worth recording that a specimen 32 inches long taken on the northern part of Georges Bank, September 22, 1929, had one egg capsule measuring 3 by 2¼ inches (exclusive of tendrils) in each oviduct, and that a male, 35¼ inches long had nearly ripe milt, but a number of other large females taken at the same time were barren.

Prickly skates caught on Georges Bank in September 1929, had been feeding on fish, shrimps, spider crabs, anemones, and worms; this is the first definite information as to the diet of this skate.

Brier skate, *Raja eglanteria* Bosc

An unusually large one, 37¼ inches long, was taken off Woods Hole, Mass., in August 1932.

Additional to the few Gulf of Maine records of this skate already reported are two specimens taken on Nantucket Shoals, near Round Shoal Buoy, by the *Halcyon*, one in July, the other in September 1924. This is a shoal water species, the deepest capture made by *Albatross II* between southern New England and the offing of Chesapeake Bay being in 38 fathoms.

Smooth skate, *Raja senta* Garman

The smooth skate, formerly believed rare in the Gulf of Maine, is now known to be quite generally distributed on our offshore fishing banks, as well as on soft bottom in the deeper parts of the gulf. We have taken it commonly on Georges Bank, in South Channel, in the deep water (80–100 fathoms) just off Cashes Ledge, near Jeffreys Ledge, and off Chatham. The shoalest capture was from 25 fathoms.

The largest specimen obtained was 24 inches long.

Barn-door skate, *Raja stabuliforis* Garman

Young specimens are seldom reported, hence it is of interest to record one of 7½ inches taken on the western edge of Nantucket Shoals July 14, 1930, in 28 fathoms. This fish had essentially the same characters as the adult. The range of the barn door skate is now known to extend northward to the western part of the Grand Bank of Newfoundland.

Torpedo, *Narcacion nobilianus* (Bonaparte)

As no torpedoes had been reported to the eastward of Cape Cod since 1896, the captures of a 52-inch specimen weighing 78 pounds, on the southwest part of

Georges Bank, December 8, 1930, and of another of 39 inches at Provincetown, July 28, 1931, deserve mention here.

Chimaera, *Chimaera affinis* Capello

It was formerly believed that the chimaera did not exceed a length of about 3 feet, but a specimen measuring 49 inches in length, 17½ pounds in weight dressed, was taken October 15, 1930, 85 miles south by west of Cape Sable in a depth of about 400 fathoms (Firth, 1931, p. 9).

Common sturgeon, *Acipenser sturio* Linnaeus

Although sturgeon have seldom been reported from offshore, the recent captures of a 268-pound fish in South Channel the end of April 1928, of another of 420 pounds in April 1929, of a 335-pound fish trawled on Browns Bank in April 1936, and of a 435-pound fish on Georges Bank, latitude 41°00′ N., longitude 67°45′ W., on January 7, 1931, indicate that they are to be occasionally found on our outer fishing banks.

Short-nosed sturgeon, *Acipenser brevirostris* LeSueur

A 30-inch specimen, taken at Provincetown about 1907, now in the collection of the Museum of Comparative Zoology, is the only reliable record for the Gulf of Maine. This record was omitted from "Fishes of the Gulf of Maine" (Bigelow and Welsh, 1925).

Eel, *Anguilla rostrata* (LeSueur)

The known range of the American eel in northern waters has been extended to the west coast of Greenland (Jensen, 1926, p. 101).

American conger, *Conger oceanica* (Mitchill)

The American conger, long considered identical with the European, has recently been shown by Schmidt (1931) to be a distinct species, characterized by having fewer (140–149) vertebrae than the European (154–163 vertebrae); a relationship paralleling that between the American and European eels of the genus *Anguilla.*

The American conger ranges along the continental shelf northward to Cape Cod. Its southern boundary cannot be stated until the congers of the coasts of North and South America have been critically compared.

Additional to the few records of larvae already reported from the Gulf of Maine are those of two specimens (4¼ inches long) picked up on the beach at Newburyport, Mass., in November 1929, which were sent to us for identification.

Dr. Johannes Schmidt's discovery [4] of very young larvae in the West Indian region, but nowhere else, points to this as the chief, if not the only, spawning ground of the American conger.

Snake eel, *Pisodonophis cruentifer* Goode and Bean

Goode and Bean's (1896, p. 147) record of this species from Jeffreys Bank—the only one for the gulf—was omitted from "Fishes of the Gulf of Maine." A number of specimens have been taken recently between the offings of Nantucket and of Cape Henry, Va., in depths ranging from 24 to 245 fathoms by the *Fish Hawk* and the *Albatross II.*

[4] See Schmidt, 1931, p. 602, for a discussion of this question.

Herring, *Clupea harengus* Linnaeus

The northern limit to the known range of the herring in the Western Atlantic has been extended to the west coast of Greenland by Jensen (1926, p. 101).

Herring are so seldom taken in any large numbers on the offshore banks that it is of interest to record a catch of 2,800 pounds in South Channel and 3,000 pounds on the northern edge of Georges Bank, in October 1931.

Mass destruction of young herring, cast up on the beaches has occurred from time to time in various harbors in the Gulf of Maine. A recent occurrence of this sort was reported by Dr. Austin H. Clark, who, in Manchester Harbor on the north side of Massachusetts Bay, early in August 1925, observed that the mud flats were white with stranded herring which measured 3 to 5 inches in length. Another such destruction took place in the same harbor in the summer of 1928.

Alewife, *Pomolobus pseudoharengus* (Wilson)

So little is known about the habits or migrations of the alewife while at sea that it is of interest to record the capture by *Albatross II* of 18 adults, 10 to 11 inches long, by otter trawl, seventy odd miles off Barnegat, N. J., on March 5, 1931.

Blueback, *Pomolobus aestivalis* (Mitchill)

The maximum length of this herring is usually given as about 1 foot but we have seen examples of it ranging up to 15 inches.

The capture of seven adult specimens by *Albatross II*, on March 5, 1931, about 70 miles off Barnegat, N. J., suggests that, like its relative the sea herring, the blueback moves out from land, and passes the cold season near the bottom, thus throwing some light on the probable winter home of the Gulf of Maine stock.

Thread herring, *Opisthonema oglinum* (LeSueur)

The capture of a single specimen, 7 inches long, off Monomoy Point at the southern angle of Cape Cod in August 1931, extends the known range of this southern herring to the Gulf of Maine. Occasionally the thread herring is taken off southern New England; it was even reported as rather common in Buzzards Bay and Vineyard Sound in the summer of 1885. As it is essentially a tropical fish it is not apt, however, to reach the gulf except as the rarest of strays.

Round herring, *Etrumeus sadina* (Mitchill)

This herring, recorded by Bigelow and Welsh (1925, p. 91) as *Etrumeus teres* DeKay, appears very rarely to stray past Cape Cod. Hence, it is of interest to record the capture of one specimen in Yarmouth River which empties into Casco Bay, and one in the bay itself, on September 15, 1924.

Anchovy, *Anchoviella mitchilli* (Cuvier and Valenciennes)

This species is listed by Bigelow and Welsh (1925, p. 124) as *Anchovia mitchilli.* The subgenus Anchoviella Fowler differs from the subgenus Anchovia Jordan and Evermann chiefly by having much fewer gillrakers, the former having about 35 to 50 and the latter 100 or more.

Striped anchovy, *Anchoviella epsetus* (Bonnaterre)

A record from off the Presumpscot River, near Portland, October 8, 1930 (Kendall 1931, p. 11) is the first for the Gulf of Maine. This anchovy is now known from as far northward as Halifax harbor where a number were seined September 29, 1931 (Vladykov 1935, p. 3).

Argentine, *Argentina silus* Ascanius

Until recently the argentine was considered rare in our waters, for only odd examples had been brought in from widely scattered localities. The development of otter trawling proved that argentines are in reality fairly common around the edge of Georges Bank and off Cape Cod in deep water. Thus, along the northern and northwestern slopes of the bank and to the eastward of Cape Cod, in depths of 80 to 100 fathoms, it is not unusual for a haul of the trawl to bring in from one to a dozen, and as much as 15,000 pounds has been reported by one boat during a week's fishing (Firth 1931, p. 11). It also occurs in the deep central basin of the gulf, for the *Albatross II* has recently (July 1931) trawled a specimen in 115 fathoms off Mount Desert Rock.

Pearlsides, *Maurolicus pennanti* (Walbaum)

Additional Gulf of Maine records of this species include one specimen 41 mm long taken from the stomach of a cod, on Platts Bank, July 27, 1924; one 43 mm long, also from a cod's stomach, on Cashes Ledge, August 16, 1928; and four, 32 to 39 mm long, from the stomachs of two pollock, caught in 20 fathoms, 7 miles southeast of Bakers Island, Mount Desert, Maine, July 24, 1930.

Viperfish, *Chauliodus sloanei* Bloch and Schneider

A specimen found in the stomach of a swordfish caught in the gully between Browns and Georges Banks in 1931 is the second to be definitely recorded from within the Gulf of Maine.

Lancetfish, *Alepisaurus ferox* Lowe

A record of a 5½-foot specimen of this rare fish caught alive in the surf on Block Island, R. I., March 12, 1928, is of especial interest even though outside the limits of the Gulf of Maine. An excellent photograph, sent in by Mrs. Elizabeth Dickens, shows the upper lobe of the caudal prolonged as a long filament, which most of the specimens so far seen have lost. This specimen had been feeding on small dogfish.

Needlefish, *Scomberesox saurus* (Walbaum)

A specimen gaffed at the surface from the *Albatross II* on northern Georges Bank, September 20, 1928, is the only definite offshore record for the Gulf of Maine although the needlefish has been taken in various localities there alongshore.

Trumpetfish, *Fistularia tabacaria* Linnaeus

Recent reports of the trumpetfish at Port Mouton, Nova Scotia, and on the south coast of Newfoundland, show that this tropical species may stray much farther north than previously supposed.

Pelagic pipefish, *Syngnathus pelagicus* Linnaeus

A single specimen 3½ inches long, taken on Georges Bank (lat. 42°09′ N., long. 66°41′ W.) September 20, 1927, by the *Albatross II*, is the only Gulf of Maine record. This specimen was dipped up with a mass of gulf weed (Sargassum) and was the only one found in a large amount of weed that was examined.

Common pipefish, *Syngnathus fuscus* Storer

Pipefish are rarely taken on bottom far from the immediate shore waters, hence it is of interest to report the capture of four specimens 4½ to 6 inches long at a depth of 19 fathoms 10 miles south of No Mans Land, February 5, 1930.

Northern barracuda, *Sphyraena borealis* DeKay

A specimen about 2 inches long found alive in the surf at Nauset Beach, Cape Cod, September 26, 1930, by Dr. Edward P. Richardson, is the only record thus far reported for the Gulf of Maine. Young fry, a few inches long, are taken, however, from time to time in the region of Vineyard Sound and Buzzards Bay on the southern coast of New England, from July to December.

Mackerel, *Scomber scombrus* Linnaeus

The body length of the mackerel is erroneously given as about three and one-half times the depth by Bigelow and Welsh (1925, p. 188); actually, it is four to five and one-half times the depth.

A small mackerel taken at Cape Lookout, N. C., in February 1925 (Coles, 1926, p. 105), extends the known range southward beyond Cape Hatteras.

Recent captures of a mackerel weighing 7½ pounds,[5] and of another of 7¼ pounds, 26 inches long, both of which we, ourselves, examined, shows that occasional giants occur, for the weight seldom exceeds 4 pounds or the length 22 inches.

Tuna, *Thunnus thynnus* (Linnaeus)

Larger catches of tuna have been made within the Gulf of Maine in recent years partly, at least, because of an increased market demand for the fish. Thus, compared with the 69,868 pounds recorded for Massachusetts and Maine in 1919, the catch of 1934 amounted to 356,904 pounds, of which 254,076 pounds came from Cape Cod. The Nova Scotian shore of the Gulf of Maine yielded about 24,000 pounds in 1924 and 10,000 pounds in 1929. At present the annual catch for the gulf is probably between 300,000 and 400,000 pounds. Assuming an average weight of 300 pounds (probably too little, for the average weight of about 90 tuna caught off the coast of Maine in 1926 was about 540 pounds), this would represent a thousand or more fish. Off the outer coast of Nova Scotia, where tuna have been taken in larger numbers than within the Gulf of Maine, the annual catches from 1917 to 1933 have fluctuated between 152,000 and 1,550,000 pounds.

The heaviest New England fish on record, taken off Rhode Island about 1913, weighed 1,225 pounds, while four or five fish have been brought into Boston that weighed approximately 1,200 pounds. Another fish weighing 1,300 pounds was shipped in 1924 from Nova Scotia to Boston (Sella, 1931, p. 61).

[5] Atlantic Fisherman, August 1925.

Small and moderate sized tuna (below 100 pounds) are comparatively rare in the Gulf of Maine. However, schools composed of individuals estimated to weigh not more than 40 to 70 pounds were observed around Boston lightship July 13 and 14, 1935.[6] None below 20 pounds has been recorded within the gulf, but off southern New England, especially near Block Island, small tuna are sometimes caught, there being an unusual run of them (8 to 12 pounds) in 1928. Thus it is probable either that the lower temperatures of the Gulf of Maine are a barrier to the smaller-sized tuna, or that they find less favorable feeding grounds there than do the larger sizes.

Off the New England coast the first schools are sighted late in June or early July to the southward of Block Island, over depths of about 85 fathoms, and a few days later they appear inshore. At first the fish are hungry, and there is some reason to believe that their summer migrations follow their breeding period. An example of their seasonal abundance in the shore waters of the coast of Maine may be had from the catches made in the vicinity of Casco Bay in 1926, where about 70 fish were taken in July, 17 in August, 3 in September, and 1 on October 4.

Common bonito, *Sarda sarda* (Bloch)

Two fish were reported from the mouth of Kennebec River in July and one in September 1930, and one from southern Nova Scotia (Vladykov, 1935, p. 7) in the latter month.

In looking through the records of the catches made by a certain set of pound nets at Provincetown over a period of 10 years, we find the earliest catch for that locality was in July (1915), and the latest on October 4 (1919).

Spearfish, marlin, *Makaira albida* (Poey) [7]

No spearfish were reported in the Gulf of Maine from about 1880 until 1925. Since then, however, seven specimens have been brought in, all in summer, one of them from off Portland, the others from Georges, Browns, and Sable Island Banks, the last being the most northerly record for the species in the western North Atlantic. These specimens ranged from 5 feet to nearly 16 feet in length and from 21 to about 700 pounds in weight.

Additional descriptive data based on two New England specimens examined by us are as follows: The first dorsal fin of one specimen has 47 stiff rays, the other fish having 48. This fin is separated from the second dorsal by a space equal to the length of the latter in the one fish, by a shorter space in the other. The first anal fin (2 spines and about 12 or 13 rays), situated below the rear part of the first dorsal, is triangular, its first rays forming a sharp angle.

Swordfish, *Xiphias gladius* Linnaeus

The largest swordfish definitely recorded from the Gulf of Maine was one, caught in the summer of 1921 by Capt. Irving King and landed at the Boston Fish Pier, that weighed 915 pounds dressed—hence, upward of 1,000 pounds alive (Fishing Gazette, September 1921, p. 13). The specimen was not measured, but the sword being more than 5 feet, the total length of the fish must have approximated 15 feet.

[6] Data furnished by J. W. Lowes.

[7] Recorded by Bigelow and Welsh (1925, p. 227) as *Tetrapturus imperator* (Bloch and Schneider).

In 1931, another large fish was caught, 644 pounds in weight, dressed, 13 feet in length, with a sword measuring 3 feet 8 inches.

Young swordfish are so rarely reported off the New England coast that it is of interest to record the capture of a 2-foot fish, weighing 7¾ pounds, taken by the *Dacia* on a trawl line September 2, 1931, on Georges Bank.

Pilotfish, *Naucrates ductor* (Linnaeus)

Up to 1925 only three definite records for the Gulf of Maine had come to hand. Since then we have learned of the capture of six more pilotfish, off Portland, in Provincetown Harbor, to the southeast of Cape Cod, and on the northern edge of Georges Bank, during the summer and fall months in the years 1921, 1924, 1929, 1931, and 1933. Vladykov (1935, p. 6) reports two specimens from Sable Island Bank and one from Sambro, off Nova Scotia, in the period 1932–34.

Rudderfish, *Seriola zonata* (Mitchill)

The known range of the rudderfish has been extended northward to Halifax, Nova Scotia (Leim, 1930, p. xlvi, as *S. dumerili*).

One fish was caught on a smelt hook off a Portland wharf in September 1921; a 5½-inch fish was taken off Boston in September 1929; another, 17½ inches long, from South Channel the same month; and a 6-inch specimen on Nantucket Shoals in August 1930.

Mackerel scad, *Decapterus macarellus* (Cuvier and Valenciennes)

One specimen, 7 inches long, was taken in a trap at Richmond Island, off Cape Elizabeth, in September 1931, this being only the second recorded for the Gulf of Maine.

Saurel, *Trachurus trachurus* (Linnaeus)

One specimen of this fish, rare to the northward of Woods Hole, Mass., was taken in Casco Bay on August 12 and another near Castine Bay, Maine, on October 15, 1930 (Kendall, 1931, p. 11).

Big-eyed scad, *Trachurops crumenopthalma* (Bloch)

Two specimens, recently taken off Cape Cod, one at Provincetown, the other about 8 miles off the beach at Chatham, are the only positive records of this species for the Gulf of Maine. As it is caught from time to time, however, in the summer and fall as far northward as Woods Hole, it may be expected to round the cape occasionally. This scad has been recorded from Canso, Nova Scotia by Cornish (1907, p. 85).

Hardtail, *Caranx hippos* (Linnaeus)

A hardtail taken off Provincetown in 1933 is the second reported from the Gulf of Maine. Several specimens about 2 inches long were taken the summer of 1933 in Musquodoboit Harbor, Nova Scotia (Vladykov, 1935, p. 4).

Hardtail, *Caranx crysos* (Mitchill)

One fish was taken off Chatham in 1933.

Lookdown, *Selene vomer* (Linnaeus)

During the autumn of 1933 many small lookdowns were reported from traps at the mouth of Casco Bay, one also from Beverly Farms, and another from North Truro, an unusual incursion, for only three specimens had previously been recorded in the Gulf of Maine. Jones (1882 p. 89) and Honeyman (1886 p. 328) record this species (young) as occasional in the shore waters of Nova Scotia, presumably along the east coast.

Leatherjacket, *Oligoplites saurus* (Bloch and Schneider)

A specimen taken in a trap off the outer beach at Chatham is the only record for the Gulf of Maine.

Bluefish, *Pomatomus saltatrix* (Linnaeus)

For many years no bluefish had been reported north of Cape Ann, until 1925, when one was caught off Halifax, Nova Scotia. This seems to have presaged a temporary extension of range, for numbers of them visited the inner coasts of the gulf northward to Casco Bay in the summer of 1927, while in 1930 the bluefish was again reported at Halifax (two specimens) and at Port Mouton, Nova Scotia (one specimen, Leim, 1930, p. xlvi).

Common dolphin, *Coryphaena hippurus* Linnaeus

A dolphin about 3½ feet long taken 60 miles south-southwest of Cape Sable, in the deep gully between Browns and Georges Banks by the trawler *Natalie Hammond*, August 15, 1930, is the first Gulf of Maine record. The specimen is now in the collection of the Boston Society of Natural History.

Opah, *Lampris regius* (Bonnaterre) [8]

A specimen about 3 feet long was taken in July 1925, on Western Bank, southwest of Sable Island, by the schooner *Falmouth* (Radcliffe, 1926), while another of about the same size stranded on the beach at Hyannis, Mass., on September 17, 1928.

Johnson's sea bream, *Taractes princeps* Johnson

A fish taken on Browns Bank, off Cape Sable in January 1928 is the first record of this species for the western Atlantic. This bream previously was known only from Madeira, in the eastern Atlantic. For a detailed account and comparison with allied species see Bigelow and Schroeder (1929).

Butterfish, *Poronotus triacanthus* (Peck)

Recent records show that the northward range of this species extends to the east coast of Newfoundland, as well as to Nova Scotia as has long been known.

It now seems well established that the butterfish actually withdraw from the gulf when they disappear in the autumn, as they do from the immediate shore waters farther south, and from inland waters such as Chesapeake Bay. Until very recently the winter home of the butterfish was unknown; but as they are now often taken in the winter otter trawl fishery recently established off the coast between Chesapeake

[8] This species was given as *Lampris luna* (Gmelin) by Bigelow and Welsh (1925, p. 242).

Bay and Cape Hatteras, it appears that they move out to sea to winter on the outer part of the continental shelf as do several other common Gulf of Maine fishes.

The illustrations of larvae 2.1 and 3.4 mm long credited by Kuntz and Radcliffe (1918) to the butterfish and reproduced by Bigelow and Welsh (1925, fig. 116, *c* and *d*) have since been proved to belong to one of the hakes.

Harvestfish, *Peprilus alepidotus* (Linnaeus)

Five or six specimens were reported caught in floating traps at Richmond Island, off Cape Elizabeth, Maine, in July 1929, while another was taken at the mouth of the Damariscotta River, Maine, in August 1933, the most northerly record for the species.

Striped bass, *Roccus lineatus* (Bloch)

The striped bass considerably increased in abundance along both shores of Cape Cod between 1928 and 1932, then decreased again as illustrated by the following catches reported for Barnstable County, Mass.: 1928, 8,060 pounds; 1929, 18,665 pounds; 1930, 27,385 pounds; 1931, 33,600 pounds; 1932, 30,926 pounds; 1933, 4,500 pounds. Anglers as well as commercial fishermen have also caught some numbers along the Eastham-Chatham Beaches and marshes during the past few years, while a 44¾ pound bass was caught near Brant Rock on the southern shore of Massachusetts Bay, in November 1930. A small stock seems also to have built up in the brackish tributaries of Plum Island Sound north of Cape Ann, for some were taken in Parker River by anglers during the few years previous to 1930, while in that year (when fishing restrictions were relaxed) 8,700 pounds were reported thence, though smaller numbers since then. But this increase did not extend northward beyond Massachusetts waters, for the commercial reports from the States of New Hampshire and Maine did not mention bass at all in 1924, or in 1928–33.[9]

Striped bass so rarely stray away from the immediate shoreline that it is of interest to mention the capture of a 6-pound fish in a gill net on Cod Ledge, 3 or 4 miles off Cape Elizabeth, Maine, October 15, 1931.

Sea bass, *Centropristes striatus* (Linnaeus)

Sea bass are seldom taken within the Gulf of Maine, and even on the southern New England coast are rarely caught later than early November, hence the reported capture of a 5-pound fish in December 1930, 5 miles east of Pollock Rip Lightship, in 24 fathoms, is noteworthy.

Triggerfish, *Balistes carolinensis* Gmelin

Previous to 1925, only one specimen of the trigger fish had been reported from the Gulf of Maine. Actually, this species must drift over the offshore rim of the gulf more often than the paucity of early records would suggest, for a specimen was recorded from Casco Bay in August 1931; another was taken in 1932 near Plymouth; a third, 15 inches long, was gaffed at the surface, on the southeast part of Georges Bank, from the fishing vessel *Huntington Sanford*, in July 1929; and two small fry, 2 to 3 inches in length, were picked up on the northeast part of the bank in mid-September 1927, by the *Albatross II*. The fact that these last were taken with gulf weed (Sargassum) suggests that triggerfish are most apt to appear on the banks with the latter.

[9] No statistics are available for 1925–27.

Filefish, *Monacanthus hispidus* (Linnaeus)

The filefish appears in the inner parts of the gulf only as a stray from warmer seas, recent records being that of a fish taken off Seguin, September 12, 1929, one off Portland lightship, July 17, 1931, and a 6-inch fish at Provincetown, November 6, 1929. On the offshore banks, however, it is to be expected more frequently (which accords with its southern origin) for the *Albatross II* gathered 181 small fry 1 to 2 inches long, on the northeastern part of Georges Bank among floating gulf weed (Sargassum) in September 1927; while a larger one was picked up to the southeast of Cape Cod in that same month of 1930.

Filefish, *Monacanthus ciliatus* (Mitchill)

A 7-inch fish taken in a Provincetown trap in November 1929 is the second (and only recent) record of this species within the Gulf of Maine (Firth, 1931, p. 13). A straggler has been reported, however, from Newfoundland—far to the north of its previously known range.

Unicornfish, *Alutera scripta* (Osbeck)

Two specimens of this fish, 5 and 5½ inches long, respectively, caught on the western edge of Georges Bank, constitute the first Gulf of Maine record (Mac Coy, 1931a, p. 16).

Puffer, *Spheroides maculatus* (Bloch and Schneider)

A specimen taken off Long Island, Portland Harbor, on July 24, 1933, is the first to be recorded from the northern boundary (Casco Bay) of this species since 1896.

Rosefish, *Sebastes marinus* (Linnaeus)

It is now known that rosefish may be born in the Gulf of Maine as early as the end of April, for in 1930 we saw gravid females during the last half of that month. In July 1931 the *Albatross II* trawled many gravid females, 10 to 13½ inches long, in the central basin of the gulf; one of these, 13 inches long, contained approximately 20,500 young 6 to 7 mm long, ready to be spawned.

The fact that we obtained many young fish 2½ to 5¾ inches in length, off the coast of Maine from April to August, suggests that this is the approximate size attained during their first year of life.

Recent catches of 75–625 rosefish per haul in a trawl by the *Atlantis* in 70–130 fathoms in the western and northeastern parts of the gulf are evidence of the abundance of this species over the soft bottoms of the basins, as well as in other parts of the gulf. The commercial importance of this species has greatly increased of late, the reported landings having risen from 1,288,000 pounds in 1934 to 14,100,000 pounds in 1935.

Black-bellied rosefish, *Helicolenus dactylopterus* (De la Roche)

A fish 13 inches long, trawled on the eastern edge of Georges Bank in 150 fathoms, October 6, 1929 (Firth, 1931, p. 13), is the first record for this species within the Gulf of Maine. In addition to previous records from outside the gulf, a number of small fish (1¼ to 3½ inches) were trawled off southern New England in 80 to 118 fathoms during 1930.

Hook-eared sculpin, *Artediellus uncinatus* (Reinhardt) [10]

This sculpin is now known to be generally distributed in the Gulf of Maine in depths greater than 20 to 30 fathoms. Thus, in addition to the Massachusetts Bay records of many years ago, we have recently taken it repeatedly near Mount Desert, off Cape Elizabeth, near Jeffrey's Ledge, around Cashes Ledge, along the northern slopes of Georges Bank, in the southeastern part of the basin of the gulf, and at the entrance to the deep gully between Georges and Browns Banks, in depths ranging from 20 to 150 fathoms. Individual hauls have yielded up to six or eight specimens, both on hard and on soft bottom.

After examining specimens from New England waters and comparing published drawings of European fish, we can find no major differences between the hook-eared sculpins of the eastern and western Atlantic.[11]

Mailed sculpin, *Triglops ommatistius* Gilbert

This sculpin is not as rare in the Gulf of Maine as was formerly supposed, for during the past few years we have trawled specimens near Mount Desert, in Massachusetts Bay, off Cape Ann, off Cape Cod, and around the northern slope of Georges Bank, in depths of 20 to 140 fathoms, in various months from spring to autumn. The most southerly locality was about 10 miles east of Chatham.

Longhorn sculpin, *Myoxocephalus octodecimspinosus* (Mitchill)

Numerous young specimens 1½ to 2 inches long taken in September, and 3 to 3½ inches in February, suggest that the longhorn sculpin is about 2 to 3 inches long at 1 year of age, spawning as it does in late fall.

Deep-sea sculpin, *Cottunculus microps* Collett

A specimen, about 2 inches long, trawled by the *Albatross II* on the northern slope of Georges Bank, in a depth of 120 fathoms, on July 24, 1931, is the third record for the Gulf of Maine proper.

Sea raven, *Hemitripterus americanus* (Gmelin)

The fact that fish of both sexes with gonads only partially developed have recently been found on Nantucket Shoals late in June, added to previous captures of ripe females off southern New England in November and December shows this to be a late fall and early winter spawner. The sea raven is a prolific fish, for a female 20 inches long that we caught off Boothbay Harbor, Maine, in April 1925, contained about 10,000 eggs. The fact that these were definitely of two sizes, the smaller averaging 1.5 mm in diameter, the larger about 3 mm, raises the interesting question whether individual sea ravens may spawn more than once during the year.

The sizes of the few young sea ravens that have been taken in the Gulf of Maine suggest that they reach a length of 2 to 4 inches by the middle of the first summer, when 6 to 8 months old; and about 6 inches by the following April, at an age of 1½ years.

[10] Given as *Artediellus atlanticus* Jordan and Evermann by Bigelow and Welsh (1925, p. 314).

[11] Jordan, Evermann, and Clark (1930, p. 377) in the Check List of Fishes placed *Artediellus atlanticus* Jordan and Evermann in the synonymy of *A. uncinatus* Reinhardt.

Sea snail, *Neoliparis atlanticus* Jordan and Evermann

The sea snail, previously unknown offshore, has recently been taken on Georges and on Browns Banks. Its range has recently been found to extend as far southward as the offing of Atlantic City, N. J. (Lat. 39°20'N.). Most of the specimens were found living in scallop shells (*Pecten magellanicus*), as is so often the case.

Striped sea snail, *Liparis liparis* (Linnaeus)

This sea snail was formerly known as far southward as New York but the *Albatross II* has taken it off Delaware Bay and the *Grampus* off Assateague, Va. (Welsh, 1915, p. 2).

Red-winged sea robin, *Prionotus strigatus* (Cuvier)

A specimen was taken off Monhegan, Maine, in 40 fathoms, in an otter trawl November 19, 1933. This is the most northerly record for this straggler in the Gulf of Maine.

Remora, *Remora remora* (Linnaeus)

Recent Gulf of Maine records of this species include one found on the bottom of a lobster trap in Portland Harbor in 1931, probably brought in by a schooner from the West Indies; one found sucking to the gills of a blue shark (*Prionace glauca*) that was caught on the northeast edge of Georges Bank, August 1, 1931; one in Cape Cod Bay in September 1934, and one off Provincetown in August 1935, taken by C. W. Lowes on blue sharks; also two specimens, 6 and 17 inches long, respectively, taken on August 3, 1932, 220 miles east-southeast of Cape Ann. Previously it had been recorded only once from the Gulf of Maine.

Rock eel, *Pholis gunnellus* (Linnaeus)

Recent records show that the rock eel occurs in considerable numbers on the offshore banks in the Gulf of Maine down to at least 40 fathoms and occasionally even to 100 fathoms (Schroeder, 1933, p. 5) as well as inshore. So many have been found in the stomachs of cod and pollock caught on Nantucket Shoals, Georges Bank, Browns Bank, Cashes Ledge, etc., that it must be an important food of these two species.

The range of the rock eel recently has been found to extend south to the latitude of Delaware Bay, where in February 1930 *Albatross II* trawled two specimens in 23 and 38 fathoms, respectively.

Snake blenny, *Lumpenus lampetraeformis* (Walbaum)

Recent captures, by *Albatross II*, of adult snake blennies (one specimen each) off Mount Desert, off Boone Island, and on Stellwagen Bank, in depths ranging from 28 to 88 fathoms, added to earlier records from Massachusetts Bay and from the Bay of Fundy region, show that this species is generally distributed over the gulf, as records of its larvae had suggested. So slender and active is this fish that it can easily escape through the meshes of any of the nets used by commercial fishermen, hence it is seldom reported.

Color notes taken from a 12-inch specimen are as follows: The body had brown markings on a whitish ground, the head being pale brown. The dorsal fin was marked obliquely with 18 pale bars, the caudal transversely with 8. The anal rays were pale brown against a colorless membrane, the ventrals white, while the pectorals were tinged with brown.

One of 19 inches caught on the eastern slope of Stellwagen Bank in 42 fathoms in July 1931 is the largest on record.

Shanny, *Leptoclinus maculatus* (Fries)

One specimen of this stray from the north was trawled on the northeast part of Georges Bank in August 1926 and four (4 to 4½ inches long) were taken off Chatham, Cape Cod, in 28 fathoms, May 1, 1930, by the *Albatross II*. This is the most southerly record for the species.

Arctic shanny, *Stichaeus punctatus* (Fabricius)

A specimen 4½ inches long of this arctic species, taken one-half mile off Little Duck Island near Mount Desert, Maine, from the stomach of a cod, on April 30, 1930, is the first record for the Gulf of Maine; the only record indeed to the southward of Newfoundland. This specimen was in such good condition that it unquestionably had been living in the immediate vicinity.

Radiated shanny, *Ulvaria subbifurcata* (Storer)

This shanny was previously known to be rather common in the northeastern part of the gulf, and enough have now been found in the stomachs of cod caught on Cashes Ledge, Georges Bank, Nantucket Shoals, and other offshore grounds to show that it is widespread in other parts of the gulf as well, on hard bottom. The deepest capture was in 45 fathoms.

Wrymouth, *Cryptacanthodes maculatus* Storer

Recent captures of two specimens in the central basin of the Gulf of Maine, July 1931, in 88–95 fathoms, of three in August 1936, in 72–100 fathoms, and of another on the continental slope between 245 and 325 fathoms, shows that this species is not as closely restricted to the vicinity of the coast as previously supposed and that it reaches considerably greater depths.

The locality of the capture (taken by *Atlantis*) last mentioned (lat. 39°31′ N; long. 72°16′ W.) also extends the known range somewhat farther south.

Spotted wolffish, *Anarrhichas minor* Olafsen

This Arctic species is seldom taken within the Gulf of Maine, hence the capture of a small specimen, weighing 3¼ pounds, on a trawl, off Portand Lightship on April 23, 1927, is worthy of mention. On the Scotian banks, however, it is not so uncommon, for we have records of 2, 37 and 54 inches long, respectively, caught on Sable Island Bank in January 1934 and 5 more in March of that year. Usually about 5 to 10 from this general region are landed each year at the Boston Fish Pier.

Eelpout, *Zoarces anguillaris* (Peck)

Many small specimens from 1.8 inches long upward, have recently been collected along our coast between Maine and New Jersey, including (within the gulf) Mount Desert, Stellwagen Bank, Georges Bank, and the vicinity of Chatham, suggesting that the eelpout breeds successfully throughout this range. And as all the young thus far taken have been caught in depths of 20 to 45 fathoms, probably this is the usual spawning zone. Although eelpouts have seldom been reported deeper than 50

fathoms, *Albatross II* recently (July 1931) trawled a number in the basin of the gulf as deep as 90 fathoms.

The sizes, in different months, of the young fry show that eelpouts in the Gulf of Maine grow to a length of about 2 inches in the first 6 months of their lives, and 3 inches in 9 months, agreeing in this respect with the growth-schedule of Bay of Fundy eelpouts derived by Clemens and Clemens (1921, p. 74) from the annual rings on the otoliths. Small specimens 5 to 6½ inches long taken from February to May are probably about 1½ years old.

Young eelpouts, up to 3 or 4 inches long, are checkered along the sides, and irregularly blotched on the back with light and dark brown, with a small but prominent black spot, which fades out with growth, on the anterior part of the dorsal fin.

Wolf eel, *Lycenchelys verrillii* (Goode and Bean)

The recorded range of the wolf eel, previously known only off the coasts of New England and Nova Scotia, has now been extended southward to the offing of New York (Beebe, 1929, p. 18).

The wolf eel is more common within the Gulf of Maine, in deep water, than was formerly supposed, for in the autumn and summer of 1928 and 1930 the *Albatross II* trawled 61 specimens, 6 to 6½ inches long, in the deep basin to the westward of Jeffreys Ledge, in about 90 fathoms of water. It was also found scattered over the central basin of the gulf, in July 1931, in 95 to 123 fathoms.

Silver hake, *Merluccius bilinearis* (Mitchill)

The wintering ground of the Gulf of Maine stock of silver hake has been the subject of so much speculation that the capture by the *Albatross II*, of many specimens between the offings of No Mans Land and off Cape Hatteras in depths ranging from 12 to 146 fathoms, in February 1930 at temperatures of 4.2° to 10.6° C. (39.5° to 51° F.), deserves mention. Such wide ranges of temperature indicate that the silver hake are well distributed on these offshore grounds during the winter.

Young fish are rarely found close to shore within the gulf. Offshore, however, the *Albatross II* and *Atlantis* have trawled large numbers between 2 and about 8 inches long in widely scattered localities and in depths ranging from 20 to 115 fathoms.

Measurements of young silver hake,[12] recently obtained in the Gulf of Maine indicate that a length of 6–7 inches is attained at about 1 year of age.

Pollock, *Pollachius virens* (Linnaeus)

Recent tagging experiments verify the earlier view that the pollock which appear in the cold months of the year off New York and New Jersey are winter migrants from the region of Nantucket Shoals. In general the pollock in the Gulf of Maine are not migratory although occasional fish may make long journeys.

Cod, *Gadus callarias* Linnaeus

Extensive tagging experiments (Schroeder, 1930) have proved that the appearance of cod in winter southward along the coasts of New York and New Jersey in commercial quantities represents a regular annual mass migration from Nantucket Shoals followed by a return migration in spring. But only scattering fish join this

[12] Several hundred specimens.

winter migration from the more northerly and easterly parts of the Gulf of Maine. It has been known that many of these cod spawn on the southern wintering grounds, but it was not until the spring of 1930 that large numbers of fry were obtained there. At that time (April) *Albatross II* trawled hundreds of fry 1½ to 2½ inches long on bottom, the most southerly catch being in latitude 36°21′ N.[13]

Haddock, *Melanogrammus aeglefinus* (Linnaeus)

The haddock, formerly unknown beyond the Straits of Belle Isle, in the western Atlantic, has now been reported from West Greenland (Jensen and Hansen, 1930, p. 52). From Icelandic waters comes a record of a giant haddock 44 inches long and weighing about 37 pounds (Thompson, 1929, p. 29).

Long-finned hake, *Urophycis chesteri* (Goode and Bean)

The capture of several specimens on the northern edge of Georges Bank in September 1929, in 85 to 100 fathoms, and of many to the westward and in the central basin of the Gulf of Maine the summer of 1931, in 70 to 140 fathoms, suggests that this species is more plentiful in the gulf than was previously supposed.

This hake is said to be a summer spawner but very little is known concerning its rate of growth, hence we report captures of 3 fish 57 to 71 mm on April 26, 1931, and of 16 fish of 74 to 110 mm taken late in July, suggesting that a length of 4 or 5 inches is reached at 1 year of age.

Spotted hake, *Urophycis regius* (Walbaum)

The scarcity of this hake within the Gulf of Maine is emphasized by the fact that not a single one was captured there in the numerous hauls made recently by the *Albatross II*. To the southward, however, many were trawled between Cape Hatteras and the offing of Delaware Bay in 5 to 45 fathoms (chiefly in less than 20 fathoms) from February to May 1930 and 1931.

Although the spotted hake reaches a length of at least 16 inches, large fish are relatively rare. The longest of about 600 specimens taken on 14 stations by the *Albatross II* was only 130 mm (5⅛ inches). In the largest catch (Apr. 8) the dominant size was 2 to 2½ inches.

Four-bearded rockling, *Enchelyopus cimbrius* (Linnaeus)

The rockling has recently (July 1931) been trawled in the central basin of the Gulf of Maine where it was expected, but heretofore unrecorded. The fact that one was taken in latitude 36°56′ N., off Cape Charles, Va., on February 10, 1930, in only 12 fathoms, shows that in the most southerly parts of its range, it is not restricted to deep water, as previously supposed.

Cusk, *Brosme brosme* (Müller)

A fish 40 inches long and weighing 27 pounds, trawled by *Albatross II* in the central part of the Gulf of Maine, in 120 fathoms, is the largest definitely recorded from the Gulf of Maine.

[13] These were taken during the course of O. E. Sette's mackerel investigations.

Common grenadier, *Macrourus bairdii* Goode and Bean

Recent records show that the grenadier is comparatively common on muddy bottom in the gulf, at depths greater than about 90 fathoms and that it may occasionally be taken shoaler, for one was reported from the slope of Jeffreys Ledge in about 50 fathoms during March 1934. The capture of a ripe male in late September verifies the earlier suggestion that the grenadier is an autumn spawner. The largest fish taken by *Albatross II* was 16 inches long. This grenadier has now been taken as far eastward as the Grand Banks of Newfoundland (Nfld. Rpt., 1933 (1934), p. 116).

American plaice, *Hippoglossoides platessoides* (Fabricius)

Recent trawling by *Albatross II* and *Atlantis* proves this species to be generally distributed even in the deeper parts of the central basin of the gulf, to a depth of at least 120 fathoms. A specimen 15½ inches long caught off Montauk Point, N. Y., in 112 fathoms, February 6, 1930, is the most southerly and westerly record.

As this flounder is a spring spawner it may be assumed that bottom stages 69 to 80 mm long trawled off Cape Cod, May 1, were about 1 year old, and 85 to 118 mm fry found at several localities in July and August were between 1¼ and 1½ years old, those of 8–10 inches, 2¼ to 2½ years.

Four-spotted flounder, *Paralichthys oblongus* (Mitchill)

This flounder, formerly thought rare to the east of Cape Cod, has recently been found here and there on the southern half of Georges Bank. Previously known only as far southward as New York, many have been trawled by the *Albatross II* south to the Virginia Capes (lat. 36°45′ N.).

The fact that captures were made in 23 to 112 fathoms in February (7 stations), 31 to 52 fathoms in March (two stations), 10 to 85 fathoms in April (eight stations), 15 to 35 fathoms in May (four stations), 11 to 47 fathoms in June (five stations), and 41 fathoms in July (one station) indicates that it is present and widely distributed in this general depth zone the year round.

The capture of ripe specimens as late as mid-July shows that the breeding season is not limited to spring, as formerly supposed, but extends well into the summer.

Rusty dab, *Limanda ferruginea* (Storer)

Capture of a specimen, in the offing of Hog Island, Va. (lat. 37° 41′ N.) considerably extends the known range to the southward. The captures of young dabs 2 to 4 inches long in February (17 fish), 2¼ to 4½ inches in April (26 fish), 2⅓ to 5⅔ inches in May (10 fish), 3 to 5 inches in June (3 fish) and 3 to 6⅓ inches in July (13 fish) yield the first data as to rate of growth. According to this growth schedule the rusty dab reaches a length of approximately 5 inches at 1 year of age.

Winter flounder, *Pseudopleuronectes americanus* (Walbaum)

The recovery, off Chatham and on Nantucket Shoals, of winter flounders tagged and released at Woods Hole proves that some of them, at least, may wander for longer distances than previously supposed.

Georges Bank flounder, *Pseudopleuronectes dignabilis* Kendall

This flounder, previously known only from the Georges Bank area, is now reported from the eastern edge of the Scotian banks and the western part of the Grand Banks of Newfoundland (Nfld. Rept., 1934 (1935), p. 79).

Witch flounder, *Glyptocephalus cynoglossus* (Linnaeus)

The witch flounder has recently been found to be generally distributed in the central basin of the Gulf of Maine where the *Albatross II* and *Atlantis* trawled it down to 140 fathoms, in July 1931 and in August 1936, respectively. Goode and Bean's (1896, p. 433) record of it in latitude 34°39′ at a depth of 603 fathoms (omitted in Bigelow and Welsh, 1925) shows that it ranges southward to the offing of Cape Hatteras in deep water. But the most southerly record of it in shoal water is a specimen taken by *Albatross II* in 10 fathoms off Virginia (lat. 37°50′).

Many specimens from 3 to 5 inches and from 7 to 8½ inches long were taken from July to September suggesting that the witch reaches a length of about 4 inches at 1 year and about 8 inches at 2 years of age.

Gulf Stream flounder, *Citharichthys arctifrons* [14] Goode

This little flounder was formerly believed to reach a length of only about 4 inches but recently the *Albatross II* collected many specimens up to 7 inches long.

Recent trawling experience extends knowledge of its distribution by showing that it may occur as shoal as 12 fathoms, and that it finds its northeastern boundary off the southeastern slope of Georges Bank and its southwestern boundary off Cape Hatteras. Usually only a few specimens are taken in any given trawl haul, even further to the west and south where the species appears to be most common; hence, a catch of about 100 made by the *Albatross II*, off Montauk Point, N. Y., in 50 fathoms, is noteworthy.

Apparently, it spawns over a long season, from spring through summer, for we have found females with well-developed ovaries in February while Goode had ripe ones in September. Although the Gulf Stream flounder is not large enough and thus far has been found too scarce to be of commercial value, we can witness that it is excellent on the table.

American goosefish, *Lophius americanus* Cuvier and Valenciennes

Recent investigations by Berrill (1929) and by Procter et al. (1928) make it appear that the American goosefish, given as *Lophius piscatorius* in "Fishes of the Gulf of Maine" (Bigelow and Welsh, 1925, p. 524), is specifically distinct from the European.

Very small goosefish are seldom reported, hence captures of 1 of 10 inches in February, 1 of 10 inches in April, 2 of 7½ and 10 inches, respectively, in May, 3 of 6¾ to 9 inches in July, and 3 of 4 to 4¼ inches in August between latitudes 43°21′ N. and 37°36′ N. in depths ranging from 35 to 140 fathoms, are of interest.

Sargassum fish, *Histrio histrio* (Linnaeus)

A single specimen about 4¾ inches long, picked up in a purse seine near the surface over the west central part of Georges Bank, by the schooner *Old Glory* on September 15, 1930 (Firth, 1931, p. 14), extends the known range of this fish to the Gulf of Maine.

[14] Parr (1931) has made a revision of the genus *Citharichthys* of the western Atlantic.

Deep-sea angler, *Mancalias uranoscopus* (Murray)

A 24½-inch specimen of this uncommon fish was trawled on Georges Bank February 9, 1927, by the fishing steamer *Ripple;* this is the only record of a member of this family (Ceratiidae) from New England waters (Parr, 1932, p. 12).

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ADAPTATION OF THE FEEDING MECHANISM OF THE OYSTER (*Ostrea gigas*) TO CHANGES IN SALINITY

By A. E. Hopkins

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 21

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1936

For sale by the Superintendent of Documents, Washington, D. C. - - - - - - - - - - - - - - - - - - Price 10 cents

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By A. E. HOPKINS, Ph. D., *Aquatic Biologist, United States Bureau of Fisheries*

CONTENTS

	Page
Introduction	345
Material and methods	346
Description of experiments	347
Series I	348
Series II	350
Series III	351
Series IV	353
Series V	355
Series VI	356
Series VII	356
Discussion	360
Summary	362
Literature cited	363

INTRODUCTION

Natural beds of oysters are found characteristically in such inshore waters as the coastal estuaries and bays in which there is a considerable dilution of the ocean water by land drainage. Prytherch (1934), in an extensive monograph describing an experimental study of the ecology of *Ostrea virginica*, concluded that successful propagation of oysters depends upon the presence in the water of copper ions required by the swimming larvae before attachment, or setting, may take place. In nature the copper is introduced into sea water in solution in the fresh water of rivers, thereby locating natural oyster grounds where they are subject to frequent changes in salinity.

Referring to *O. virginica*, Churchill (1920) stated:

> Oysters are found in water ranging in density from 1.002 to 1.025 (about 2.5 to 33.0 parts per mille), but cannot withstand densities lower than 1.007 (9 parts per mille) for indefinite periods. In general they seem to thrive best in densities between 1.011 and 1.022 (14.36 to 28.80 parts per mille).

This range apparently refers to areas in which natural oyster beds are located, or those areas in which propagation takes place.

The feeding activities, however, may not be most efficient at the same range of salinity or density as in the case of propagation. It may frequently be observed that oysters grown on those grounds where seeds are caught most effectively do not fatten as well as those grown in different areas. Oyster growers typically catch seeds in one place and transplant them to localities which experience has shown to be favorable for

[1] Bulletin No. 21. Approved for publication June 4, 1936.

fattening. It appears possible that salinity may be one of the important factors influencing the feeding of oysters.

The gills of oysters, by means of cilia, pump a stream of water from which food particles are filtered and passed along definite grooves to the labial palps, which convey them to the mouth (Nelson, 1923b). The rate at which water is pumped was used by Galtsoff (1928) as a criterion of the rate of feeding under different conditions of temperature. Nelson (1921, 1923a) kept records of the opening and closing of oysters immersed in the open bay along with those of temperature, salinity, turbidity, etc. He concluded that the oyster feeds most rapidly on the flood tide even when the density is approximately the same as during ebb tide. He concluded also that for *O. virginica* a density of 1.008 (10.42 parts per mille) is the lowest at which feeding will go on, and that the minimum density required varies in proportion to that of the water in which the oysters have been grown. His method, however, was to study the opening or closing of oysters under different conditions, judging an open specimen as actively feeding. But, as will be shown below, an oyster may be open without feeding, though clearly when it is closed feeding is impossible.

The mechanism of physiological adaptation to changes in salinity is not the question primarily discussed in this paper. This study deals with the pumping activity of the gills as influenced by salinity, although it is realized that final explanation of the results is a matter of cellular physiology.

MATERIAL AND METHODS

Because of their relatively large size, specimens of *Ostrea gigas* are most favorable material for experimental study. This species is imported from Japan as small seeds and grown in various waters of the Pacific coast. In portions of Puget Sound propagation occurs, and the resulting well-shaped, large oysters were used in these tests.

The method employed has already been described (Hopkins, 1933). A simple lever, resting with the least possible weight upon the upper (right) valve of the specimen, served to record on a kymograph paper the position and movements of the valves, as affected by activity of the adductor muscle. A paper cone, thoroughly waterproofed with a solution of celluloid in acetone, attached to a system of levers made of lightweight straw, was placed so that all water pumped by the gills struck the cone. The recording tip of the straw was made of a sliver of cellophane, and this made its record on the kymograph paper directly below that of the lever recording shell movements. Fixed levers continously recorded the zero positions—the closed position of the shell and the level of cessation of pumping by the gills.

Since the salinity of the water had to be maintained at a constant level, it was necessary to employ a method for continuous aeration and circulation. For this purpose small centrifugal pumps, made of celluloid (Hopkins, 1934) were used. Two of these pumps were used to circulate and aerate the water, without causing any strong currents which might disturb either the oyster or the mechanism for recording the relative rate at which the gills pump. An extra aquarium was interposed between the experimental chamber and the pumps for the control of temperature. In this aquarium either an electric-light bulb or an immersion heater was so controlled that the temperature in the experimental chamber was maintained during all tests at between 17° and 19° C. This temperature level was chosen because it had been previously determined (Hopkins, 1933, 1935) to be most favorable for stability of

the adductor muscle, resulting in the shells remaining at almost their optimum degree of openness. At 20° C. or above the valves tend to become more closed, although the gills themselves pump more rapidly up to between 27° and 28° C.

The salinity of the running water at the laboratory varied generally between 26 and 29 parts per mille. Water of a lower salinity was prepared in a tank, large enough for several changes of water in the experimental aquaria, by mixing the laboratory water with pure spring water. Control tests showed this method to be adequate, for specimens behaved identically in bay water of salinity 28 parts per mille and in water of the same salinity made by mixing spring water and concentrated bay water.

The water level in the experimental tanks was marked so that occasional small additions of spring water prevented more than very slight changes in salinity due to evaporation. The pH of the water varied only slightly, between 7.7 and 8.0, in harmony with that of water on the oyster grounds.

Specimens for experimentation were always kept in the running sea water of the laboratory for several days or weeks before use. During the first one or more days after being placed in the experimental aquarium, a specimen was tested in water of approximately the same salinity as the running laboratory sea water. In making a change of water, of either the same or a different salinity, the water was drained from the experimental tanks, which were then flushed out thoroughly with the new water before being filled to the correct level. To save time, the new water was warmed to the experimental temperature (17°–19° C.) before being siphoned in.

Some specimens were mounted upon a base of plaster of paris and sand, while others were set rigidly upon a small celluloid frame. No ill effect of the plaster of paris was noted.

After completion the kymograph papers were marked off exactly into 5-minute periods for analysis. Planimeter measurements were made of the area enclosed between the record line and the reference line during each 5-minute period. These measurements are considered in the following descriptions as representing S (the degree of openness of the shell) and F (the relative rate of flow of water through the gills) during each 5-minute period.

DESCRIPTION OF EXPERIMENTS

These experiments were started for the purpose of determining whether there is any relationship between salinity and the rate at which water is pumped. It was thought that adaptation to a change in salinity would occur quite quickly, since in their natural environment oysters are subject to frequent and sometimes extreme salinity variations, and it was planned to make a change, allow the pumping mechanism to reach a stable level of activity, then to change again. In this manner it was hoped that sufficient values might be obtained to permit graphical analysis of the relationship between salinity and the rate of feeding.

It soon became evident, however, that such a procedure would require a long period of time, even with only one specimen. Adaptation was found to be extremely slow, and the variations in degree of openness of the valves and in rate of pumping are so great even under conditions of constant salinity and temperature that any test would have to be carried on for many days, or even weeks. It was, therefore, decided to attack the problem by making a study of the process of adaptation following changes in salinity with respect to shell movements and gill activity.

The nature of the results and the different lengths of time during which specimens were subject to water of different salinities make it impossible to present the data obtained in any manner other than by description of the tests with each specimen. Seven such series are described below.

SERIES I

This was the first specimen on which detailed experiments were performed. The salinity at the beginning was 29.40 parts per mille and records were kept for thirty-seven 5-minute periods, or 185 minutes. Then, on the same day, the salinity was lowered to 26.96 parts per mille and the activity recorded for the next 205 minutes, or forty-one 5-minute periods. The records taken at the two salinities (table 1, series I) are closely similar, although the averages in the former case are S, 8.53; F, 6.45; and in the latter case, S, 7.13; F, 5.40. Obviously the results are inadequate for comparison because of the short duration of exposure to each medium.

On the following day the salinity was lowered still further to 24.03 parts per mille and records kept for forty-seven 5-minute periods. The low F values during early treatment at this salinity, as shown in the table, indicate a marked effect of the change, though later values appear to be in harmony with those obtained at the original higher salinities.

The effect of lowering the salinity is more strikingly shown in the tests of the next 2 days (Nov. 9 and 10), after changing the salinity from 24.03 to 17.76 parts per mille. Although during the first day the shell remained approximately as wide open as previously, only a feeble stream of water was pumped by the gills. In figure 1 the consecutive 5-minute values are shown graphically, to illustrate the slow

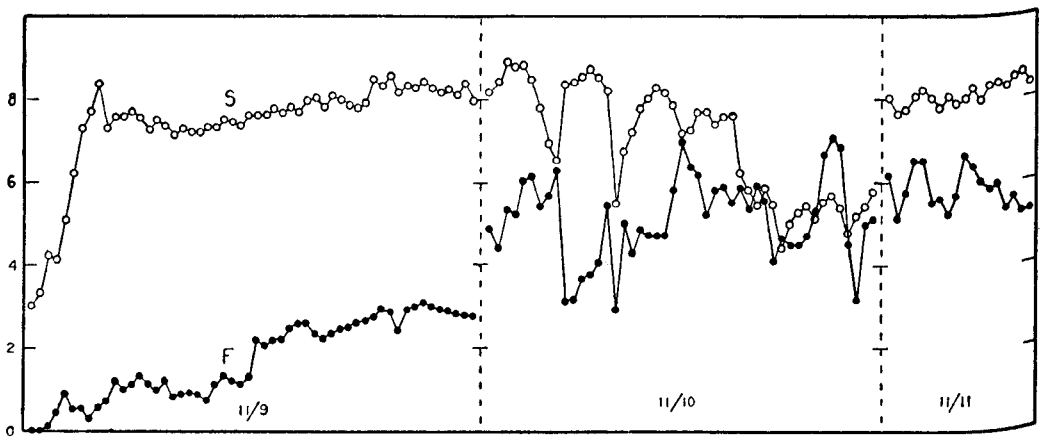

FIGURE 1.—Values of *S* and *F* showing adaptation during 3 days to a salinity of 17.76 p. p. m. following a change from 24.03 p. p. m. Series I. 17°–19° C.

adaptation of the gill mechanism (F) while the valves (S) quickly recovered their normal degree of openness. It is doubtful that adaptation was completed even after more than 2 days. However, the salinity was changed (Nov. 11) to 28.50 to test adaptation to a rise in salinity. Records were kept on the first day for fifty-four 5-minute periods. Within a very short time after the change, the values of F rose almost to normal, though not until the next day did the shell open wide enough to permit completely normal gill activity.

After the specimen had been in this water for 4 days the salinity was again lowered to 22.20 parts per mille. Adaptation to this change was relatively rapid,

occupying but a few hours. On the following day the medium was changed to a salinity of 29.46, and adaptation was almost immediate.

During the preceding tests it appeared that adaptation to a considerable change in salinity is a very slow process, much of which occurs between the recordings on consecutive days. In order to obtain records of as many details as possible of the early stages of adaptation, the salinity was reduced to 14.60 parts per mille and during the following 12 hours records were taken which provided one hundred and twenty-five 5-minute periods. In figure 2 the results are given in detail for the

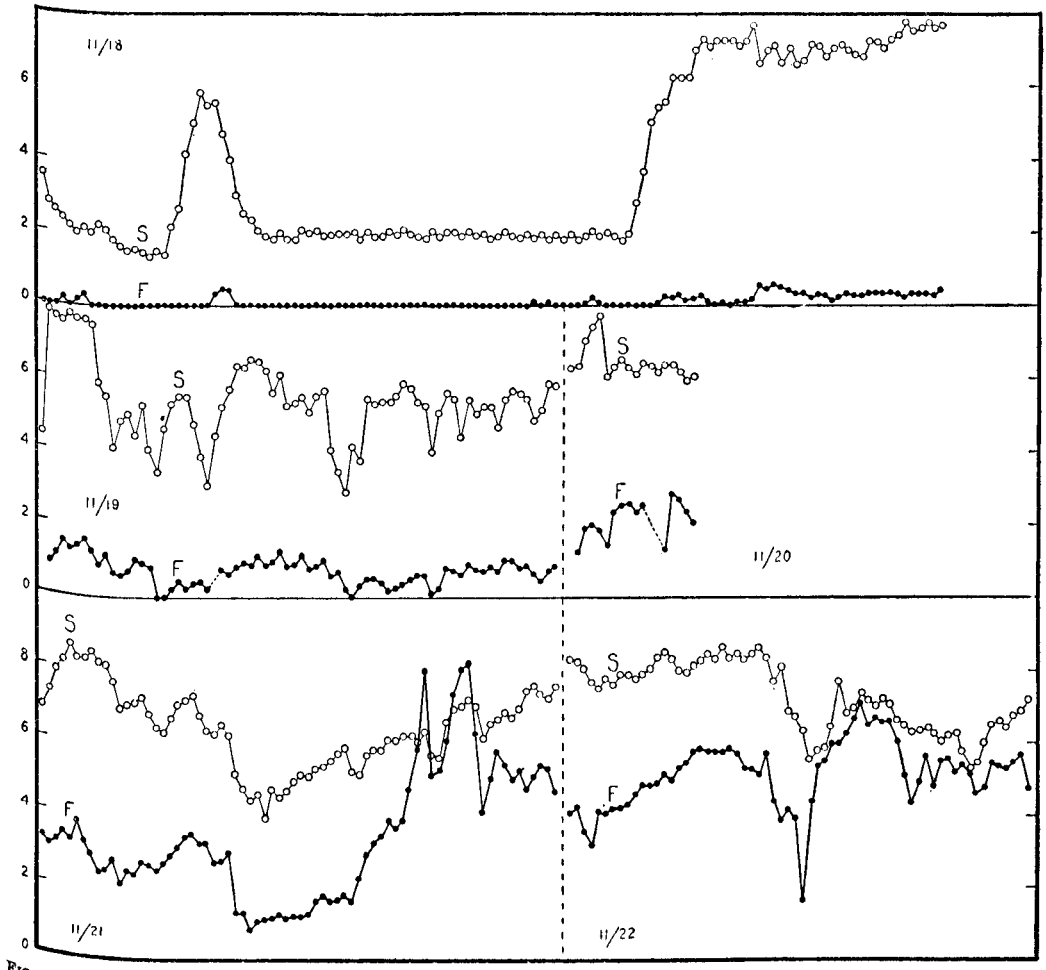

FIGURE 2.—Adaptation to salinity of 14.60 p. p. m. following a change from salinity of 29.46 p. p. m. Series I. Values of *S* and *F* refer to consecutive 5-minute periods. 17°–19° C.

5 days during which this salinity was used. For the first 8 hours (Nov. 18), with minor exceptions, the valves remained relatively close together, and almost no water was pumped. During the following hour the shell consistently became wider open and the gills produced a slight flow of water. Recording was continued for several hours more, but the rate of flow increased very little. However, during the following 4 days the gills steadily recovered, though large variations both in rate of flow and in degree of openness of the valves may be noted. Even after 5 days of treatment recovery could not be called complete, for the values of F never reached the

previous levels. (See series I, table 1.) When the salinity was then raised to 28.56 the specimen became adapted to a comparable level within a few hours.

SERIES II

Preliminary tests in a salinity of 28.87 parts per mille were carried on only during 1 day (thirty-six 5-minute readings), although it later appeared that they should have been continued for several days more (series II, table 1). When the salinity was changed to 22.70 parts per mille for 2 days and then to 28.74 parts per mille, the correct level of adaptation was reached. After 3 days in the latter a relatively slight change was made to a salinity 25.08 parts per mille. A graph (fig. 3) is reproduced showing the gradual adaptation following the change. Within about 4 hours adaptation proceeded almost to completion, as may be seen in the figure by comparing the values of S and F with those of the previous day, when higher salinity was used, as well as with those of the following day.

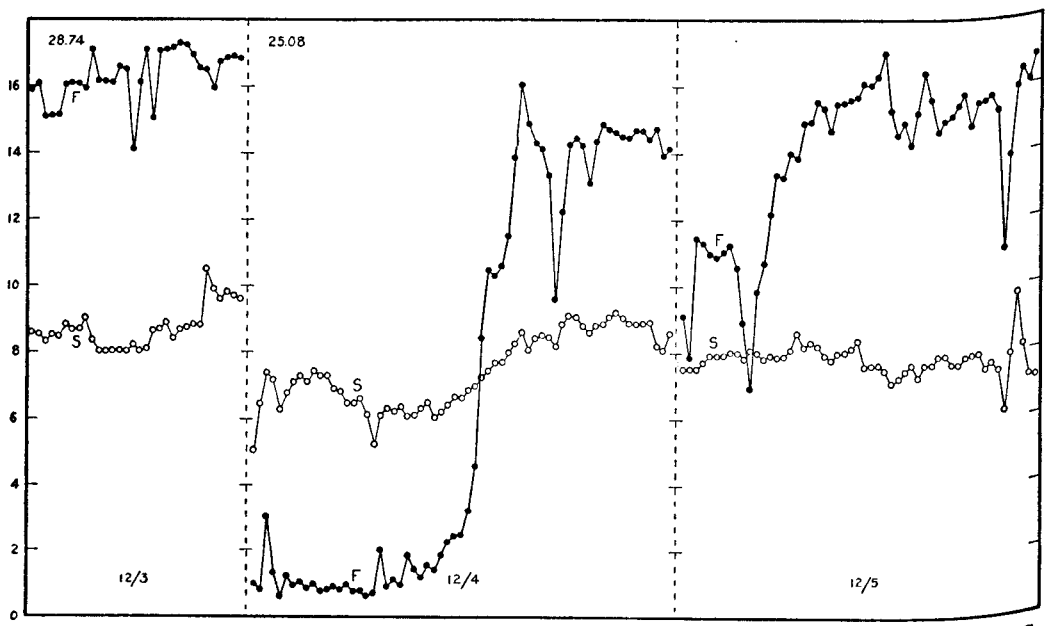

FIGURE 3.—Adaptation of *S* and *F* (5-minute values) following change in salinity from 28.74 to 25.08 p. p. m. Series II. 17°-19° C.

After returning the specimen to a salinity 28.94 parts per mille for 1 day, the water was changed to a salinity of 17.85 parts per mille, a step considerably greater than that just described. During the first several days (series II, table 1) it appeared that adaptation was slowly occurring, but during the remainder of the 11 days there was no further obvious recovery. The valves did not remain open wide enough to permit free flow of water. Yet when the salinity was raised to 27.27 parts per mille recovery was so rapid that activity seemed to be almost at its normal level within 2 or 3 hours.

A considerable difficulty in the analysis of these data lies in the fact that two activities are concerned, namely, the degree of openness of the shell (S) and the rate at which water is pumped (F). The latter is dependent upon the former, and it appears that both functions are influenced independently by changes in salinity. However, even under constant conditions of temperature and salinity, there is a

tremendous variation in the degree of openness. The rate of pumping of water is the activity which primarily is being studied, for on this depends the rate of feeding; but this activity may not be isolated from the influence of the adductor muscle save by propping the valves open; in which case the results would be of little significance with respect to the reactions of the oyster as a whole to environmental factors.

In a previous publication (Hopkins, 1933) it was shown that, at constant temperature, the rate of flow of water through the gills increases as the valves become wider open. By plotting the results of certain series to show the relationship between S and F it is possible to find whether observed effects are due to changed activity of the gills or only to the effect of the position of the valves. Such a graph is shown in figure 4, in which the results for all of the tests with a salinity of 17.85 parts per mille are given in solid points and those taken with a salinity of about 28 parts per mille in open circles. In spite of the fact that the points are considerably dispersed, they fall into relative alinement.

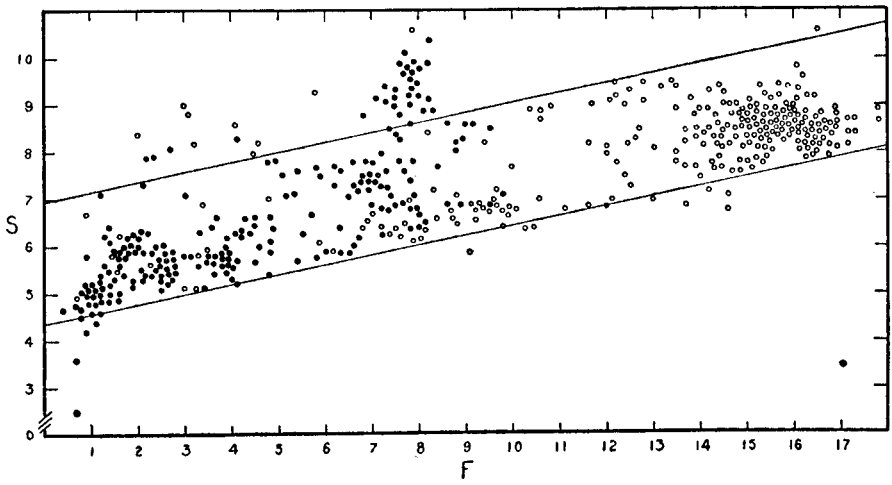

FIGURE 4.—Relationship between S (degree of openness of shell) and F (rate of flow) at salinity of 17.85 p. p. m. (solid points) as compared with 28 p. p. m. (open circles). Series II. 17°–19° C.

Most of the points resulting from low salinity represent low values of both S and F, but they fall into general alinement with values obtained with the higher salinity. This indicates that at least a large part of the low F readings at the lower salinity (series II, table 1) may be due to the effect of the position of the valves. Yet, also, a good many of these points are high on the S scale but much lower on the F scale as compared with the values obtained at high salinity. The trend of the low salinity curve appears to be much steeper than the other. The significance of the graph is that both the adductor muscle, by controlling shell position, and the gill mechanism were in this case responsible for the lack of complete adaptation to the lower salinity. Tests with other specimens throw further light on the subject.

SERIES III

The preceding two series of tests were concerned with changes in salinity between about 14 and about 29 parts per mille. It was noted that adaptation to a reduction in salinity is quite slow as compared to that following a rise. The question presented itself as to whether this difference was due to the fact that the specimens had been

living in water of the higher salinity (28–29 parts per mille) and consequently any change from this level produced a pronounced effect, while restoration of this level merely permitted normal activity.

The reactions were studied when the specimen was transferred into water of a salinity of 39.10, after 2 days of study at 28.55 and 28.27 parts per mille. Since pure ocean water has a salinity of only 35 to 36 parts per mille, there is no possibility that the specimen could already be adapted to water of even higher salinity. The results of the entire series are summarized in table 1, series III. It may readily be observed that the specimen became adapted quickly to the abnormally high level. In figure 5 the values of S and F are given in detail to show the reactions during the first 2 days in this high salinity. After about 3 hours the specimen was pumping water at a rate only a little below normal, and within the following 4 hours it appeared to become completely adapted, as judged by degree of openness and rate of pumping. Tests of the following day are given on the graph for comparison.

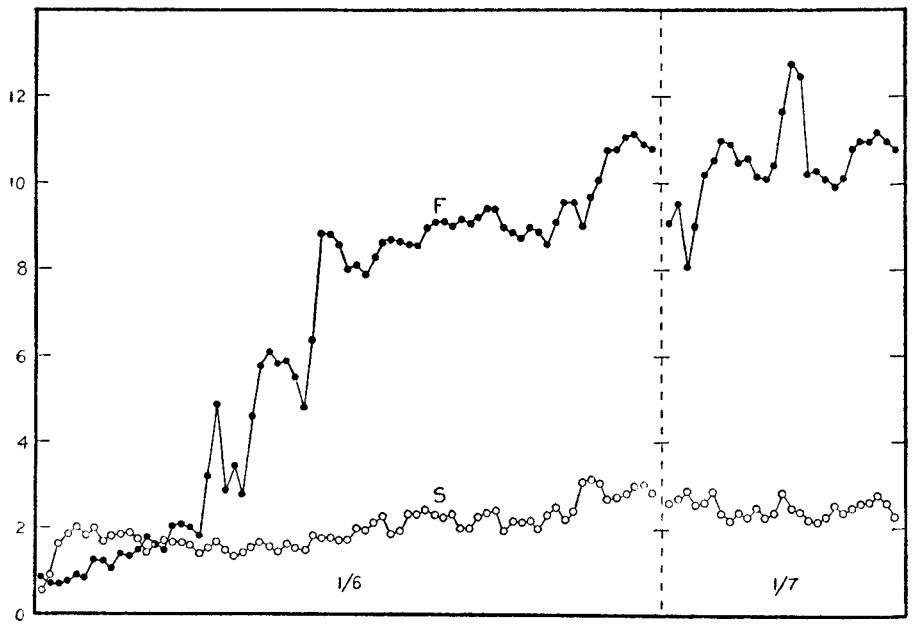

FIGURE 5.—Adaptation of 5-minute values of *S* and *F* to salinity of 39.10 p. p. m. following change from 28.27 p. p. m. Series III. 17°–19° C.

On the other hand, adaptation proceeded at the same slow rate as previously observed when the salinity was lowered to 28.04 parts per mille, as shown in figure 6. At least 3 days were required for restoration of the rate of pumping previously observed, although the valves were much wider open than at the higher salinity. The effect of lowering the salinity in this case appears to be entirely upon the gill mechanism, rather than upon the organs controlling position of the valves.

Since the specimen appeared to function so well in a salinity of 39.10 parts per mille, a short test was made to give a general idea of the upper limit to which it could become adapted. A salinity of 56.32 parts per mille, twice that of the ordinary bay water, was used and records kept for 4 days (series III, table 1). During the first day the shell remained entirely closed, and on the second it opened only to a small degree. However, as the valves became sufficiently far apart the gills were

able to produce a slight flow of water. On the fourth day the valves were abnormally wide open, gaping, although the gills were able to function and produce a slight current. Tests would have been continued save that gaping is generally indicative of loss of tonus of the adductor muscle and death of the organism. However, the oyster was placed in running laboratory water, where, after some days, it apparently recovered completely.

SERIES IV

The experiments described above suggest a marked sensitivity of the oyster to lowered salinity, while the effect of raising the salinity is very temporary. In one case (series I) the salinity was lowered to 14.60 parts per mille and the specimen did not become completely adapted even after 5 days. It is of importance to know approximately the lower salinity limit at which the oyster is able to feed, for in nature the species is frequently subjected to water ranging in salinity from almost pure ocean water to fresh water. Before making such an experiment this specimen (series IV, table 1) was tested for 2 days in water of a salinity of 28.06 parts per mille, after which the salinity was raised to 36 parts per mille and left for 2 days while records were kept to show the progress of adaptation.

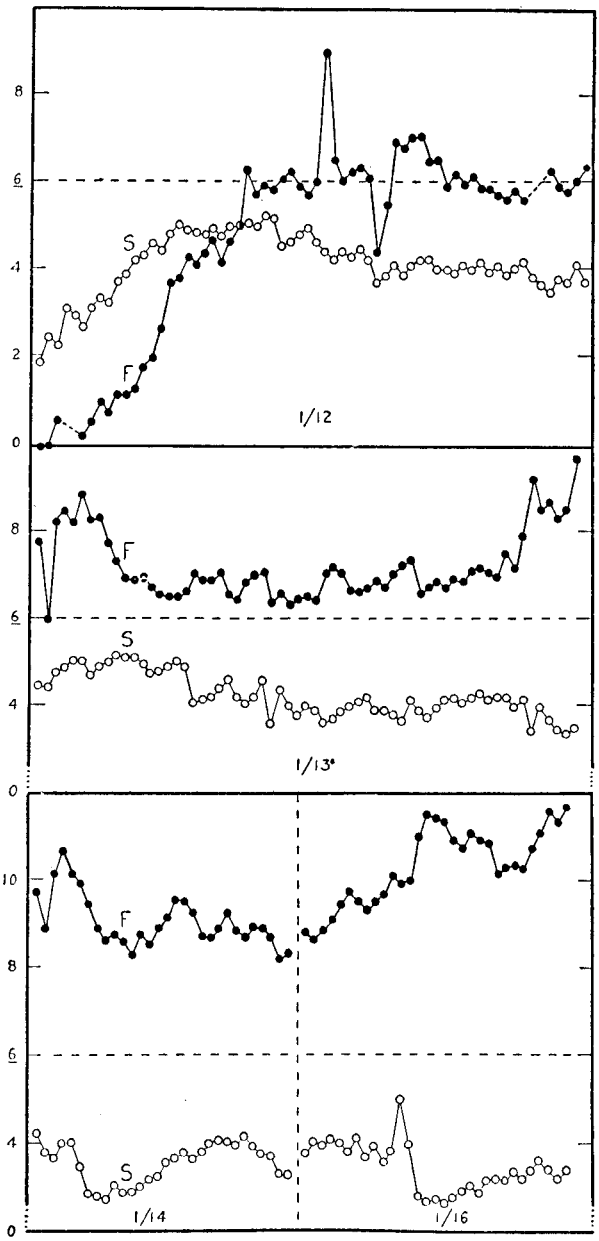

FIGURE 6.—Graph of 5-minute values of S and F showing progressive adaptation to salinity 28.04 p. p. m. following change from 39.10 p. p. m. For reference the value, 6, is shown as broken line. Series III. 17°–19° C.

The results of this change to higher salinity are in harmony with other similar changes already described (fig. 7), for the specimen became completely adapted within a few hours, although the initial effect of the change was to reduce the rate of pumping almost to zero. When the salinity was then reduced to 28.17 parts per mille (fig. 8) adaptation during the first few hours was rapid, but it was not until the third day

that the gills were able to pump at the previous rate, even though the valves were well apart.

These tests occupied 10 days, during which time the specimen was highly active and adaptable. At about noon on the tenth day (series IV, table 1) the salinity was reduced to 10.59 parts per mille and a few records kept during the rest of the day. However, the shell remained almost entirely closed. On the next 2 days kymograph records were not made, for the valves were only slightly open and no water was pumped. On the third day the valves had opened wider and the activity was recorded on the kymograph. Only occasionally was a little water discharged either on this day or during the entire 20 days that water of this salinity was used. After the first few days the valves were generally open to a normal degree, and consequently it was the gills themselves that failed to function. The tests were continued for as long as 20 days with the hope that some indication of adaptation of the gill mechanism would appear.

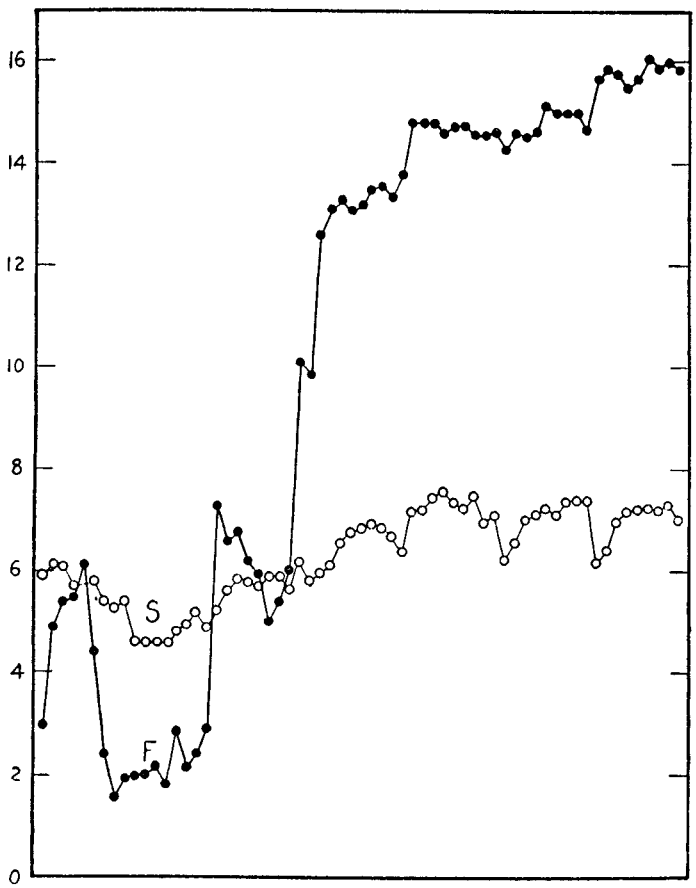

FIGURE 7.—Adaptation of *S* and *F* (5-minute values) to salinity of 36 p. p. m. following change from 28.06. Series IV. 17°–19° C.

In an attempt to locate as exactly as possible the minimum salinity required for functioning of these organs, the salinity was then raised slightly to 12.94 parts per mille and maintained for 4 days. Results being similar to those in the preceding tests, the salinity was again raised to 15.01 parts per mille for 2 days, but without any indication of increased activity. Even when the salinity was raised to 27.92 parts per mille the specimen did not show any sign of recovery. It only remained abnormally wide open, as it has been during many days in water of low salinity. It was clear that subjection to a salinity as low as 10.59 parts per mille for a considerable period of time had done some damage which was not readily repaired even after restoration of more favorable conditions. In fact, it was only after the specimen had been in running sea water for about 2 weeks that it appeared to pump a vigorous stream of water.

Incidentally, the behavior of the oyster during all tests after the introduction of the low salinity was different from the normal in that the quick, partial closures

which occur with characteristic frequency in a normal specimen almost never were to be observed. The oyster acted almost as if anaesthetized, although the shell varied considerably in degree of openness. All movements, however, were slow. Nevertheless, secretion of shell proceeded at a rapid rate, and when the experiment was discontinued several millimeters of thin new shell had been added to the margins of the valves.

SERIES V

In the preceding series the specimen was left in a salinity of 10.59 parts per mille for 20 days, resulting in damage to the pumping mechanism. It was desirable to know whether shorter exposure to such a salinity would have the same harmful effect. A specimen was therefore tested thoroughly for 2 days in water of high salinity (27.35 parts per mille), during which time it reacted favorably, pumping vigorously (series V, table 1). After being changed to a salinity of 10.64 parts per mille, the valves remained at first only slightly open but during the next 2 days opened abnormally wide. As in the previous series, almost no water was pumped. After 4 days of treatment, the salinity was raised to 27.39 and records kept for 5 days. Within about 2 hours after the change the gills began to pump a small stream. Beyond this, however, there was no further recovery during the 5 days. The shell opened wider and wider, but never was more than a feeble circulation of water produced by the gills.

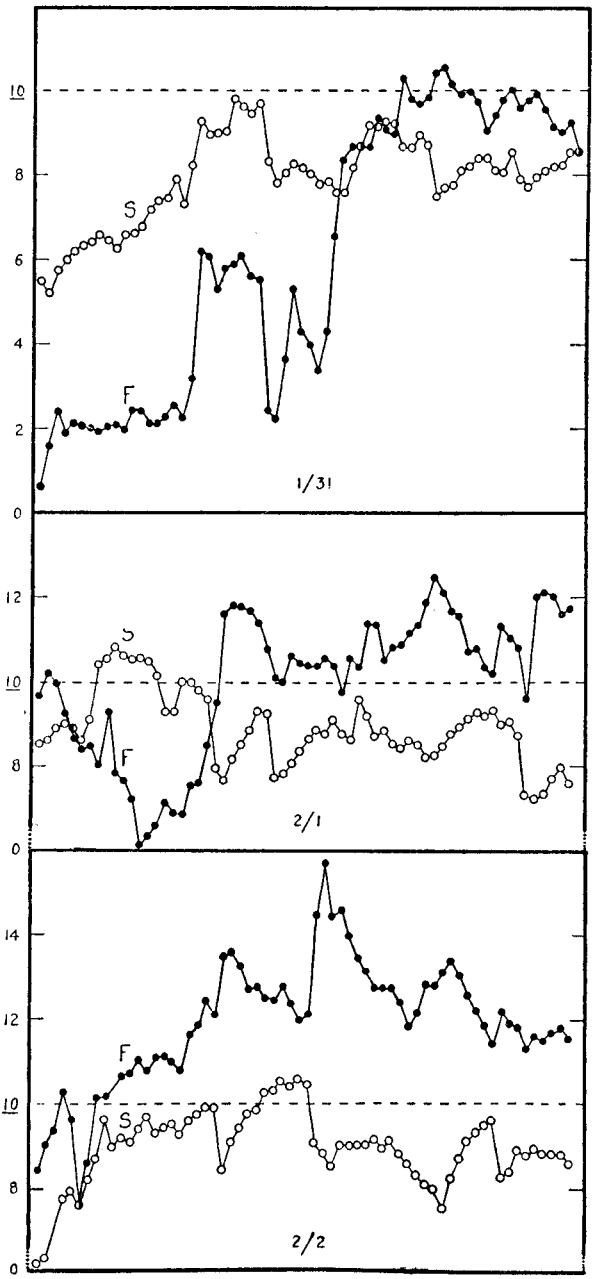

FIGURE 8.—Five-minute values of *S* and *F* during adaptation to a salinity of 28.17 p. p. m. after change from 36 p. p. m. The value, *10*, is shown as broken line for reference. Series IV. 17°–19° C.

The results are similar to those described in series IV, with the difference that in the present series exposure to low salinity had not been sufficiently prolonged to produce the harmful effect to as great a degree.

SERIES VI

With this specimen another attempt was made to obtain comparative data on the reactions to a series of salinities, the changes being made in relatively small steps. The summarized results are shown in figure 9 and table 1, series VI. After 4 days in a salinity of 28.31 parts per mille, during which there was some variability in activity, the salinity was reduced to 23.57 parts per mille and left for 4 days. Adaptation appeared to be quite rapid on the first 2 days; but on the fourth day, for unknown reasons, the value of F was lower than before.

When the salinity was changed to 20.90 parts per mille adaptation was apparently complete on the second day. However, reduction to 16.31 resulted in an entirely different behavior, the specimen becoming adapted within a few hours to a certain low level of pumping which was maintained without improvement during the entire period of the test (6 days). Examination of figure 9, as well as the results of preceding tests, leads to the suggestion that salinities below about 20 parts per mille become more and more strikingly unfavorable in their effect.

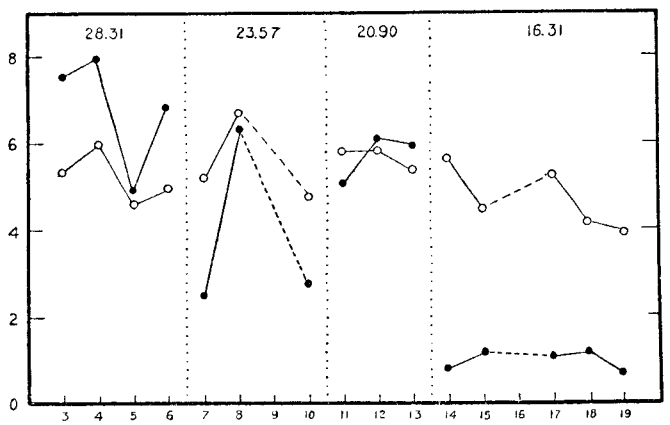

FIGURE 9.—Graph of daily averages of values of S (degree of openness) and F (relative rate of flow) at different salinities. Series VI. 17°–19° C.

Whether adaptation would take place in such instances to the extent that water would be pumped at the same rate as at higher salinities may not definitely be stated, but it is clear that adaptation is extremely slow.

SERIES VII

In those experiments which have already been described it was indicated that when specimens are placed in water of a salinity of about 15 to 17 parts per mille the rate of pumping is greatly reduced and adaptation is very slow, possibly never reaching the level observed at higher salinities. It was also shown that a salinity as low as 10 to 11 parts per mille results not only in almost complete stoppage of the flow of water through the gills but also in a harmful effect from which recovery, after return to high salinity, is extremely slow. It would appear that the lower salinity limit which the oyster can tolerate lies somewhere between 10 and 15 parts per mille. This experiment was performed in order to locate this limit more exactly (series VII, table 1).

Preliminary tests were carried on over a period of 9 days with a salinity of 25.09 parts per mille before changing to a salinity of 13.00 parts per mille. During the first day at the lower salinity the valves did not open wide and there was no flow of water. On the next day it looked as if the specimen was going to become well adapted, but during the following days this rate of activity was not maintained. During 8 days of treatment in water of this salinity only a sluggish stream was pumped as compared with the activity observed during the preceding

tests. The activity in this salinity was only slightly less rapid than that recorded in series I, when a salinity of 14.60 parts per mille was employed. A salinity of about 13 parts per mille appears to be but little more favorable than a salinity of about 10.5 parts per mille as studied in series IV and V. In the latter cases, however, the specimens were not able readily to recover from the harmful effect.

This specimen quickly became adapted to a salinity of 25.53 parts per mille, and in spite of the fact that it had been in the water of lower salinity for 8 days it recovered completely within 2 days. The progress of adaptation in this case is one of the best examples obtained, and a graph (fig. 10) is reproduced showing all of the 5-minute values of S and F. After the first 2 hours, during which the valves were not wide open and almost no water was pumped, the shell consistently opened wider and the rate of flow of water increased. It may be noted that considerable adaptation took place overnight between recordings of the 2 days. This graph suggests also the close correlation between degree of openness and rate of pumping.

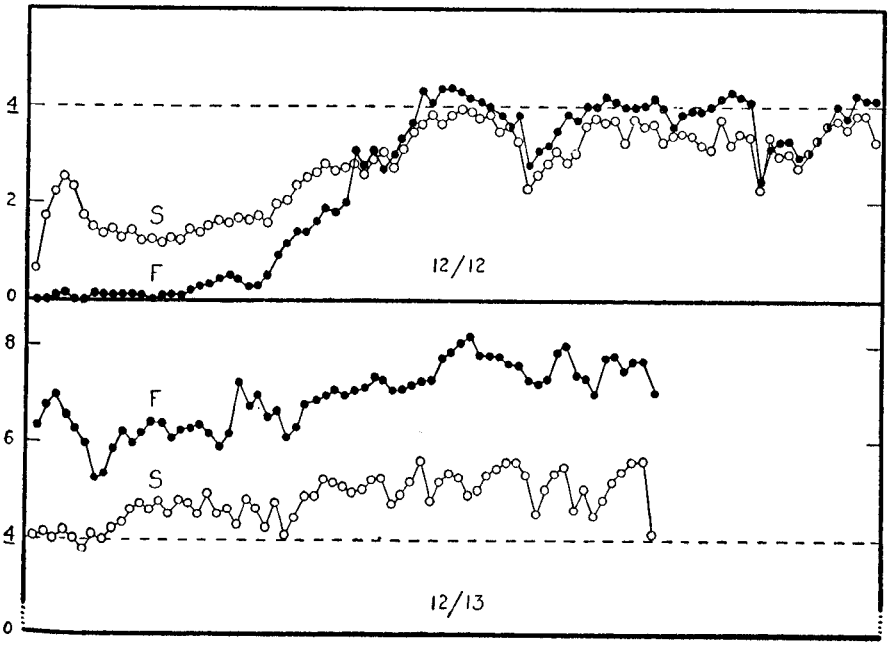

FIGURE 10.—Adaptation of *S* and *F* (5-minute values) to salinity of 25.53 p. p. m. following change from 12.93 p. p. m. Series II, 17°–19° C. The value, *4*, is shown by a broken line for reference.

In many cases of adaptation it is difficult to determine whether the rate of pumping at any time is due to the rate of activity of the gills or to the degree of openness of the valves, which thereby determine how much water may be pumped. By plotting the values obtained during the 2 days when the specimen was in water of a salinity of 25.53 parts per mille, to show the correlation between S and F (fig. 11), it was clearly shown that the points, with a few exceptions due to the initial effect of the change in salinity, fall into definite alinement; that is, the relationship between rate of flow and degree of openness was the same on the first day, when the specimen was beginning to become adapted, and on the second day, when adaptation was almost complete. This is interpreted as direct evidence that adaptation in this case was entirely under the control of the adductor muscle, regulating the

valves, while the gills themselves become adapted quickly. In this respect these results are entirely different from those obtained in series IV and V, in which, after the salinity was raised following treatment in about 10.5 parts per mille, the shells

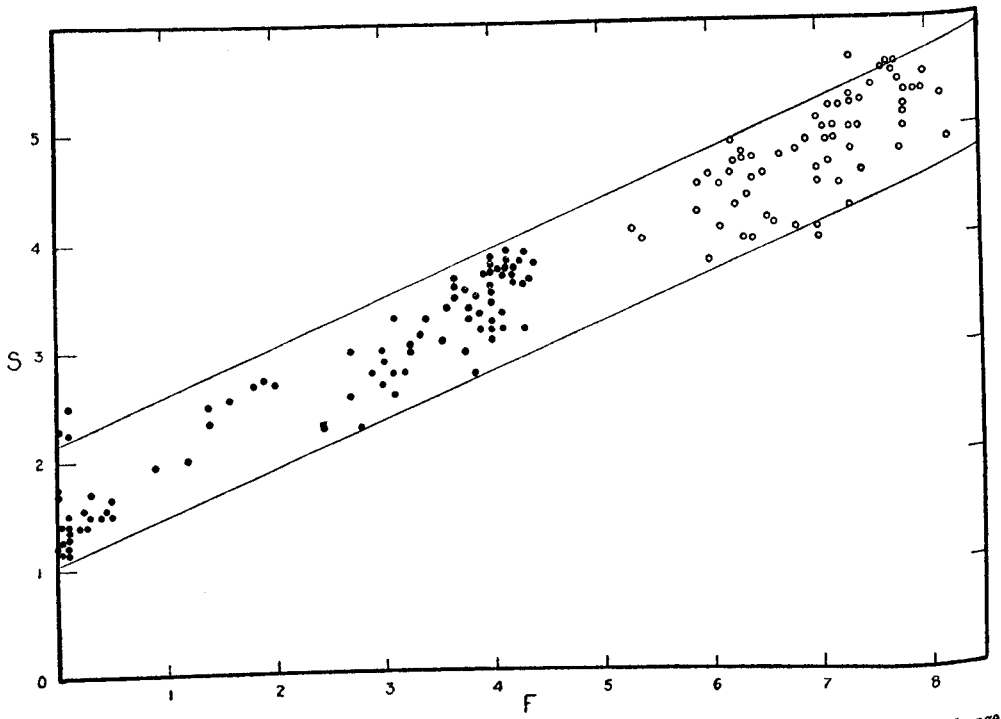

FIGURE 11.—Relationship between S and F during the first (solid points) and second (open circles) days following change in salinity from 12.93 p. p. m. to 25.53 p. p. m. Series II. (See fig. 10.)

remained wide open but the gills were inactive. Between 10.5 and 13 parts per mille, then, there is a tolerance limit, below which there appears to be a destructive effect.

TABLE 1.—*Daily averages of values of S (degree of openness of shell) and F (relative rate of flow of water)*

[17°–19° C.]

SERIES I

Date	Salinity (parts per mille)	Number of 5-minute periods	S (average)	F (average)	Date	Salinity (parts per mille)	Number of 5-minute periods	S (average)	F (average)
Nov 7	29.40	37	*8.53*	*6.45*	Nov. 14	28.50	65	7.99	5.61
Nov. 7	26.96	41	*7.18*	*5.40*	Mean		[1]162	*7.03*	*6.25*
Nov. 8	24.03	47	*7.50*	*6.19*	Nov. 15	22.205	79	*7.63*	*7.62*
Nov. 9	17.76	54	7.42	1.21	Nov. 16	29.46	71	*7.66*	*9.08*
Nov. 10	17.69	47	6.98	5.12	Nov. 18	14.60	125	3.84	.09
Nov. 11	17.69	18	8.15	5.79	Nov. 19	14.60	72	5.35	.70
Mean		[1]119	*7.35*	*3.46*	Nov. 20	14.60	18	7.18	2.15
Nov. 11	28.50	54	5.62	4.67	Nov. 21	14.57	72	6.43	3.43
Nov. 12	28.50	43	7.35	9.20	Nov. 22	14.57	64	7.28	5.17
					Mean		[1]351	*5.48*	*1.93*
					Nov. 23	28.56	51	*6.00*	*4.85*

SERIES II

Nov. 28	28.87	36	*6.33*	*7.29*	Dec. 7	28.94	63	*7.73*	*17.67*
Nov. 29	22.70	71	7.47	5.69	Dec. 8	17.85	29	5.07	.23
Nov. 30	22.70	71	8.17	9.34	Dec. 9	17.85	36	6.98	6.06
Mean		[1]142	*7.82*	*7.51*	Dec 12	17.83	54	8.83	6.92
Dec. 1	28.74	72	8.38	13.31	Dec. 13	17.83	48	6.08	4.40
Dec. 2	28.74	81	8.73	15.48	Dec. 14	17.83	24	5.67	3.88
Dec. 3	28.74	32	8.60	16.47	Dec. 15	17.83	17	5.65	2.79
Mean		[1]185	*8.58*	*14.81*	Dec. 16	17.83	27	4.77	1.20
Dec. 4	25.08	63	7.47	6.95	Dec. 17	17.83	17	5.96	1.69
Dec. 5	25.08	54	7.80	13.90	Dec. 18	17.83	9	5.22	1.08
Mean		[1]117	*7.62*	*10.14*	Mean		[1]261	*6.43*	*3.98*
					Dec. 19	27.27	53	*7.48*	*12.42*

SERIES III

Jan. 4	28.55	50	*2.89*	*6.44*	Jan. 12	28.04	60	4.15	4.86
Jan. 5	28.27	54	*3.03*	*9.13*	Jan. 13	28.04	63	4.26	7.32
Jan. 6	39.10	71	2.01	6.30	Jan. 14	28.04	30	4.13	9.73
Jan. 7	39.10	36	2.58	10.01	Jan. 16	28.04	31	4.06	11.04
Jan. 9	39.10	36	3.54	8.72	Mean		[1]184	*4.08*	*7.53*
Jan. 10	39.10	33	3.57	9.05	Jan. 17	56.32	18	0	0
Jan. 11	39.10	65	3.95	9.10	Jan. 18	56.32	27	1.27	.03
Mean		[1]241	*3.09*	*8.34*	Jan. 19	56.32	37	1.95	.68
					Jan. 20	56.32	10	7.89	.52
					Mean		[1]92	*2.01*	*.33*

SERIES IV

Jan. 25	28.06	50	5.67	9.14	Feb. 15	10.48	18	2.86	0
Jan. 26	28.06	45	7.00	16.70	Feb. 16	10.48	17	8.50	0
Mean		[1]95	*6.60*	*12.44*	Feb. 17	10.48	51	10.63	.36
Jan. 27	36.00	63	6.32	10.32	Feb. 18	10.48	14	10.97	.22
Jan. 28	36.00	46	8.15	14.20	Feb. 20	10.48	36	9.46	.38
Jan. 29	36.00	51	8.40	12.83	Feb. 21	10.48	18	5.47	0
Jan. 30	36.00	64	8.78	12.75	Feb. 23	10.48	28	7.08	0
Mean		[1]224	*7.89*	*12.39*	Mean		[1]398	*7.80*	*.16*
Jan. 31	28.17	65	8.08	6.21	Feb. 24	12.94	54	8.38	.19
Feb. 1	28.17	64	8.89	10.04	Feb. 25	12.94	45	11.24	.06
Feb. 2	28.17	64	9.12	12.15	Feb. 27	12.94	28	11.21	.31
Feb. 3	28.17	18	7.81	7.66	Mean		[1]126	*10.02*	*.17*
Mean		[1]211	*8.61*	*8.85*	Feb. 28	15.01	61	11.74	.19
Feb. 3	10.59	14	.38	0	Mar. 1	15.01	55	13.01	.14
Feb. 6	10.59	36	5.57	.40	Mean		116	*12.35*	*.17*
Feb. 7	10.59	36	3.42	0	Mar. 2	27.92	54	11.87	.07
Feb. 8	10.59	54	6.74	0	Mar. 3	27.92	52	12.12	.03
Feb. 9	10.59	36	7.37	0	Mean		[1]106	*12.00*	*.05*
Feb. 11	10.59	17	8.37	0					
Feb. 13	10.59	23	10.01	.46					

[1] Total.

TABLE 1.—*Daily averages of values of S (degree of openness of shell) and F (relative rate of flow of water)*—Continued

SERIES V

Date	Salinity (parts per mille)	Number of 5-minute periods	S (average)	F (average)	Date	Salinity (parts per mille)	Number of 5-minute periods	S (average)	F (average)
Mar. 7	27.35	61	3.67	7.81	Mar. 13	27.39	54	5.46	1.26
Mar. 8	27.35	61	3.60	7.15	Mar. 14	27.39	54	5.37	1.13
					Mar. 15	27.39	63	6.41	.68
Mean		[1]122	*3.63*	*7.48*	Mar. 16	27.32	51	6.72	.65
					Mar. 17	27.32	18	8.48	.65
Mar. 9	10.64	27	.61	0					
Mar. 10	10.64	56	5.08	.03	Mean		[1]240	*6.18*	*.90*
Mar. 11	10.64	16	7.18	0					
Mean		[1]99	*4.20*	*.02*					

SERIES VI

Apr. 3	28.31	9	5.36	7.51	Apr. 11	20.90	70	5.80	5.05
Apr. 4	28.31	19	5.91	7.97	Apr. 12	20.90	23	5.88	7.07
Apr. 5	28.31	54	4.55	4.91	Apr. 13	20.90	27	5.41	5.84
Apr. 6	28.31	64	4.96	6.82					
					Mean		[1]120	*5.72*	*5.62*
Mean		[1]146	*4.95*	*6.30*					
					Apr. 14	16.31	17	5.61	.80
Apr. 7	23.57	44	5.25	2.49	Apr. 15	16.31	72	4.49	1.15
Apr. 8	23.57	25	6.69	6.39	Apr. 17	16.31	52	5.26	1.08
Apr. 10	23.57	43	4.75	2.74	Apr. 18	16.31	72	4.19	1.19
					Apr. 19	16.31	27	3.94	.67
Mean		[1]112	*5.46*	*3.46*	Mean		[1]246	*4.58*	*1.07*

SERIES VII

Nov. 24	25.09	94	2.37	2.80	Dec. 7	12.98	32	4.04	.71
Nov. 25	25.09	15	3.54	5.06	Dec. 8	12.98	73	3.40	------
Nov. 27	25.09	67	4.52	6.57	Dec. 9	12.93	52	4.49	.39
Nov. 28	25.09	43	4.24	4.97	Dec. 10	12.93	11	3.81	.05
Nov. 29	25.09	55	5.06	6.54	Dec. 11	12.93	80	3.18	.24
Dec. 1	25.09	55	4.21	5.90					
Dec. 2	25.09	55	4.70	4.70	Mean		[1]440	*3.39*	*.42*
Mean		[1]384	*3.98*	*5.04*	Dec. 12	25.53	88	2.73	2.51
					Dec. 13	25.53	65	4.80	6.95
Dec. 4	13.00	80	1.18	0					
Dec. 5	13.00	31	5.71	2.27	Mean		[1]153	*3.61*	*4.40*
Dec. 6	12.98	81	3.90	.68					

[1] Total.

DISCUSSION

Organisms such as oysters which live in inshore waters, bays, and estuaries are necessarily subject to frequent changes in the density or salinity of the medium. The observations of Prytherch (1934) indicate that considerable dilution of sea water with inflowing fresh water containing copper ions is necessary for the successful propagation of the oyster. He also noted that a salinity of from 16 to 18.6 parts per mille is optimum for rate of setting, or attachment, of larvae of *O. virginica*. The natural habitat is thus limited by the salinity of the water, although it may not be assumed that diluted sea water is more favorable for growth and feeding after setting and metamorphosis have taken place. Most frequently, on the other hand, is it to be observed that those grounds which are especially favorable for catching seeds are relatively unsuited for the growing and fattening of oysters for market.

A difficulty of analysis encountered in this work is that even under uniform conditions of temperature and salinity there are marked variations in both rate of activity of the gills and degree of openness of the valves. Such variability is probably to be expected in any study of the reactions of an organism as a whole, for

innumerable factors, both internal and external, influence the activity. Lack of constancy in the rate of pumping of the gills may be traced to contraction or relaxation of the gill musculature, changes in size of the ostia caused by variations in diameter of blood vessels of the gill filaments (Elsey, 1935), secretion of mucus which impedes activity of the cilia, etc. However, in spite of such uncontrolled factors which render exact analysis difficult, the results are of sufficient uniformity to warrant definite conclusions.

The experimental results described above suggest that an important factor influencing the quality of oyster meats grown on different grounds is the salinity conditions. The rate at which the gills pump water, from which food particles are filtered, depends upon the salinity of the medium or, more accurately stated, upon the frequency, amplitude, and duration of changes in salinity. It is well understood that rate of pumping of water does not alone determine the rate of feeding, for the abundance of food material in the water is a variable, depending upon other factors, such as the availability of nitrates and phosphates for utilization by the microscopic plant life on which oysters feed. In some instances land drainage may bring fertilizing materials which cause prolific development of food organisms, at the same time so diluting the sea water that oysters are not able to pump sufficient water and to feed effectively.

Any significant change in salinity causes an immediate slowing or cessation in the rate of pumping. Recovery depends upon the amplitude of the change and upon whether it is to a higher or lower level. While only a few hours may be required for adaptation following a rise in salinity, several days may be necessary for recovery following the same change in the opposite direction. It was thought possible that this difference was due to the fact that the specimens had been grown in water ranging generally about 25 to 29 parts per mille and any change from this level would produce a marked effect, while restoration of this salinity resulted merely in the resumption of normal activity. However, adaptation to a further rise in salinity to 36 or 39 parts per mille, higher than oysters encounter in nature, is also rapid, but when a salinity of about 28 parts per mille is restored adaptation is very slow. Rate of adaptation following a change in salinity is also proportional to the extent of the change. Further, as the salinity becomes lower the sensitivity of the oyster to small changes increases, very much as was found (Hopkins, 1931a) with regard to temperature. It was shown that a small drop in temperature caused closure of the shell if the temperature was well below the optimum but produced no effect if near the optimum.

It appears likely that endosmosis following a reduction in salinity swells the tissues and blood vessels, such as those in the gills, resulting in decrease in the size of the pores, or ostia, through which water is forced by ciliary action. An increase in salinity, on the other hand, would involve extraction of water and consequent increase in size of the ostia. The adductor muscle is probably also affected by swelling and shrinking. The slow rate of adaptation to a lowering of salinity is in most cases clearly traceable to diminished activity of the gills, while the valves soon open as wide as, or wider than, before the change. On the other hand, a rise in salinity involves a slow accommodation in degree of openness of the shells and an almost immediate adaptation of the gill mechanism.

In certain cases there occurred what appeared to be an actual stimulation of gill activity following rise in salinity, whereby the specimen pumped more rapidly

than it had previously pumped in water of the same salinity. With respect to the above interpretation this would possibly be expected, for the ostia would be much wider open than normally after the osmotic pressure of the blood has reached equilibrium with the medium.

Living, as oysters do, in a highly changeable environment, subject to seasonal weather conditions which may cause variations in salinity between almost pure fresh water and undiluted sea water, they must necessarily have a remarkable tolerance for salinity changes. It is well known that in time of freshet oyster beds may be covered for weeks with almost fresh water without resulting in any considerable mortality. That they are able to maintain life under such conditions is probably largely due to their ability to remain closed for long periods of time (Hopkins, 1931b), protecting the actual tissues. However, the present results indicate that pumping of water and feeding probably do not go on under such extreme conditions, so that starvation would eventually take place if the low salinity were of too great duration.

It was shown above that there is a minimum limit of salinity below which pumping does not go on and a further, more lasting effect produced which renders the oyster capable of only very slow recovery after being returned to water of higher salinity. This limit appears to lie between 10.5 and 13 parts per mille. At the latter salinity only a small amount of water was pumped, but recovery was readily accomplished in a high salinity. These results compare favorably with Nelson's (1921) estimate of a salinity of about 10.42 parts per mille as the lowest at which *O. virginica* can feed, although his conclusion was based upon whether or not the shell remained open.

Pumping activity was approximately the same at salinity ranging from about 25 to about 39 parts per mille, although the latter value is considerably higher than that of pure ocean water. A salinity as high as 56 parts per mille is obviously unfavorable, and, although pumping some water, the specimen gaped and would probably have soon died. From an ecological standpoint it is the lower limit that is of importance, for seldom are oysters in nature forced to adjust themselves to a salinity higher than that of the ocean.

The oyster appears to be increasingly sensitive to changes in salinity below about 20 parts per mille, possibly indicating that the optimum is higher. The results do not permit one to state the optimum salinity, but it would appear to be well above 20 parts per mille, possibly as high as 30 or 35 parts per mille. It may be that the optimum depends upon the medium to which the particular oysters have been accustomed for generations, that specimens from beds in relatively fresh bays would react differently from those grown in more saline water, as suggested by Nelson (1923a). Most likely, however, little difference of this nature is to be expected, save that a longer time would be required for adaptation of specimens from the water of higher salinity.

SUMMARY

1. Adaptation of the feeding mechanism of the oyster to changes in salinity was studied by recording on the kymograph the degree of openness of the valves and the relative rate of flow of water pumped by the gills.

2. Both the activity of the gills and that of the adductor muscle, which by controlling the position of the valves determines the size of the inhalent and exhalent apertures, are markedly affected by any considerable change in salinity. The initial effect of such a change is to cause partial or complete contraction of the adductor muscle and slowing or cessation of the flow of water.

3. Recovery, or adaptation, following a rise in salinity is very rapid as compared with adaptation following the same change in the opposite direction. The former may require a few hours, while several days may be necessary in the latter case.

4. The rate of adaptation depends upon the degree of change and upon the extent of departure from optimum salinity. It is probable that, as the salinity departs further from the optimum, adaptation would never be so complete that water would be pumped at the normal rate.

5. Because of the great variability in activity of the gills and in degree of openness even under conditions of constant salinity and temperature, the results do not justify exact statement of the optimum salinity. However, the optimum is probably not greatly different from that of ocean water, for salinities between about 25 and 39 parts per mille appear to produce similar effects.

6. While the oyster will tolerate a salinity as high as 39 parts per mille, higher than that of pure ocean water, and pump at the maximum rate, a salinity of 56 parts per mille, is definitely too high for it to tolerate.

7. As the salinity is reduced below about 20 parts per mille the oyster becomes increasingly sensitive. A longer time is required for adaptation to relative stability, and it is probable that the rate of pumping would never become as high as that observed at salinities of about 28 parts per mille.

8. The lower limit of tolerance, or the minimum salinity at which water is pumped effectively, is between 10.5 and 13 parts per mille. At the former salinity almost no water is pumped, although the valves remain well open.

9. At a salinity of about 13 parts per mille little water is pumped, even after several days are allowed for adaptation, but recovery to normal activity occurs readily following restoration of a higher salinity.

10. A salinity as low as 10.5 parts per mille produces a harmful effect, after which recovery in water of high salinity is extremely slow. This effect appears to be within the gill mechanism rather than the adductor muscle.

11. A change to a lower salinity appears to affect the gill mechanism primarily, while following a rise in salinity the adductor muscle tends to hold the valves closer together than normally, resulting in a slower rate of pumping even though the gills may be well adapted.

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U. S. DEPARTMENT OF COMMERCE
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BUREAU OF FISHERIES
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DETECTION AND MEASUREMENT OF STREAM POLLUTION

By M. M. ELLIS

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 22

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1937

For sale by the Superintendent of Documents, Washington, D. C. - Price 20 cents

DETECTION AND MEASUREMENT OF STREAM POLLUTION [1]

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CONTENTS

	Page
Introduction	365
Stream pollutants and aquatic environment	366
Physical and chemical characteristics of waters suitable for fresh-water stream fishes	366
General field methods	368
Water samples	369
Mud samples	369
Plankton	369
Fresh-water mussels	369
Fish	370
Equipment	370
Dissolved oxygen	370
Hydrogen-ion (pH) limits	379
Ionizable salts	383
Specific conductance	383
Carbon dioxide	386
Fixed carbon dioxide (chiefly calcium and magnesium carbonates)	386
Free carbon dioxide	388
Iron	390
Ammonia	391
Suspensoids	394
Depths	396
Stream pollutants, etc.—Continued.	
Physical, etc.—Continued.	
Ionizable salts—Continued.	
Temperature	397
Bottom conditions as affected by stream pollution	398
Action of pollutants on fishes	400
Injuries to gills and external structures	400
Pollutants entering the body of the fish and exerting true toxic action	402
Lethality of specific substances occurring in stream pollutants	403
General consideration	403
Test animals	404
Goldfish	405
Daphnia magna	406
Water types	406
Specific lethality tables	408
Osmotic pressure and sodium chloride	408
Acids	409
Compounds of various metals	413
Miscellaneous compounds	416
Lethal limits of 114 substances which may be found in stream pollutants	417
Acknowledgments	433
Bibliography	433

INTRODUCTION

The menace of pollution to our inland streams and rivers is too well known to require definition. In fact, unsightly and noisome conditions due to pollution are encountered so often that they have come to be accepted by many as the usual order of things. It is true, however, that many cases of pollution could be remedied and the streams so affected restored to an acceptable state for recreation, fishing, and

[1] Bulletin No. 22. Approved for publication, Sept. 1, 1936. The present study is presented as the first of three dealing with pollution hazards to fresh-water fishes. The second will discuss trade wastes and chemical effluents, and the third, the cumulative effects of dilute pollutants.

general use with reasonable expense, if all parties concerned would cooperate. To obtain this cooperation, it is necessary to understand the situation and to judge it fairly. Much confusion and misunderstanding has arisen in attempts to define the extent of pollution and to place the responsibility for damage to fisheries, because of the lack of available information on the conditions to be defined.

In the present paper findings from the widely scattered scientific literature supplemented by the experimental and field work of various agencies have been brought together covering (1) the conditions which should be maintained if good fish faunae are to thrive, and (2) the specific effects of various types and components of effluents which now pollute our streams.

It is hoped that the use of this information will make possible the definition of undesirable conditions with fairness both to the industrialist, who must use water and streams, and to the citizen, who is entitled to enjoy these same streams.

With the limits of both the required stream conditions and of the pollutant lethalities better understood, corrective measures can be recommended intelligently, for remedial action can only be instituted when the cause and the severity of the pollution are known. The United States Bureau of Fisheries is engaged at present in such investigations based on findings presented here.

STREAM POLLUTANTS AND AQUATIC ENVIRONMENT

PHYSICAL AND CHEMICAL CHARACTERISTICS OF WATERS SUITABLE FOR FRESH-WATER STREAM FISHES

The various effluents, municipal, industrial, and otherwise which comprise collectively stream pollutants may be detrimental to fishes and other aquatic life either indirectly through quantitative alterations in those substances which give fresh waters their inherent characteristics, as dissolved oxygen, carbonates, and hydrogen ions, or directly because of specific physiological and toxic effects on the aquatic organisms themselves. Many effluents are of complex composition, however, and are harmful to aquatic life through both changes in the aquatic environment and through definite toxic actions. Therefore, in determining the effects of stream pollutants on aquatic biota and particularly on fishes, it has been necessary to study both the modifications in the environment and the specific physiological actions attributable to the different pollutants.

The many substances which are carried in solution and suspension by a stream, collectively determine whether the waters of that stream in themselves present conditions favorable or unfavorable for fishes and other aquatic organisms; and any individual fish in the stream is affected not only directly by these substances, but indirectly through their action on other forms of aquatic life which comprise in a very restricted environment the food, the enemies, and the competitors of the particular individual. The definition of the amounts of these substances which should be present in water in order to maintain a suitable environment for fishes, or which may be tolerated by fishes under favorable conditions, is therefore much more involved than the designation of standards for water for human consumption, which concern but a single, air-breathing, non-aquatic animal, man.

Water standards for fishes and other aquatic organisms, moreover, are not identical with those standards which will define water as potable for human beings or satisfactory for industrial use. Water may be serviceable for many industries and yet not support fish life, or fishes may thrive in water which would be unsafe for human consumption due to the presence of particular bacteria as typhoid, or certain compounds harmful to man, as the western alkalis.

The definition of waters as suitable for aquatic life is complicated still further by the fact that various species of fishes and other aquatic animals and even individuals of different ages of the same species have different degrees of tolerance to deviations from the ideal environment, and to the cumulative effects of many stream pollutants. Consequently, the presence or even the survival for a time of fishes in waters suspected of pollution does not in itself constitute evidence that these waters are either satisfactory or safe for fishes.

In spite of the various confusing factors which have been set forth in the preceding paragraphs, it is essential in order to determine the extent and degree of pollution in any given stream to define as far as possible the limits of variation in the several components of those aquatic complexes which desirable fishes will tolerate and in which they will still thrive. Neither minimal lethal nor arbitrary standards will suffice. The limiting values for the various substances in stream waters, with references to the effects on aquatic life, as presented here have been obtained through the correlation of data of four sorts: (*a*) The amounts of these substances found in natural waters where fishes were successfully maintaining themselves, (*b*) studies of streams which as far as could be determined were unpolluted and which, therefore, presented natural conditions, (*c*) the physiological responses of fishes and other aquatic animals to variations in the concentrations of these substances, and (*d*) the survival of aquatic forms when exposed to these substances over long periods under controlled conditions. These data have been drawn from the existing literature, and from field and laboratory studies by the staff of the Columbia (Mo.) field unit of the United States Bureau of Fisheries during the past 5 years (Ellis, 1935a).

In the present consideration of water standards for fish and other aquatic animals the dissolved and suspended substances have been divided into two groups, namely, those constituting the complex favorable to fishes in natural unpolluted waters, i. e., those substances to which the fresh-water fishes are physiologically adapted; and, those substances which are added from time to time to natural waters by man and his agencies, and to which the individual fish must adapt itself. There is, of course, some overlapping between the two groups since certain forms of pollution merely alter the amounts of specific substances normally found in streams, as in the case of the acid wastes from wire-nail mills, which effluents raise the acid ions, the iron and the sulphates, all of which occur in small quantities in most streams, to levels toxic or detrimental for aquatic forms, with, of course, disastrous results.

Throughout the application of these data and standards it must be borne in mind that individual fishes and various species of fish have different degrees of resistance and tolerance. Consequently, some fishes may be found in waters where less favorable conditions than those here designated obtain, since both the minimal and maximal limits immediately compatible with life have been avoided, for these limits cannot be regarded as desirable or physiologically reasonable in determining a

suitable environment for fishes any more than for man. An effort has been made, therefore, to present usable and reasonable standards of water suitability favorable to fish life; that is, standards defining waters in which a mixed fauna of fresh-water fishes of the common warm water types including desirable centrarchids, cyprinids, catostomids, and silurids, as well as such tolerant forms as carp and gar, will thrive. Various lethal limits are also set forth.

It must also be pointed out that these standards of suitability must be maintained throughout the periods of low water, maximal temperature, and maximal liability to pollution, since a deviation in the amount of any of several substances, as dissolved oxygen, acids, or salts, to the critical level for only a few hours may so change conditions in a considerable portion of an otherwise favorable stream, that months or years may be required to reestablish the former fish fauna and normal balance of aquatic species.

In a large series of field studies it has been shown that the natural, inherent water conditions of most streams can be ascertained satisfactorily for pollution studies as regards fisheries problems by determining repeatedly at different times of the night and day and at various seasons of the year the (1) dissolved oxygen, (2) pH, (3) ionizable salts, (4) carbon dioxide, fixed and free, (5) total ammonia, and (6) suspensoids, since the determinations of these factors not only give specific data concerning particular conditions, but also concerning several complexes which vary in even unpolluted streams and which are definitely affected by many forms of pollution.

From determinations made at many stations where good mixed fish faunae were present, it was found that the values from the above determinations in favorable waters, i. e., waters supporting good mixed fish faunae, fell within rather definite limits, and that deviations from these limits in our inland streams were almost always indicative of conditions unfavorable to aquatic life. However, these values alone, which cover only the more basic, inherent conditions which must be maintained in any stream if it is to support a good fish fauna and on which conditions of specific pollution are superimposed, will not suffice for the complete definition of water as favorable for aquatic life, since the absence of specifically toxic substances must also be demonstrated before the water can be finally approved as unpolluted.

GENERAL FIELD METHODS

Throughout these studies, both for the determination of water suitability standards and of pollution conditions, certain routine procedures were followed, in addition to the special investigations which the conditions in the particular locality required, in order that certain data from all localities could be compared fairly and without the skewing which results from haphazard sampling.

The stations at which samples were taken in each locality were selected as representative of the various complexes of conditions presented. Whenever possible, samples were taken at intervals throughout the night and day and at different times during the season. Many of the stations included in this report have been visited repeatedly during the past 5 years.

Although in this paper the detailed data concerning the findings on plankton, bottom organisms, fresh-water mussels, and fish population are not presented, since various general statements concerning findings on these animals have been included

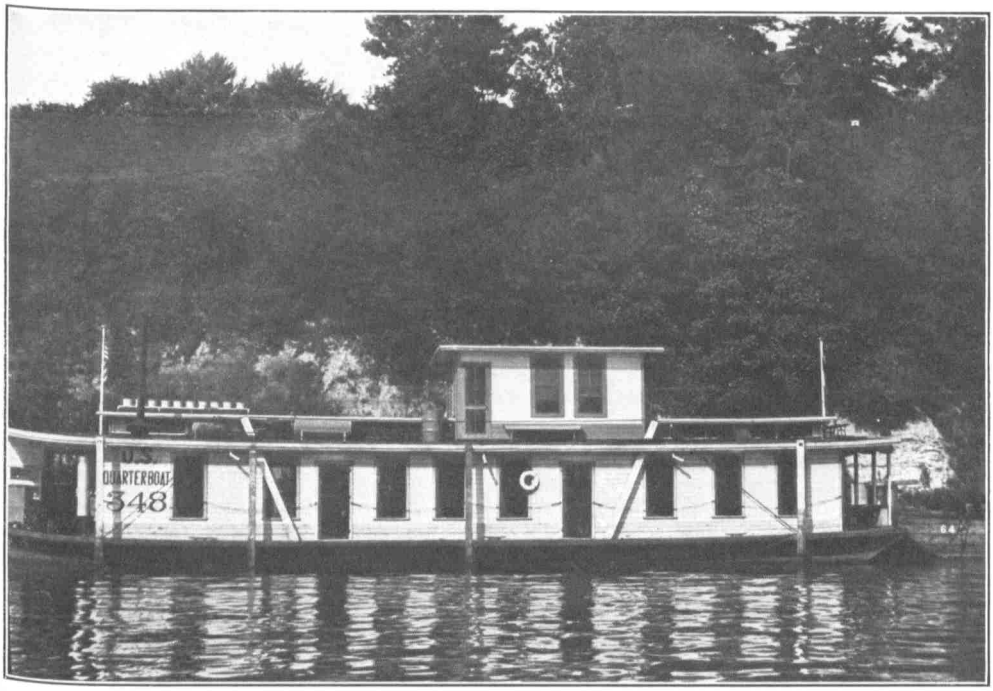

FIGURE 1.—U. S. Quarterboat *348*, the floating laboratory of the United States Bureau of Fisheries.

FIGURE 2.—U. S. Fisheries cruiser *56*, equipped with sounding and sampling booms and field-laboratory apparatus. Two such cruisers were used on the larger rivers and streams.

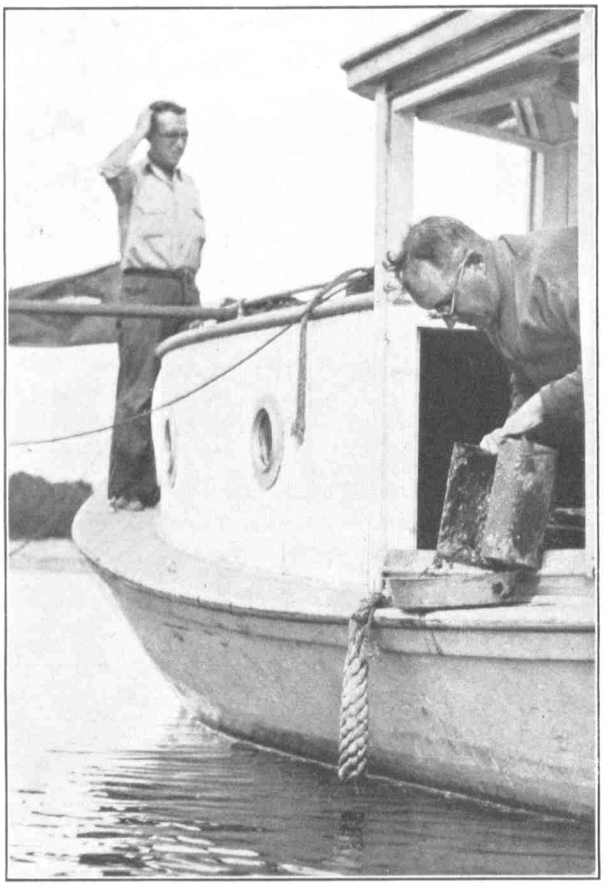

FIGURE 3.—Collecting bottom samples from cruiser with Peterson dredge.

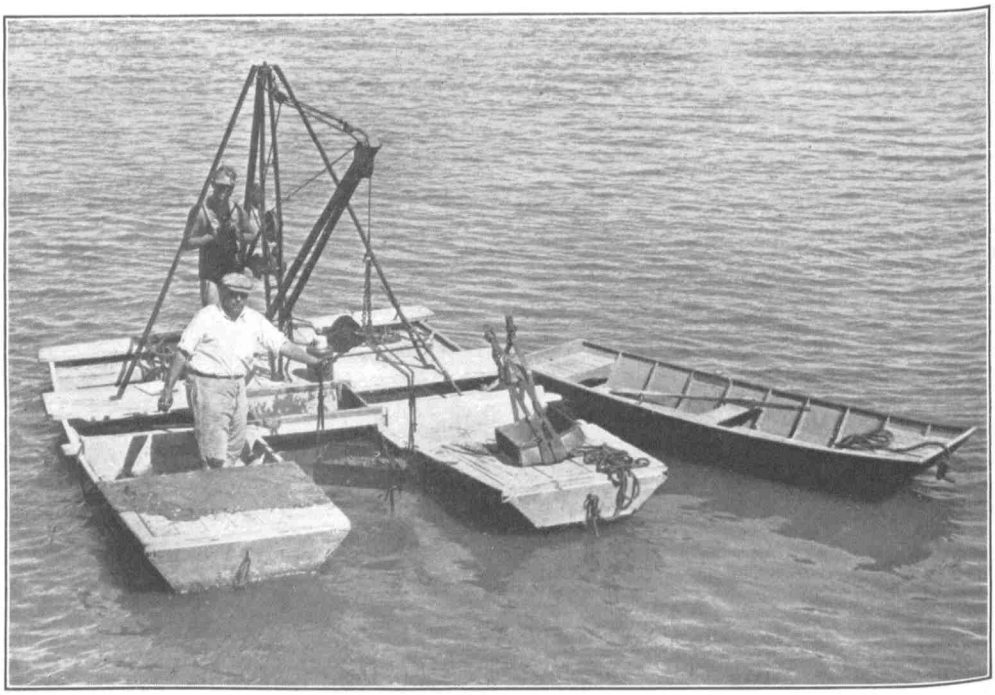

FIGURE 4.—Mussel dredge in operation from catamaran. This dredge was used in the study of bottom conditions where rocks and other obstructions made use of Peterson dredge impossible.

and since the studies of these forms constitute part of the routine background for the interpretation of the pollution hazards, the field methods employed in connection with the entire pollution study operations have been given.

Water Samples

At each station water samples were collected by means of a brass sampler of the general type described by Kemmerer, Bovard, and Boorman (1923) and transferred at once without aeration to 300-cubic-centimeter glass-stoppered, self-sealing magnesium-citrate bottles. The first or top water samples were taken at a depth of from 1 to 2 feet, the actual surface water (the first few inches below the surface) being avoided in the general sampling because the dissolved gases in the water in immediate contact with the air do not present a true picture of the dissolved gases in the main mass of the water in the stream (this fact is discussed more fully under dissolved oxygen). Whenever the depth was greater than 3 feet a second set of water samples, bottom samples, were taken about 3 inches above the floor of the stream. Intermediate samples were collected between the top and bottom at levels from 5 to 10 feet apart wherever the depth of the water justified such sampling.

Mud Samples

Bottom mud samples were obtained with a Peterson dredge properly weighted to bring up about one-half cubic foot of bottom from an area approximately 1 foot square. These mud samples were divided into aliquot parts, some of which were dried (see fig. 3) or fixed with various reagents for chemical determinations, and others were sieved through a series of Monell screens for qualitative and quantitative studies of the bottom fauna.

Plankton

Plankton counts were made from the catch obtained by pumping slowly 1 cubic meter of the water under consideration through a standard silk bolting cloth plankton net, supported in the water and provided with a glass trap bottle of 250-cubic-centimeters capacity in which the organisms accumulated uninjured. On some of the river lakes, as Lake Pepin and Lake Keokuk, a trawl supported by a boom and operated over the side of a cruiser was used both for plankton and the larger surface animals.

For purposes of quick field diagnosis of water conditions only net plankton were used, although in the detailed studies of plankton both nano- and macroplankton were determined.

Fresh-Water Mussels

At the stations where fresh-water mussels were to be taken a heavy mussel dredge (see fig. 4) operated from a catamaran was used. This dredge, which was found to be very effective to a depth of 8 or 9 inches in the mud of the river floor, brought up approximately 1½ cubic feet of river bottom with the contained organisms. Quantitative as well as qualitative studies were possible, therefore, from these dredgings.

Fish

The fish fauna was studied from collections made with various types of nets and seines. Several hauls were made in each of the various portions of the habitat under consideration and usually the entire catch preserved. If the entire catch were too large, representative collections from it were made and the total bulk of the catch noted.

EQUIPMENT

In the field studies reported in this discussion several types of equipment have been used. In the major stream surveys U. S. Quarterboat *348* (see fig. 1), which is fully equipped with chemical and hydrobiological laboratories, together with living quarters for 12 people, was used as the base from which the operations were conducted. Attached to the quarterboat for these investigations were two 35-foot cruisers (U. S. Fisheries *53* and U. S. Fisheries *56*, see fig. 2) which were specially equipped with dredging, sounding, and sampling apparatus, together with portable chemical units for such determinations and preparations as required immediate attention in the field. On certain streams where it was not feasible to move the quarterboat and cruisers, support and cooperation in equipment was given by various Government, State, and private agencies, including the loan of vessels and the use of equipment at hand.

For certain stream studies automobile trucks carrying compact biochemical, biophysical, and hydrobiological apparatus were also used extensively. These mobile units were found to be very effective, as long distances could be covered quickly and the equipment taken to the specific site of the pollution problem to be investigated. (See fig. 5.)

The detailed experiments, most of the bioassay work, and various analyses and tests which could not be made in the field were conducted at the United States Bureau of Fisheries laboratories at the University of Missouri. Here, through the excellent cooperation afforded by the University of Missouri, the Bureau has a research laboratory suite of eight rooms specially equipped for biochemical, physiological, and biological work, in which various pieces of apparatus devised particularly for these pollution studies are in operation.

DISSOLVED OXYGEN

The modifications of the Winkler method for oxygen determinations as described by Kemmerer, Bovard, and Boorman (1923) and as given by American Public Health Association (1933) were followed in both the field and laboratory analyses for dissolved oxygen. The data are reported in parts per million (p. p. m.) unless otherwise specified.

In figures 6, 7, 8, and 9 are presented the results of 5,809 determinations of dissolved oxygen made at 982 stations on fresh-water streams and rivers of the United States during the months of June to September, inclusive, 1930–35. Natural lakes and ponds are excluded, the data covering only conditions in stream and river waters during the warm season. This season was chosen since the oxygen carrying power of water decreases and the metabolic demands of aquatic animals for oxygen increase as the temperature of water rises.

FIGURE 5.—One of the field-laboratory trucks, showing stream-side operations. These trucks were equipped with apparatus and chemicals, sampling and collecting outfits, dredges, and seines. Each truck unit was able, therefore, to make detailed investigations at any stream site which could be reached by car.

From these 5,809 cases, all determinations made at stations where good, mixed, fish faunae were found at the time of sampling, were selected for a composite regardless of the actual amount of dissolved oxygen present. For purposes of this comparison good, mixed, fish faunae were defined as faunae including representatives of the fine fish group (trout, or bass, sunfish, perch, and other spiny-rayed fishes), of the rough fish group (suckers, buffalo, and catfish), and of the minnow series, in good condition

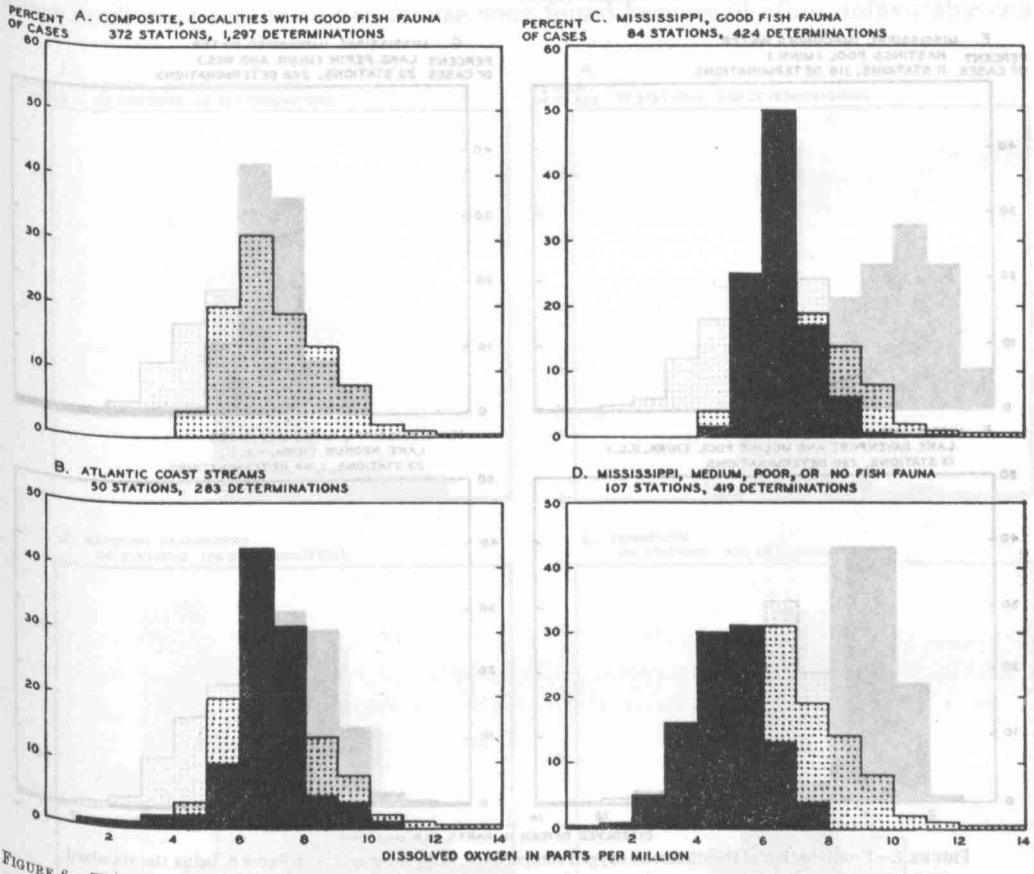

FIGURE 6.—The stippled graph is a composite of dissolved oxygen values for all stations at which good mixed fish faunae were found, each river system being given equal weight to avoid skewing due to differences in actual numbers of cases. Each solid black graph presents all oxygen data for a single river unit regardless of presence or absence of fish at sampling stations. Direct evaluation of each river unit can be made in terms of the preferences of good fish faunae from the stippled graph on which the black graph is superimposed.

at the time the samples were taken. Naturally, the exact species composition of these good, mixed faunae varied to some extent with the river system.

This composite selected as explained, includes 1,297 determinations of dissolved oxygen from 372 stations. Figure 6*A* gives the distribution of the dissolved oxygen values for this composite. To avoid skewing due to uneven number of cases from the different localities the various river systems were given equal weights in determining the percentages.

From figure 6*A* it may be seen that during the warm season the waters at 96 percent of the good fish faunae stations carried 5 p. p. m. or more dissolved oxygen, and that in all of the 5,809 cases good, mixed fish faunae were not found in waters carrying less than 4 p. p. m. dissolved oxygen. These data collected from localities where the fish had had opportunity to choose for themselves point very strongly to 5 p. p. m. as the lower limit of dissolved oxygen, if the complex is to maintain a desirable fish faunae under natural river conditions.

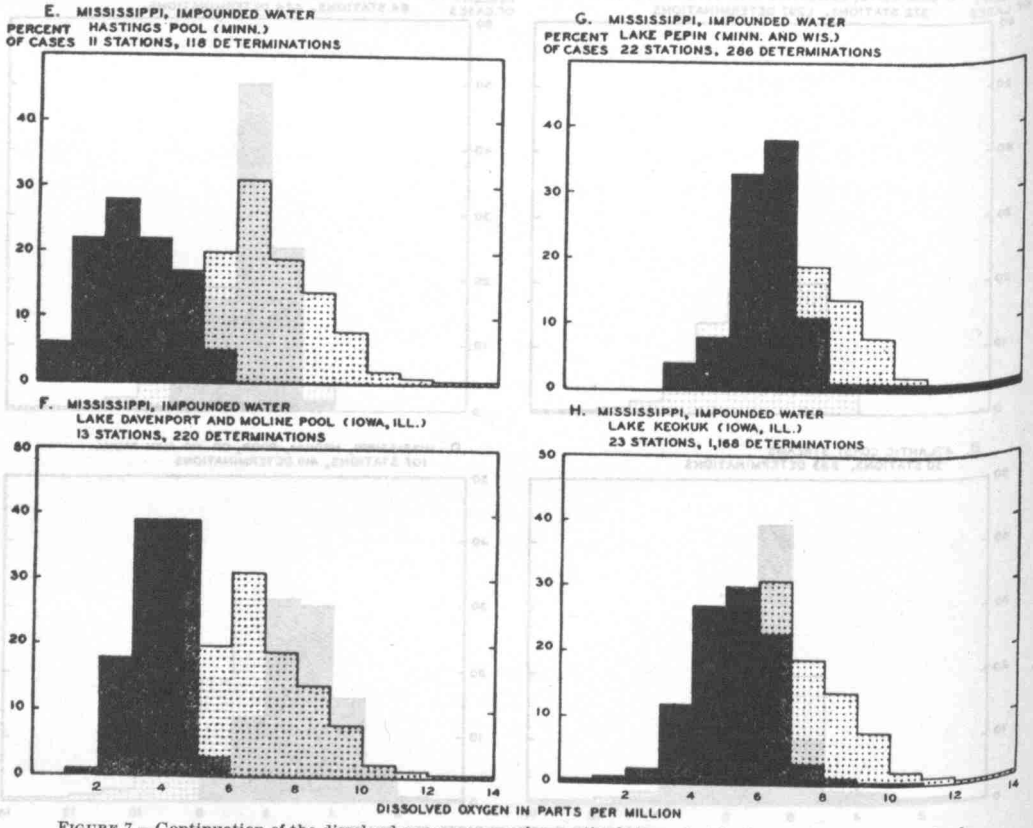

FIGURE 7.—Continuation of the dissolved oxygen comparisons, stippled graph *A* in figure 6, being the standard.

It may be suggested in the absence of other data that the aggregation of the good fish faunae in waters containing 5 p. p. m. or more dissolved oxygen does not constitute proof that this amount of oxygen was required by these fishes, and that some other factor or factors delimit these complexes where good fish faunae were found. However, experimental data presented in another portion of this section support the view that dissolved oxygen is definitely one of the determining factors in these favorable complexes.

A comparison of graphs *C* and *D* in figure 6, with the composite *A*, however, brings out the fallacy, for river waters at least, of the suggestion which has been made at times that the determination of dissolved oxygen or dissolved oxygen in terms of oxygen demand is sufficient alone to define water as suitable or unsuitable for fish life. Graph 6*C* gives the distribution of the dissolved oxygen value for all stations in

the Mississippi River where good fish faunae were found and graph 6*D* for all stations in the Mississippi River where medium, poor, or no fish faunae were found regardless of type of pollution. In this comparison the water at over 98 percent of the stations where good fish faunae were found carried 5 p. p. m. or more dissolved oxygen, and the water at 52 percent at stations where medium, poor, or no fish faunae were found carries less than 5 p. p. m. dissolved oxygen, but the water at 48 percent of the stations where medium, poor, or no fish faunae were found because of other unfavorable con-

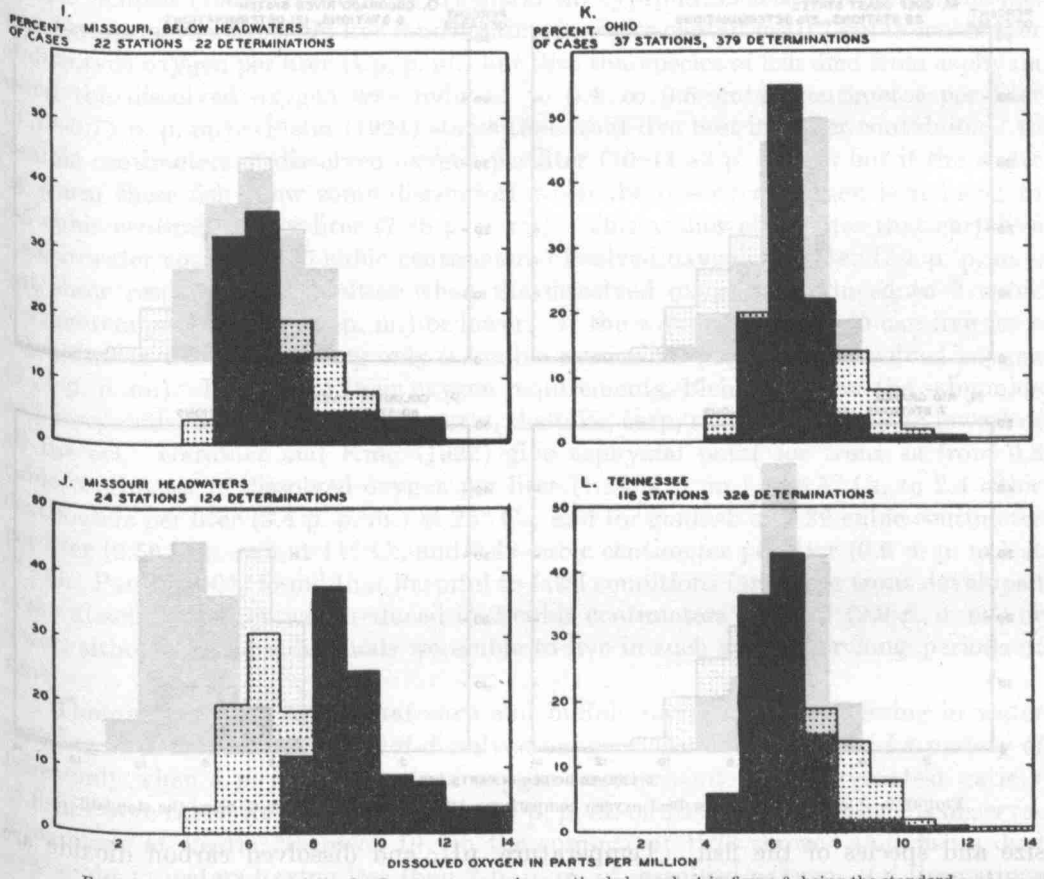

FIGURE 8.—Continuation of dissolved oxygen comparisons, stippled graph *A* in figure 6, being the standard.

ditions, carried 5 p. p. m. or more dissolved oxygen due to current action and other factors in spite of the polluting materials.

Three other observations may be made from these studies of warm-season dissolved-oxygen values in the various streams and river lakes. Low dissolved oxygen was found more frequently in the impounded waters of streams, particularly if the impounded waters were subject to organic pollution, than in the more rapidly flowing portions of these same streams (see graph 7*E* of Hastings Pool, a notoriously polluted portion of the Mississippi River, and graphs 7*F* and 7*H*); headwater streams, especially those in mountainous regions usually have high dissolved oxygen, and the range of

dissolved oxygen to be expected in flowing streams both polluted and unpolluted is in general from 0 to 14 p. p. m.

For the final evaluation of the various findings presented from the field studies on dissolved oxygen, experimental data covering the oxygen requirements of fresh-water fishes must also be considered, as both the amount of oxygen consumed by the fish and the minimal amount of dissolved oxygen which will barely support life vary with the combinations of environmental factors operating at the time, and with the

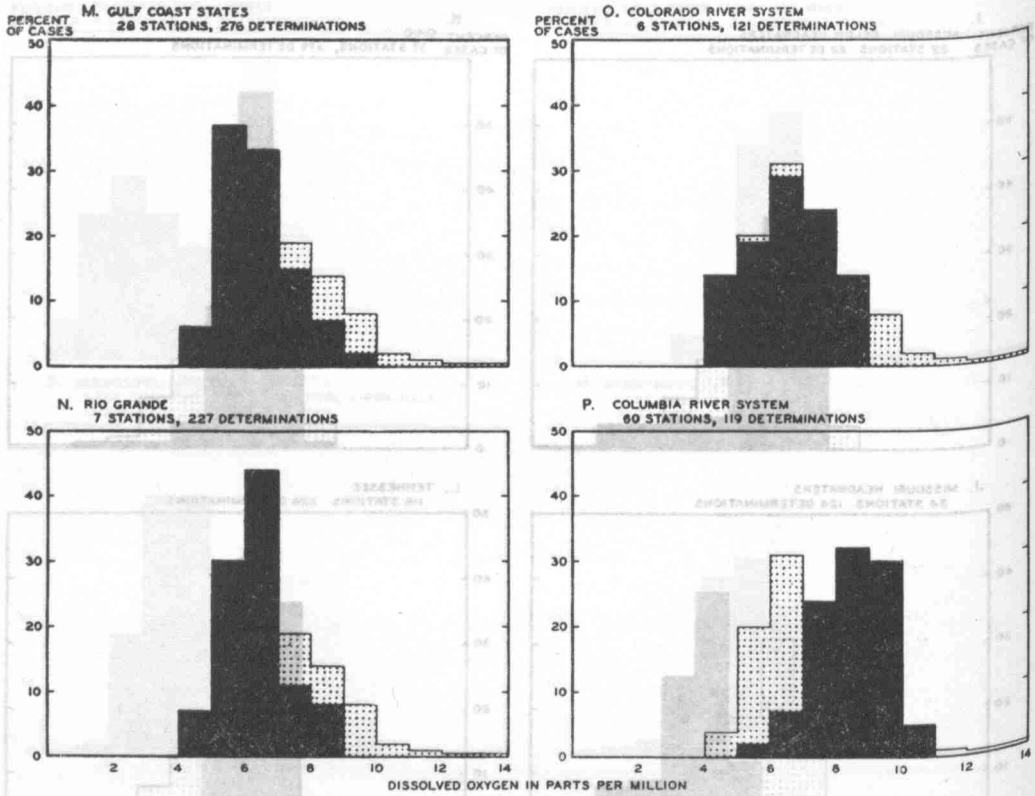

FIGURE 9.—Continuation of dissolved oxygen comparisons, stippled graph *A* figure 6, being the standard.

size and species of the fish. Temperature, pH, and dissolved carbon dioxide are particularly important in this connection.

Many observers have pointed out that the metabolism of, and consequently the oxygen consumed by, fishes and other aquatic animals follows in general the van't Hoff law with reference to temperature so that the actual amount of oxygen removed from the water by the individual fish will vary with the temperature regardless of the amount of oxygen present until a near-lethal point is reached (Keyes, 1930). Ruttner (1926) states that the oxygen consumption of many aquatic animals is almost doubled with each rise of 10° C., within physiological limits, and Powers (1922 and 1932) has pointed out correlations between the utilization of oxygen by fishes at low oxygen tensions and the pH and carbonate systems.

The variation in the amount of oxygen consumed by fresh-water fishes of different species is apparent from the work of Gardiner, King, and Powers (1922) who give the oxygen consumption of the brown trout as from 90 to 200 cubic centimeters per kilo of body weight per hour at temperatures between 4° and 20° C.; of the goldfish as 16 to 90 cubic centimeters; and of the eel 9 to 60 cubic centimeters.

The lower limit for dissolved oxygen—that is, the point at which the dissolved oxygen—is so reduced as to present a lethal condition for fishes is equally difficult to define. Kupzis (1901) reports that in general the cyprinid, *Leuciscus erythrophthalmus* (the European roach), could live for sometime in water containing 0.7 cubic centimeter of dissolved oxygen per liter (1 p. p. m.) but that this species of fish died from asphyxia when the dissolved oxygen was reduced to 0.4 to 0.5 cubic centimeter per liter (0.57–0.71 p. p. m.). Plehn (1924) states that trout live best in water containing 7 to 8 cubic centimeters of dissolved oxygen per liter (10–11.43 p. p. m.), but if the water be warm these fish show some discomfort when the dissolved oxygen is reduced to 5.5 cubic centimeters per liter (7.86 p. p. m.). This author also states that carp live well in water containing 5 cubic centimeters dissolved oxygen per liter (7.1 p. p. m.), but show respiratory difficulties when the dissolved oxygen is reduced to 3 cubic centimeters per liter (4.3 p. p. m.) or lower. If the water be cold, carp can live for a short time in water containing only 0.5 cubic centimeter per liter of dissolved oxygen (0.71 p. p. m.). In order of their oxygen requirements, Plehn lists first the salmonids and coregonids, then the barbe, the rutte, the pike, carp, tench, goldfish, and lowest of all the eel. Gardiner and King (1922) give asphyxial point for trout as from 0.8 cubic centimeter of dissolved oxygen per liter (1.14 p. p. m.) at 6.5° C., to 2.4 cubic centimeters per liter (3.4 p. p. m.) at 25° C.; and for goldfish as 0.39 cubic centimeter per liter (0.56 p. p. m.) at 11° C., and 0.42 cubic centimeter per liter (0.6 p. p. m.) at 27° C. Paton (1904) found that harmful to fatal conditions for young trout developed if the dissolved oxygen were reduced to 2 cubic centimeters per liter (2.9 p. p. m.) or lower, although some individuals were able to live in such waters for long periods of time.

Thompson (1925) states that carp and buffalo have been found living in water carrying as little as 2.2 p. p. m. of dissolved oxygen. As a rule, he found a variety of fishes only when 4 p. p. m., dissolved oxygen were present, and the greatest variety of fishes were taken from waters carrying 9 p. p. m. of dissolved oxygen. His observations made at Peoria Narrows, Ill., in the summer of 1923 showed that fishes died over night in waters having less than 2 p. p. m. of dissolved oxygen. Of the various species of Illinois fish discussed by Thompson the dogfish, *Amia calva*, seemed to be the most sensitive to low oxygen tensions and the carp, the most resistant.

From the various observations cited above, which may be taken as representative of the voluminous literature on the oxygen requirements of fishes, it may be seen that the upper limit of dissolved oxygen at which asphyxia may be expected in fresh-water fishes if there be no unusual complicating factors, is in general about 3 p. p. m. at 25° C. In evaluating the dissolved oxygen level as a lethal hazard to fish life, this upper asphyxial limit must be considered rather than the lower minimal limit of dissolved oxygen which can be tolerated by some fish for varying periods, particularly under the conditions of rapid or abrupt oxygen reduction presented in so many of the experimental studies, since the actual hazard to fish life begins at the oxygen level where

death may be expected even if some more hardy individuals survive temporarily or for some time at lower oxygen levels.

It is well established for many animals and man, however, that the asphyxial oxygen level, the oxygen level which will support life if profound compensations be made, and the oxygen level at which respiratory, cardio-vascular, and other systemic compensations begin are three quite different values. The latter—that is, the oxygen level at which respiratory and circulatory compensations are initiated—marks the lower limit as regards oxygen percentage of the favorable respiratory environment, although this oxygen level is much higher than the lethal oxygen level for these same species. It has been shown (Ellis, 1919) that although man lives in air normally containing 21-percent oxygen, and the collapse point for most human beings is reached when the oxygen in the air breathed is reduced to approximately 6 percent, that human respiratory compensation to reduced oxygen begins at about 18 percent oxygen. Applying this same principle to fishes in the present studies it has been found that individual goldfish, perch, catfish, and other species of fresh-water fishes in good condition and from favorable environments if placed in water of constant flow, favorable composition, and temperature (20° to 25° C.) may show respiratory compensations in rate and volume or both when the dissolved oxygen in this water is reduced only a little below 5 p. p. m. As there are various factors influencing the exact point at which this respiratory compensation begins, the details will be presented elsewhere; but the important finding in connection with the present discussion is that even under conditions as favorable as may be met with in fresh-water streams, respiratory compensations by fishes to oxygen reduction may begin when the dissolved oxygen level is still almost 5 p. p. m. From these studies the case of a perch which made respiratory compensation to reduced oxygen largely by rate is presented (fig. 10) as typical.

This finding that respiratory compensations by fresh-water fishes to oxygen reduction may begin when the dissolved oxygen of water is lowered only to approximately 5 p. p. m. is in accord with the statement of Plehn (1924) that carp show respiratory difficulties when the dissolved oxygen is reduced to 4.3 p. p. m. and gives physiological background for the differences in fish faunae between waters carrying 4 p. p. m. or less dissolved oxygen and those carrying 5 p. p. m. or more dissolved oxygen, as reported in our field studies.

Considering the data from all sources and particularly from the field and laboratory studies presented here 5 p. p. m. of dissolved oxygen seems the lowest value which may reasonably be expected to maintain in good condition varied fish faunae of warm-water fishes in our inland streams, if the water temperature be 20° C. or above. This statement does not mean that 5 p. p. m. dissolved oxygen is the lethal point for fresh-water fishes but designates 5 p. p. m. as approximately the lower limit of favorable conditions. The fact that fish on occasion can tolerate for a period of hours or even days water carrying less than 5 p. p. m. dissolved oxygen does not justify the acceptance of such conditions as defining any stream as suitable for fishes, in view of the data presented on the natural preference by fresh-water fishes for waters containing 5 p. p. m. or more of dissolved oxygen, and the experimental evidence from various sources that vital compensations may be called for in waters carrying less than 5 p. p. m. dissolved oxygen at temperatures of 20° C. or above.

Besides it is recognized in the various fields of animal husbandry, including aquiculture and pisciculture, that if any variety of animal is to be successful and thrive merely sublethal conditions are not adequate.

The application of this observation concerning sublethal conditions is particularly important in pollution investigations, for a reduction of dissolved oxygen increases the lethality of many stream pollutants, especially those injurious to the gills (v. i.). For example, it was found that certain concentrations of various metallic salts and

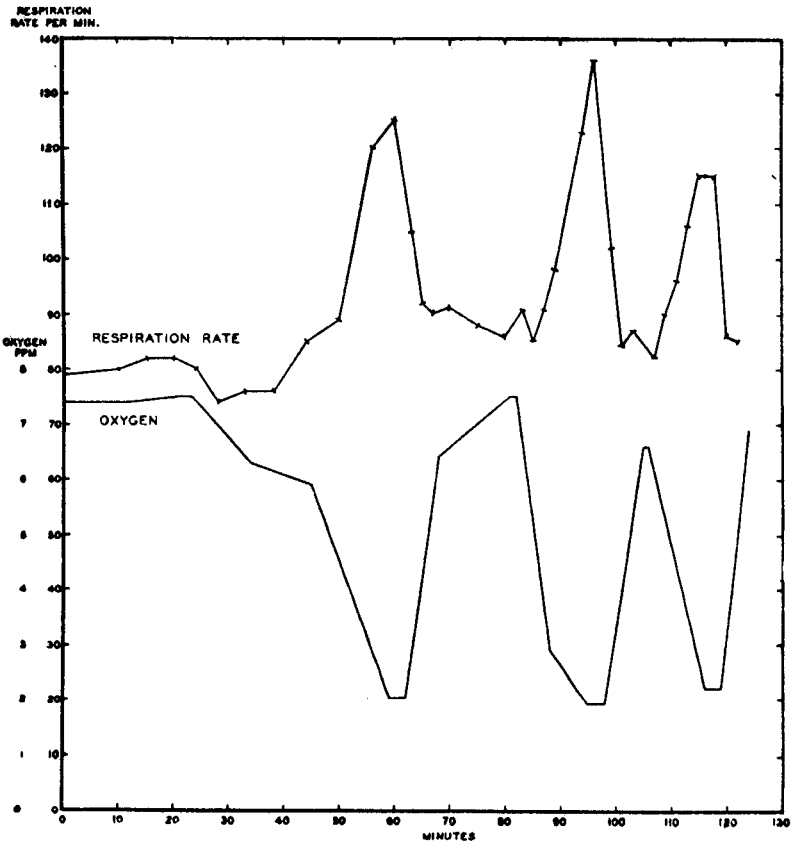

FIGURE 10.—Changes in the respiration rate of a 4½-inch yellow perch, *Perca flavescens*, correlated with changes in the dissolved oxygen content of the surrounding water, temperature 18 degrees centigrade.

acid wastes were consistently more injurious to fish when the dissolved oxygen contained in the water thus polluted was comparatively low, but still sublethal, than when the dissolved oxygen was high. This difference in lethality correlated with dissolved oxygen obtained in spite of the fact that these specific pollutants neither reacted with nor were removed by dissolved oxygen regardless of the amount of oxygen present.

The dissolved oxygen content of unpolluted streams normally varies with at least four major sets of factors, namely, (*a*) physical conditions such as stream flow, stream fall, and temperature, which influence the saturation of water with oxygen from the air; (*b*) oxygen produced by aquatic plants; (*c*) oxygen removed by aquatic organisms both plant and animal; and (*d*) the oxygen demand of the organic detritus

in the stream. Effluents polluting streams alter this dissolved oxygen balance chiefly through increasing the oxygen demand. Pollutants may create oxygen demand in any of three ways or combinations of these; that is, by the addition of quantities of organic matter of a putrescible sort, among which may be mentioned domestic sewage, packing-plant wastes, beet-sugar waste, and hide vat liquor from tanneries; through the action of various reducing chemicals as certain sulphite wastes from paper mills, sulphide and iron wastes from mines, and certain spent dyes from leather works; and by killing large masses of aquatic vegetation which subsequently decompose. Many effluents which create oxygen demand are also harmful to aquatic organisms because of specific toxic effects.

The determination of the biochemical oxygen demand of various effluents affecting the dissolved oxygen balance in the stream does not necessarily, therefore, give a true evaluation of the pollution hazards produced by these effluents; for various species of warm-water fishes will live in water having high oxygen demand, due to domestic sewage or industrial wastes rich in organic material but without specific toxic substances, if the dissolved oxygen level be maintained above 5 p. p. m. and the aeration be sufficient to blow off the excess of other gases as carbon dioxide, methane, and sulphur derivatives. The biochemical oxygen demands of such effluents as have high oxygen demands must be taken into account, however, if these wastes are poured into streams, in order to compute the dilution required to prevent this oxygen demand from lowering the dissolved oxygen in the stream to an unfavorable level.

Two examples of the effect of dissolved oxygen on the lethality of effluents free from specific toxic substances but presenting large pollution hazards because of high oxygen demands will suffice. The tan vat liquor from a tannery on the upper Mississippi River in spite of the high oxygen demand of this waste was not only tolerated readily when properly aerated and unmixed with the toxic chemical effluents from the plant by various warm water fishes but materially increased the production of plankton when added to the river water. Findings from the sewage treatment system of the city of Munich, Germany, also demonstrate that high biochemical oxygen demand in itself need not be a pollution hazard to fresh-water fishes. In this system, water from the River Isar is mixed with prepared sewage and impounded for the commercial raising of rainbow trout and carp. This procedure was very successful over a period of years in the production of commercial quantities of both trout and carp. The following statement from a recent English review of the work of this plan (Engineering, 1935) may be quoted in this connection:

> The proportion of fresh water to sewage should be at least 5:1, and the proportion of oxygen not less than 5 cubic centimeters per litre (7.1 p. p. m.). If these conditions are maintained, the micro-organisms will flourish, absorbing and destroying all impurities and providing the food for the completion of the process. In such circumstances the fish will suffer no ill effects, although, as is well known, trout are most susceptible to any impurity.

The oxygen balance of streams may also be affected by oils which exclude oxygen from the surface of the stream and prevent proper reaeration of the water. Oil is rarely poured into streams in such quantities as to present this difficulty, however. Again sewage and industrial sludges are often particularly harmful in reducing the dissolved oxygen through their biochemical oxygen demands during the winter season when ice covers the stream surface and interferes with the reoxygenation of the water.

HYDROGEN-ION (pH) LIMITS

Hydrogen-ion concentration measurements in the laboratory and aboard Quarterboat *348* were made electrometrically with calomel and quinhydrone electrodes (Leeds, Northrup Co., Philadelphia, type 7701–A1). In the field the Youden apparatus (W. M. Welch Co., Chicago, type 5270) bridging the quinhydrone electrode against standardized phthalate solution was used because of greater portability. When field conditions were such that neither of these two pieces of apparatus were available, the determinations of hydrogen-ion concentrations were made colorimetrically by the method of Gillespie (1920). Sterile tubes, solutions, and stoppers were used in preparing the tube series for the Gillespie sets, which were calibrated against the calomel electrode and kept in a dark box except when measurements were being made. Although fractional values were recorded (i. e., hundredths), in presenting the data the value is given to the nearest tenth pH.

The hydrogen-ion concentration of the inland streams of the United States, southern Canada, and northern Mexico, excepting badly polluted portions of these waters, as seen in a review of some 10,000 readings made during the past 5 years, lies in general between values of pH 6.7 and pH 8.6, with the extreme range (in our data) of pH 6.3 and pH 9.0 in streams for which no specific pollution factor affecting the hydrogen-ion concentration was readily observable. Swamp waters, bog streams, and particularly swamp lakes not infrequently show an acidity between pH 4.5 and pH 6.0, yet at the same time may support mixed fish faunae. In some small western streams and pools containing fishes examined by the writer in North Dakota, Montana, and New Mexico an alkalinity of pH 9.5 was occasionally found in alkali districts or near mineral springs. In such waters small poeciliids and cyprinids were uniformily the dominant fishes.

In figures 11, 12, 13, and 14, 7,228 pH readings from inland stream waters representing 1,125 localities are presented. These data were collected during the warm season, June to September, 1930–35, and are comparable with the dissolved oxygen data in the preceding section. The composite, figure 11*A*, was constructed from 2,280 readings representing 409 localities where good fish faunae, as previously defined, were found. This composite covers a range between pH 6.3 and pH 9.0, with 97 percent of the cases between pH 6.7 and pH 8.6. Superimposing the graph of the composite on the graphs presenting the data from the various river systems, however, shows that, except in cases of extreme pollution, the pH values as such of stream waters, both polluted and unpolluted, do not differ materially from those of the composite.

The data from the various river systems (other than the composite) are presented without regard to pollution, except that no pH readings of water in the immediate vicinity of flumes and conduits from which effluents were escaping have been included. The extreme pH range of the flowing waters of inland streams of the United States, both polluted and unpolluted, as found in these field studies was pH 3.9 to pH 9.5, although various effluents poured into these same waters were found to range from pH 1.0 to pH 11.0 at the point of entrance into the stream. These observations show that dilution and the buffer action of various substances

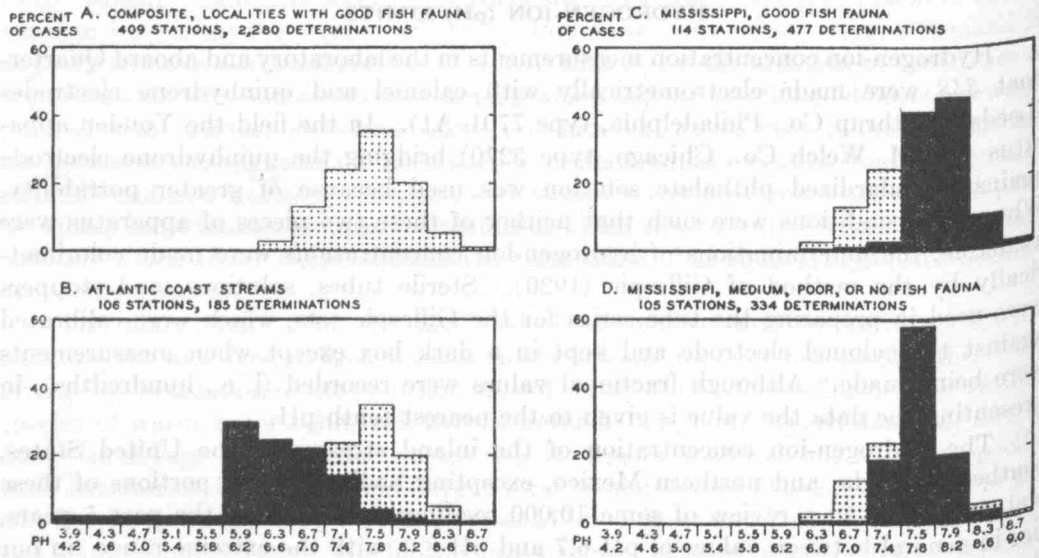

FIGURE 11.—Comparisons of pH values of various river units. Composite and black graphs as explained under figure 6.

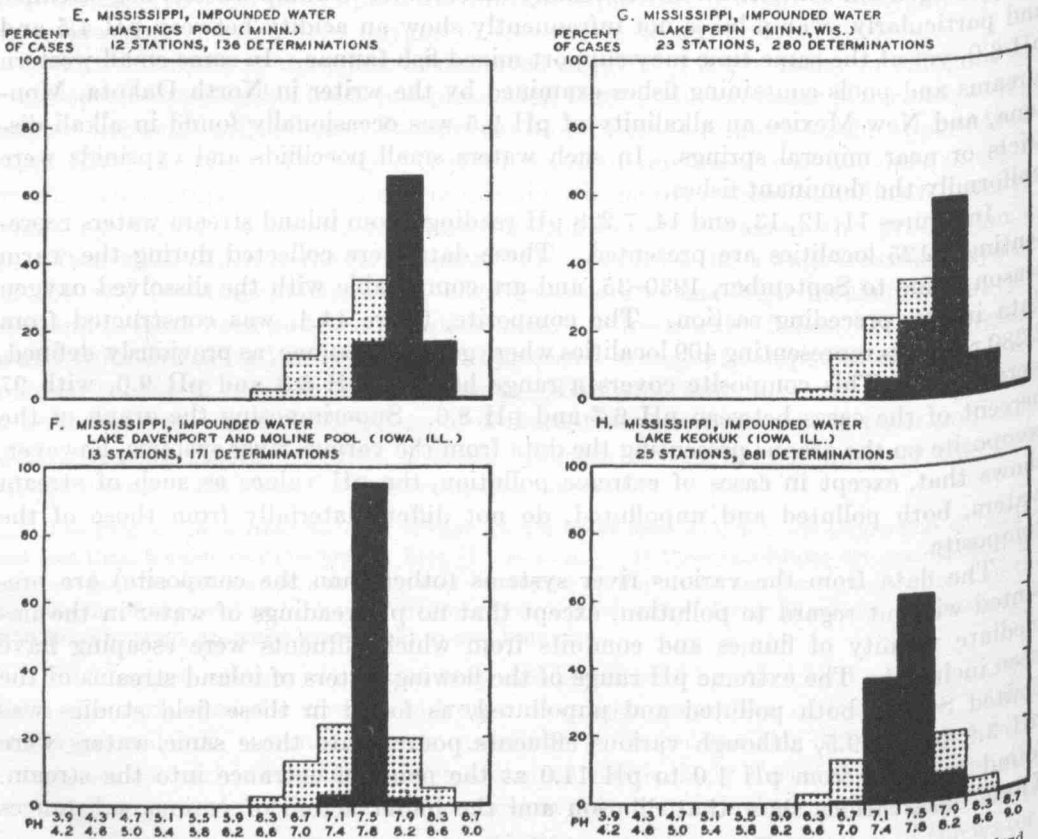

FIGURE 12.—Continuation of comparisons of pH values for various river units, stippled graph *A* figure 11, being the standard

in the river waters do change the pH values of the extremely acid and extremely alkaline wastes rather rapidly to the range of the composite pH 6.3 to pH 9.0.

Reviewing all of the field pH data it may be observed within the general range of unpolluted water, pH 6.7 to pH 8.6, that mountain streams, particularly headwater streams, are in general more acid than plains or lowland streams. The Columbia River data (fig. 14*P*) bring out this comparison in the bimodal distribution of the pH values, since portions of the Snake River flowing through plains and desert regions and the mountainous headwaters of both the Snake and Columbia Rivers

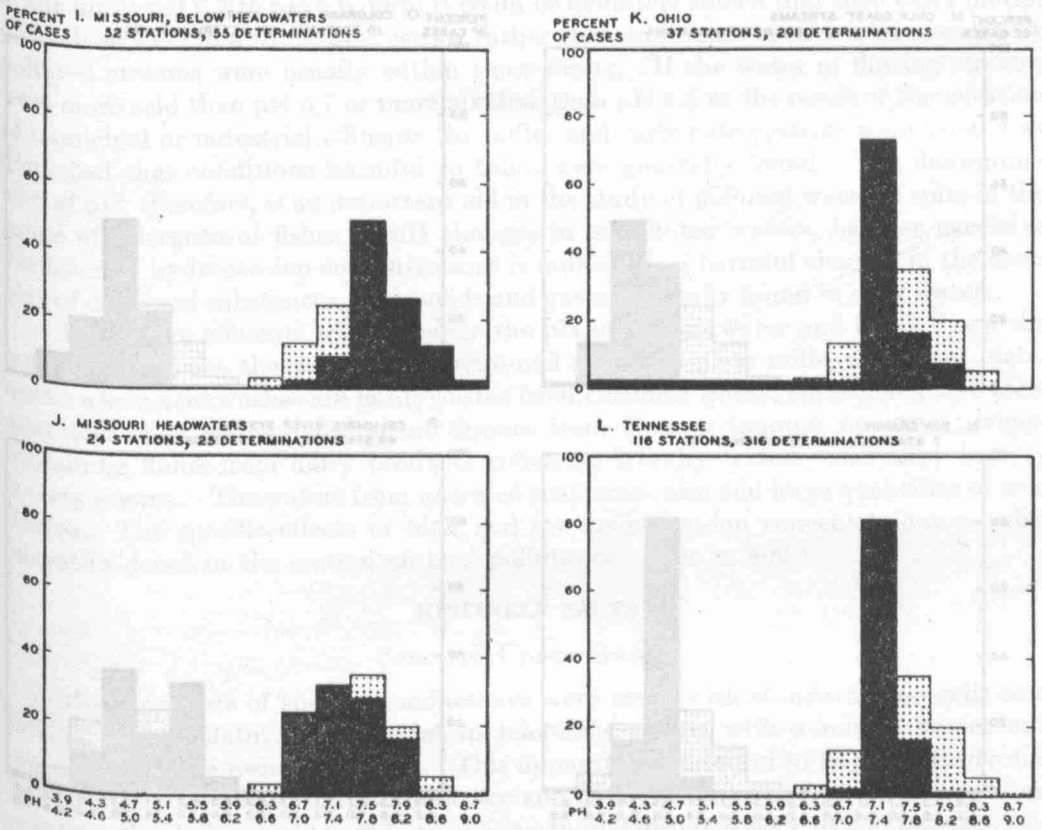

FIGURE 13.—Continuation of comparisons of pH values, stippled graph *A* figure 11, being the standard.

are included in this graph. This same distribution of pH values is also apparent in the graphs presenting the findings in the two parts of the Missouri River system (figs. 13*I* and 13*J*). The explanation of these distributions of pH values is clear when the carbonates and conductivities of these waters are also considered (v. i.), as the headwater streams contain much less dissolved solid matter than the plains, lowland, and desert streams. The effects of acid pollution are evident in the Ohio River (fig. 13*K*), and of general pollution and some bog waters in the Atlantic coast streams (fig. 11*B*).

The field observations presented here agree in general with the statement made by Shelford (1929) that the hydrogen-ion concentration from pH 6.5 to pH 8.5 may

be expected in most uncontaminated fresh-water streams and lakes; and with the observations of Powers (1921 and 1929); and of Juday, Fred, and Wilson (1924).

Experimental tests have demonstrated that many species of fresh-water fishes have a great tolerance for variations in hydrogen-ion concentrations over a wide range. Creaser (1930) showed brook trout to have a voluntary toleration of hydrogen-ion concentrations from pH 4.6 to pH 9.5. Brown and Jewell (1926) found catfish and perch living in apparently good condition in a bog lake, the water of which ranged from pH 4.4 to pH 6.4; and also in a glacial lake nearby, the water of which varied

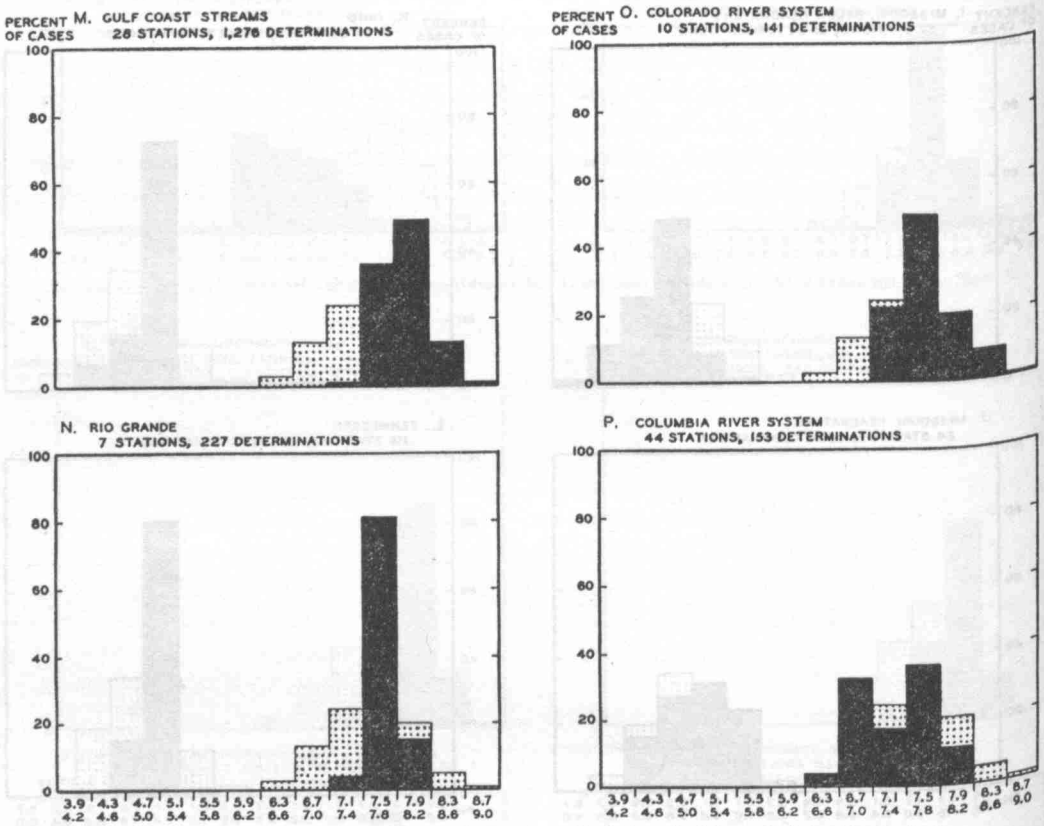

FIGURE 14.—Continuation of comparisons of pH values, stippled graph *A* figure 11, being the standard.

from pH 8.2 to pH 8.7. These workers demonstrated that the fishes from the two lakes survived transfer from either lake to the other. Wiebe (1931a) reports goldfish survive rapid changes from pH 7.2 to pH 9.6; largemouth black bass, from pH 6.1 to pH 9.5; smallmouth black bass, from pH 6.6 to pH 9.3; and sunfish from pH 7.2 to pH 9.6. Powers (1930) in reviewing the problem summarizes the existing data by saying that aquatic organisms are able to withstand a wide range in pH. The writer has confirmed this statement with gammarids, daphnia, unionids, and planaria, as well as for goldfish, perch, and catfish, in connection with pollution tests.

It might seem, therefore, from both the field data and laboratory findings that the pH values of stream water would be of little consequence in pollution studies and in determining standards of water suitability. However, the pH of natural water is

determined by substances in solution—particularly carbonates, carbon dioxide, various salts, and a few organic substances—which collectively constitute a poor to fair buffer system; so that water more acid than pH 6.7 or more alkaline than pH 8.6 is not found generally in our inland streams, unless there be some unusual factor in the complex. Pond water, bog water, and lake water vary over a wider range, but the combination of stream flow, aeration and buffer substances holds the hydrogen-ion concentration of the larger rivers, the smaller streams, and even many brooks within the limits described. In pollution studies, therefore, it has been found advisable to view with suspicion any stream water having an hydrogen-ion concentration outside of the limits pH 6.7 to pH 8.6, until it could be definitely shown that such extra limital pH values were due to natural causes rather than to human agencies, as even badly polluted streams were usually within these limits. If the water of flowing streams were more acid than pH 6.7 or more alkaline than pH 8.6 as the result of the addition of municipal or industrial effluents the buffer and carbonate systems were usually so disturbed that conditions harmful to fishes were generally found. The determination of pH, therefore, is an important aid in the study of polluted water in spite of the range of tolerance of fishes to pH changes in unpolluted waters, because excessive variation in hydrogen-ion concentrations is indicative of harmful changes in the complex of dissolved substances, both solids and gases, normally found in river water.

Among the effluents which change the pH of stream water and break down the buffer systems are the wastes from wire-nail mills, tin-plate mills, and other metal works where acid washes are used; wastes from chemical works, particularly dye mordant and soda compounds; spent liquors from chrome tanning processes; whey-containing fluids from dairy products concerns; laundry waters; and some battery factory wastes. The waters from unsealed coal mines also add large quantities of acid wastes. The specific effects of high and low hydrogen-ion concentrations are discussed in detail in the section on acid pollutants. (See p. 409.)

IONIZABLE SALTS

Specific Conductance

Measurements of specific conductance were made with standard glass cells containing coated platinum electrodes in telephone circuit with a microhummer and standard variable resistance units. This apparatus was found to be very sturdy and was regularly used both in the laboratory and in the field. For convenience in presentation, the data are expressed as specific conductance in mho$\times 10^{-6}$ at 25° C.

Unpolluted natural waters contain in solution small quantities of carbonates, chlorides, phosphates, and sulphates, usually some nitrates and nitrites if organic matter be present, and traces of many other salts which vary with the region through which the stream flows. The metallic ions represented are largely calcium, magnesium, sodium, potassium, iron, and manganese, with traces of various other elements. Owing to the fact that carbon dioxide is supplied to stream water from so many sources, carbonates are the dominant salts; but because of the low solubility of most carbonates and also of most phosphates, the mineral content of river water never rises very high unless some particular substance is added to the water which will raise the solubility of these compounds or transform them into other more soluble compounds. All of the substances in solution in river water collectively exert

osmotic pressure on the aquatic organisms living in the water, and many of these compounds are physiologically active, so that fresh-water fishes and other animals living in these streams have become adapted to the physical and physiological actions of this salt complex.

Small variations in several of these salts may cause small variations in the species composition, particularly the invertebrates, of the faunae at any given station. Most aquatic species, however, will tolerate changes of considerable magnitude in the relative amounts of these salts normally present in flowing waters, if the very small total amount which is usually present be not exceeded. For example, the fixed carbonates in the upper Tennessee River were found to vary from 0.4 to 30 cubic centimeters per liter (computed as CO_2 by volume) without affecting the general composition of the aquatic fauna, and from 0.3 to 55.5 cubic centimeters in Spider Creek, a tributary to the Wabash River.

The specific quantities of most of the substances comprising this salt complex are not so important as the total quantity of soluble matter involved (see section on osmotic pressure), since even the small quantities of these compounds present in ordinary soil run-off are in excess of the physiological needs of most fresh-water organisms. As in general these substances are ionizable, measurements of the specific conductance of a large number of polluted and unpolluted waters were made. The summarized data are presented in figure 15.

These determinations of specific conductance of inland fresh waters show that, excepting the streams in the plains and desert regions, the specific conductance of those portions of inland streams and rivers which were supporting good, mixed fish faunae in general lay between 150 and 500 mho $\times 10^{-6}$ at 25° C.

This uniformity of water composition in flowing streams holds even in the very deep holes of rivers. Two cases—Pan Eddy, in the Tennessee River, and the deep hole off Grand Tower, Ill., in the Mississippi River—are presented as typical in table 1.

Only in the very deep portions of river lakes, such as Lake Wilson in the Tennessee and Elephant Butte Reservoir in the Rio Grande, is there any marked stratification of the waters. In the deeper portions of some of these impounded waters (see table 4) definite thermal stratification, with the attendant changes in turbidity, dissolved oxygen, pH, and other physiochemical features of the water, develop in midsummer at levels variously determined by the general climatological features of the region and the level and amount of draw-off as made for the needs of industry and navigation. In such river lakes a warm, more turbid stream—the hyperlimnorrheum—flows over a colder, clearer lake—the hypolimnion—with a rather well-delimited thermocline lying between these. This condition of stratification obtains, however, only during a portion of the warm season. Specific data for one station on Lake Wilson (see table 4) show such stratification of the waters when it was at its height. During the colder portions of the year there is a rather complete mixing of the waters at all depths, even in Lake Wilson. Details of these hydrobiological data of various river lakes are presented elsewhere.

The specific conductance of mountain stream waters was generally in the lower part of this range, unless excess carbon dioxide were present. However, in the streams of the western plains and desert areas, particularly those carrying the more alkaline

waters, as the Snake (Columbia River system), the Rio Grande (below headwaters), the Colorado and Gila Rivers, and the upper Missouri and Yellowstone below the mountains, a specific conductance of 2,000 mho was not unusual, the general range of specific conductance of these streams being between 200 and 2,000 mho, with

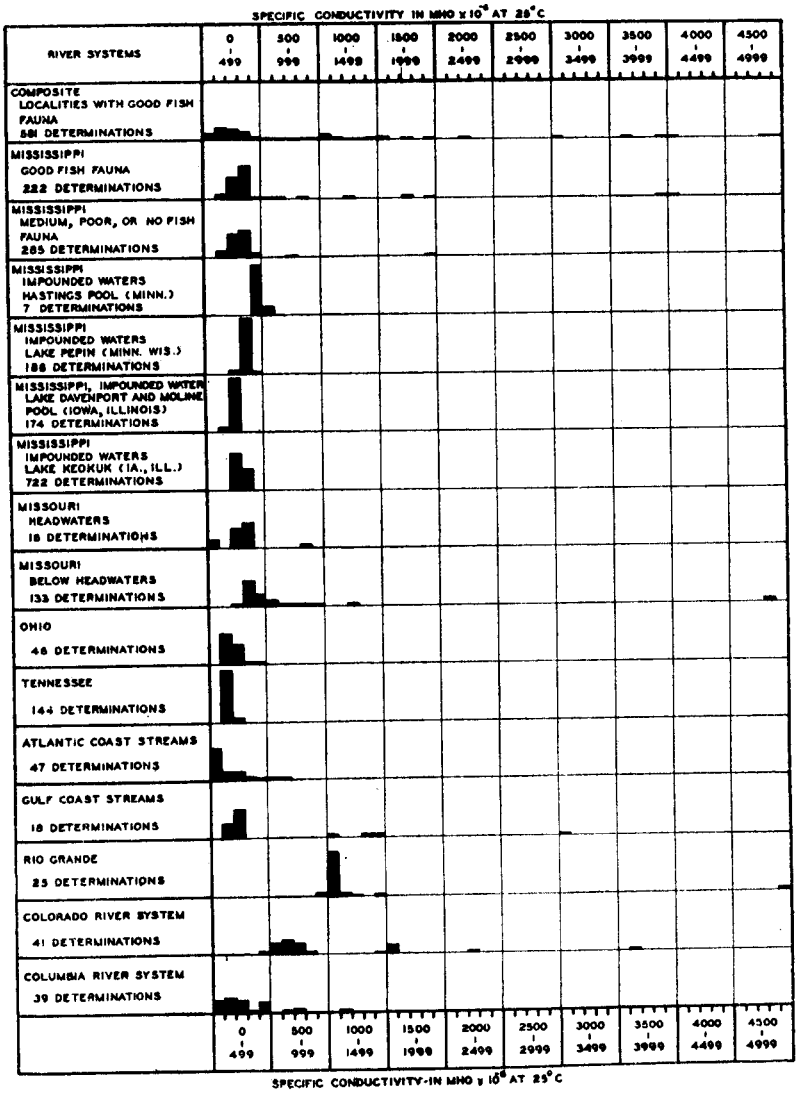

FIGURE 15.—A comparison of the specific conductivity values of the waters of various river units.

extreme readings of almost 5,000 mho $\times 10^{-6}$ at 25° C. However, good mixed fish faunae of such species as normally inhabit these western streams were usually not found in waters with specific conductance greater than 2,000 mho $\times 10^{-6}$ at 25° C. These high conductivity values for certain western waters were clearly due to the natural high solids content of these waters which drain areas rich in the various soluble alkalis.

From the field studies on specific conductance it was found advisable in pollution studies to look for specific pollutant action if the conductivity of the water exceeded 1,000 mho in all types of streams except those draining the more alkaline regions, or 2,000 mho in the case of the western streams discussed above, for the specific conductance is very readily raised by acid and salt pollutions of several sorts.

Specific conductance, therefore, offers a ready method for detection of salt and acid pollution, as produced by water from oil wells, by wastes from industries using salts or strong acids, and by soluble salts of heavy metals. This method was used very satisfactorily by the writer in determining the extent of downstream pollution from lead and zinc mines in the Coeur d'Alene district in Idaho (Ellis, 1932), and in following pollution by acid mine waters from coal mines in Tennessee and West Virginia.

Carbon Dioxide

Determinations of free, half-bound and fixed carbon dioxide were made by the methods of Seyler as described by Kemmerer, Bovard, and Boorman (1923) and American Public Health Association (1933). The data are expressed as cubic centimeters of carbon dioxide per liter.

Fixed carbon dioxide (chiefly calcium and magnesium carbonates)

In figures 16 and 17 the data from 6,770 determinations of fixed carbon dioxide in flowing streams of the United States and southern Canada collected during the warm season, June to September, inclusive, 1930–35, are presented. The extreme range of fixed carbonates varied from almost 0 to 70 cubic centimeters per liter, with 40 cubic centimeters per liter as the usual upper limit. A composite of determinations from waters where good fish faunae were thriving (fig. 16*A*) covered the entire range from 0 to 70 cubic centimeters per liter. In this composite 96 percent of the 2,190 analyses showed the stream water to carry less than 50 cubic centimeters per liter of fixed carbon dioxide and 53 percent lay between 10 and 30 cubic centimeters per liter. Comparing these findings with the classification of lake water given by Birge and Juday (1911), it may be seen that most of the flowing waters fell in the second class, designated as medium waters; and that the large percent of the river and stream waters could be classified as either soft or medium. Hard waters were distinctly in the minority.

Reviewing this composite in connection with the findings on fixed carbonates in the waters of the various river systems, it is evident that between 10 and 40 cubic centimeters of fixed carbon dioxide may be expected in most of the fresh-water streams of the United States. Fixed carbon dioxide in itself, however, does not seem to be a determining factor in classifying flowing waters as suitable or unsuitable for fresh-water fishes. Various limnologists have pointed out the importance of fixed carbonates in maintaining food supply, and, therefore, fish faunae of various lakes (Welch, 1935), but from the data on rivers and streams presented here it must be concluded that either carbonates are not limiting factors or that they are always present in sufficient quantities to meet the needs of the stream biota. An exception to this last statement, however, must be taken at least in the case of fresh-water mussels, as carbonates do constitute a very vital limiting factor for these animals.

In general, it was found that the fixed carbonates vary with the character of the country drained, mountain streams in regions where igneous rocks dominate being very low in fixed carbonates and streams traversing limestone country or alkaline soil being relatively high. However, it must be added that excepting the headwater streams in mountainous regions the fixed carbonate load of flowing stream water was rarely less than 5 cubic centimeters per liter.

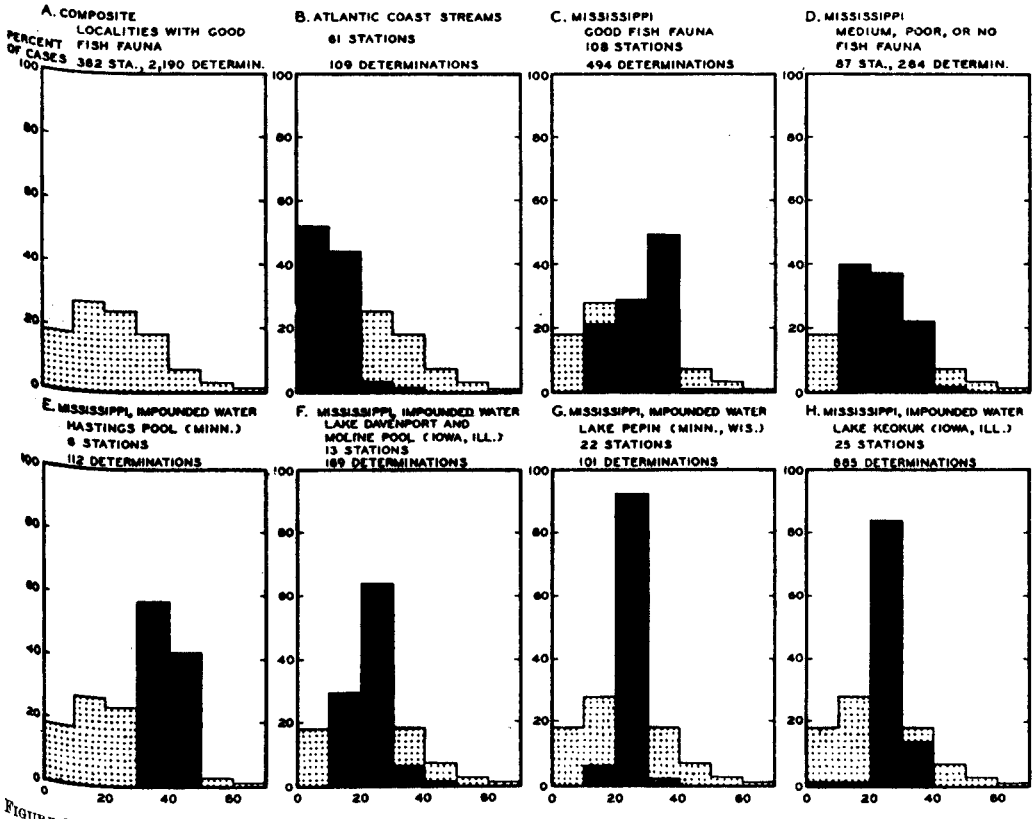

FIGURE 16.—Fixed carbon dioxide values (as cubic centimeters of carbon dioxide per liter, bottom line) for the waters of various river units. Stippled and black graphs composed as explained under figure 6.

In pollution studies, although fixed carbonates may not be important in defining particular water as suitable or unsuitable for good fish faunae, the fixed carbon dioxide is of large importance in evaluating the extent of certain types of pollution and in determining the amount of dilution required to render certain effluents relatively harmless to aquatic life. The fixed carbon dioxide of the stream water is the major buffer against which both acid and alkali pollutants act, and the fixed carbonate must be taken into consideration, therefore, when the maximal nontoxic dilution of any effluent is to be determined. This problem is discussed more fully under acid wastes, but it may be pointed out here that the toxicity to fishes and other aquatic life of many of the common acids is much greater in distilled water or water carrying very little fixed carbon dioxide than in water carrying 20 to 60 cubic centimeters per liter of fixed carbon dioxide. The reason is obvious because of the buffer and

neutralizing actions of these fixed carbonates on free acids. Again, the fixed carbon dioxide is of considerable importance in detoxifying various effluents, particularly those carrying salts of heavy metals, by precipitating various compounds, since many carbonates are relatively insoluble and, therefore, are removed at least temporarily from the waters during precipitation. This is discussed more fully in the section on metallic poisons.

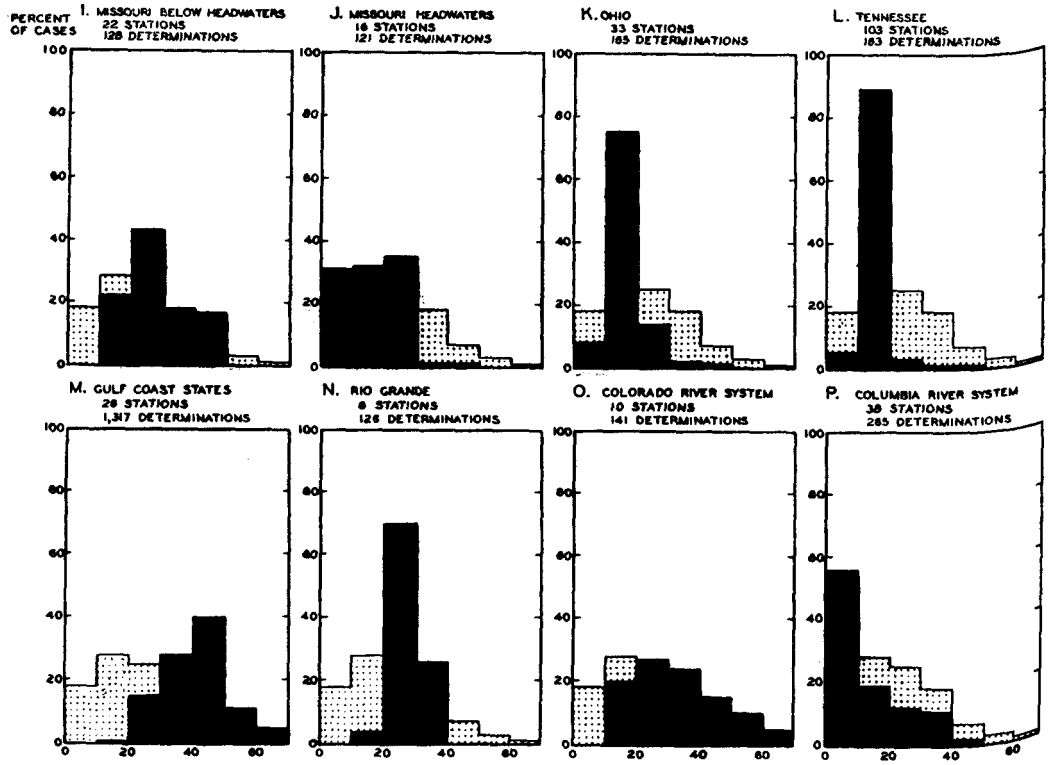

FIGURE 17.—Continuation of comparisons of fixed carbon dioxide values, stippled graph *A* figure 16 being the standard.

FREE CARBON DIOXIDE

Figures 18 and 19 present the data from 3,351 determinations of free carbon dioxide in various streams of United States. From these figures, and particularly from the graph of the composite, it may be seen that river and stream waters, where good fish faunae were found, carried consistantly less than 5 cubic centimeters of free carbon dioxide per liter, 90 percent of the waters where good fish faunae were taken carrying less than 2 cubic centimeters of free carbon dioxide per liter. It must be pointed out in this connection that conditions in moving streams are quite different as regards free carbon dioxide from those obtaining in lakes and ponds. Due to the constant turnover of river and stream waters because of current action, there is a very uniform mixing of water from surface to bottom (see data from Grand Tower on the Mississippi and Pan Eddy in the Tennessee (table 1)), so that the free carbon dioxide, as well as the other dissolved gases, is quite uniformly distributed throughout the

stream. Again, the movement of the current facilitates the constant reaeration of stream waters with a tendency for these waters to lose carbon dioxide to the air as soon as the carbon-dioxide tension in the water exceeds that of the surrounding air, which is usually quite low (2 to 4 parts per 10,000). Both of these conditions, together with the usual presence of calcium and magnesium salts in stream waters, tend to keep these flowing streams more alkaline than pond, lake, and bog waters, so that in many river waters the alkalinity is raised to a point where there is little or no uncombined carbon dioxide.

TABLE 1.—*Characteristics of water at different depths in deep holes of flowing rivers, showing general uniformity of composition at any given station due to mixing action of current*

I. UPPER TENNESSEE RIVER, AT PAN EDDY, 18 MILES BELOW CHATTANOOGA, TENN., AUG. 21, 1931, AIR TEMPERATURE, 23° C.

Depth in feet	Water temperature, degrees centigrade	pH	Specific conductivity in mho×10^{-6} at 25° C.	Fixed carbon dioxide, cubic centimeters per liter	Dissolved oxygen parts per million	Light penetration, millionth intensity depth in millimeters
S[1]	28.0	7.3	169	15.4	5.6	544
10	28.0	7.2	169	15.4	5.5	561
20	27.9	7.3	169	14.9	5.7	561
30	27.9	7.3	169	14.9	5.9	561
40	27.8	7.3	169	14.9	6.0	561
50	27.8	7.3	169	14.9	5.7	561
60	27.8	7.3	169	14.9	5.2	561
70	27.8	7.4	169	15.2	5.5	552
80	27.8	7.4	169	15.2	5.7	552
90	27.8	7.4	169	15.2	5.5	544
100	27.6	7.4	169	15.4	5.6	536
110	27.7	7.3	168	14.9	5.7	528
120	27.8	7.3	168	14.9	6.1	521
130	27.8	7.3	167	15.1	5.9	513

II. MISSISSIPPI RIVER, OFF TOWER ROCK, NEAR GRAND TOWER, ILL., SEPT. 8, 1931, AIR TEMPERATURE 30.5° C.

S[1]	26.2	7.5	340	26.4	5.3	129
10	26.0	7.5	341	26.6	5.1	125
20	25.8	7.6	339	26.8	5.3	125
30	26.0	7.5	337	26.4	5.3	122
40	26.0	7.5	338	26.4	5.3	129
50	26.0	7.5	340	26.4	5.3	120
60	26.0	7.5	331	26.6	5.3	122
70	26.2	7.4	338	26.7	5.3	122
80	26.0	7.4	342	26.7	5.3	125
90	26.0	7.4	339	26.8	5.4	122
100	26.0	7.4	338	26.8	5.4	119
110	26.0	7.4	341	26.8	5.3	124

[1] Surface, i. e., top 12 inches of water.

The specific toxicity of carbon dioxide for aquatic organisms is well known and is discussed under acid wastes. From all of the field data and in view of the experimental findings presented, the determination of free carbon dioxide was found to be a valuable aid in pollution studies, and river and stream waters carrying more than 3 cubic centimeters of free carbon dioxide per liter were checked carefully for some source of organic pollution. Values in excess of 3 cubic centimeters per liter usually were indicative of such pollution in our flowing inland streams. The relatively high free carbon dioxide as compared with the composite found in Hastings Pool in the upper Mississippi River and in the polluted portions of the Atlantic coast streams and other systems are evident from the graphs presented in figs. 18*E* and 18*B*.

IRON

Iron determinations were made by the method of American Public Health Association (1933), using permanent standards of cobalt and platinum salts.

A limited number of total iron determinations were made in typical localities for correlation with studies of water from abandoned coal mines. Eighty-three determinations of total iron in waters of Mississippi, Missouri, Ohio, Tennessee, Atlantic coast, and Gulf coast systems gave the following grouping:

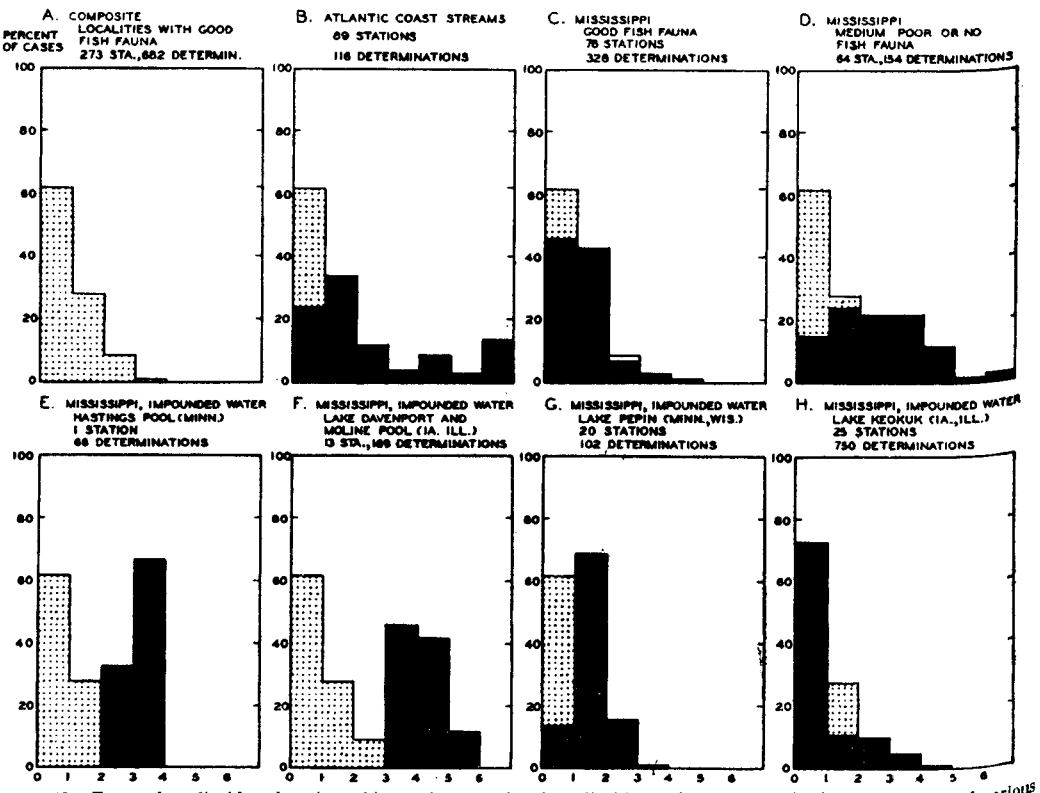

FIGURE 18.—Free carbon dioxide values (as cubic centimeters of carbon dioxide per liter, bottom line) for the waters of various river units. Stippled and black graphs composed as explained under figure 6.

At stations where good fish faunae were found (75 cases) the free iron ranged from a trace to 30 p. p. m., with 69 of these 75 cases below 10 p. p. m. In streams polluted with either mine waters or chemical effluents carrying iron compounds the total iron ran much higher, the maximum found in this series being 202 p. p. m. in waters of a stream of high acidity (pH 4.4) flowing from a coal mine in operation near Turley, Tenn. Iron in quantities above 100 p. p. m. was associated with acidity above average and when such conditions were found chemical or mine pollutions were suspected.

In the experimental tests (see section on heavy metals) it was found that 100 p. p. m. of total iron were not immediately harmful to either fish or daphnia; and that such quantities, unless a constant flow were maintained, were usually diminished during the first few days of experimental tests as a result of precipitation so that the

free iron in the water did not exceed 20 p. p. m. Iron as it occurs in most natural flowing waters, therefore, is not a major limiting factor in the distribution of fishes in fresh-water streams. Besides in fresh-water streams and rivers the constant reaeration of water readily offsets any important oxygen loss through iron compounds, as has been reported from bog lakes and certain deep lakes where large quantities of iron were found.

In pollution studies of the inland fresh-water streams, therefore, the determination of total iron is helpful in locating the source of acid in highly acid waters, as a

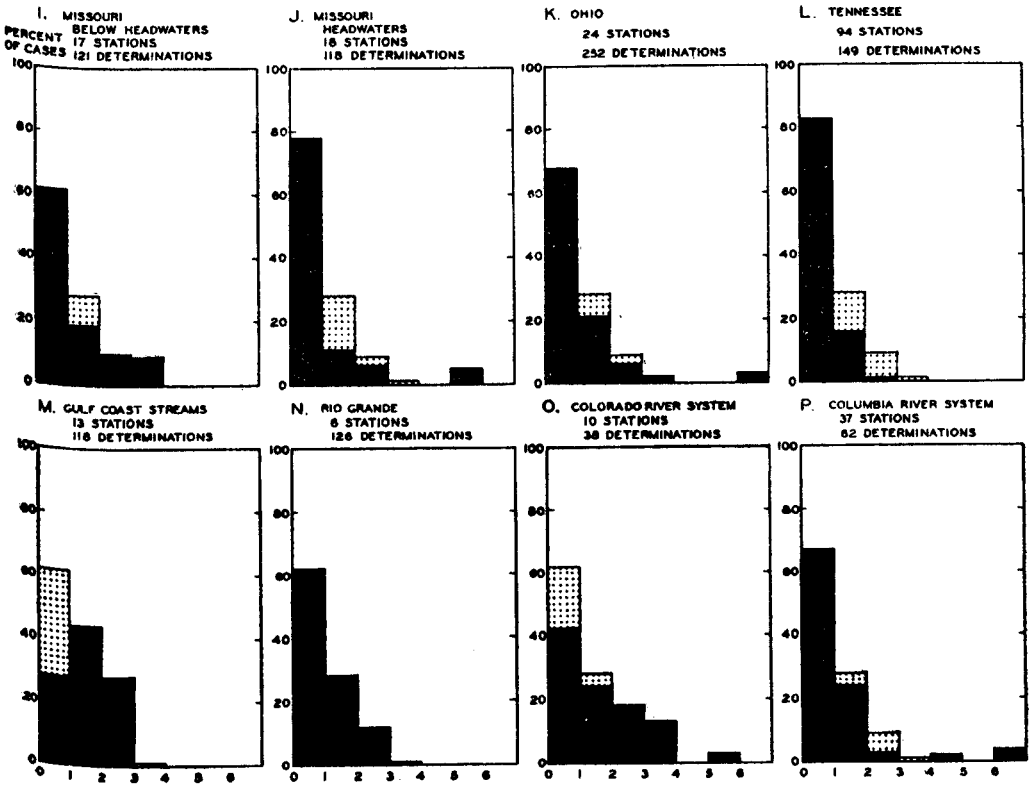

FIGURE 19.—Continuation of comparisons of free carbon dioxide values, stippled graph *A* figure 18, being the standard.

combination of high iron and high acidity suggest the source of acidity as pyrite or coal beds if no specific chemical effluent is responsible for these conditions.

AMMONIA

Total ammonia determinations were made by the Nessler method as described by American Public Health Association (1933).

Decomposing organic matter, if nitrogenous, will liberate into stream water, ammonium compounds representing a considerable portion of the total nitrogen. As ammonium compounds present at once both a hazard due to the high toxicity of ammonium carbonate for most aquatic animals, and an important source of nitrogen

for the lower plants in the aquatic food chain, ammonia determinations give a significant index of the balance between stream purification through the consumption and elimination of ammonium compounds formed during the disintegration of organic detritus, and the amount of such organic wastes received by the stream. In natural unpolluted waters organic detritus consists primarily of the remains of the organisms, both plant and animal, dying in the stream and adjacent waters, together with such organic matter as may be brought into the stream by surface run-off water. In unpolluted water, therefore, the amount of ammonia and ammonium compounds (chiefly ammonium carbonate) is usually very small.

The West Riding Rivers Board (1930) found the ammonia content of the River Wharfe, an unpolluted stream, to vary between 0.0 and 0.17 p. p. m.; Butcher, Pentelow, and Woodley (1927) state the ammonia content of the river Itchen, normally to be less than 0.1 p. p. m. with a maximum of 0.25 p. p. m.; Pearsall (1930) found the waters of various English lakes to carry less than 0.01 p. p. m.; Domogalla, Juday, and Peterson (1925) report the ammonia in Lake Mendota to vary between 0.0073 and 0.76 p. p. m.; and unpolluted portions of Wisconsin River above Rhinelander, Wis. (Wisconsin State Board of Health, 1927) averaged 0.096 p. p. m. ammonia. In field studies by the Columbia, Mo., unit similar ammonia values, all below 0.9 p. p. m., were obtained from analyses of unpolluted flowing stream waters.

Polluted streams, even if carrying only a very small load of organic wastes, present quite a different picture and, as Winslow and Phelps (1906) have pointed out, from one-third to one-half of the total nitrogen of sewage will be in the form of free ammonia, largely as ammonium carbonate; and sewage will carry from 15 to 35 p. p. m. or more of total nitrogen. Wiebe (1931b) reported a maximum of 0.224 p. p. m. ammonia in the Mississippi River at Fairport, Iowa. Ellis (1935b) found from 0.36 to 1.16 p. p. m. ammonia in the Mississippi River at Davenport, Iowa, during low waters in the month of July (1934) in portions of the river that were not badly polluted and which were at the time supporting bass, catfish, and other warm-water fishes; and from 0.24 to 3.80 p. p. m. of ammonia in the badly polluted waters of the Mississippi River during September 1935 between St. Louis, Mo., and Cairo, Ill. In the highly polluted Blackstone River, the Massachusetts State Board of Health (1913) reported 11.7 p. p. m. of ammonia. Similarly the writer has found 5.68 p. p. m. of ammonia in the Cache la Poudre River in Colorado at a point where there was heavy pollution with beet sugar factory wastes.

In table 2 a group of ammonia data typical of the field findings by the Columbia, Mo., unit are presented. These data include no determinations from the immediate vicinity of sewers or other outlets pouring organic wastes into the streams, and no determinations from restricted local portions of streams in which unusual organic pollution was found. These data show the general range of dissolved ammonia which may be expected in our flowing streams during the warm season, and under the usual conditions of municipal and industrial pollutions.

The composite series includes the ammonia values from all these stations collectively at which good fish faunae as previously defined were taken, and the Mississippi and coastal series include all stations in these systems regardless of fish faunae.

TABLE 2.—*Dissolved ammonia in various stream waters during the warm season, June to October, inclusive, 1934*

[For convenience of comparison, data are expressed as percents of total number of determinations for each stream unit]

River system	Number of stations	Number of determinations	Dissolved ammonia in parts per million						
			0.0–0.9	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	Greater than 6.0
Composite [1]	72	178	21	58	21	(2)			
Entire Mississippi system	182	478	24	49	22	3	2	(2)	(2)
Coastal streams	58	91	7	55	33	1	1	1	

[1] Derived from ammonia determinations at 72 stations throughout the entire Mississippi system and in coastal streams, at each of which stations good mixed fish faunae and associated organisms were thriving.
[2] Less than 0.5 percent.

It may be seen that excepting the restricted local areas where heavy pollution was found (data not presented in this table) the dissolved ammonia in flowing streams in general lies below 3 p. p. m. This is due to a variety of physical and chemical factors, chief among which is the constant turn-over of the moving stream waters. The good fish faunae showed a preference to waters containing less than 2 p. p. m. dissolved ammonia, as 79 percent of the cases of this group were found in water containing less than 1.9 p. p. m. dissolved ammonia. The remaining 21 percent were apparently thriving in waters containing between 2 and 3 p. p. m. dissolved ammonia, with one case (the maximal indicated by footnote 2 in the 3–3.9 column) in waters carrying 3.5 p. p. m. dissolved ammonia. This maximal dissolved ammonia value among the stations where good fish faunae were taken was found at Reeds Landing, Minn., where the Mississippi River was flowing rapidly over a sandy bottom at a point just below extensive beds of aquatic vegetation in the foot of Lake Pepin. It must be noted that without exception those waters carrying 2 to 3 p. p. m. ammonia and at the same time supporting the good fish fauna were high in dissolved oxygen; that is, 5.5 to 7 p. p. m., were of low turbidity, and were flowing over good bottoms. Toleration of dissolved ammonia above 2 p. p. m. under field conditions was always associated with otherwise good to exceptionally favorable conditions.

The toxic effects of ammonia compounds have been the subject of many investigations; and aquatic animals have been shown to be particularly sensitive to ammonium carbonate, the form in which ammonia is most frequently found in inland waters, (Shelford, 1917; Belding, 1928; Steinmann, 1928; and McCay and Vars, 1931). Thirty p. p. m. of ammonia will kill some tench, trout, and salmon rather rapidly (Weigelt, 1885), and 55 to 77 p. p. m. will kill shiners and carp in a few minutes to a few hours (Clark and Adams, 1913). A review of the literature on ammonia, however, shows that some observers obtained toxic effects with much smaller quantities.

Ellis and Chipman (1936) have repeated many of the earlier tests and extended the observations to daphnia and gammarids, as well as fish, finding that pH is a large factor in regulating the toxicity of ammonium compounds for aquatic animals, ammonium salts becoming more toxic in more alkaline media. This fact explains the relatively high toxicity of ammonium carbonate to aquatic organisms as compared with other ammonium salts. From these data (presented in section on ammonia pollutants) curves were drawn showing that the toxicity of ammonium compounds increases 200 percent or more between pH 7.4 and pH 8.0. The lower limit of toxicity

(death in 10 days or less, depending upon conditions of experiments) was found to be near 2.5 p. p. m. of ammonia. Some acclimatization to ammonia is possible, and it is well known that individuals of various species of fish may be found in water containing 3 to 10 p. p. m. of ammonia. However, the existing literature and the data from our experiments indicate that under average stream conditions with pH value 7.4 and pH 8.5, 2.5 p. p. m. of ammonia will be harmful to many individuals at least of the common aquatic species.

Therefore, in view of the small amount of ammonia found in unpolluted natural flowing waters, 1.5 p. p. m. dissolved ammonia was considered the maximal amount of dissolved ammonia not suggestive of specific organic pollution. In flowing streams 2 to 3 p. p. m. were almost always associated with definite organic pollution and values above 3 p. p. m. in our field studies were always traceable to sewage or factory effluents.

SUSPENSOIDS

The amounts of finely divided suspensoids in various waters and light penetration into these waters were determined by a photoelectric apparatus described by Ellis (1934).

The suspensoids—that is, particulate matter in suspension in inland fresh waters—consists normally of erosion silt, organic detritus (as discussed under ammonia), bacteria, and plankton. Each component of this mixture, with the exception of plankton, may be greatly augmented by man's agencies, as quantities of powdered rock, cellulose pulp, sawdust, semisolid sewage, and other debris are added to natural waters.

Parts of some streams, as the Yellowstone and Missouri—draining areas in which natural erosion has been proceeding rapidly—have been muddy with their loads of erosion silt since before the earliest records by man and have as a result limited fish faunae. In a large proportion of the inland streams, however, erosion silt, organic detritus, and bacteria were formerly in balance over a considerable portion of the year and conditions favorable to aquatic life maintained, although now and then floods and other unusual conditions killed many aquatic animals in these streams by inundations of silt. With the advent of civilized man and unrestricted deforestation, agriculture, and other uses of the earth's surface, the erosion problem has become gigantic, and the effects of the loads of erosion silt carried by these once relatively clear streams overwhelming on aquatic life in many places.

Erosion silt and other suspensoids (disregarding any specific toxic action of suspensoid wastes) affect fisheries directly by covering the bottom of the stream with a blanket of material which kills out the bottom fauna, greatly reduces the available food, and covers nests and spawning grounds; and also by the mechanical and abrasive action of the silt itself which may clog and otherwise injure the gills and respiratory structures of various aquatic forms, including many fishes and mollusks (Ellis, 1936a). The mechanical action of silt and other suspensoids may not be severe or even harmful to the gills and other structures of the free-swimming fish which move about above the bottom and are not mired down by the settling deposits of the suspensoids, if the amounts of the suspensoids in the water are not too great and if the action of the suspensoids is uncomplicated by other pollutants. Normal fish and many other swimming animals secrete continuously quantities of mucus which wash away

suspensoid particles as they lodge on the gills and other exposed parts. Consequently, healthy and uninjured fishes can move through very muddy water or water carrying considerable quantities of pulps (Cole, 1935b), sawdust, and other suspensoids and receive little or no mechanical injury to the gills. However, as has been pointed out by Marsson (1911), small amounts of various acids, chemical wastes, and other substances which in themselves either injure the gills or alter the flow of mucus may greatly augment the mechanical action of the suspensoids, with serious results to the fish, so that through the combined action of these chemical agents and the suspensoids the abrasive action on the gills may be increased or the gills matted with deposits which under more favorable conditions would have been washed away by the mucus.

Indirectly, but none the less effectively, erosion silt affects fisheries by screening out the light, by "laking down" organic wastes, and thus increasing the oxygen demand at the bottom of the stream, and by retaining many forms of industrial effluents as oils, chemical wastes, and pulps in beds on the floor of the stream, with disastrous results to the bottom fauna.

Summarized data on turbidity of and light penetration into various stream waters are presented in table 3.

TABLE 3.—*Turbidity of stream waters as measured by light penetration (millionth intensity depth in meters) in various river systems during June to September, inclusive, 1932–35*

[For convenience of comparison, data are expressed as percents of the total number of determinations for each stream unit]

River system	Number of stations	Number of determinations	Light penetration expressed as millionth intensity depth in meters					
			Clear	Cloudy	Turbid	Very turbid	Muddy	Very muddy
			5.00–∞	4.99–1.00	0.99–0.50	0.49–0.30	0.29–0.15	0.14–0
Composite, streams supporting good mixed fish fauna [1]	202	514	35	24	17	9	9	6
Mississippi, flowing streams, good fish fauna	52	237	4	11	8	16	25	36
Mississippi, flowing streams, medium, poor, or no fish fauna	79	260	1	18	11	14	38	18
Mississippi, impounded water, Hastings Pool (Minn.)	1	17		100				
Mississippi, impounded water, Lake Pepin (Minn.-Wis.)	12	73	11	88		1		
Mississippi, impounded water, Lake Davenport and Moline Pool (Iowa-Ill.)	13	175		51	19	19	4	7
Mississippi, impounded water, Lake Keokuk (Iowa-Ill.)	16	571		19	28	20	16	17
Missouri, headwaters, clear streams (Mont.-Wyo.)	5	15		20	60	20		
Missouri, below headwaters (Mont., Wyo., Colo., Nebr., Kans., Mo.)	19	23	44	31	4		4	17
Ohio (Pa., W. Va., Ohio, Ky., Ind., Ill.)	41	82	12	5	15	7	48	13
Tennessee, flowing streams (Ky., Tenn., Miss., Ala.)	93	158	11	8	32	32	17	
Atlantic-coast streams (Maine to S. C., inclusive)	11	16	36	37	18			9
Gulf-coast streams (Fla. to Tex.)	11	111		18	46	18		18
Rio Grande, flowing streams (Tex., N. Mex., Ariz.)	6	25	88		4			8
Colorado, flowing streams (Ariz.-Nev.)	7	36	67	22	8	3		
Columbia, flowing streams (Idaho, Mont., Wash., British Columbia)	17	31	49	39	3	3	3	3

Grand totals: Stations, 585; light-penetration determinations, 2,344

[1] Derived from light-penetration determinations made at 202 stations in the Mississippi, Missouri, Tennessee, Atlantic coast, Gulf coast, Rio Grande, Colorado, and Columbia systems, at each of which stations good mixed fish faunae and associated organisms were thriving. Each of these 8 stream units are given equal value in the expression of the composite.

From the fieldwork on unpolluted streams in areas where surface erosion was not materially influenced by man and where water conditions were otherwise favorable, it has been shown by Ellis (1936a) that the millionth intensity depth (i. e., the level at which the light entering the surface of the stream would be reduced to one-millionth of its surface intensity) for clear unpolluted streams carrying little or no erosion material is 50 meters or more, and that in streams carrying a heavy load of erosion silt, like the Missouri River, the millionth intensity level may be reduced to less than 100 millimeters. Until erosion is brought under control little can be done in demanding a minimum amount of silt and consequently no standard has been suggested here, but data from over 6,000 determinations on inland streams show that the silt load of these streams should be reduced so that the millionth intensity level would not be less than 5 meters, if conditions even approximating those of times past when erosion was held in check by forest and grasslands are to be restored, in the average inland stream of the United States. The detrimental nature of erosion silt as regards fisheries is discussed more fully by Ellis (1936a).

However, particulate matter introduced by man into streams can be regulated, and the detrimental action of various types of suspensoid pollutants is discussed under that heading.

DEPTHS

As various depths of water are selected by different species of aquatic animals, and even by different ages of the same species in many cases, there is naturally no single optimum depth of stream water for all types of aquatic life. Depth studies of streams and flowing waters, however, bring out differences between waters of natural lakes and those of flowing streams and river lakes.

Current action in flowing streams mixes the water so thoroughly and continuously that in general the composition of the aquatic environment as presented by the water itself varies but little from a few inches below the surface to a few inches above the bottom of the stream. The temperature of the water, its turbidity, dissolved solids content, pH, and even dissolved gases content are much the same throughout the bulk of the stream at any given station, if there be definite current action. Sloughs and other rather isolated lateral areas, particularly those containing large masses of aquatic vegetation, are of course excepted, but even in such cut-off portions of streams the actual differences in water characteristics as compared with the main stream mass are often small.

Of significance in pollution studies, these depth data show that pollutants may be expected to mix rather rapidly and completely with the waters in streams and even river lakes unless these river lakes be more than 50 feet deep, and even in those river lakes unless the seasonal conditions are such as to promote the stratification just described in the deeper portions of such lakes; and that the products of bottom pollution will also be distributed throughout the waters of the stream below such pollution.

TABLE 4.—*Characteristics of water at different depths in river lakes produced by impounding flowing rivers*

I. LAKE WILSON[1]

Depth in feet	Water temperature, degrees centigrade	pH	Specific conductivity in mho x 10^6 at 25° C.	Fixed carbon dioxide, cubic centimeters per liter	Dissolved oxygen parts per million	Light penetration, millionth intensity depth in millimeters
8[2]	30.2	7.4	177	13.4	7.5	2,053
10	30.2	7.6	178	12.9	7.3	2,053
20	29.5	7.4	181	13.2	6.1	1,297
30	29.0	7.5	178	12.9	5.8	1,075
40	28.6	7.5	175	12.9	5.7	1,075
50	28.2	7.5	173	12.9	5.1	972
60	27.8	7.3	161	12.9	3.6	1,075
70	22.9	7.2	167	15.4	.2	9,036
80	21.9	7.2	158	15.0	.2	9,036
90	21.5	7.1	159	15.0	.2	6,910
100	20.9	7.2	159	15.4	.1	6,262
110	20.8	7.2	162	15.9	.2	5,335

II. ELEPHANT BUTTE RESERVOIR[3]

8[2]	33.0	8.1	1,009	29.5	7.1	6,823
3	33.0	8.1	1,062	28.7	7.2	6,823
6	23.8	8.1	1,024	28.7	5.9	14,344
10	23.0	8.1	1,017	28.1	5.5	13,414
20	22.8	7.6	1,022	28.4	6.1	28,874
30	21.5	7.6	1,081	29.3	5.9	30,254
40	19.8	7.6	1,107	29.1	6.2	63,987
50	19.6	7.6	1,068	29.2	6.5	63,987
60	18.8	7.6	1,070	29.0	6.6	63,987
70	18.0	7.6	996	29.6	6.8	61,237
80	17.8	7.6	1,067	29.8	5.1	61,237
90	17.6	7.6	1,045	30.2	5.1	63,987
100	17.1	7.6	1,059	30.7	5.3	63,987
110	16.9	7.6	1,052	30.4	5.1	61,237
125	16.9	7.5	1,123	30.7	4.7	63,987

III. LAKE KEOKUK[4]

8[2]	27.8	7.5	285	27.8	6.7	1,170
10	27.5	7.5	287	28.0	6.6	1,170
20	27.0	7.5	285	28.3	5.8	1,103
33	27.0	7.5	290	28.3	5.4	1,065

[1] Tennessee River near Florence, Ala., station 385, July 30, 1931, air temperature 31.3° C. A deep river lake showing midsummer stratification.
[2] Rio Grande River, near Hot Springs, N. Mex., station 829, June 15, 1935, air temperature 33.0° C. A deep lake showing partial stratification at time of these observations.
[3] Surface, i. e., top 12 inches of water.
[4] Mississippi River near Keokuk, Iowa, station 80, Sept. 22, 1932, air temperature 30.3° C. A medium to shallow river lake showing little or no stratification.

TEMPERATURE

As the temperature of the water has bearing on several factors associated with the general problems of pollution, such as dissolved oxygen carrying power of the water, the rate of bacterial decomposition of organic pollutants, and the metabolic demands of the aquatic organisms themselves, the temperature range of flowing streams and river lakes during the warm season is presented in table 5. These data include no headwaters in mountainous regions, and give, therefore, the water temperature range to be expected in the average inland stream of the United States during the summer months, which season as has been pointed out under the discussion of dissolved oxygen presents certain specific pollution hazards.

TABLE 5.—*Water temperatures of inland streams, exclusive of headwaters in mountainous regions, during warm season, June to September, inclusive, 1930–35*

River system	Number of stations	Number of cases	Percent of cases						Minimum degrees, Centigrade	Maximum degrees, Centigrade
			14.0°–17.9° C.	18.0°–21.9° C.	22.0°–25.9° C.	26.0°–29.9° C.	30.0°–33.9° C.	Above 34° C.		
Composite [1]	726	4,545	13	16	35	31	5	(2)	15.0	36.6
Entire Mississippi system	447	2,887	12	12	46	27	3	(2)	15.0	35.2
Coastal streams into Gulf of Mexico [3]	39	1,367	7	14	32	36	9	2	16.8	36.6

[1] Includes flowing streams at stations at which fish were found in Mississippi, Missouri, Tennessee, Ohio, coastal streams flowing into Atlantic Ocean and Gulf of Mexico, Rio Grande, Colorado, and Columbia system.
[2] Less than 1 percent.
[3] Exclusive of Mississippi system.

Considering the composite in table 5, it may be seen that in spite of the high air temperatures which prevail in many parts of the United States during the summer months, often for periods of days, stream temperatures above 34° C. are not common, and that 95 percent of the 4,545 cases listed in table 5 lie below 30° C. On the other hand, 66 percent of these 4,545 cases lie between 22° and 30° C. For comparison with the composite in this table, data from the entire Mississippi system and from the coastal streams of the Gulf States, Texas to Florida, inclusive, are also presented. In the Mississippi system 73 percent of the cases fell between 22° and 30° C., and 68 percent of the cases in the Gulf States have the same range.

In evaluating biochemical oxygen demand, dissolved oxygen content, and specific toxicity values for pollution studies therefor, a water temperature range during the warm season from 15° to 36° C. may be expected in the average inland stream of the United States, with the probability of 66 percent or more that these water temperatures will lie between 22° and 30° C. During the other portions of the year—that is, outside of the warm season—the water temperatures of these streams in localities north of the freezing line will fall, with 0° C. as the limit. Our field data also show that south of the usual freezing line—that is, in streams of southern Texas, Alabama, and Florida—temperatures as low as 10° C. are not unusual during the midwinter season.

The true headwater streams, particularly those in mountainous regions, present a different temperature range even during the summer months. The maximal temperatures for various streams which could be definitely classified as mountainous headwaters, as found in our field studies, were rarely above 10° to 15° C., with the average values lying around 10° C. or even lower.

BOTTOM CONDITIONS AS AFFECTED BY STREAM POLLUTION

In most stream-pollution studies, conditions at the bottom must be considered, since the bottom of the stream contributes a considerable part of the food of stream fishes through the organisms of the bottom fauna which are either eaten directly by fishes or which are included in the food chains of various species of fishes. Besides, portions of the bottom usually in the shallower parts of the stream provide nesting sites for certain species. However, as the stream bed may change from rock and coarse gravel to fine clay in the course of a few hundred yards, and as there is a wide variation in habitat preference of the many desirable organisms which inhabit stream

bottoms, it is very difficult to define all of the conditions at the bottom of a stream which may or may not be suitable for bottom inhabitants and therefore affect the fish fauna; for over this already complicated association of rock, soil, debris, and living organisms pollution may spread a blanket of silt, sludges, pulps, and poisonous fluids.

Studies of the bottom faunae of polluted streams, particularly those carrying quantities of organic pollution, have shown that many of the bottom species of unpolluted streams are very sensitive to pollution conditions, so that as pollution progresses the normal bottom fauna changes giving way to certain more tolerant species of tubificid worms, chironomid midges, sphaeriid mollusks, and leeches. Consequently, various investigators (Marsson, 1911; Suter and Moore, 1922; Turner, 1927; Richardson, 1928; Wiebe, 1928), in connection with other data have correlated the presence of certain bottom forms with different degrees of stream pollution, and a few such species of bottom organisms have come to be used to some extent as indices of pollution. Richardson (1928) however, in discussing 49 bottom species definitely associated with pollutional or subpollutional conditions in the Illinois River points out the difficulties attending the use as indices of pollution, of even such species as the tubificid worm, *Tubifex tubifex*, and the midge, *Chironomus plumosus*, which are commonly regarded as characteristic of pollutional conditions bordering on septic. The problem of index species is greatly complicated by the fact that the number of individuals of any particular index species may vary from zero over a wide range in adjacent parts of any polluted stream as the result of conditions other than those produced by pollution.

In the present studies, bottom samples were taken throughout the field work as a part of the regular routine. Reviewing the results of the examinations of many hundreds of bottom samples, there is no doubt that bottom samples are a necessary part of any pollution study, and that the findings concerning the bottom organisms are very valuable when considered with the chemical and physical data. However, the writer agrees with the statement of Richardson (1928, p. 410), in connection with his Illinois River studies, that index species are of service in pollution studies only when used with the greatest caution, and when checking with other indicators.

With due regard to the limitation just discussed, three organisms—namely, the water mold, *Sphaerotilus natans*, the rattail maggot, *Eristalis* sp., and the sludge fly, *Psychoda* sp.—were often found helpful in delimiting the septic zone near the source of extensive organic pollution; and the tubificid worms, *Tubifex* sp. and *Limnodrilus* sp., and the larvae of the red midge, *Chironomus* sp. (particularly *Chironomus plumosus*), if their presence or absence were supported by the chemical and physical analyses and by the data concerning the biological complex as determined from repeated samplings, were frequently used in defining the extent of bad to moderate organic pollution. In the lesser degrees of organic pollution and in most cases of chemical pollution index species as such were of little value.

On the other hand, the abundance of the various species comprising the bottom fauna and particularly the species composition of the bottom fauna at various stations in the polluted area were usually of large value, regardless of the sort of pollution, when correlated with the physical and chemical data. Gross pollution of several kinds was quickly detected from bottom samples both by the physical and chemical conditions

of the mud itself and by the paucity or absence of bottom fauna, often represented only by dead shells and other remains. Dredgings readily demonstrated such gross pollution by silt, sewage, pulps, tars and heavy oils, mine tailings, rock powders from quarry operations, and such organic wastes as starch effluents, sizings from cloth mills, and distillery slops.

Downstream from a region of gross pollution the biological analyses of the bottom faunae were often particularly significant when compared with the bottom faunae in similar situations in comparable unpolluted waters (if possible of the same stream) in showing the selective effects of some pollutants, and the downstream extent of pollution.

Many chemical wastes have high specific gravity and consequently tend to follow the stream bottom for some distance before complete mixing is accomplished by stream current action. Often downstream dredgings showed complete absence of bottom life of any type for some distance below the outlets of flumes carrying such chemical wastes, and the limits of the zones in which the bottom faunae had been killed out yielded valuable information concerning the points at which the effluent had been diluted to a nontoxic level.

ACTION OF POLLUTANTS ON FISHES

Regardless of the effects on the environment, many pollutants affect fishes directly by some specific action on the living organism itself. These pollutants can be grouped, therefore, according to the locus of injury and method of action of the various active substances which the effluents contain (Ellis, 1936b).

INJURIES TO GILLS AND EXTERNAL STRUCTURES

The higher concentrations of almost all effluents and all lethal concentrations of some types of pollutants kill by their actions on the gills of the fish before little, if any, of the material causing the death of the fish passes beyond the gills. Such substances kill, therefore, by a combination of chemical and physical injuries rather than by true toxic action. The salts of several heavy metals, some acids, and some special chemicals as trinitrophenol combine readily with the mucus secreted by the fish's skin, mouth, and gills, forming insoluble compounds.

If the dilution of the pollutant of this type be great enough, or if the supply of the pollutant be limited so that it acts on the fish only a short time, the secretion of additional mucus may wash away the precipitated compound as fast as it is formed, or may carry away the larger masses of the precipitate before serious damage to the fish results. If, however, the concentration and exposure time are large enough (very small quantities of several heavy metal salts suffice, v. i.), the precipitated insoluble compound covers the body, the lining of the mouth, and the gills. (See fig. 21.) Disastrous results follow the covering of the gills with these precipitates, and death supervenes very rapidly from the respiratory failure. In our experiments with salts of heavy metals and various other compounds producing death by precipitation of insoluble matter on the gills, the precipitate was found to cause death as the result of a combination of three conditions which individually or collectively disturbed the proper functioning of the respiratory and circulatory mechanisms.

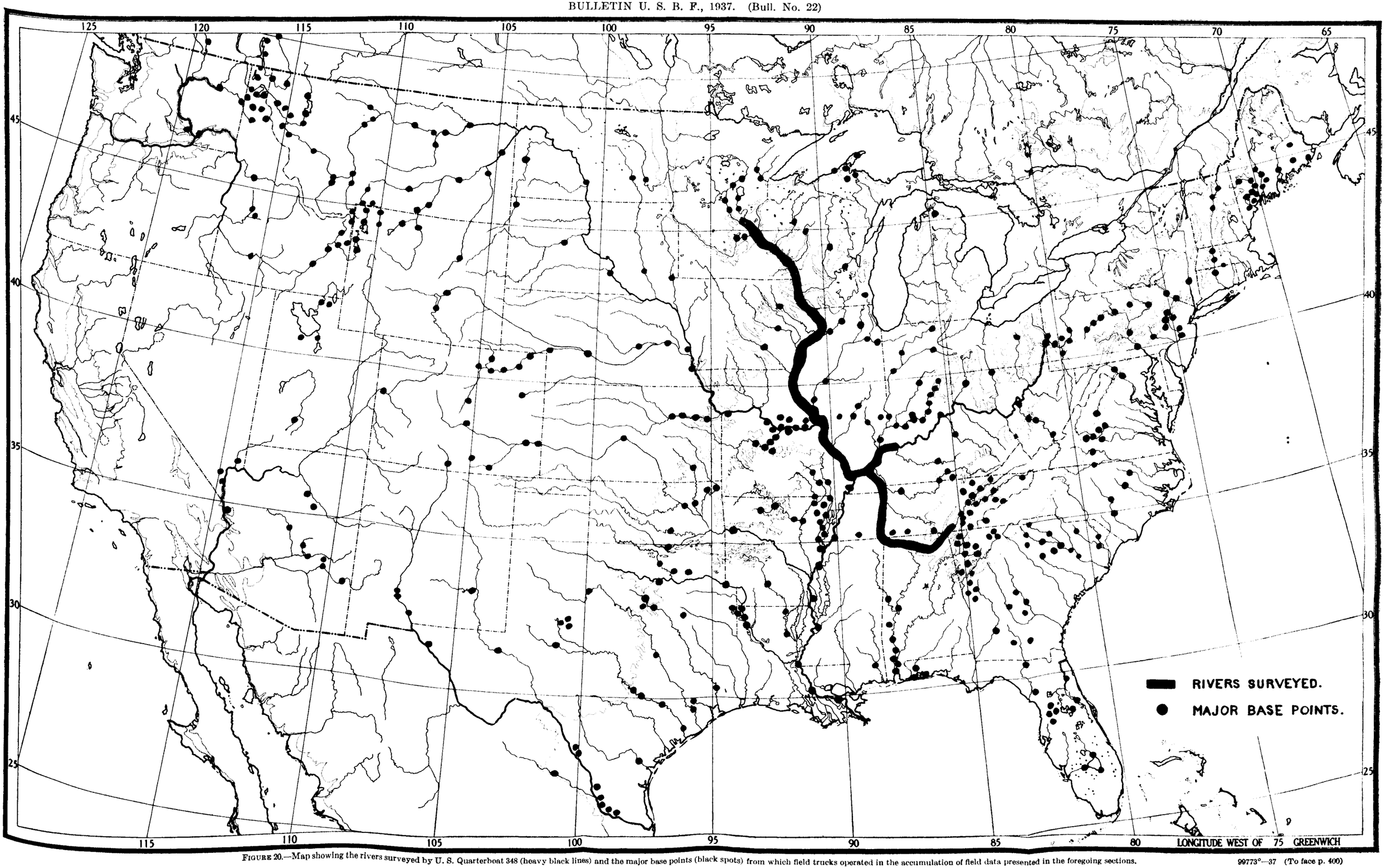

FIGURE 20.—Map showing the rivers surveyed by U. S. Quarterboat 348 (heavy black lines) and the major base points (black spots) from which field trucks operated in the accumulation of field data presented in the foregoing sections.

In the weaker concentrations of such effluents and harmful substances, the precipitate coated the gill filaments and filled the filament interspaces so that the water pumped through the mouth and onto the gills for the aeration of the blood could not reach the cells of the gill filaments. Consequently, the aeration of the blood with its accompanying gas exchanges was prevented, and sooner or later death followed from a combination of anoxemia and carbon-dioxide retention.

If still larger masses of flocculent precipitate were formed, as was the case when the stronger effluents were tested, the interlamellar spaces were clogged and movement of gill filaments became impossible. This condition affected the circulation of the blood in the gills, in that stasis of the blood in the gill capillaries usually follows cessation of movement of gill filaments in a short time. Kolff (1908) in her studies of fish hearts found that the pulsation of the heart is only one of the forces necessary to drive the blood through the gill capillaries, and that the movements of the gills are important in maintaining the gill capillary circulation.

If the scales be removed from the midventral portion of the precardial region of a pithed goldfish and a tiny steel needle (the minuten nadeln on which entomologists mount very small insects) be forced through the body wall and into the pericardial cavity, when proper adjustment is made, this needle, if examined under a binocular microscope, can be seen to swing with each heart beat. Using this procedure the rate of the uninjured and unexposed heart in situ can be recorded for hours. Such fish, when the gills were perfused via the mouth with water containing salts of heavy metals or other substances producing these heavy mucoid precipitates, continued their normal respiratory movements and heart action until the precipitate clogged the gills and mechanically prevented the movement of the gill filaments. At that time an abrupt change in the activities of the heart was usually noted, the heart action dropping to about one-half its former rate. Heart block also often developed at this time. When these changes in heart rate and heart action were noted, the gill capillaries were always found to be gorged with blood on the efferent or cardiac side and showed practically complete to complete stasis of the blood in the capillaries. This same condition of blood stasis in the gill capillaries was noted in other fish in which anoxemia was produced by exposure to water containing little or no dissolved oxygen shortly after cessation of respiratory movements, so that the importance of the respiratory movements for the maintenance of capillary circulation in the gills was well established. After its rate had dropped to approximately one-half normal, the heart continued to beat for hours (in some cases for over 24 hours), although the circulation through the gills was completely blocked. In fishes which had ceased to make movements of any sort, either respiratory or general, after prolonged exposure to water low in dissolved oxygen, the hearts were found to be beating even when these fishes were opened under oil to exclude even momentary aeration of the pericardial fluid.

The various substances producing these heavy precipitates, as well as many other pollutants (acetic acid, volatile extracts of crude oil, and others) which did not form precipitates with mucous secretions on the gills, also produce death by asphyxia through direct damage to the gill filament cells, which in turn cause stasis of the blood in the gill capillaries. Death from anoxemia and circulatory failure in the gills, therefore, was regularly found in fishes dying either in waters containing

low oxygen or in the stronger hypertonic solutions of various salts and other chemicals, regardless of the formation of any sort of mucoid precipitate.

In connection with gill damage, it must be pointed out that the weaker concentrations of various pollutants which do not damage the gills rapidly enough to cause speedy respiratory and circulatory failures must also be considered as pollution hazards if these solutions be even slowly toxic to the cells of the gill, for Smith (1929) has demonstrated that the gills of fresh-water fishes (carp and goldfish) are important excretory structures, removing from 6 to 10 times as much nitrogenous wastes as the kidneys. Keys and Willmer (1932) have found special cells associated with chloride secretion in the gills of various fishes, including fresh-water species. Damage to the gills from pollutant substances in the water can result, therefore, in the impairment of other functions, particularly those of salt balance and excretion in addition to respiration and circulation as already described, without actual toxic action on the internal vital organs of the fish.

POLLUTANTS ENTERING THE BODY OF THE FISH AND EXERTING TRUE TOXIC ACTION

The gills, the lining of the mouth, and the skin are the main portals of entry through which toxic substances can be absorbed into the body of the fish. However, Bond (1933) concludes that the bony fishes and many fresh-water invertebrates have little or no permeability to a variety of substances. The writer has been able to confirm this relative nonpermeability of the external structures of various fresh-water fishes, particularly the gills, for a number of substances. The active agents in various stream pollutants, therefore, may be still further subdivided into those which can enter the body of the fish through external structures as various volatile compounds from crude oil, dilute chlorine, ether, chloroform, methyl mercaptan, and formaldehyde, and those which do not enter or at least enter very slowly through the external structures as certain arsenic compounds.

The main internal channel for the absorption of injurious and toxic substances is the gastrointestinal tract. The writer, using colloidal dye methods, has found that many fresh-water fishes refuse to swallow water containing various types of effluents for sometime after being placed in such water, for as has been pointed out by Smith (1930) most of the water required for the formation of urine in the fresh-water fish is probably taken in through the lining of the mouth. However, after varying intervals, usually 48 hours or more, fresh-water fish swallow some of the surrounding water even if not fed, suggesting that the water needs of the body are not entirely supplied through absorption by the external surface or the lining of the mouth. The swallowing of polluted water allows any of the injurious or toxic substances which this water may contain direct access to the mucosa of the gastrointestinal tract. Harmful substances may, therefore, either damage the lining of the intestinal tract or may be absorbed from the gastrointestinal tract, and in this way gain access to the internal vital organs. Consequently, another group of pollutants can be designated as those acting on the fish after ingestion into the gastrointestinal tract. It is through this portal that many cumulative poisons enter the body of the fish during long-time exposures to concentrations of pollutants which may at the time seem harmless.

Arsenic may be cited as an example of a substance which can be accumulated by the fish via the gastrointestinal tract after long exposure to low concentrations.

To summarize, on the basis of locus of injury to the fish, stream pollutants may be classified as—

(1) Those substances injurious to the gills and other external structures of the fish without any marked absorption beyond the gills. Death of the fish exposed to these pollutants results from anoxemia, through respiratory and circulatory failure, and through interference with the excretory functions of the gills.

(2) Those substances killing the fish by specific toxic action after absorption through the gills, the lining of the mouth, and other external structures.

(3) Those substances killing the fish by specific toxic action after absorption from the gastrointestinal tract, which region they have reached in water swallowed by the fish.

LETHALITY OF SPECIFIC SUBSTANCES OCCURRING IN STREAM POLLUTANTS

GENERAL CONSIDERATIONS

In this section, data from the literature and from experimental assays made during the present studies are presented covering the lethality of various substances which are the active harmful agents in different types of stream pollutants. These biochemical and biophysical findings in general may be applied to pollution conditions ranging from acute to mild; although in the evaluation of all individual cases of pollution, caution must be exercised, as biological data of any sort are rarely suitable for rigid application. One particular component of a given waste may constitute the major pollution hazard of that waste; in fact, the dangerous qualities of many wastes center largely around one substance in each effluent rather than the effluent mixture as a whole. In such cases, lethality tables are particularly helpful, but the synergistic and antagonistic actions of other substances in the stream water as well as in the waste itself must be borne in mind always. For example, the lethality of copper sulphate for fishes under certain conditions is decreased by the presence of calcium chloride and increased by sulphuric acid, and both of these compounds occur free or combined in certain industrial wastes. Again the toxic actions of small amounts of chlorine and of ammonia on aquatic life singly are different from the actions of the same quantities of these substances when both are present, since together they may form either ammonium chloride or chloramine, depending upon conditions; and the toxicity of the resultant mixture may vary accordingly.

From the data presented in the following tables, however, the harmless, injurious, and lethal ranges of various substances may be computed readily with reasonable accuracy for particular pollution cases if due regard be given to the chemical and physical conditions of the water of the stream involved. Tests should be made, of course, to detect the presence of unusual and unexpected substances in the local complex which might alter the action of the pollutant.

In addition to the appraisal of the pollutant on the basis of the lethal action of its major component or components, when the pollution is acute, mild, or intermittent,

under which headings a large percent of the pollution cases may be classified, the possibility of cumulative effects must be considered when determining remedial measures or dilutions. Cumulative effects from very low concentrations of some substances which seem harmless to fish life over a period of 10 to 14 days present difficult problems. Some of these are discussed in subsequent portions of this section.

TEST ANIMALS

In the course of the work on the lethality of stream pollutants 30 species of fresh-water animals (see table 6), including 17 species of fish, 6 species of crustaceans, and 7 species of fresh-water mussels, have been used in one connection or another as test animals.

TABLE 6.—*Species of test animals*

Species	Common name	Species	Common name
FISH		AMPHIPODS	
1. *Perca flavescens*	Yellow perch.	18. *Gammarus fasciatus*	Gammarid.
2. *Micropterus salmoides*	Largemouth black bass.	19. *Eucrangonyx gracilis*	Do.
3. *Lepomis incisor*	Blue gill.	ENTOMOSTRACANS	
4. *Lepomis humilis*	Orange-spotted sunfish.	20. *Daphnia magna*	Daphnia.
5. *Ameiurus nebulosus*	Common bullhead.	21. *Bosmina sp*	Cladoceran.
6. *Ictalurus punctatus*	Channel cat.	22. *Cypris sp*	Ostracod.
7. *Agosia nubila*	Long-nosed dace.	23. *Cyclops* sp	Copepod.
8. *Leuciscus balteatus*	Dace minnow.	FRESH-WATER MUSSELS	
9. *Notemigonus chrysoleucas*	Golden shiner.	24. *Tritogonia verrucosa*	Buckhorn.
10. *Notropis delicious*	Straw-colored minnow.	25. *Megalonaias gigantae*	Washboard.
11. *Hybognathus nuchalis*	Silvery minnow.	26. *Quadrula trapezoides*	Small washboard.
12. *Pimephales promelas*	Fathead minnow.	27. *Fusconaia undata*	Pigtoe.
13. *Cyprinus carpio*	German carp.	28. *Actinonaias carinata*	River mucket.
14. *Carassius auratus*	Common goldfish.	29. *Lampsilis anodontoides*	Yellow sand-shell
15. *Salmo irideus*	Rainbow trout.	30. *Lampsilis siliquoidea*	Fat mucket.
16. *Salmo clarkii*	Cut-throat trout.		
17. *Lepisosteus platostomus*	Short-nosed gar.		

From these studies and from the voluminous literature of bioassay methods and physiological and pharmacological experiments in which these and many other forms of aquatic life have been used as bioreagents, two animals—the common goldfish, *Carassius auratus*, and the entomostracan, *Daphnia magna*—were selected for the standard tests. This procedure, i. e., the use of standard test animals, is recognized in other fields of biological investigation in which the frog, the rat, and the guinea pig have established positions as assay animals, and makes possible direct comparisons of data on the actions of a variety of substances over a wide range of conditions. No single test animal combines all of the desirable qualities and in making a choice both availability and physiological suitability for the problem in hand must be considered. As the variety of aquatic animals which may be affected by stream pollution is large, a lethality range for each pollutant and effluent must be established, as the specific sensitivities of various aquatic species are not the same, although they may live in the same aquatic complex. However, if the pollutant destroys any one of the major species in the complex, the entire fauna in that part of the stream may suffer as a result. The selection of goldfish and daphnia gave a combination by which the maximal and minimal limits of toxicity of any given pollutant for different stream complexes could be ascertained rapidly and with reasonable accuracy.

GOLDFISH

Goldfish of any size up to 6 inches are easily obtainable in quantity from commercial goldfish farms, are relatively inexpensive, and stand shipment well. The practical considerations, although important in the selection of a test animal, are of course secondary to the physiological characteristics of the goldfish which make it particularly suitable for the bioassays of stream pollutants. The goldfish is tolerant of confinement and can be kept in laboratory containers and aquaria for months, making both short-time and long-time tests, uncomplicated by excitement and the attendant endocrine disturbances, possible under controlled conditions. The amount of oxygen consumed by the goldfish is not large per unit of weight, and this fish does not succumb to low oxygen as quickly as many other fresh-water fishes. In fact, the uninjured goldfish if permitted can obtain sufficient oxygen to maintain itself for some time in water very low in or even devoid of dissolved oxygen merely by skimming and breaking the surface film of the water. Because of these facts, the toxic action of many substances which would be volatilized or oxidized by the constant aeration of water required to maintain various other species of fish can be ascertained, using goldfish as reagents; and the specific parts played by the oxygen demand, the external action, and the internal effects of the pollutant on the fish determined separately. On the other hand, if the combination of anoxemia and toxic action of the pollutant are desired, goldfish can be placed in closed containers, or merely prevented from reaching the surface layer of the water by submerged strips of glass which do not interfere with either the movement of the water or with its surface reaeration.

By comparative tests the relative resistance of the goldfish to poisons, injury, and anoxemia was found to be equal to or greater than that of bass, perch, or catfish, and definitely greater than the resistance of trout or most fresh-water minnows. The minimal lethal concentration of any effluent or pollutant for goldfish established, therefore, approximately the maximal concentration of that pollutant which ought not to be exceeded if any fresh-water fish were to survive in waters polluted with such effluent.

An added advantage in the use of the goldfish as a test animal is the already large literature on this fish in both physiological and pharmacological fields, in which the usefulness of this animal as a bioassay reagent is well established (Munch, 1931; Powers, 1917).

The stock goldfish used for these tests were obtained in lots as needed from a commercial goldfish farm, and were held in flowing water in large hatchery tanks at a temperature ranging from 17° to 21° C. All goldfish were of the standard carp-form variety, i. e., the various ornamental varieties were excluded. The fish were fed regularly every third day a ration of prepared shrimp meal, and *Myriophyllum* growing in the tank was available at all times. For routine tests 3-inch goldfish (60 to 90 millimeters in length), weighing between 3 and 5 grams, were selected as standard. Larger sizes were used for special tests as required.

DAPHNIA MAGNA

The second test animal, *Daphnia magna*, which is found in the quiet backwaters of various river systems (Surber, 1936), and which is raised extensively as food for young fish, was chosen because of its high sensitivity to most stream pollutants. Comparative tests showed this animal to be more sensitive even than trout, so that the minimal lethal concentration for daphnia of a given pollutant gave approximately the maximal dilution from which damaging effects on fresh-water fishes and many other fresh-water animals could be expected (exclusive of certain cumulative effects). Consequently, between the minimal lethal concentration for daphnia on the one hand and the minimal lethal concentration for goldfish on the other, the gamut of lethal concentrations of any pollutant or effluent under conditions comparable to those of particular pollution cases could be defined rather definitely.

Daphnia proved to be an excellent test animal with which to obtain a quick orientation concerning the relative toxicity of effluents of unknown lethality, since this animal is quite free from the protective mucous secretion which safeguards fish for a time against many pollutants.

Daphnia were also valuable in studying the cumulative effects of some pollutants, as under favorable controlled conditions a new parthenogenetic generation could be expected every 5 to 8 days.

Like that of the goldfish, the scientific literature on daphnia is extensive, and the general physiology and reactions of this animal are well known. The use of daphnia as a bioreagent is also well established (Munch, 1931; Adams, 1927; Billiard, 1925).

The daphnia used in these tests were raised from original stock secured in Texas, pedigreed strains being established and lines of parthenogenetic clones secured for the assay work. The daphnia colony is maintained in a series of large glass jars, each containing four liters of water; and the animals fed bacterial nutrient material prepared from cottonseed meal as described by Chipman (1934).

All assay tests were made in a constant temperature cabinet (see fig. 22) at 25° C. One hundred fifty daphnia of the same age (usually 4 days old) from the same strain were placed in each jar containing 3 liters of the solution to be tested, i. e., in a known dilution of the pollutant, using water from the same source as that in which the daphnia were living as the diluent. No abrupt changes in temperature were permitted, and the solution was well aerated before the daphnia were placed in it. Every 48 or 72 hours, depending upon the type of test, the animals in each jar were concentrated in a pyrex glass trap devised for this work, counted, and returned to the same or fresh solution as desired. When young appeared they were removed and carried in separate jars containing the same concentration of the pollutant as that of the original jar. In this way the mortality of each succeeding generation as well as the rate of reproduction could be followed.

WATER TYPES

When determining the specific lethality of any given pollutant for a particular case, water from the stream into which the effluent was being poured, taken just upstream from the point at which the pollutant entered the stream and filtered through bolting cloth to remove large masses of suspensoids and the macroplankton was used as the diluent water. In this way the pollutant was mixed with the same water as

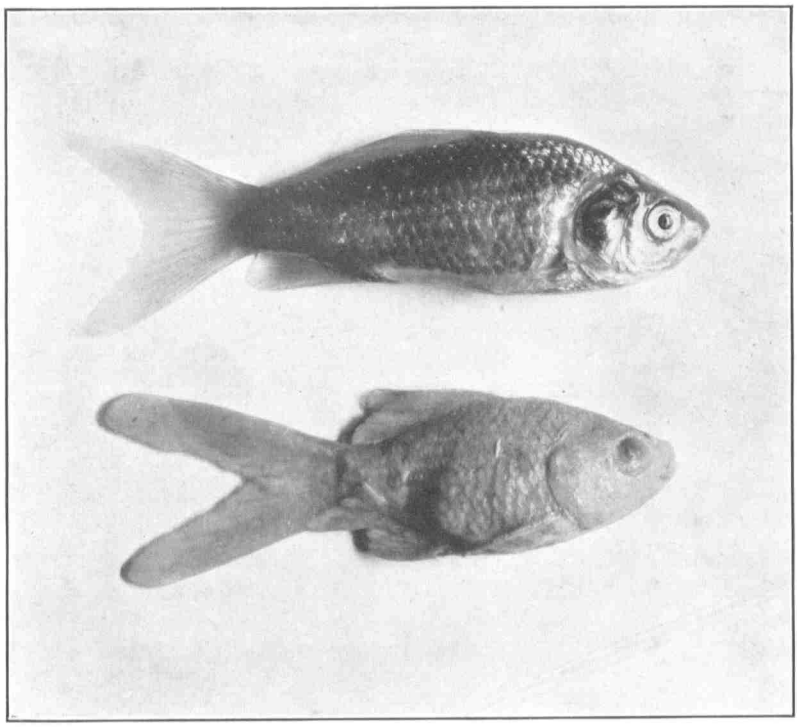

FIGURE 21.—Top, normal goldfish; bottom, goldfish killed in copper sulphate. Note thick deposit of opaque copper-mucoid precipitate covering body, fins, and eyes. This type of precipitate is produced by many wastes containing compounds of heavy metals.

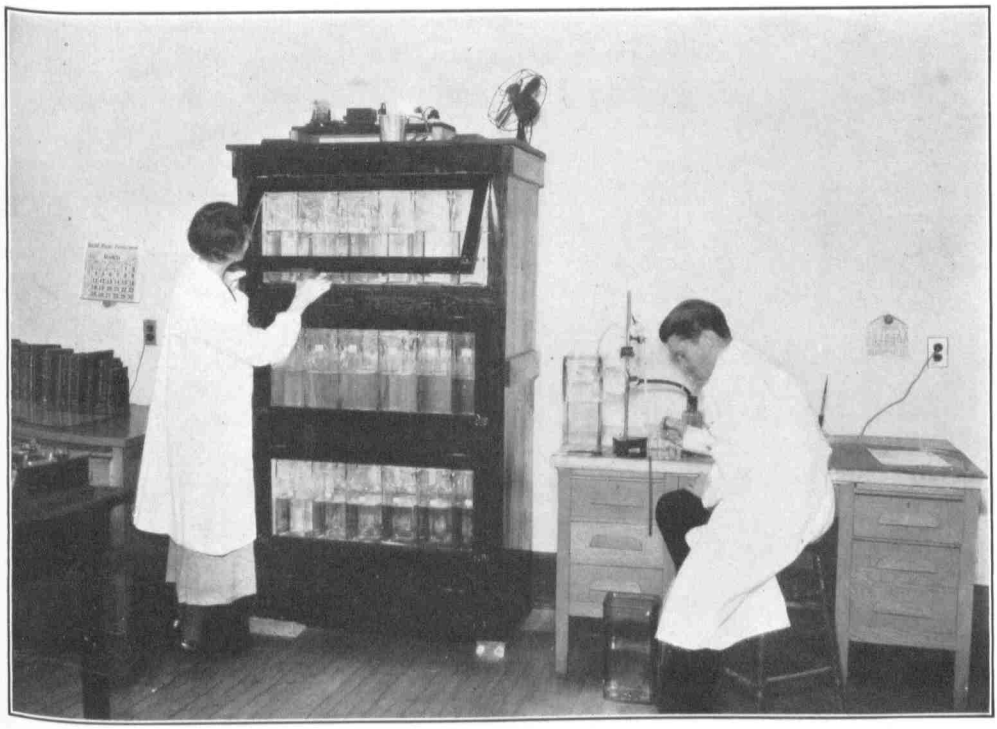

FIGURE 22.—Constant-temperature apparatus in which *Daphnia magna* were used as test reagents for toxicity of various stream pollutants. Assistant at the right is operating a concentrator preparatory to counting *Daphnia*.

in the actual case of pollution under consideration and the same chemical interreactions were possible. When it was not feasible to use stream water at the site of the pollution, unpolluted water from a comparable stream was diluted or fortified until the salt content, the conductivity, the carbonates, and the pH were essentially the same as those of the stream water in question. This was made possible by the field and laboratory analyses of the waters of the stream. This method of compounding a synthetic stream water, although laborious at times, gave very satisfactory comparative results. Control tests were also made in each investigation using glass-distilled water as the diluent for certain critical concentrations.

In making the assays of pollutants, regardless of the diluent water, no material was removed after making the dilution; i. e., even if precipitates or colloidal suspensions were formed on the addition of the pollutant to the diluent water, the fishes or daphnia were exposed to the action of the entire mixture. Many substances which are precipitated in stream and river water are nevertheless slightly soluble in water, particularly if small quantities of carbon dioxide and other compounds be present, so that portions of the precipitate might continue to redissolve for hours or days, and insoluble substances even though precipitated to the bottom of the stream constitute supplies of various ions which may be drawn into the water as others are removed. Again, some of these precipitated materials are dissolved or chemically changed by the action of various substances in or on the body of the fish or daphnia, or by the excretory products of these animals, so that particles of precipitated material lodging temporarily on the gills might be dissolved by the carbon dioxide there, or other particles swallowed by the fish might be acted upon by the digestive fluids of the animal. In view of these complicating factors, the tests made in stream waters are much more valuable in obtaining the actual hazards to aquatic life than those made in distilled water.

In the basic data tests (see tables 7, 8, 9, 10, 11, 12, and 13) four types of water were used as diluents, namely, glass-distilled water for the chemical controls in which the specific and uncomplicated action of the substance was studied, and soft, medium, and hard water (following the classification of Birge and Juday, 1911), i. e., with fixed carbonates less than 5 cubic centimeters per liter, 5 to 22 cubic centimeters per liter and over 22 cubic centimeters per liter, respectively, for the general lethality tests. Ranges of lethality were obtained in this way which are applicable within the limitations previously discussed to most stream waters of the United States, since the hardness of these natural stream waters is dependent almost entirely on the calcium and magnesium carbonates which exists in different degrees of concentrations in the interior waters.

The soft and hard natural waters were obtained at Columbia, Mo.; the hard water representing a typical limestone drainage, and the soft water a typical clay drainage. The medium water was obtained from the upper Mississippi River. In the tables the pH and specific conductance are given both for the original water and for the mixture as modified by the pollutant, so that the fluctuations in the diluent water itself and in the mixture as the result of the action of the pollutant on the salt and buffer balances may be followed in each case.

SPECIFIC LETHALITY TABLES

OSMOTIC PRESSURE AND SODIUM CHLORIDE

Many effluents carry soluble substances exerting considerable osmotic pressure, and because of that property are capable when sufficiently concentrated of withdrawing water from the gills of fishes and from other delicate external organs of various aquatic organisms, with the attendant damage to the living cells. High concentrations of many sorts of pollutants present this danger quite independently of any toxic, chemical, or corrosive action they may have on aquatic life. The toxic and chemical actions of various salts in stream pollutants may be in part offset by the presence of other substances; but the osmotic action of all of the components of the mixture may be lethal regardless of their mutual antagonisms or specific toxicities, consequently the osmotic pressures of concentrated effluents must be regarded as potential hazards until these substances are sufficiently diluted to be within the limits of osmotic pressure tolerated by fresh-water fishes.

Garrey (1916) finds, using the straw-colored minnow, *Notropis blennius*, as a reagent, that fresh-water fishes tolerate an osmotic pressure of the external medium equal to that of their own blood if the various salts and substances in the water are balanced against each other so as to exclude the specific toxic effects. As the blood of fresh-water fishes contains approximately 0.7-percent sodium chloride, together with small quantities of calcium and potassium salts, the limit of osmotic pressure tolerated in the external medium by fresh-water fishes is therefore near 6 atmospheres, or the approximate equivalent of 7,000 p. p. m. of sodium chloride (common salt) in the surrounding water.

In table 7 data are presented showing the effect of common salt in medium water (Mississippi River water) on test goldfish. This water, of course, contained small quantities of calcium and magnesium salts, which served to some extent to offset the specific toxic action which sodium chloride has in distilled water. (See sodium chloride, p. 429.) These river-water tests confirm the work of Garrey (1916), as sodium chloride killed quickly in concentrations greater than 10,000 p. p. m., and was not lethal in concentrations of 5,000 p. p. m. or less. The survivals in a concentration of 10,000 p. p. m. sodium chloride in river water ranged from 4 to 7 days, and the predicted maximal nonlethal concentration of sodium chloride on the basis of osmotic pressure alone in terms of the osmotic pressure of fish blood would be approximately 7,000 p. p. m.

TABLE 7.—*Survival of goldfish in solutions of sodium chloride: diluent, filtered Mississippi River water*[1]

Concentration ration by weight	Parts per million	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time[2]
		Water	Solution	Water	Solution	
1:20	50,000	7.8	7.7	236	62,669	30 to 40 minutes.
1:50	20,000	7.8	7.7	235	31,336	1 to 2 hours.
1:67	14,925	7.8	7.7	235	25,254	10 to 12 hours.
1:80	12,500	7.8	7.7	235	25,200	24 to 36 hours.
1:100	10,000	7.8	7.7	235	18,772	4 to 10 days.
1:200	5,000	7.8	7.7	235	4,156	∞
1:1,000	1,000	7.8	7.7	235	2,328	∞
1:10,000	100	7.8	7.7	235	455	∞
1:100,000	10	7.8	7.7	235	245	∞

[1] Condition of experiments as described in table 8.
[2] Minimal and maximal survival times as found in these experiments. Infinity sign indicates survival greater than 25 days without any apparent injury to fish.

In practical pollution work, therefore, any effluent as long as its osmotic pressure is greater than 6 atmospheres may be expected to be lethal to fresh-water fishes regardless of any specific toxic properties. Below this osmotic pressure the toxic, chemical, and corrosive characteristics of wastes will be the major determining factors in its lethality. Brine wastes, however, often present pollution hazards largely because of their osmotic pressures.

ACIDS

High acidity is a characteristic of a large number of wastes, so that the action of uncombined acid is one of the major problems of stream pollution. In determining the lethality of acid wastes, both the actual acidity—that is, the pH or hydrogen-ion concentration of the polluted water carrying acid effluent—and the specific acid involved must be considered, as acid wastes do not kill merely because of a particular degree of acidity.

In table 8 a summary of an extensive series of experiments on the lethality of 11 acids found in stream pollutants is presented. It is obvious, first of all, from this table that it is futile to attempt to designate a given p. p. m. value as marking the lethal point for any particular acid as the buffer substances and dissolved salts of the water into which acid waste is poured will determine the amount of free acid or hydrogen-ions available. The actual conditions, therefore, presented to aquatic life following the addition of a given number of p. p. m. of a particular acid to soft water will be quite different from those presented by the same amount of that acid when added to hard water, with of course all sorts of intermediate possibilities between these two extremes. For example, 134 p. p. m. of sulphuric acid killed goldfish in from 6 to 90 hours when added to soft water, but were not lethal when added to hard water.

TABLE 8.—*Survivals of 700 goldfish in various concentrations of 11 acids found in industrial wastes* [1]

Substances	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time [2]	Constituent of—
				Water	Solution	Water	Solution		
Acetic acid	1:70	14,286	Hard	8.0	3.0	641	936	26 to 33 minutes	Beet-sugar wastes.
Do	1:201	4,975	do	8.0	3.5	641	749	30 to 36 minutes	
Do	1:631	1,585	do	8.0	4.0	641	673	50 to 60 minutes	
Do	1:1,000	1,000	do	7.8	4.5	645	693	50 minutes to 1 hour 30 minutes.	
Do	1:1,005	995	do	8.0	4.5	641	652	2 hours to 5 hours 50 minutes.	
Do	1:1,077	929	do	7.9	4.6	641	662	1 to 6 hours	
Do	1:2,365	423	do	8.0	5.0	641	676	4 hours 45 minutes to 20 hours.	
Do	1:2,871	348	do	8.0	5.5	641	675	20 hours to ∞	
Do	[3] 1:10,000	100	do	7.8	6.8	645	675	48 hours to ∞	
Do	[3] 1:100,000	10	do	7.8	7.3	645	688	∞	
Do	[3] 1:1,000,000	1	do	7.8	7.6	645	680	∞	
Benzoic acid	1:1,000	1,000	do	7.8	4.8	666	593	29 to 50 minutes	Coal-tar wastes.
Do	1:5,000	200	do	7.8	5.9	666	598	7 hours 16 minutes to ∞	
Chromic acid	1:1,000	1,000	Very soft	6.2	1.4	<50	3,680	15 to 23 minutes	Tannery wastes.
Do	1:1,250	800	Hard	7.8	5.4	647	844	3 hours 21 minutes	
Do	1:2,500	400	do	7.8	5.9	647	724	15 hours 18 minutes to 28 hours 24 minutes.	
Do	1:5,000	200	do	7.8	6.4	647	716	60 hours 24 minutes to 84 hours.	
Do	1:10,000	100	do	7.8	7.3	647	689	∞	
Do	1:10,000	100	Very soft	6.2	4.0	<50	469	30 to 35 minutes	
Citric acid	1:400	2,500	Hard	8.0	3.0	641	841	55 to 86 minutes	Citrus-fruit products wastes.
Do	1:698	1,433	do	8.0	3.5	641	654	3 hours to 3 hours 30 minutes.	
Do	1:1,119	894	do	8.0	4.0	641	542	4 to 28 hours	
Do	1:1,600	625	do	8.0	4.5	641	494	∞	

TABLE 8.—*Survivals of 700 goldfish in various concentrations of 11 acids found in industrial wastes* [1]—Continued

Substances	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time [2]	Constituent of—
				Water	Solution	Water	Solution		
Hydrochloric acid	[3] 1:1,000	1,000	do	7.8	1.8	680	3,481	10 to 15 minutes	Chemical wastes.
Do	1:5,100	196	do	8.0	3.0	641	1,221	1 hour 15 minutes to 1 hour 30 minutes.	
Do	1:5,614	178	do	8.0	3.5	641	930	1 hour 23 minutes to 2 hours 15 minutes.	
Do	1:6,011	166	do	8.0	4.0	641	912	4 hours 28 minutes to 6 hours 32 minutes.	
Do	1:6,299	159	do	8.0	4.5	641	853	∞	
Do	[3] 1:10,000	100	do	7.8	6.9	645	654	∞	
Do	[3] 1:100,000	10	do	7.8	7.5	645	650	∞	
Do	[3] 1:1,000,000	1	do	7.8	7.7	645	648	∞	
Lactic acid	1:326	3,068	do	8.0	3.0	641	1,100	40 to 50 minutes	Dairy industries wastes.
Do	1:706	1,416	do	8.0	3.5	641	765	1 hour 12 minutes to 1 hour 45 minutes.	
Do	1:1,530	654	do	8.0	4.0	641	600	6 to 43 hours	
Do	1:2,324	430	do	8.0	4.6	641	566	∞	
Nitric acid	1:1,333	750	do	7.8	3.4	666	1,625	30 to 50 minutes	Chemical wastes.
Do	1:5,000	200	do	7.8	4.9	666	818	∞	
Do	1:10,000	100	do	7.9	7.9	652	698	∞	
Oxalic acid	1:1,000	1,000	do	7.8	2.6	666	2,620	25 to 30 minutes	Dye, tanning and bleaching wastes.
Do	1:5,000	200	do	7.9	5.3	652	405	∞	
Do	1:10,000	100	do	7.9	6.8	652	524	∞	
Do	1:17,000	59	Very soft	6.2	4.5	<50	146	∞	
Do	1:40,000	25	do	6.2	5.8	<50	119	∞	
Do	1:100,000	10	Hard	7.9	7.6	652	662	∞	
Sulphuric acid	[3] 1:1,000	1,000	do	7.8	2.2	645	1,381	30 to 45 minutes	Coal- and iron-mine waters.
Do	1:5,922	169	do	7.8	3.0	640	1,203	50 minutes to 1 hour 10 minutes.	
Do	1:7,000	143	Soft	6.4	3.5	583	790	2 hours 30 minutes to 5 hours 17 minutes.	
Do	1:7,000	143	Hard	7.8	3.5	640	1,170	2 hours to 2 hours 20 minutes.	
Do	1:7,250	138	Soft	6.4	3.9	583	753	5 to 6 hours	
Do	1:7,250	138	Hard	7.8	4.0	640	868	4 hours to ∞	
Do	1:7,450	134	Soft	6.4	4.3	583	675	6 hours 12 minutes to 96 hours.	
Do	1:7,450	134	Hard	7.8	4.5	640	756	∞	
Do	[3] 1:7,500	133	do	7.8	5.0	645	673	∞	
Do	[3] 1:10,000	100	do	7.8	6.8	645	698	∞	
Do	1:17,000	59	Very soft	6.2	3.2	<50	450	1 hour to 1 hour 15 minutes	
Do	1:60,000	17	do	6.2	4.5	<50	93	∞	
Do	[3] 1:100,000	10	Hard	7.8	7.5	645	692	∞	
Do	1:120,000	8	Very soft	6.2	5.6	<50	85	∞	
Do	[3] 1:1,000,000	1	Hard	7.8	7.5	645	695	∞	
Tannic acid	1:1,000	1,000	do	7.8	6.4	666	631	2 hours 38 minutes to 3 hours 48 minutes.	Tannery wastes.
Do	1:5,000	200	do	7.9	7.3	652	652	7 hours 26 minutes to 9 hours 26 minutes.	
Do	1:10,000	100	do	7.9	7.6	652	652	9 hours 40 minutes to 20 hours 20 minutes.	
Do	1:100,000	10	do	7.9	7.8	652	652	∞	
Tartaric acid	1:1,000	1,000	Very soft	6.2	3.2	<50	900	20 to 25 minutes	Winery wastes.
Do	1:1,000	1,000	Hard	7.8	3.9	655	727	3 hours to 3 hours 20 minutes.	
Do	1:5,000	200	do	7.8	4.6	655	700	∞	
Do	1:10,000	100	Very soft	6.2	3.6	<50	205	3 hours to 3 hours 33 minutes.	
Do	1:100,000	10	do	6.2	4.9	<50	<50	∞	

[1] Standard goldfish weight 3 to 5 grams used. Each fish in individual glass container carrying 3 liters of solution. Dissolved oxygen 6 to 7 p. p. m.; temperature maintained between 18° to 23° C. Diluent waters discussed on page —.

[2] Minimal and maximal survival times as found in these experiments. Infinity sign indicates survival greater than 4 days without any apparent injury to the fish.

[3] Initial volume of 3 liters per fish replaced by constant flow apparatus at rate of 1 liter per hour.

Considering the actual acidity of the resultant mixture of acids and a given hard water, the most acid mixtures in which goldfish survive 4 days or more were pH 4.0, sulphuric acid; pH 4.5, hydrochloric and citric acids; pH 4.6, lactic acid; pH 4.9, nitric and tartaric acids; pH 5.5, acetic acid; pH 5.8, oxalic acid; pH 5.9, benzoic acid; pH 7.3, chromic acid; and pH 7.8, tannic acid. To this comparison,

it must be added, as previously pointed out in the section on pH of natural water, that Brown and Jewell (1926) found fish living in a bog lake where the acidity of the water was pH 4.5 due to the action of carbon dioxide and organic acids leached from the surrounding bog vegetation. It is evident from all of the data in table 8 that no matter what the diluent water be, as far as hydrogen-ion concentration alone is concerned, the acidity near the magnitude of pH 4.0, regardless of the acid or acid-salt combinations producing this acidity, will be lethal for fresh-water fishes if that concentration of acidity be maintained. All acid concentrations more acid than pH 4.0 were lethal. In concentrations less acid than pH 4.0 the penetrative properties and the lethality of the kation of the acid must also be considered, for it may be seen that at any given pH the relative lethality varies with the particular acid involved.

On the basis of p. p. m. of acid present, disregarding the pH factor, the acids may be arranged in order of lethality as follows: Tannic acid, 10 p. p. m.; chromic acid, 100 p. p. m.; sulphuric acid, 130 p. p. m.; hydrochloric, 159 p. p. m.; benzoic, nitric, oxalic, and tartaric, each 200 p. p. m.; acetic acid, 348 p. p. m.; lactic, 430 p. p. m.; and citric, 625 p. p. m., in the particular hard water tested. The exact p. p. m. values are not so significant, for they will vary to some extent with the hardness of the diluent water; but the group shows the general order of magnitude of the relative lethality for these common pollutant acids.

Fishes are killed by acid wastes first through the precipitation and coagulation of the mucus on the gills and by the coagulation of the gill membranes themselves. If this coagulation of gills and gill secretions does not take place, the death of the fish is attributable to the lethal action of the kation of the acid. Combinations of these two actions are not uncommon, i. e., both precipitation and specific toxic action may contribute to the death of the fish. The precipitation of the mucus and of the proteins within the gill membrane cells themselves progresses rapidly when the relative acidity of the mixture is more acid than pH 4.5 because of the acidity itself, but this precipitation may be enhanced by the action of the kation of the acid. Tannic, chromic, and nitric acids all have marked affinity for living protoplasm, forming insoluble compounds with certain protein constituents of living tissue very promptly; in fact, all three of these acids are used as histological fixing agents to kill protoplasm. In the previous comparison on the basis of pH value, the minimal lethal concentration of these acids shows that tannic, chromic, and nitric killed goldfish in solutions less acid than the lethal solutions of sulphuric, hydrochloric, citric, and lactic acids. Acetic acid has high penetrative properties and causes a swelling of tissues which is very destructive to the living cells, so that although this acid does not coagulate the gill membrane and gill mucus like hydrochloric acid, it does disrupt the cells of gill membrane with disastrous results. Consequently, it is not surprising to find that acetic acid kills goldfish at pH of 5.5.

Reviewing all of the data on acid wastes, it seems that the truly acid effects must be limited largely to those acids which kill at a hydrogen-ion concentration more acid than pH 5.0; while in the cases of those acids killing at hydrogen-ion concentration less acid than pH 5.0, lethality factors other than hydrogen-ion concentration play the major part. Of course, as the hydrogen-ion concentration of the surrounding medium in which the fishes and other aquatic animals are living becomes more acid than pH 7.2 to 7.4 (the normal values for most living cells),

detrimental effects which may act synergistically with the specific toxic actions of the substances producing such deviations in pH must be expected.

In this connection, it must be pointed out that although the lethality limits of acid wastes as given here are applicable to immediate or intermittent pollution the cumulative effects must also be considered. When goldfish were kept in water at pH 4.5 produced by addition of small quantity of sulphuric acid, this amount of sulphuric acid, although tolerated for a few days without apparent injury to the fish, seemed definitely detrimental to goldfish in exposures longer than 2 weeks, even though some fishes can tolerate pH 4.5 in the natural habitat when this degree of acidity is produced by carbon dioxide and acids from decaying vegetation in bog and swamp lakes. It may be necessary, therefore, to add sulphuric and other acids to the lists of those producing specific toxic effects when long-time experiments in progress are completed.

Table 9 presents data concerning the effects of acids on daphnia comparable to those given in table 8 for fishes. In the cases of daphnia which do not produce volumes of protective mucus to remove or in part buffer down the acid in the effluents to which they may be exposed, the maximal acidity of the solutions in which there was any survival by daphnia was around pH 5.4. It is significant in this connection to recall that the isoelectric point at which many proteins found in living tissue are precipitated is pH 5.5. The daphnia tests, therefore, suggest strongly that were fishes unprotected by mucus the lethal hydrogen-ion concentration for acids in general would be near pH 5.5, and explain the detrimental effects of acid wastes to the stream faunae in general even though the particular concentration may be survived by some fishes. In waters less acid than pH 5.5 the same relative lethalities of the various acids were found for daphnia as for fishes.

TABLE 9.—*Survivals of 4,500 Daphnia magna in various concentrations of 5 acids found in industrial wastes* [1]

Substance	Concentration ratio by weight	Parts per million	pH		Specific conductivity $mho \times 10^{-6}$ at 25° C.		Survival time	Final percent mortality
			Water	Solution	Water	Solution		
Acetic acid	1:1, 333	750	7.4	4.0	470	516	5 hours	100
Do	1:2, 000	500	7.4	4.6	470	491	do	100
Do	1:5, 333	188	7.4	5.0	470	461	do	100
Do	1:8, 000	125	7.4	5.4	470	460	24 to 72 hours	75
Citric acid	1:2, 666	375	7.6	4.0	425	532	1 to 2 hours	100
Do	1:4, 210	248	7.6	4.6	425	491	2 to 17 hours	100
Do	1:5, 405	185	7.6	5.0	425	490	10 to 17 hours	100
Do	1:8, 340	120	7.6	5.5	425	466	24 to 72 hours	40
Do	1:12, 500	80	7.6	5.9	425	440	∞	0
Hydrochloric acid	1:14, 545	69	7.4	4.0	452	660	1 to 4 hours	100
Do	1:15, 384	65	7.4	4.5	452	650	do	100
Do	1:16, 667	60	7.4	5.0	452	614	4 to 17 hours	100
Do	1:17, 777	56	7.4	5.4	452	595	17 to 72 hours	80
Lactic acid	1:3, 470	288	7.6	4.0	442	493	3 hours	100
Do	1:4, 280	234	7.6	4.5	442	463	do	100
Do	1:5, 230	191	7.6	5.0	442	443	6 to 48 hours	100
Do	1:5, 880	170	7.6	5.5	442	441	26 to 72 hours	66
Sulphuric acid	1:20, 000	50	7.3	3.5	324	610	1 to 3 hours	100
Do	1:26, 667	38	7.3	4.0	324	484	24 hours	100
Do	1:33, 333	30	7.3	4.5	324	389	do	100
Do	1:34, 479	29	7.3	5.0	324	381	24 to 72 hours	100
Do	1:50, 000	20	7.6	6.5	375	387	168 hours	0
Do	1:100, 000	10	7.6	7.3	375	375	do	0
Do	1:1, 000, 000	1	7.6	7.6	375	375	do	0
Do	1:10, 000, 000	0.1	7.6	7.6	375	375	do	0

[1] Standard daphnia, 5 days old, from parthenogenic clones were used. For each dilution 150 animals were carried in glass jars containing 4 liters of the solution, and these jars held at 25° C. in constant temperature chamber. The diluent was soft water (see p. 406) from the same source as that in which the stock colonies of daphnia were living. A control of 150 animals in 4 liters of this water without test substance was maintained for each series.

COMPOUNDS OF VARIOUS METALS

Compounds of many metals are rapidly lethal, because these compounds coagulate and precipitate the mucus secreted by the gills of fishes (Carpenter, 1930) and many of the proteins in the living cells. This action has been explained in the discussion of the effects of pollutants on fishes (p. 400). In addition, some metallic salts, such as ferric chloride, if present in sufficient quantities may increase the acidity of the water to a level dangerous for aquatic life and combine this hazard with that of the metallic coagulant.

Since the carbonates and phosphates of many metals are relatively insoluble in water, the hardness of waters receiving effluents containing compounds of the heavier metals is an important factor in determining the immediate lethality of such effluents to fishes, as a considerable portion of these metals may be precipitated from the effluent by the salts in the water. This factor has led to much confusion concerning the absolute limits of lethality of metallic compounds for fishes, since various observers have used different kinds of test water, ranging from distilled to very hard. Unless the hardness of the water in question and particularly the amounts of carbon dioxide, both fixed and free, be known the limits of lethality of any particular metallic compound in any given water are difficult to estimate even though there may be ample data on the specific toxicity of that compound. Besides, the factors of synergy and antagonism between the metallic compound itself and other compounds in the water or effluent which do not precipitate this metallic compound must be considered. Examples of this action are presented in table 10 for copper sulphate.

TABLE 10.—*Influence of other salts in solution upon the toxicity of copper sulphate to gold fish* [1]

Series	Copper sulphate concentration		Sodium nitrate concentration		Calcium chloride concentration		pH		Specific conductivity mho × 10^{-6} at 25° C.		Average survival time
	Ratio by weight	Parts per million	Ratio by weight	Parts per million	Ratio by weight	Parts per million	Water	Solution	Water	Solution	
A	1:100,000	10					7.1	4.0	<50	112	2 hours 30 minutes.
B	1:100,000	10	1:2,000	500			7.1	5.7	<50	806	3 hours.
C	1:100,000	10	1:1,000	1,000			7.1	5.7	<50	1,478	3 hours 45 minutes.
D	1:100,000	10	1:500	2,000			7.1	5.8	<50	2,749	6 hours 10 minutes.
E	1:100,000	10	1:333	3,000			7.1	5.8	<50	4,020	6 hours 15 minutes.
F	1:100,000	10	1:250	4,000			7.1	6.0	<50	5,413	6 hours 30 minutes.
G	1:100,000	10	1:200	5,000			7.1	6.0	<50	6,668	6 hours 40 minutes.
H	1:100,000	10	1:167	6,000			7.1	6.4	<50	7,734	5 hours.
J	1:100,000	10	1:143	7,000			7.1	6.2	<50	9,013	5 hours 30 minutes.
K	1:100,000	10	1:125	8,000			7.1	6.3	<50	10,113	4 hours.
L	1:100,000	10	1:2,000	500	1:20,000	50	7.1	6.3	<50	1,513	5 hours 15 minutes.
M	1:100,000	10	1:1,000	1,000	1:20,000	50	7.1	6.3	<50	1,541	5 hours 30 minutes.
N	1:100,000	10	1:500	2,000	1:20,000	50	7.1	6.4	<50	2,825	6 hours 30 minutes.
O	1:100,000	10	1:333	3,000	1:20,000	50	7.1	6.5	<50	3,984	9 hours 30 minutes.
P	1:100,000	10	1:250	4,000	1:20,000	50	7.1	6.4	<50	5,350	12 hours 30 minutes.
Q	1:100,000	10	1:200	5,000	1:20,000	50	7.1	6.4	<50	6,573	12 hours 45 minutes.
R	1:100,000	10	1:167	6,000	1:20,000	50	7.1	6.5	<50	7,866	8 hours.
S	1:100,000	10	1:143	7,000	1:20,000	50	7.1	6.5	<50	8,763	7 hours.
T	1:100,000	10	1:125	8,000	1:20,000	50	7.1	6.5	<50	10,338	Do.
U			1:333	3,000			7.1	7.3	<50	4,221	(2).
V			1:250	4,000			7.1	6.7	<50	5,350	80 hours.
W			1:200	5,000			7.1	6.8	<50	6,620	37 hours.
X			1:167	6,000			7.1	6.9	<50	7,798	6 hours 30 minutes.

[1] Glass distilled water was used in these tests. Other conditions as described in table 8.
[2] Survival greater than 4 days, fish apparently unaffected.

It may be noted in this table that the addition of progressively larger quantities of sodium nitrate to the copper sulphate solution increased the survival time of fishes from 2 hours 30 minutes to 6 hours 40 minutes, up to a concentration of 1 : 200 for sodium nitrate. Beyond that concentration the osmotic action of the sodium nitrate became unfavorable (see osmotic pressure, p. 408) and the survival time decreased with a further increase of sodium nitrate, i. e., sodium nitrate, which does not precipitate copper, both increased and decreased the survival time of fishes exposed to the lethal action of same amounts of copper sulphate according to the concentration of sodium nitrate present. The second half of this table shows the marked increase in survival time from 2 hours and 30 minutes in the copper sulphate alone to 12 hours 45 minutes in the same strength of copper sulphate solution to which both sodium nitrate and calcium chloride were added. The amount of calcium chloride used was very small, namely, 50 p. p. m., and in this concentration no precipitate formed, yet this quantity of calcium chloride greatly enhanced the protective action of the sodium nitrate against the lethal action of copper sulphate.

These discussions of the precipitation of metallic compounds out of effluents and of the synergistic and antagonistic actions of compounds which do not precipitate the particular metal in question show, both specifically in the case of effluents carrying compounds of metals and in general in the case of all stream pollutants carrying chemical wastes, that field examinations of local conditions, analyses both of the effluents and the water receiving these effluents, and bioassays of the mixtures of the two must be made before the lethal limits of such wastes can be determined.

In table 11 summarized data from a large series of tests covering the lethality limits of certain compounds of eight metals found in commercial effluents are presented. From these data the expected lethal ranges and the relative lethality of these eight compounds in various types of water, together with the changes in salt balance and relative acidity produced by these compounds, may be estimated if uncomplicated by substances other than those normally found in stream water, or by excessive amounts of those substances.

TABLE 11.—*Survivals of 850 goldfish in various concentrations of salts of 8 metals found in industrial wastes* [1]

Substance	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time [2]	Constituent of—
				Water	Solution	Water	Solution		
Aluminum potassium sulphate.	[3] 1:1,000	1,000	Hard	7.8	5.5	678	1,247	1 to 10 hours	Tannery wastes.
Do	[3] 1:10,000	100	do	7.8	6.8	678	736	12 hours to ∞	
Do	[3] 1:100,000	10	do	7.8	7.6	678	584	∞	
Do	1:1,000,000	1	do	7.8	7.7	678	677	∞	
Cobaltous chloride	1:1,000	1,000	Very soft	6.2	6.6	<50	1,906	28 to 29 hours	Electroplating wastes.
Do	1:1,000	1,000	Hard	7.8	7.2	647	2,265	30 to 31 hours	
Do	1:10,000	100	Very soft	6.2	6.5	<50	308	168 hours to ∞	
Cupric sulphate	[3] 1:1,000	1,000	Glass distilled	7.0	5.6	<50	1,123	1 to 2 hours	Copper and brass industries wastes.
Do	[3] 1:1,000	1,000	Hard	7.8	6.8	690	1,348	1 hour to 2 hours 20 minutes.	
Do	[3] 1:10,000	100	do	7.8	7.0	671	637	3 hours to 11 hours	
Do	1:10,000	100	do	7.9	7.0	635	637	3 to 41 hours	
Do	[3] 1:100,000	10	do	7.9	7.6	635	671	11 to 72 hours	
Do	1:100,000	10	do	7.9	7.7	635	700	48 hours to ∞	
Do	[3] 1:1,000,000	1	do	7.9	7.5	635	640	72 hours to ∞	

TABLE 11.—*Survivals of 850 goldfish in various concentrations of salts of 8 metals found in industrial wastes* [1]—Continued

Substance	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10^{-6} at 25° C.		Survival time [2]	Constituent of—
				Water	Solution	Water	Solution		
Ferrous sulphate	[3] 1:1, 000	1, 000	do	7. 7	6. 4	594	1, 307	2 to 10 hours	Wire and tinplate mills wastes.
Do	[3] 1:10, 000	100	do	7. 7	6. 7	594	649	∞	
Do	[3] 1:100, 000	10	do	7. 7	7. 4	594	598	∞	
Do	[3] 1:1, 000, 000	1	do	7. 7	7. 6	594	600	∞	
Ferric chloride	1:1, 000	1, 000	Very soft	6. 2	2. 4	<50	2, 156	1 hour to 1 hour 10 minutes.	
Do	1:10, 000	100	do	6. 2	3. 4	<50	334	1 hour to 1 hour 20 minutes.	
Do	1:10, 000	100	Hard	7. 8	5. 5	647	700	∞	
Do	1:100, 000	10	Very soft	6. 2	5. 0	<50	<50	∞	
Lead nitrate	[3] 1:1, 000	1, 000	Hard	7. 8	6. 4	678	2, 500	2 to 3 hours	Mining and smelting wastes.
Do	[3] 1:10, 000	100	do	7. 8	6. 8	678	775	80 hours to ∞	
Do	[3] 1:100, 000	10	do	7. 8	7. 4	678	678	∞	
Do	[3] 1:1, 000, 000	1	do	7. 8	7. 5	678	673	∞	
Nickelous chloride	1:1, 000	1, 000	Very soft	6. 3	6. 3	<50	1, 876	6 hours to 18 hours 30 minutes.	Electroplating wastes.
Do	1:1, 000	1, 000	Hard	7. 8	7. 4	647	2, 218	12 to 18 hours	
Do	1:10, 000	100	Very soft	6. 3	6. 3	<50	253	19 hours 25 minutes to 50 hours 25 minutes.	
Do	1:100, 000	10	do	6. 5	6. 5	<50	95	200 to 210 hours	
Stannous chloride	1:1, 000	1, 000	Very soft	6. 4	3. 5	<50	2, 380	1 hour to 1 hour 30 minutes.	Brass industries wastes.
Do	1:1, 000	1, 000	Hard	7. 8	3. 8	647	1, 609	4 to 5 hours	
Zinc sulphate	[3] 1:1, 000	1, 000	do	7. 8	7. 2	678	1, 538	1 to 4 hours	Mining and smelting wastes.
Do	[3] 1:10, 000	100	do	7. 8	7. 6	678	780	∞	
Do	[3] 1:100, 000	10	do	7. 8	7. 6	678	678	∞	
Do	[3] 1:1, 000, 000	1	do	7. 8	7. 6	678	678	∞	

[1] Experimental conditions as in table 8.
[2] Minimal and maximal survival times as found in these experiments. Infinity sign indicates survival greater than 4 days without any apparent injury to the fish.
[3] Initial volume of 3 liters per fish replaced by constant flow apparatus at rate of 1 liter per hour.

Another hazard from wastes containing compounds of various metals is the cumulative effect. Even though precipitated out, compounds carrying these metals, as long as they remain in the stream, on the bank, or on the floor of the stream, are subject to re-solution if conditions in the waters change (in many cases only slightly), and to ingestion by fish and other aquatic animals during feeding.

The case of lead salts will suffice for example. Carpenter in a series of papers (1924, 1925, 1926, 1927, and 1930) has shown that the lethal action of lead compounds on fishes in cases where the more soluble lead salts are present is due to the precipitation of mucus and proteins in and on the gills by the lead ion, and that the absorption and, therefore, the internal poisoning of fishes by lead compounds under these conditions is negligible during moderately short exposures. This conclusion has been confirmed by Behrens (1925) using a very delicate test (the radio-activity of an isotope of lead) which demonstrated the distribution of lead throughout the body of the fish.

However, the writer in long-time experiments in which goldfish were kept in glass containers, the bottoms of which were covered with finely powdered lead ore (lead sulphide, which is very insoluble in water), found cumulative effects which resulted in the death of fish after 61 days of such exposure, although there were no casualties in the controls carried under identical conditions except for the presence of lead ore. Although these experiments which are being followed further do not in themselves prove that the cumulative action was that of lead alone or of lead in conjunction with some other substance (i. e., traces of other substances in the ore may

have been responsible for these cumulative effects), these experiments do show that precipitated and insoluble substances on the bottom of the stream can be a definite pollution hazard over a long period of time due to cumulative action. Again, the writer has found that insoluble zinc ore (zinc sulphide) carried by a stream and deposited on flats adjacent to the main stream bed during high water when exposed to the actions of sunlight, air, and moisture produced quantities of zinc sulphate, a freely soluble and definitely toxic compound which was leached back through into the stream subsequently by rains and high waters (Ellis, 1932).

The synergistic physiological action of many compounds is well known, and the work of Macht and Leach (1930) on goldfish and other types of animals may be cited in this connection, as these writers found that two or more octylic alcohols were synergistic in their action on the respiratory and neuromuscular mechanisms of animals.

MISCELLANEOUS COMPOUNDS

In tables 12 and 13 the relative toxicities of 13 other substances found in industrial wastes or otherwise constituting stream pollution hazards are presented. The changes in hydrogen-ion concentration and salt balance are shown, as in the tables giving the data on acids and metallic compounds. It may be seen, however, that the substances listed in tables 12 and 13 do not kill because of changes either in pH or salt balance, i. e., in these two tables are included representatives of those substances which, if detrimental, are so because of specific toxic action after entering the body of the fish. Phenol produces paralysis of the neuromuscular mechanisms and hemolyzes the blood; potassium xanthate in high dilution acts after several days on the gastrointestinal tract; amyl alcohol quickly induces a semiparalyzed condition with marked incoordination, yet the fish may live for days in this state before dying; and sodium selenite causes a slow decline in the general activities of the fish.

TABLE 12.—*Survival of goldfish in solutions of sulphur and selenium compounds* [1]

Substance	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time [2]	Constituent of—
				Water	Solution	Water	Solution		
Ammonium sulphide	[3] 1:1,000	1,000	Hard	7.7	7.9	681	938	15 minutes to 1 hour 30 minutes.	Sewage and organic wastes.
Do	[3] 1:10,000	100	do	7.7	7.8	681	735	72 hours to ∞	
Do	[3] 1:100,000	10	do	7.7	7.7	681	681	∞	
Do	[3] 1:1,000,000	1	do	7.7	7.7	681	681	∞	
Hydrogen sulphide	[3] 1:1,000	1,000	do	7.8	6.5	670	734	45 minutes to 1 hour	Do.
Do	[3] 1:10,000	100	do	7.8	7.3	670	676	3 to 4 hours	
Do	[3] 1:100,000	10	do	7.8	7.6	670	661	96 hours to ∞	
Do	[3] 1:1,000,000	1	do	7.8	7.7	670	670	∞	
Sodium sulphite	[3] 1:1,000	1,000	do	7.8	7.6	676	2,017	3 to 72 hours	Paper-pulp-mill wastes.
Do	[3] 1:10,000	100	do	7.8	7.6	676	864	96 hours to ∞	
Do	[3] 1:100,000	10	do	7.8	7.6	676	678	∞	
Do	[3] 1:1,000,000	1	do	7.8	7.8	676	677	∞	
Sodium selenite	1:1,000	1,000	Very soft	6.4	7.5	<50	753	1 hour to 1 hour 30 minutes.	Certain soils.
Do	1:1,000	1,000	Hard	7.8	7.4	647	1,141	1 hour to 2 hours 10 minutes.	
Do	1:10,000	100	Very soft	6.4	7.5	<50	107	20 hours 56 minutes to ∞.	
Do	1:10,000	100	Hard	7.8	7.7	647	723	8 hours to 19 hours 30 minutes.	
Do	1:100,000	10	Very soft	6.4	7.3	<50	<50	98 to 144 hours	

[1] Conditions of experiments described in table 8.
[2] Minimal and maximal survival times as found in these experiments. Infinity sign indicates survival greater than 4 days without any apparent injury to the fish.
[3] Constant flow as described in table 8.

The specifically toxic substances which do enter the body of the fish can be grouped therefore according to their specific pathological and pharmacological effects much as in the case of man; and these poisons which do enter the body of the fish constitute important pollution hazards in high dilution, since the high dilutions may be tolerated by the fish for a short time without apparent harmful results. Consequently, the compounds in this miscellaneous group must be considered individually in evaluating pollution hazards.

TABLE 13.—*Survivals of goldfish in solutions of various chemicals found in industrial wastes* [1]

Substance	Concentration ratio by weight	Parts per million	Diluent water	pH		Specific conductivity mho×10⁻⁶ at 25° C.		Survival time [2]	Constituent of
				Water	Solution	Water	Solution		
Ammonium carbonate	[3] 1:1, 000	1, 000	Hard	7.7	8.1	718	2, 644	1 to 2 hours	Organic wastes, gashouse wastes.
Do	[3] 1:10, 000	100	do	7.7	7.8	718	956	4 to 10 hours	
Do	[3] 1:100, 000	10	do	7.7	7.7	718	727	∞	
Do	[3] 1:1, 000, 000	1	do	7.7	7.7	718	718	∞	
Amyl alcohol (iso)	1:1, 000	1, 000	do	7.8	7.8	647	666	17 to 71 hours	Distillery wastes.
Do	1:10, 000	100	do	7.8	7.8	647	647	82 hours–∞	
Do	1:100, 000	10	do	7.8	7.8	647	647	94 hours–∞	
Do	1:1, 000, 000	1	do	7.8	7.8	647	647	161 hours–∞	
Bromine	1:1, 000	1, 000	do	8.0	6.7	646	673	20 to 40 minutes	Chemical industries wastes.
Do	1:2, 500	400	do	8.0	7.4	646	659	30 minutes to 1 hour 10 minutes.	
Do	1:10, 000	100	do	8.0	7.6	646	649	1 hour to 3 hours 25 minutes.	
Do	1:50, 000	20	do	8.0	8.0	646	646	15 to 96 hours	
Do	1:100, 000	10	do	8.0	8.0	646	646	∞	
Chlorine	1:10, 000	100	do	7.9	7.4	653	640	54 minutes to 1 hour 30 minutes.	Do.
Do	1:100, 000	10	do	7.9	7.9	653	653	5 hours 15 minutes to 48 hours.	
Do	1:500, 000	2	do	7.9	7.9	653	653	17 to 48 hours	
Do	1:1, 000, 000	1	do	7.9	7.9	653	653	96 hours to ∞	
Cresylic acid	1:1, 000	1, 000	do	7.8	7.8	639	654	14 to 30 minutes	Livestock disinfectants and flotation wastes.
Do	1:10, 000	100	do	7.8	7.8	639	641	5 to 31 hours	
Do	1:100, 000	10	do	7.8	7.8	639	640	46 to 96 hours	
Do	1:1, 000, 000	1	do	7.8	7.8	645	645	93 to 120 hours	
Do	1:10, 000, 000	0.1	do	7.8	7.8	645	645	120 hours to ∞	
Phenol	[3] 1:1, 000	1, 000	do	7.8	7.6	690	587	15 to 30 minutes	Livestock disinfectants and gashouse wastes.
Do	[3] 1:10, 000	100	do	7.8	7.6	690	593	60 to 72 hours	
Do	[3] 1:100, 000	10	do	7.8	7.8	690	690	72 hours to ∞	
Do	[3] 1:1, 000, 000	1	do	7.8	7.8	690	690	∞	
Potassium xanthate	[3] 1:3, 125	320	do	8.1	8.8	669	900	5 to 24 hours	Mine flotation wastes.
Do	[3] 1:6, 250	160	do	8.1	8.6	669	776	12 to 24 hours	
Do	[3] 1:12, 500	80	do	8.1	8.4	669	731	12 to 36 hours	
Do	[3] 1:100, 000	10	do	8.1	8.1	669	669	48 to 96 hours	
Sodium chlorate	[3] 1:10, 000, 000	0.1	do	8.1	8.1	669	669	4 to 5 days	
Sodium fluoride	1:1, 000	1, 000	do	8.0	7.7	645	753	∞	Distillery wastes and certain soils.
Do	1:1, 000	1, 000	Very soft	6.4	6.4	<50	2, 162	12 to 29 hours	
Do	1:1, 000	1, 000	Hard	7.8	7.0	647	2, 346	60 to 102 hours	
	1:10, 000	100	do	7.8	7.3	647	943	∞	

[1] Condition of experiment described in table 8.
[2] Minimal and maximal survival times as found in these experiments. Infinity sign indicates survival greater than 4 days without apparent injury to the fish.
[3] Constant flow as described in table 8.

LETHAL LIMITS OF 114 SUBSTANCES WHICH MAY BE FOUND IN STREAM POLLUTANTS

In this section summaries of the lethal limits of individual substances, together with bibliographic references and statements concerning the test animals used and conditions of the experiments, are presented. These data have been massed from the literature and from the writer's own experiments (M. M. E.). In these summaries no attempt has been made to include all existing references, but instead

sufficient data to give a definite idea of the relative lethality of the substance in question under conditions which may be encountered in the streams of the United States. Only fresh-water fishes and fresh-water organisms have been considered. It is hoped that these summaries will prove helpful in evaluating specific pollution conditions when used in conjunction with the data presented in preceding sections. However, as has been pointed out repeatedly in this paper, arbitrary application of lethality data to specific pollution problems is absolutely impossible owing to the many limiting factors, various of which have been discussed in previous sections.

Any student of the toxicity of the components of industrial and municipal effluents to fishes and other aquatic life will find the pioneer work of Penny and Adams (1863) and of Weigelt, Saare, and Schwab (1885) starting points for the investigations of the commoner substances. However, much progress has been made in the study of the factors limiting the action of many pollutants, since these experiments and the lethality values given by these earlier observers have been quoted too often without regard to more recent findings.

Important advances have been made in the measurement of stream-pollution hazards of particular effluents through the isolation from these effluents of various compounds of highly toxic nature, which compounds were formerly overlooked or disregarded because the actual amounts of these substances present in the effluent were quite small. These highly toxic compounds, some of which are volatile or may otherwise disappear from the effluent after a time, have been responsible for the wide discrepancies in lethality of the waste as a whole as reported by different observers working on the same type of effluent.

In the present list of substances which may be participants in stream-pollution problems, several compounds have been included which are little known except to the professional chemist, although the harmful properties of these substances have been demonstrated in connection with certain industrial effluents. The list of these less familiar compounds will undoubtedly grow, both as investigations of particular effluents are completed and as chemical engineering produces new commercial processes. The long series of dyes, many of which are highly toxic to aquatic life, used in industries and arts have not been included in this list of possible stream pollutants because the dye wastes are largely mordant, bleach and processing liquors containing only traces of the dyestuffs themselves which industry has found too costly to waste. The conservation of these expensive dye compounds by the manufacturing concerns has been very apparent to the writer in several recent investigations of plants dyeing fabric, paper, and leather.

Acetic acid, $CH_3 \cdot COOH$. Vinegar acid

Beet-sugar pulp waste; some winery wastes; soured fruit wastes; and vinegar works. Penny and Adams (1863), 114 p. p. m. killed minnows in 20 hours, but 286 p. p. m. not fatal to goldfish; M. M. E., 100 p. p. m. in hard water killed some goldfish, *Carassius auratus*, and 125 p. p. m. killed cladocerans, *Daphnia magna*, in 24–72 hours.

Acetone, $(CH_3)_2CO$

Gas and coal-tar wastes; paint and chemical industries. Shelford (1917), 14,250–15,050 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*.

Acridine, $C_6H_4(N.CH)C_6H_4$

Gas tar oils; dye industries; water sterilization. Adams (1927), 5 p. p. m. in Nile River water killed cladocerans, *Daphnia sp.*, and copepods, *Cyclops sp.*

Alcohols

See amyl alcohol, butyl alcohol, ethyl alcohol, methyl alcohol, and octyl alcohol.

Aluminium ammonium sulphate, $Al(NH_4)(SO_4)_2$. Ammonium alum

Dye works and cloth printing industries. Weigelt, Saare, and Schwab (1885), 523 p. p. m. in tap water caused large trout to float on side after 10 hours' exposure.

Aluminium potassium sulphate, $AlK(SO_4)_2$. Alum or potassium alum

Dye works; tanneries; leather works. Penny and Adams (1863), 250 p. p. m. killed goldfish and minnows; Weigelt, Saare, and Schwab (1885), 544 p. p. m. in tap water killed California salmon in 6 hours, and medium trout in 15 hours; M. M. E., 1,000 p. p. m. in hard water killed goldfish, *Carassius auratus* in 1–10 hours, 100 p. p. m. killed goldfish in 12–96 hours, although some survived this strength over 100 hours.

Alums

See aluminium ammonium sulphate, aluminium potassium sulphate, and ferric potassium sulphate.

Ammonia

See ammonium hydroxide.

Ammonium carbonate, $(NH_4)_2CO_3$

Gas wastes; wool-washings; tannery effluents. Clark and Adams (1913), 155–197 p. p. m. fatal to shiners and carp in a few minutes to a few hours; Shelford (1917), 600–800 p. p. m. killed orange-spotted sunfish, *Lepomis humilis* in 1 hour; M. M. E., 100 p. p. m. in hard water killed goldfish in 4–10 hours, 48 p. p. m. in 6 days, 10 p. p. m. tolerated for more than 100 hours without apparent effect.

Ammonium chloride, NH_4Cl. Sal ammoniac

Gas wastes; various chemical wastes. Clark and Adams (1913), 180 p. p. m. in tap water, no effect on shiners or carp; Wells (1915b), 535 p. p. m. in tap water killed bluegills, *Lepomis pallidus* in 4 hours 45 minutes, and same amount in distilled water killed bluegills in 18 days; Shelford (1917), 700–800 p. p. m. killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Powers (1917), 1,712 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 6–18 hours; M. M. E. 268 p. p. m. in hard water, killed goldfish in 6 days; 535 p. p. m. killed cladocerans, *Daphnia magna*, in 6 hours.

Ammonium ferrocyanide $(NH_4)_4Fe(CN)_6$

Gas wastes. Shelford (1917), 150–200 p. p. m. killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Ammonium hydroxide, NH_4OH

Wool washings; chemical wastes; gas wastes. Since ammonia gas NH_3 unites readily on mixing with water forming the hydroxide, these two compounds are considered together here. Clark and Adams (1913), 9.4 p. p. m. (ammonium hydroxide) did not kill shiners, carp, and large suckers but 13 p. p. m. killed all these fishes, 20 p. p. m. being fatal in 15 minutes; Belding (1928), 6.25 p. p. m. killed brook trout in 24 hours; Weigelt, Saare, and Schwab (1885), 250 p. p. m. (ammonia) killed trout in 2 hours; Shelford (1917), 7–8 p. p. m. (ammonia) in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; M. M. E., 2–2.5 p. p. m. (ammonia) in hard water fatal to goldfish, *Carassius auratus*, and yellow-perch, *Perca flavescens*, in 24 hours to 4 days.

Ammonium nitrate, NH_4NO_3

Chemical industries; manufacture of explosives; in fertilizers. Wells (1915b), 800 p. p. m. in tap water killed bluegills, *Lepomis pallidus*, in 3.9 hours; in distilled water lethal to bluegills in 16 days; Powers (1917), 4,545 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 90 hours.

Ammonium sulphate, $(NH_4)_2SO_4$

Chemical wastes; gas wastes; fertilizers. Wells (1915b), 66 p. p. m. in tap water killed bluegills, *Lepomis pallidus*, in 3 hours, 30 minutes, in distilled water lethal to bluegills in 17 days; Shelford (1917), 420–500 p. p. m. in tap water killed *Lepomis humilis*, in 1 hour; M. M. E., 264 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 6 days or less.

Ammonium sulphide, $(NH_4)_2S_x$

Chemical wastes; in wastes from some beet-sugar processes; in some gas wastes. M. M. E., 100 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 72 hours, 10 p. p. m. in hard water, goldfish survived more than 100 hours of exposure.

Ammonium thiocyanate, NH_4CNS. Rhodanammonium

Gas wastes; chemical industries. Shelford (1917), 280–300 p. p. m. in tap water killed orange-spotted sunfish in 1 hour; Demyanenko (1931), 200 p. p. m. lethal for fish.

Amyl alcohol (iso), $C_5H_{11}OH$

Chemical wastes; in some distillery wastes. M. M. E., 100 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 82 hours, 1 p. p. m. killed goldfish in 161 hours.

Aniline, $C_6H_5NH_2$

Dye wastes; chemical industries; gas wastes. Shelford (1917), 1,020–1,122 p. p. m. killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Demyanenko (1931), 250 p. p. m. lethal for fishes.

Arsenic trioxide, white arsenic

See sodium arsenate.

Barium chloride, $BaCl_2$

Some chemical wastes; some alkaline pools. Powers (1917), 5,000 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 12–17 hours.

Benzoic acid, $C_6H_5 \cdot COOH$

Gas wastes. Shelford (1917), 550–570 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; M. M. E., 200 p. p. m. in hard water killed goldfish in 7–96 hours.

Blue Vitriol

See cupric sulphate.

Bromine, Br_2

Chemical industries; bromine plant wastes. Penny and Adams (1863), 29 p. p. m. killed minnows and goldfish; M. M. E., 20 p. p. m. in hard water killed goldfish in 15–96 hours, 10 p. p. m. in soft water lethal for cladocerans, *Daphnia magna*.

Butyl alcohol (iso), C_4H_9OH

Paint and varnish solvents; some chemical industries. Powers (1917), 250 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 7–20 hours.

Cadmium chloride, $CdCl_2$

Pigment works; calico printing; chemical wastes. Powers (1917), 0.0165 p. p. m. in distilled water killed goldfish in 8 hours 40 minutes to 18 hours.

Cadmium sulphate, $CdSO_4$

Same sources as cadmium chloride. Carpenter (1927), 1,042 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in 3 hours.

Calcium chloride, $CaCl_2$

Wastes from bromine and salt works; in waters from oil wells; antidust road surfacing. Wells (1915b) 555 p. p. m. in tap water caused pathological degeneration of tail fin of rock-bass, *Amblo-plites rupestris*, in an exposure of 1 week; Garrey (1916), 2,775 p. p. m. in distilled water killed straw-colored minnows, *Notropis blennius*, in 2–4 days, but this species did not succumb to 277 p. p. m. in distilled water in 5–7 weeks; Powers (1917), 7,752 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 22–27 hours; Wiebe, Burr, and Faubion (1934), 5,000 p. p. m. killed golden shiners, *Notemigonus crysoleucas*, in 143 hours.

Calcium hydroxide, $Ca(OH)_2$. Lime

Tannery-wastes; leather works. Weigelt, Saare, and Schwab (1885), 700 p. p. m. in tap water killed trout in 26 minutes; Marsh (1907), 18 p. p. m. (as calcium oxide) fatal to trout fry.

Calcium nitrate, $Ca(NO_3)_2$

Some chemical wastes. Powers (1917), 6,061 p. p. m. in distilled water killed goldfish, in 43–48 hours.

Calcium oxide, CaO. Unslaked lime

Forms calcium hydroxide, q. v., immediately on addition to water.

Carbon bisulphide, CS_2

Gas wastes; as a solvent in various chemical industries. Weigelt, Saare and Schwab (1885), a 7 minute exposure to 5,000 p. p. m. killed trout 2 days later; Shelford (1917), 100–127 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Carbon dioxide, CO_2

From sewage and any decomposing organic wastes (see section on carbon dioxide in natural waters). Wells (1918), 113,925–151,900 p. p. m. in tap water killed fresh-water fishes.

Carbon monoxide, CO

Motorboat exhausts; in water returned to streams from cooling systems of engines using fuel oil if mixed with exhaust gases. Wells (1918), 1,160 p. p. m. in tap water killed straw-colored minnow, *Notropis blennius*, in 1 hour; the blunt-nosed minnow, *Pimephales notatus*, in 1 hour 55 minutes; the orange-spotted sunfish, *Lepomis humilis*, in 5 hours 40 minutes; the green sunfish, *Lepomis cyanellus*, in 6 hours; 11,314 p. p. m. under same conditions killed the black bullhead, *Ameiurus melas*, in 9 hours 55 minutes.

Chloramine, NH_2Cl

Water purification systems either as chloramine or formed from small quantities of ammonia and chlorine in the water. Coventry, Shelford, and Miller (1935), 0.3–0.4 p. p. m. in tap water killed trout fry at once, and 0.06 p. p. m., trout fry in 48 hours; 0.4 p. p. m. killed sunfish and bull-heads; 0.76 p. p. m., hardy minnows; and 1.2 p. p. m., large carp and bullheads.

Chloramine-T, $CH_3 \cdot C_6H_4SO_2NNaCl$

Water purification systems. Adams (1927), 5 p. p. m. in Nile River water killed cladocerans, *Daphnia sp.*, and copepods, *Cyclops sp.*

Chlorine, Cl_2

Water purification systems; various chemical wastes. Adams (1927), 2 p. p. m. in Nile River water killed cladocerans, *Daphnia sp.*, and copepods, *Cyclops sp.;* Davis (1934), 1 p. p. m. killed coarse fish; M. M. E., 1 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 96 hours; and 0.5 p. p. m. in soft water killed cladocerans, *Daphnia magna*, in 72 hours or more.

Chloride of lime, or bleaching powder

This substance is of uncertain composition as usually found. Its lethal properties as regards aquatic life are largely dependent upon the amount of chlorine which is liberated when the bleaching powder is added to the water. The potential amount of chlorine available in the sample under question must be known before its toxicity can be estimated. Much confusion exists in the previous reports because of that fact and consequently no limits are given here.

Chromic acid, H_2CrO_4

Chrome tannery wastes. M. M. E., 100 p. p. m. in hard water did not kill goldfish, *Carassius auratus*, in 100 hours' exposure; the same amount in very soft water killed goldfish in 30–35 minutes.

Citric acid, $(COOH)CH_2C(OH)(COOH)CH_2COOH$

Wastes from industries using citrus fruits. M. M. E., 894 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 4–28 hours; 625 p. p. m. in hard water was not lethal to goldfish in 100 hours exposure; 120 p. p. m. in soft water killed cladocerans, *Daphnia magna*, in 24–72 hours.

Cobaltous chloride, $CoCl_2$

Pigment works; chemical industries. M. M. E., 1,000 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 30–32 hours; 10 p. p. m. in soft water fatal to some goldfish in 168 hours; others survived exposure to this amount for longer periods.

Copper, Cu_2

See various cupric compounds. As Moore and Kellerman (1905) have pointed out and as is discussed here under the action of heavy metals, the amount of copper required to produce lethal results varies greatly with the water, and particularly the carbonates. These writers state that "in water containing carbonates, if the amount of dissolved CO_2 is very low the basic carbonate of copper formed may be considered insoluble; if, however, the water should contain a fair amount of CO_2 it would bring the copper carbonate at least partially into solution." Copper compounds are used as algicides and occur in many industrial wastes.

Cresol, general formula $C_6H_4(OH)(CH_3)$

A mixture of the various isomeric compounds of this group. The mixture and the individual compounds occur in gas wastes in varying proportions and the mixture is used in various sheep dips and other preparations for the disinfecting of livestock. Both gas wastes and dipping vats have on occasion been the sources of stream pollution by this substance. This mixture and two of the component isomers are discussed below.

Cresol

Adams (1927), 10 p. p. m. in Nile River water killed cladocerans, *Daphnia sp.*, and copepods, *Cyclops sp.;* Demyanenko (1931), 17–20 p. p. m. lethal for fishes.

Orthocresol

Shelford (1917), 55–65 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; M. M. E., 10–20 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 3–5 days.

Paracresol

Shelford (1917), 80–90 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Southgate, Pentelow, and Bassindale (1933), 6.2 p. p. m. in tap water caused trout, *Salmo irideus*, to float helpless on their backs in 1 hour 40 minutes, if the water carried *circa* 10 p. p. m. of dissolved oxygen and in 13 minutes if the water carried only 3 p. p. m. dissolved oxygen.

Cresylic acid, a mixture of isomeric cresols and xylenols

Mine floatation wastes; sheep and cattle dips. M. M. E., 0.1 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 5 days and 1 p. p. m. in 6–48 hours; 0.1 p. p. m. in soft water killed cladocerans *Daphnia magna*, in 72 hours.

Cupric chloride, $CuCl_2$

Powers (1917), 0.0188 p. p. m. in distilled water killed goldfish in 3 hours 30 minutes to 7 hours; Carpenter (1927), 672 p. p. m. in distilled water killed the minnow, *Leuciscus phoxinus*, in 82 minutes.

Cupric nitrate, $Cu(NO_3)_2$

Dilling and Healey (1926), 0.0188 p. p. m. in tap water killed many tadpoles and interfered with the development of those which survived.

Cupric sulphate, $CuSO_4$. Blue vitriol

Because of the wide use of this compound in both industry and in aquatic investigations, and because of the variation in limits of lethality copper sulphate as given by many writers, owing to differences in water, in carbonate content, and in associated substances, a larger number of references have been included for copper sulphate than for most compounds in this list. Penny and Adams (1863), 10 p. p. m. fatal to goldfish and minnows, but 5 p. p. m. under the conditions of their tests were not lethal to these fishes; Moore and Kellerman (1905), 0.143 p. p. m. in hatchery water (Cold Spring Harbor, N. Y.), maximum strength tolerated by brook trout, and 0.33 p. p. m. maximum for carp and suckers, 0.4 p. p. m. for catfish, 0.5 p. p. m. for goldfish, 1.33 p. p. m. for sunfish, 2 p. p. m. for black bass; Carpenter (1927), 399 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in 62 minutes; Catt (1934), 0.5 p. p. m. in lake water not lethal to white perch and yellow perch in 15 hours, but 1 p. p. m. in lake water killed white and yellow perch in 1 to 10 hours; M. M. E., 2 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 24–96 hours; catfish, *Ameiurus nebulosus*, in 96–200 hours; 1 p. p. m., some goldfish in 72 hours; 1.25 p. p. m., the amphipods, *Gammarus fasciatus* and *Eucrangonyx gracilis*, in 17–20 hours; 10 p. p. m., the isopod, *Mancasellus macrourus*, in 16–48 hours; 1 p. p. m. in distilled water killed cladocerans, *Daphnia magna*, in 15 minutes to 2 hours, and 0.25 p. p. m. in distilled water in 30 minutes to 3 hours.

Ethyl alcohol, C_2H_5OH

Fermented organic wastes, particularly fruit pulps, brewery and distillery wastes. Weigelt, Saare, and Schwab (1885), a 2-hour exposure to 10,000 p. p. m. in tap water survived by tench, *Tinca vulgaris*, without injury; Powers (1917), 250 p. p. m. in distilled water killed goldfish in 6–11 hours.

Ethyl amine, $C_2H_5NH_2$

Gas wastes. Shelford (1917). 400–800 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Ferric chloride, $FeCl_3$

Dye industries; some ore milling operations; various chemical wastes. Powers (1917), 9 p. p. m. in distilled water killed goldfish in 20 hours; Carpenter (1927), 270 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in 90 minutes; M. M. E., 100 p. p. m. in very soft water killed goldfish, *Carassius auratus*, in 1 hour to 1 hour 30 minutes, but same quantity of ferric chloride in hard water was not detrimental to goldfish in a 96-hour exposure.

Ferric potassium sulphate, $FeK(SO_4)_2$. Ferric alum

Dye mordant; calico printing. Weigelt, Saare, and Schwab (1885), 1 minute exposure to 10,000 p. p. m. not fatal to tench.

Ferric sulphate, $Fe_2(SO_4)_3$

Chemical industries; as a coagulant for sewage precipitation. Clark and Adams (1913), 0.716 p. p. m. in distilled water killed shiners, carp, and suckers in 12–24 hours.

Ferrous sulphate, $FeSO_4$. Green vitriol or copperas

Waters from mines containing pyrites; in pickle liquor from industrial plants cleaning iron plate or wire. Weigelt, Saare, and Schwab (1885), 2,721 p. p. m. in tap water killed trout and California salmon in 31–66 minutes; Clark and Adams (1913), 2.9 p. p. m. in distilled water killed shiners, carp, and suckers in 4–24 hours; Carpenter (1927), 315 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in about 3 hours; M. M. E., 1,000 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 2–10 hours, 100 p. p. m. in hard water apparently not harmful to goldfish in a 96-hour exposure.

Gallic acid, $C_6H_2(COOH)(OH)_3$

Dye wastes; tannery wastes; some chemical wastes. Penny and Adams (1863), 143 p. p. m. killed goldfish and minnows.

Glycerol, $(CH_2OH)_2CHOH$. Glycerine

Soap factories. Weigelt, Saare, and Schwab (1885), tench survived 16-hour exposure at 8° C. to 100,000 p. p. m. in tap water without apparent effect.

Hydrochloric acid, HCl. Muriatic acid

In effluents from many chemical processes. Weigelt, Saare, and Schwab (1885), 1,000 p. p. m. in tap water caused trout to overturn helpless in 2–5 minutes; Wells (1915a), 3.6 p. p. m. in distilled water killed green sunfish, *Lepomis cyanellus*, in 48 hours. Standing Committee on Rivers Pollution (1924), 200 p. p. m. in distilled water produced general collapse in perch and roach; M. M. E., 166 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 4–7 hours; 157 p. p. m. in hard water apparently did not injure goldfish in over 100 hours' exposure; 56 p. p. m. in soft water killed cladocerans, *Daphnia magna*, in 17–72 hours.

Hydrogen sulphide, H_2S

Produced by decomposition of many types of organic effluents, both municipal and industrial, and occurs in many trade wastes, chemical wastes, and gas wastes. This gas which readily dissolves in water is not only harmful in itself but in its decomposition may produce colloidal sulphur, which is also a pollution hazard. Weigelt, Saare, and Schwab (1885), a 3-hour exposure to 100 p. p. m. in tap water was fatal to tench, *Tinca vulgaris*, 8 days later, and 10 p. p. m. in tap water caused trout to float on back in 15 minutes; Shelford (1917), 4.9–5.3 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Belding (1929), 0.086 p. p. m. lethal for brook trout, *Salvelinus fontinalis*, 3.8 p. p. m. for the sucker, *Catostomus commersonii*, 4.3 p. p. m. for aquarium goldfish, *Carassius auratus*, and 6.3 p. p. m. for carp, *Cyprinus carpio;* M. M. E., 10 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 96 hours or less, 5 p. p. m. killed some goldfish in 200 hours, and 1 p. p. m. in soft water killed cladocerans, *Daphnia magna*, in 72 hours or less.

Iodine, I_2

Rarely found free in stream water. Penny and Adams (1863), 28.5 p. p. m. killed minnows and goldfish.

Iron, Fe_2

See various ferric and ferrous compounds.

Lactic acid, $CH_3CH(OH)COOH$

A component of various dairy industries wastes. M. M. E., 654 p. p. m., in hard water killed goldfish, *Carassius auratus*, in 6–43 hours, but 430 p. p. m. in hard water apparently was not harmful to goldfish in exposures of over 100 hours; 170 p. p. m. in soft water killed cladocerans, *Dapghnia magna*, in 26–72 hours.

Lead, Pb_2

Compounds of this metal are found in many industrial wastes and in effluents from various mining and ore milling operations. These compounds are highly toxic as has been discussed under

action of heavy metals on fishes and other aquatic organisms. Two general statements concerning the lethality of lead may be given here. Other references follow under the several salts of lead. Carpenter (1927) believes that as little as 0.33 p. p. m. of lead may be lethal to fresh-water fishes, and Dilling, Healey, and Smith (1926) found that 4 p. p. m. of colloidal lead retarded the growth of young plaice.

Lead acetate, $Pb(C_2H_3O_2)_2$. Sugar of lead

Rushton (1922), 10 p. p. m. in stream water killed yearling trout; Carpenter (1925), 5 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in 4–16 hours, and 10 p. p. m. in distilled water, if renewed every other day, killed goldfish in 12 days.

Lead nitrate, $Pb(NO_3)_2$

Rushton (1922), 10 p. p. m. in stream water killed trout in 2 hours 15 minutes; Carpenter (1925), 250 p. p. m. in distilled water killed goldfish in 4–5 days and minnows, *Leucisus phoxinus*, in 2–3 hours; Dilling and Healey (1926), 1.6 p. p. m. retards growth of tadpoles and 3.3 p. p. m. lethal for tadpoles in tap water; Carpenter (1930), 165 p. p. m. in distilled water, if given sufficient exposure will kill steel-colored minnow, *Notropis whipplii;* common shiner, *Notropis cornutus;* blunt-nosed minnow, *Hyborhynchus notatus;* silver-mouthed minnow, *Ericymba buccata;* sucker-mouthed minnow, *Phenacobius mirabilis;* creek chub, *Semotilus atromaculatus;* stoneroller, *Campostoma anomalum;* common sucker, *Catostomus commersonii;* chub sucker, *Eriomyzon sucetta;* Johnny darter, *Boleosoma nigrum;* fan-tailed darter, *Etheostoma flabellare;* log perch, *Percina caprodes;* and bluegill, *Lepomis pallidus;* M. M. E., 100 p. p. m. in hard water fatal to goldfish, *Carassius auratus*, in 80 hours; 10 p. p. m. in hard water, without apparent injury to goldfish, in 96 hours' exposure.

Lead sulphate, $PbSO_4$

Carpenter (1925), 25 p. p. m. in distilled water killed goldfish, *Carassius auratus*, in 4 days, and minnows, *Leuciscus phoxinus*, in 2–3 hours.

Lithium chloride, LiCl

Found in some mineral springs. Powers (1917), 3,750 p. p. m. in distilled water killed goldfish in 22–27 hours.

Magnesium chloride, $MgCl_2$

A component of various waste waters from oil wells, and some industrial wastes. Garrey (1916), 476 p. p. m. in distilled water killed straw-colored minnow, *Notropis blennius*, in 4–6 days; Powers (1917), 6,757 p. p. m. in distilled water killed goldfish in from 78 hours to 21 days; Wiebe, Burr, and Faubion (1934), 5,000 p. p. m. in distilled water killed golden shiner, *Notemigonus crysoleucas*, in 96 hours.

Magnesium nitrate, $Mg(NO_3)_2$

Powers (1917), 12,500 p. p. m. killed goldfish in 14–16 hours.

Mercuric chloride, $HgCl_2$. Corrosive sublimate

Weigelt, Saare, and Schwab (1885), 500 p. p. m. in tap water killed large trout in 54 minutes; Carpenter (1927), 13.6 p. p. m. in distilled water killed minnow, *Leuciscus phoxinus*, in 42 minutes.

Methyl alcohol, CH_3OH

A solvent in many industrial operations. Weigelt, Saare, and Schwab (1885), a 2-hour exposure to 10,000 p. p. m. in tap water was tolerated by trout without apparent injury; Powers (1917), 250 p. p. m. in distilled water killed goldfish in 11–15 hours.

Methyl mercaptan, CH_3SH

A highly toxic constituent of sulphite paper pulp waste. Cole (1935a), 1 p. p. m. in lake water killed white bass, *Roccus chrysops*, in 1 hour, 45 minutes, or less; yellow perch (*Perca flavescens*), largemouth black bass (*Micropterus salmoides*), smallmouth black bass (*Micropterus dolomieu*), and bluegill (*Lepomis pallidus*), in 6–8 hours; and rock bass (*Ambloplites rupestris*), in 11 hours.

Muriatic acid

See hydrochloric acid.

Naphthenic acids and naphthene derivatives

These compounds are listed among the solutes which may occur in refinery wastes (American Petroleum Institute, 1935), and Kupzis (1902) believes the naphthenic compounds to be among the most toxic substances to fish, passing from crude oil into water. Kupzis (l. c.), using fractions containing the naphthenic acids extracted from various crude oils, gives the following lethality findings for this naphthenic acid fraction (which of course must not be considered as representing a single pure compound in this case). In tap water (hard) 3 p. p. m. killed percoid fishes, *Acerina cernua*, in 6–12 hours; 5 p. p. m. killed pickerel, *Esox lucius*, 36–48 hours; the minnow, *Abramis brama*, 72 hours; the red-eyed minnow, *Scardinius erythrophthalmus*, 26 hours; and the perch, *Perca fluviatilis*, in 16–23 hours; 20 p. p. m. killed carp, *Cyprinus carpio*, in 26–36 hours, and goldfish, *Carassius auratus*, in 8–16 hours. Several other European species tested are not listed here.

Naphthalene, $C_{10}H_8$

Aniline and coal-tar industries. Demyanenko (1931), 10 p. p. m. lethal to fish.

Nickelous chloride, $NiCl_2$

Electroplating wastes; various industrial wastes. Thomas (1924), 8.1 p. p. m. in tap water killed the top-minnow, *Fundulus heteroclitus*, in a few hours. This species, which can also live in salt water, tolerated 259.2 p. p. m. when in salt water without apparent injury during a 2-week exposure. M. M. E., 100 p. p. m. in very soft water killed goldfish, *Carassius auratus*, in 19–50 hours, and 10 p. p. m. in very soft water killed in 200–210 hours.

Nitric acid, HNO_3

Occurs in many wastes from chemical industries. It is easily broken into water and oxides of nitrogen. Weigelt, Saare, and Schwab (1885), trout after 34 minutes in 1,000 p. p. m. in tap water were helpless; Carpenter (1927), sufficient quantities to bring the water to pH 4.4 killed the minnow, *Leuciscus phoxinus*, in 7 hours, while quantity sufficient to bring the water to pH 5.2 was without apparent effect on this species of fish; M. M. E., 750 p. p. m. in hard water (see section on acids) killed goldfish, *Carassius auratus*, in 30 minutes to 1 hour, and 200 p. p. m. in hard water were without apparent effect on goldfish in exposures of over 100 hours.

Octyl alcohols, general formula $C_8H_{17}OH$

Macht and Leach (1930), 66.7 p. p. m. of primary octynol produce respiratory and neuromuscular paralysis in goldfish, *Carassius auratus*, in 15 minutes. The specific toxicity for fish of the individual octyl alcohols varied in the series of 23 which these observers studied, secondary octylic heptanol being among the least toxic, 200 p. p. m. producing paralysis in goldfish in 4 hours.

Oxalic acid, $H_2C_2O_4$

Bleaching, dying, and various chemical industries. M. M. E., 1,000 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 25–30 minutes; 200 p. p. m. in hard water produced no apparent injury during exposures of 100 hours. This acid is readily precipitated out of waters by calcium salts.

Oxygen, O_2, and **Ozone,** O_3

Although the usual problem in stream pollution is to secure enough oxygen, some of the proposed treatments for organic wastes involve high oxygenation or ozonation. It seems worth while therefore to list here some tests on the effects of high oxygen and nascent oxygen. Wiebe (1933) found changes from 5.7 p. p. m. to 40.3 p. p. m. dissolved oxygen were tolerated by largemouth black bass, *Micropterus salmoides*, smallmouth black bass, *Micropterus dolomieu*, white crappie, *Pomoxis sparoides*, bluegill, *Lepomis incisor*, orange-spotted sunfish, *Lepomis humilis*, golden shiner, *Notemigonus crysoleucas*, and goldfish, *Carassius auratus*, for at least 24 hours. Hubbs (1930) states that minnows may be killed by 0.033 p. p. m. of nascent oxygen in the water and that fishes are irritated by ozone in quantities less than 0.01 p. p. m.

Para-dichlorobenzene, $C_6H_4Cl_2$

Demyanenko (1931), 50 p. p. m. lethal to fishes.

Phenol, C_6H_5OH. Carbolic acid

An important constituent of gas wastes, many chemical effluents, and even some sewage products. Phenol may also come into streams from sheep dips and other establishments where livestock are disinfected. Shelford (1917), 70–75 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Powers (1917), 51 p. p. m. in distilled water killed goldfish in 1 hour 30 minutes to 2 hours 20 minutes; Demyanenko (1931), 16.6–20 p. p. m. lethal to fishes, some can live in 15 p. p. m., but their flesh acquires phenolic smell; Alexander, Southgate, and Bassindale (1935), 0.4–0.6 p. p. m. caused trout to overturn in 8 hours 20 minutes; Adams (1927), 10 p. p. m. in Nile River water killed cladocerans, *Daphina sp.*, and copepods, *Cyclops sp.*; M. M. E., 10 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 72 hours or less, 1 p. p. m. apparently not injurious to goldfish in exposures of 100 hours; 8 p. p. m. in soft water killed cladocerans, *Daphnia magna*.

Potassium bicarbonate, $KHCO_3$

Penny and Adams (1863), 2,000 p. p. m. killed minnows and goldfish.

Potassium chloride, KCl

Garrey (1916), 373 p. p. m. in distilled water killed straw-colored minnows, *Notropis blennius*, in 12–29 hours; Powers (1917), 74.6 p. p. m. in distilled water lethal for goldfish in 4 hours 40 minutes to 15 hours.

Potassium cyanide, KCN

Ore milling operations; chemical works; electroplating; and in effluents from coke ovens. (See Tupholme, 1933.) Powers (1917), 0.78 p. p. m. in distilled water killed goldfish in 43–118 hours; Calatroni (1928), 15 p. p. m. in tap water immobilized tadpoles with fatal results; McArthur and Baillie (1929), 65 p. p. m. killed cladocerans, *Daphnia magna;* Southgate, Pentelow, and Bassindale (1933), 0.27 p. p. m. KCN (equal to 0.11 p. p. m. CN) at temperature of 7°–9° C. caused trout to float helpless on back in about 2 hours if the dissolved oxygen in the water were *circa* 11 p. p. m., but in 10 minutes if the water carried only 3 p. p. m. dissolved oxygen; Alexander, Southgate, and Bassindale (1935) find 0.5 p. p. m. KCN (0.2 p. p. m. CN) will cause trout to overturn and become helpless in 15 minutes; M. M. E., 1 p. p. m. in river water caused glochidia of fresh-water mussels to close, rendering them incapable of attachment on fishes, and 0.1 -0.3 p. p. m., in hard water killed goldfish in 3–4 days.

Potassium dichromate, $K_2Cr_2O_7$

Ore floatation processes; chemical industries. M. M. E., 100 p. p. m. in hard water apparently not harmful to goldfish in exposures of 108 hours, 500 p. p. m. lethal to goldfish in 3 days.

Potassium ferricyanide, $K_3Fe(CN)_6$. Red prussiate of potash

Penny and Adams (1863), 2,000 p. p. m. not lethal to minnows and goldfish.

Potassium ferrocyanide, $K_4Fe(CN)_6$. Yellow prussiate of potash

Penny and Adams (1863), 2,000 p. p. m. not lethal to minnows and goldfish; Weigelt, Saare, and Schwab (1885), trout survived 1 hour exposure to 8,723 p. p. m. in tap water without symptoms.

Potassium hydroxide, KOH. Caustic potash

Soap works; from some types of ashes. Wells (1915), 56 p. p. m. in distilled water killed bluegills, *Lepomis pallidus*, in 4 hours 25 minutes, 28 p. p. m. apparently not harmful to bluegills in 10-day exposures.

Potassium nitrate, KNO_3. Saltpeter

Wells (1915b), 1,203 p. p. m. in tap water killed bluegills, *Lepomis pallidus*, in 15 days.

Potassium permanganate, $KMnO_4$

This powerful oxidizing agent is frequently used to disinfect hatchery tanks and can be applied with caution to fish themselves. Adams (1927), 5 p. p. m. in Nile River water killed cladocerans, *Daphnia sp.*, and copepods, *Cyclops sp.;* M. M. E., 10 p. p. m. in hard water killed goldfish, *Carassius auratus*, in 12–18 hours.

Potassium sulphate, K_2SO_4

Wells (1915b), 869 p. p. m. in tap water killed bluegills, *Lepomis pallidus*, in 4 days.

Potassium xanthate or potassium ethyldithiocarbonate $C_2H_5 \cdot O \cdot CS \cdot SK$

Used in ore floatation processes and on occasion to free soil from insect pests, and it is highly toxic to fishes. M. M. E., 10 p. p. m. in hard water killed goldfish in 48–96 hours, 0.1 p. p. m. in 4–5 days.

Pyrethrum

The volatile oil in this plant product is quite toxic to fishes. Bandt (1933) 5–10 p. p. m. toxic for carp.

Pyridine, C_5H_5N

In gas wastes, also in waters draining recently burned-over areas where combustion near ground has been incomplete. Shelford (1917), 1,477–1,576 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour; Powers (1917), 1,869 p. p. m. in distilled water killed goldfish in 10–30 hours; Demyanenko (1931) states 1,000 p. p. m. to have a feeble effect on fishes.

Quinoline, $C_6H_4N:CHCH:CH$

Gas wastes. Shelford (1917), 52–56 p. p. m. and 65 p. p. m. isoquinoline in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Saponin, a glucoside

Found in various plants. Ebeling (1928) points out that wastes from potato starch factories carry sufficient saponin to be dangerous to fishes, and that consequently these wastes should be highly diluted. M. M. E., 10 p. p. m. of saponin in hard water produced marked distress in goldfish in 5 hours, 100 p. p. m. rapidly fatal, killing goldfish in 7–24 hours.

Sodium arsenite, commercial preparation usually a mixture of several sodium and arsenic compounds

Some dye and tanning processes; removal of aquatic vegetation. Since arsenic trioxide is usually dissolved in sodium hydroxide, and since each lot of commercial sodium arsenite must be assayed for its arsenic content, arsenic, arsenic trioxide, and sodium arsenite are considered under this single heading. Wiebe (1930), 7 p. p. m. of As_2O_3 in Mississippi River water was not detrimental to largemouth black bass, *Micropterus salmoides*, smallmouth black bass, *Micropterus dolomieu*, white crappie, *Pomoxis sparoides*, bluegill, *Lepomis pallidus*, golden shiner, *Notemigonus crysoleucas*, bullhead, *Amieurus nebulosus*, and goldfish, *Carassius auratus*, in 148-hour exposures as shown by 3 months subsequent observation. Surber and Meehan (1931), 2 p. p. m. As_2O_3 in Mississippi River water survived by the important fish food organisms, but 2.5–4 p. p. m. killed chironomid larvae, mayfly nymphs, the fresh-water shrimp, *Hyalella*, and odonata nymphs; the isopod *Asellus* sp., survived 10–21 p. p. m.; M. M. E., 1.3 p. p. m. As_2O_3 in distilled water killed *Daphna magna*, 8 p. p. m. hard water had no appreciable effect on the fresh-water mussel, *Amblema peruviana*, but 16 p. p. m. in hard water was fatal to *Amblema peruviana* in 3–16 days.

Sodium carbonate, Na_2CO_3

Found in many chemical effluents. Clark and Adams (1913), 250–300 p. p. m. killed shiners, carp, and large suckers in tap water in a few hours; Wells (1915b), 530 p. p. m. in tap water killed bluegills, *Lepomis pallidus*, in 3 days.

Sodium chlorate, $NaClO_3$

In some effluents from chlorine and bromine works. Not markedly toxic. M. M. E., 1,000 p. p. m. in hard water produced no apparent injuries in goldfish during exposures of 5 days duration.

Sodium chloride, NaCl. Common salt

Brine works; waste waters from oil wells; effluents from some dairy industries. Garrey (1916), 2,500 p. p. m. in distilled water killed straw-colored minnow, *Notropis blennius*, in 9–24 days (solution, $\Delta=0.105$); Powers (1917), 11,765 p. p. m. in distilled water killed goldfish in 17 hours; Wiebe, Burr, and Faubion (1934), 5,000 p. p. m. in distilled water killed golden shiners, *Notemigonus crysoleucas*, in 148 hours and largemouth black bass in 200–250 hours; M. M. E., 1 p. p. m. distilled water killed cladoceran, *Daphnia magna*, in 3 hours, 5,000 p. p. m. in Mississippi River water apparently not harmful to goldfish in 25-day exposure, but 10,000 p. p. m. in Mississippi River water killed goldfish in 4–10 days.

Sodium fluoride, NaF

In certain brewery and distillery wastes; also found in some soils. M. M. E., 1,000 p. p. m. in hard water killed goldfish in 60–102 hours.

Sodium hydroxide, NaOH. Caustic soda

Soap factories; wood ashes. Clark and Adams (1913), 96 p. p. m. in tap water killed shiners, carp, and suckers in 2–10 minutes; Standing Committee on River Pollution (1924), 50 p. p. m. in distilled water was not fatal to perch and roach in a 2-hour exposure.

Sodium nitrate, $NaNO_3$. Chili saltpeter

Fertilizers. Powers (1917), 1,282 p. p. m. in distilled water killed goldfish in 14 hours; M. M. E., 4,000 p. p. m. in hard water killed goldfish in 80 hours but 3,000 p. p. m. apparently did not injure goldfish in 100-hour exposures.

Sodium selenite, Na_2SeO_3

Component of certain soils; pottery works. M. M. E., 100 p. p. m. in hard water killed goldfish in 8–20 hours, 10 p. p. m. in hard water killed in 98–144 hours.

Sodium sulphate, Na_2SO_4. Glaubers salt

Harukawa (1922), 500 p. p. m. in tap water not injurious to goldfish in 24 hours.

Sodium sulphide Na_2S

In some beet-sugar factory effluents and in some paper-pulp wastes. Weigelt, Saare, and Schwab (1885), a 1-hour exposure to 1,150 p. p. m. in tap water kill tench, *Tinca vulgaris*, 6 days later.

Sodium sulphite, Na_2SO_3

Component of various paper pulp wastes and some beet sugar factory wastes. M. M. E., 100 p. p. m. in hard water killed goldfish in 96 hours.

Stannous chloride, $SnCl_2$

M. M. E., 1,000 p. p. m. in hard water killed goldfish in 4–5 hours.

Strontium chloride, $SrCl_2$

Powers (1917), 15,384 p. p. m. in distilled water killed goldfish in 17–31 hours.

Strontium nitrate, $Sr(NO_3)_2$

Powers (1917), 9,615 p. p. m. in distilled water killed goldfish in 32–146 hours.

Sugar, cane, $C_{12}H_{22}O_{11}$. Sucrose

Garrey (1916), 34–218 p. p. m. in distilled water ($\Delta=0.198$) killed straw-colored minnow, *Notropis blennius*, in 24–48 hours.

Sulphur, colloidal, S_2

Lime-sulphur mixtures and dips; following decomposition of hydrogen sulphide in water. Harukawa (1922), 1,600 p. p. m. in tap water fatal to goldfish in 3 hours 30 minutes to 5 hours 15 minutes, and 2,100 p. p. m. in 48–71 minutes.

Sulphur dioxide, SO_2

Bleaching works; various chemical industries. Weigelt, Sarre, and Schwab (1885), 10 p. p. m. in tap water caused trout to float helpless in 10 minutes; Shelford (1917), 16–19 p. p.m. in tapwater killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Sulphuric acid, H_2SO_4. Oil of vitriol

Pickle liquor from sheet metal and wire factories; waters from coal and iron mines; various chemical wastes. Wells (1915), 7.36 p. p. m., in distilled water killed bluegills, *Lepomis pallidus*, in 60 hours, but 3.68 p. p. m. apparently harmless over period of 1 month. M. M. E., 59 p. p. m. in very soft water killed goldfish, *Carassius auratus*, in 1 hour to 1 hour 15 minutes, 138 p. p. m. in hard water in 4 hours, 100 p. p. m. in hard water apparently not injurious to goldfish in 100-hour exposures; 29 p. p. m. in soft water killed cladocerans, *Daphnia magna*, in 24–72 hours.

Tannic acid, $C_{14}H_{10}O_9$

Tannery wastes; leachings from some barks and sawmill wastes. M. M. E., 100 p. p. m. in hard water killed goldfish in 9–20 hours, but 10 p. p. m. apparently not injurious in 100-hour exposures.

Tartaric acid, $COOH(CHOH)_2COOH$

Dye wastes; mordant liquors; leather works; various chemical effluents; some winery wastes. M. M. E., 1,000 p. p. m. in hard water killed goldfish in 3–4 hours, 200 p. p. m. in hard water not injurious apparently in exposures of 100 hours, 100 p. p. m. in very soft water killed goldfish in 3 hours to 3 hours 30 minutes.

Thiophene, C_4H_4S

Gas wastes. Shelford (1917), 27 p. p. m. in tap water killed orange-spotted sunfish, *Lepomis humilis*, in 1 hour.

Tin, Sn_2

See stannous chloride.

Trade wastes

At end of this section.

Zinc nitrate, $Zn(NO_3)_2$

Dilling and Healey (1926) found that tadpoles survived 3-month exposure to 1.89 p. p. m. but failed to develop limb buds, that 5.7 p. p. m. killed most tadpoles and that 94.7 p. p. m. killed tadpoles quickly.

Zinc sulphate, $ZnSO_4$. White vitriol

Wastes from electrolytic refineries of zinc; incrustations developing from exposed zinc sulphide ores; mine tailings; several chemical effluents. Carpenter (1927), 404 p. p. m. in distilled water killed minnows, *Leuciscus phoxinus*, in 3 hours 20 minutes; M. M. E., 1,000 p. p. m. in hard water killed goldfish in 1–4 hours, 100 p. p. m. fatal to many goldfish in 5 days.

Trade wastes

Lethal limits which will be inclusive cannot be defined for sewage and trade wastes because sewage and even such specific effluents as Steffens house waste (from certain types of beet-sugar refineries) are not constant either in composition or concentration. The effects of colloidal sulphur or ferric chloride on fishes and other aquatic animals can be determined under a variety of conditions which can be duplicated, or the toxicity of any particular sample of Steffens waste, or pickle liquor from tin-plate mills, or deazoting fluid from dye works can also be ascertained with accuracy, but to attempt to define the minimal lethal concentration or the maximal dilution for all pickle liquors from samples obtained at any plant or series of plants is both unsound scientifically and unfair to the industry. Already much confusion, often to the detriment of fisheries interests, has resulted from the misuse in this connection of various statements in the literature concerning the tolerance of fishes for a given number of p. p. m. of a particular waste, when these observations were intended to apply to a specific case.

In practical tests the writer has found that wastes taken directly from their sources in the plant, i. e., not from sewers or flumes, differ widely in toxicity to aquatic life, at different plants using the same general process. Several factors contributed to these differences. For example, the process of tanning hides with chromium compounds is basically the same in all establishments using this process, but as is well known the plant chemists in the interests of economy and efficiency frequently make minor or at times even drastic changes in the process, with, of course, resultant changes in the effluents. Variations in raw material, emergencies in plant operation, and many other conditions also call for changes in procedure which result in changes in effluent composition and concentration. There is, therefore, no standard hide vat liquor waste or pickle liquor or winery effluent, even when taken at the source, which may be used with either fairness or accuracy in the estimation of the probable hazards of another plant engaged in the same work.

Besides, as the waste moves away from its source through conduits and flumes, these differences become greater owing to the addition of cooling water, wash waters, and other effluents from different parts of the plant; so that the final mixture as poured into the stream varies not only in concentration, but also in composition as the result of the sequence in which the different effluents were mixed.

However, from the studies of various wastes before mixing, the general changes which these effluents will produce in the stream complex and the types of their actions on aquatic life can be ascertained with considerable accuracy. In table 14 the usual effects of 29 common industrial wastes and of municipal sewage on the aquatic environment and the critical features of these actions as shown by a large series of field studies have been pointed out.

TABLE 14.—*Usual fisheries hazards of 30 common types of municipal and industrial effluents* [1]

Types of wastes	Changes in water affecting fishes						Bottom pollution blanket	Specific toxic action on fishes
	Decrease in dissolved oxygen	Hydrogen-ion concentration: Increase in acidity	Hydrogen-ion concentration: Increase in alkalinity	Increase in specific conductance	Increase in turbidity	Increase in ammonia		
MINERAL WASTES, LITTLE BACTERIAL ACTION								
1. Erosion silt	None	None	None	None	Critical	None	Critical	None.
2. Limestone sawmills	do	do	Possible	Moderate	do	do	do	Do.
3. Asbestos works	do	do	do	do	do	do	do	Possible.
4. Mine flotation	Possible	Possible	do	do	do	do	do	Possible to critical.
5. Coal- and iron-mine drains	do	Critical	None	do	None	do	Possible	Possible.
6. Crude oil	do	None	do	None	do	do	Possible to critical	Possible to critical.
7. Salt water from oil wells	None	do	Possible	Critical	do	do	None	Do.
ORGANIC, BACTERIAL ACTION								
8. Municipal sewage	Critical	Possible	do	Possible	Possible	Critical	Possible to critical	Do.
9. Dairy industries	do	Critical	None	Moderate	Moderate	Moderate	do	Possible.
10. Packing plants	do	Moderate	do	do	do	Critical	Critical	Do.
11. Canning factories	do	Critical	Possible	do	do	do	Possible to critical	Do.
12. Breweries and distilleries	do	None to moderate	None to moderate	do	Possible	Possible	do	Do.
13. Beet sugar, pulp wastes	do	Critical	None	do	do	do	do	Possible to critcial.
14. Paper pulp	Possible to critical.	Possible	Possible	Possible	do	do	Critical	Possible.
15. Sawdust	do	do	do	do	do	do	do	Do.
CHEMICAL PROCESSES								
16. Coal-gas wastes	Possible	do	do	Moderate	None	Critical	do	Critical.
17. Spent lubricants	do	do	None	Possible	do	None	do	Possible to critical.
18. Metal refineries	None	do	Possible	do	Possible	Possible	Possible to critical	Critical.
19. Laundries and wool washings	Moderate	None	Moderate to critical	Moderate	Moderate	Moderate to critical.	Possible	Possible.
20. Steffens house waste	do	do	Critical	Critical	do	None	do	Critical.
21. Sulphite pulp	Moderate to critical.	Possible	Moderate to critical	Moderate	do	Possible	Possible to critical	Do.
22. Strawboard waste	do	None	Critical	do	do	do	do	Do.
23. Chemical works (a)	None	do	do	do	Possible	do	None	Do.
24. Chemical works (b)	Possible	Critical	None	do	None	None	do	Do.
25. Tanneries	Moderate	Possible to critical.	Possible to critical	do	Possible	Possible to critical.	Critical	Do.
26. Dye works	Possible	None to moderate.	None to moderate	do	None	None	Possible	Do.
27. Bittern liquors	None	Critical	None	Critical	do	do	None	Possible to critical.
28. Tin-plate and wire mills	None to possible.	do	do	Moderate	None to possible.	do	Possible to critical	Do.
29. Starch factories	Possible to critical.	do	do	do	Possible	Possible	do	Do.
30. Cloth sizing	do	Possible to critical.	do	Possible	Moderate	do	do	Possible.

[1] In this table increases in both acidity and alkalinity are noted in some cases, due to the facts that two or more kinds of effluents are mixed, with one predominating at times and to changes which take place in the stream after the effluent is added.

From this table the general effects of a given effluent or comparable waste on the aquatic complex can be predicted. By field tests at the site of pollution covering the critical factors as indicated for the particular effluent (dissolved oxygen, pH, conductivity, carbonates, and other determinations for the polluted stream as the case may be), the degree of pollution can be estimated when these field data are compared with the standards given in the section on stream pollutants and aquatic environment. When specific toxic action is indicated (last section, table 14) the limits for the expected detrimental substances can be found in the section on lethal limits.

ACKNOWLEDGMENTS

The writer is particularly indebted to Dr. H. L. Motley, assistant professor of physiology, University of Missouri; to Dr. W. A. Chipman, assistant aquatic biologist, United States Bureau of Fisheries; to Mrs. M. D. Ellis, honorary fellow in physiology, University of Missouri; to Messrs. B. A. Westfall, W. G. Davis, Paul Pierce, R. O. Jones; to Mrs. Helene Pierce Chipman; and to Misses Cornealia G. Ellis, Zella von Gremp, Nelden Bickel, and Mary McConathy, bioassayists and chemists, who through their cooperative efforts as members of the staff of the Columbia, Mo., field unit, United States Bureau of Fisheries, have carried forward during the past 4 years many analyses, assays, and experiments required to give the mass of data for these studies; to the officers and employees of the Corps of Engineers, United States Army, in various river districts, who have aided these investigations in moving U. S. Quarterboat *348*, and in supplying freely river and survey data from their own work; to the many industrial concerns which have cordially opened their plants and given valuable assistance in the collection of trade waste samples; and to the University of Missouri for continued cooperation in the maintenance of the Columbia, Mo., laboratories.

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