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Contribution of the Department of Fisheries,
Québec. — No 49

**A STUDY OF SPRING AND FALL SPAWNING HERRING
(*Clupea harengus* L.) at GRANDE-RIVIÈRE,
BAY OF CHALEUR, QUÉBEC**

by
YVES JEAN

Station de Biologie marine, Grande-Rivière, Qué.
and
École Supérieure des Pêcheries, Sainte-Anne-de-la-Pocatière, Qué.



DEPARTMENT OF FISHERIES
Province of Quebec
QUEBEC
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DEPARTMENT OF FISHERIES

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1956

1. Based upon portions of a thesis accepted by the Faculty¹ of Graduate Studies, University of Toronto, in partial fulfilment for the degree of Doctor of Philosophy.

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- p. 5, par. 5, line 3. Insert "spawn" between "spawners" and "in".
- p. 6, par. 3, line 2. Read "have" instead of "habe".
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- p. 7, par. 5, line 10. Read "Because" instead of "Beaucase".
- p. 10, par. 4, line 7. Read "tows" instead of "towns".
par. 6, line 1. Read "the" instead of "a",
- p. 13. par. 4, line 5. Read "which" instead of "hich".
line 9. Insert hyphen after "February".
- p. 16, par. 1, line 2. Read "conclusion" instead of "conclusions".
- p. 18, par. 1, line 3. Read "30" instead of "39".
par. 2, line 4. Delete coma after "invertebrates".
- p. 19, second heading. Read *Temperatures* instead of "temperatures".
- p. 20, Table I, 1.4. Read "LeGall" instead of "LeCall",
- p. 27, par. 4, line 4. Read "News" instead of "New".
Delete one semi-colon.
- p. 29, par. 1, line 1. Read "of" instead of "to".
- p. 31, par. 2, line 3. Insert coma after "35 mm."
line 5. Read "vertebrae" instead of "vertabrae".
- p. 34, par. 1, line 9. Read "on young" instead of "of young".
- p. 37, par. 5, line 6. Read "1925" instead of "1929".
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- p. 38, par. 2, line 3. Read "spring" instead of "sgring".
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- p. 43, par. 3, line 3. Insert "N" between "point" and "is".
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- p. 45, par. 1, line 9. Read "distributions" instead of "distribution".
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- p. 49, par. 2, line 6. Read "ratio" instead of "ration".
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- p. 53, par. 2, line 2. Insert "year-" after "each".
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- p. 58, par. 3, line 8. Read "step" instead of "stop".
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- p. 59, par. 6, lines 1-2. Read "otoliths" instead of "otoloths".
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- p. 72, 6th ref. Read "LeGall" instead of "LeGal".
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- p. 73, 3d ref. Read "Beobatchungen" instead of "Beobatchengen".
10th ref. Read "Perlmutter" instead of "Perlmetter".
- p. 75, 12th ref. Read "Clupea harengus" instead of "Cluprs arengus".

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INTRODUCTION

Studies of the populations of several species of marine fishes have shown that the whole population is made up of more or less discrete units or "races". These correspond in a number of respects to the geographical races of many wide-ranging species on land (Dice, 1940, Mayr, 1942). Geographical races of land animals differ in such morphological characters as size, body proportions, pattern of coloration, or such physiological characters as temperature tolerance, egg production, longevity, etc.

In the case of fishes, several characters are also found to vary from one local population to another: number of vertebrae, of fin-rays, of scale rows, position and length of fins, body proportions, rate of growth, etc.

As in the case of terrestrial animals, the individuals of local populations of marine fishes can interbreed with individuals of neighbouring populations, especially near the borders of their range where a certain amount of admixture is known to occur. But local populations as a whole retain sufficient divergent characters to enable them to be separated on morphological grounds if large enough samples are taken.

*In the case of some fishes, including the Atlantic herring (*Clupea harengus* L.), seasonal as well as local separation of populations occurs (Schnakenbeck, 1931), different populations spawning at different times of the year. In some areas, Bay of Chaleur in the Gulf of St. Lawrence for instance, one group of herring spawn in the spring (May-June) and another spawn in the fall (August-September).*

Some investigators have reached the conclusion that spring and fall spawning populations of herring are separate and distinct and that the progeny of spring spawners in the spring and the one of fall spawners spawn in the fall (Johansen, 1924; Wood, 1937; Andersson, 1947; Ciegiewicz and Posadzki, 1947; Einarsson, 1951, 1952). However, a different view is held by Broch (1908), Storrow (1920), Hodgson (1925, 1929, 1934), Davis (1936) among others, who think that herring do not necessarily spawn at the same period as the one at which they themselves had been hatched.

Geographical races of terrestrial animals have been regarded as "potentially incipient species" (Mayr, 1942) if given sufficient isolation, whether geographical, ecological or reproductive. In the case of neighbouring populations of marine fishes, probably enough admixture takes place to prevent origin of separate species. In the case of seasonally distinct populations, if season of spawning is fixed so that spring hatched herring spawn only in the spring and fall hatched herring spawn only in the fall, reproductive isolation may be sufficient to lead to origin of distinct species. In fact, if reproductive isolation is complete, that is, if spring and fall spawners invariably lay their eggs at the same season as the one at which they have hatched, these two populations may have reached specific level.

It is important therefore to determine the degree to which spring and fall spawning populations of herring are thus seasonally isolated. The herring of Bay of Chaleur provided opportunity for investigating this fundamental biological problem.

In order to find out whether or not herring of Bay of Chaleur spawn at the same season as the one at which they have been hatched, the season of hatching of adult spawning fish has been determined by studying morphological structure such as scales and vertebrae which are known to be modified by water temperature during development and early life. Herring hatched in the spring develop and grow under different conditions from those to which fall hatched herring are exposed. In the spring water temperature is low but increasing. As season advances food becomes more abundant. In the fall water temperature has just passed its summer high and is decreasing. Food is also less abundant. As spring and fall larvae are exposed to different conditions of water temperature and food abundance, their early growth is likely to differ. It was discovered by Dahl in 1907 that growth of herring could be estimated from the scales. Lea (1929a, 1926b) used Norwegian herring scales as a "certificate of origin". Accordingly the scale pattern of herring hatched in the spring may differ from that of herring hatched in the fall. Vertebral number, like other meristic characters, is modified to some extent by water temperature during development (Schmidt, 1919a, 1919b; Mottley, 1934; Gabriel, 1944; Heuts, 1947; Dannevig, 1950 (quoted by Tåning, 1952), Tåning, 1952; Lindsey, 1954). With few exceptions these authors found in the laboratory an inverse correlation

between temperature during development and vertebral number, low temperature producing high vertebral number. In nature, Hubbs (1926, 1934, 1940) and Lindsey (1953) observed that fish from cold waters had in general more vertebrae than fish of the same species from warm waters. Tester (1938) found that the mean vertebral number of ten successive year-classes of the Pacific herring (Clupea palasii) varied inversely with the temperature of the water during spawning and early development.

Scales and vertebrae of adult herring can therefore be used to determine their season of origin. If season of origin of spring and fall spawners is known, it should be possible to tell whether or not herring spawn at the same season as the one at which they were hatched and accordingly to determine whether or not these two populations are distinct.

ACKNOWLEDGMENTS

The author wishes to acknowledge the assistance of Dr. J. R. Dymond, Head of the Department of Zoology of the University of Toronto and of Dr. A. Marcotte, Director, Station de Biologie marine, Department of Fisheries, at Grande-Rivière, Qué., who read the manuscript and made helpful suggestions.

MATERIAL AND METHODS

Herring populations studied were those spawning near Grande-Rivière, Bay of Chaleur, Québec. (Fig. 1).

Samples were collected at irregular intervals in 1952 and almost daily during the fishing seasons of 1953 and 1954. A total of 7,817 herring were examined. All samples but one, taken with a beach seine, were caught by means of gill-nets anchored about one-half mile from the shore near Grande-Rivière, where ripe herring occur. The depth of the water in this area is 20 m. The fact that running herring were captured in the nets indicated that herring were spawning in the area where the nets were set. The mesh of gill-nets used in 1952 ranged in size from 1½ in. to 2 3/8 in. Because of the selective action of mesh of different

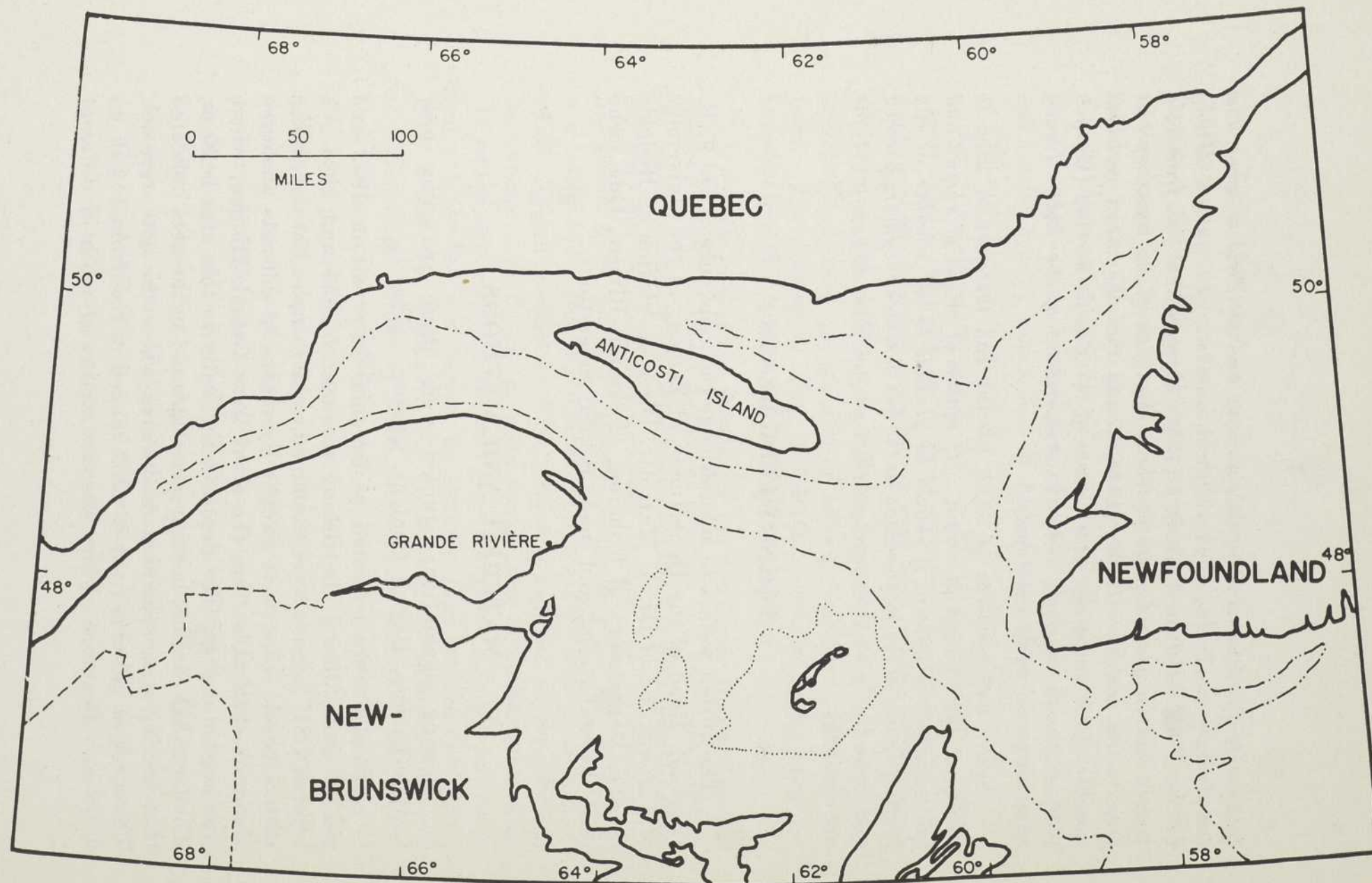


FIGURE 1.— Map of the Gulf of St. Lawrence showing location of Grande-Rivière where sampling of herring was done in 1952, 1953 and 1954.

sizes on the size of the fish, it was decided in 1953 and 1954 to use a mesh of 2 1/8 in. throughout the fishing seasons. When herring were scarce, especially in mid-summer, a second net of either smaller or larger mesh was sometimes added to the 2 1/8 in. one in 1953 and 1954.

All fish were measured on a board similar to the one described by Rounsefell (1939). Total length was measured from tip of snout to tip of lower lobe of the caudal fin in natural position and length of head from the tip of snout to the posterior margin of operculum¹.

A few scales taken from the side of the fish, opposite the tip of the pectoral fin, were mounted on microscope slides for age determination. An ordinary microfilm reader with a magnification of 14 x was used for reading the scales. The image of the scale was projected on the back of the data card and the positions of the centre of the scale and of the winter rings were marked with a pencil. A permanent record not only of age but of the position of the winter rings is thus available.

Sex and degree of maturity were noted according to Heincke's (1898) scale which distinguishes eight stages of maturity from immature (I) to recovering spent (VIII). Heincke's scale or very similar ones (Johansen, 1919; Aasen, 1952) have been used by most authors. In this investigation, however, stages II, III and IV have been fused into one and only six stages of maturity are defined as follows:

- | | |
|------------------|--|
| I — Immature. | Gonads small and transparent; both ovaries and testes alike externally. |
| II — Ripening. | Gonads fill about half of body cavity. |
| III — Ripe. | Gonads completely fill body cavity; ovaries yellowish in colour with round eggs; testes white. |
| IV — Spawning. | Slight pressure of abdomen causes extrusion of eggs and milt. |
| V — Spent. | Gonads empty and blood-red. |
| VI — Recovering. | Gonads firmer, wine-coloured. |

1. All data collected during the present investigation are kept in files at Station de Biologie marine, Grande-Rivière, Qué.

The vertebrae of all herring were counted after removal of the flesh by boiling ten minutes. The urostyle or last modified vertebra, excluded by some authors, was included in the vertebral counts made during the present investigation.

Collection and measurements of herring larvae were made from May to mid-July in 1952 and from May to mid-September in 1953 and 1954. For the collection of larvae plankton tows were made almost daily about three-quarters of a mile offshore from Grande-Rivière where the water is from 25 to 30 m. deep.

A cone-shaped net with an opening one meter in diameter was used. Curtain marquisette of rectangular mesh (35 and 24 mesh per in.) was used in 1952 and 1953. This material was replaced in 1954 by bolting silk no. 26 (25 mesh per in.). All tows, lasting 20 min. were made with the same boat at a speed of two or three knots per hr. Except when otherwise indicated, the tows were made between 9 and 10 o'clock in the morning. One tow was made at the surface and a second tow at 6 m. in 1952 and 20 m. in 1953 and 1954. The tows, having been made at the same time of day, are comparable in that respect. Two factors, however, are likely to affect catches of herring larvae — depth of sampling and cloudiness of the sky.

Statistical analysis, however, did not reveal any significant differences in the number of larvae caught at the surface and at 6 and 20 m. It has also shown that cloudiness does not affect vertical distribution of herring larvae in the area where plankton tows were made at Grande-Rivière. The mean number of larvae per daily tow was therefore calculated from both surface and sub-surface tows, irrespective of cloudiness.

Herring larvae were measured, whenever possible, the same day they were caught. In no case were the larvae measured later than one week after their capture. In the case of small samples all the larvae were measured. When the number exceeded on hundred, a random portion of 30 or 40 larvae were measured.

SPAWNING

As a temperature at which eggs develop is known to influence the number of vertebrae of fish, a study of the spawning of herring

at Grande-Rivière was undertaken mainly with a view to finding at which temperatures eggs were deposited in the spring and in the fall.

A. Spawning Periods

The extent of the spawning periods of herring at Grande-Rivière had to be determined before a study was made of water temperature at the time of egg deposition.

Several methods have been used to determine the spawning seasons of the herring, namely, collection of herring eggs, which are demersal, either by dredging (Bowers, 1952) or examining stomach contents of bottom-feeding fish (Aurich and Stier, 1939), survey of newly-hatched larvae (Einarsson, 1949) and examination of the gonads of adult herring (Hickling and Rutenberg, 1936; Runnström, 1941).

The last method is probably the most direct and was the one used in determining spawning periods at Grande-Rivière. The percentage of spawning herring (stage IV) in each sample collected at Grande-Rivière during the fishing seasons of 1952, 1953 and 1954 were determined and are given in Fig. 2.

Two spawning periods per year are shown in Fig. 2. The first one begins in late April and ends in late June or early July. Fish spawning during this period are called "spring spawners". Fig. 2 indicates for 1953 and 1954 a peak in the percentage of spring spawners present in the samples in May followed by a decline at the beginning of June. In the latter part of June another peak occurs in the percentage of spawners. Data for 1953 indicate that 87.8% of the spring spawners were caught from the beginning of the spring spawning period to June 10, and 12.2% were caught between June 10 and July 1. In 1954, 60.9% of the spring spawners were captured during the first half of the spring spawning period (to June 10) and 39.1% during the second half. The bulk of the spawning in the spring therefore takes place in May and in early June.

The second spawning period begins in mid-August (Fig. 2) and ends in late September. Fish spawning during this period are called "fall spawners".

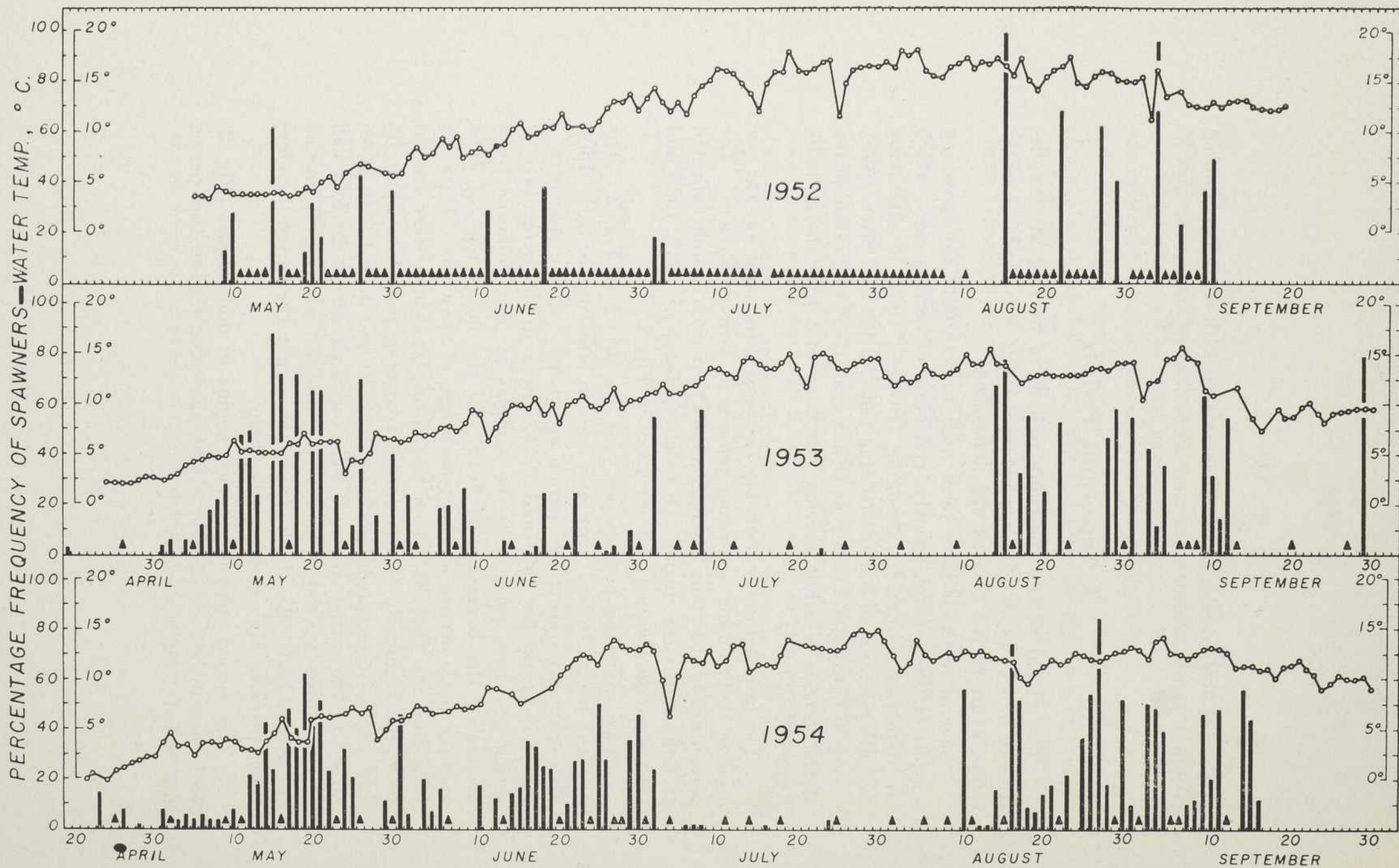


FIGURE 2.— Spawning periods of herring at Grande-Rivière in 1952, 1953 and 1954 as indicated by the percentage, in daily samples, of fish at maturity stage IV. Black triangles indicate days when no sampling was done. Temperatures are surface temperatures taken daily at the Grande-Rivière wharf.

Spring and fall spawning periods are separated by an interval of six weeks. Very few spawners are caught in July and during the first half of August.

Apparently spawning of the herring in Bay of Chaleur has occurred at the same periods for at least one hundred years. Perley (1852) wrote: "The common herring (*Clupea elongata* of DeKay and Storer) appear in the Gulf of St. Lawrence at the end of April, or early in May, and the fishing continues until about 10th June, when they retire to deep-water, having deposited their spawn. . . . Another herring appears on the coast about the 20th of August, and remains inshore for a month."

Observations made elsewhere have shown that two spawning seasons of the Atlantic herring occur in other areas as well: southeast and southwest coasts of Iceland (Johansen, 1919, 1921; LeGall, 1935; Einarsson, 1951); Faeroes (Johansen, 1921; LeGall, 1935); Baltic Sea (LeGall, 1935; Ciegiewicz and Posadzki, 1947); Scotland (Wood, 1936); Kattegat (LeGall, 1935; Johansen, 1924).

In some areas on the other hand, spawning takes place only once a year. On the Manx coast of the Irish Sea (Smith, 1924; Hsieh, 1939) spawners are caught from September to December. The east coast of England has a "fall" spawning season (Hodgson, 1928) which starts in July-August in the northern section of the coast and later farther south, in November-December at Lowestoff (LeGall, 1935). In the western part of the English Channel (LeGall, 1935) spawning takes place still later, December-January. On the Norwegian coast herring spawn only in February-March (Rass, 1936; Runnström, 1941).

In the northwestern Atlantic, Newfoundland herring spawn only in the spring, from mid-May until the end of June (Hjort, 1915; Tibbo, 1946). Herring spawn in August and September in southwestern Greenland (Jensen, 1939).

In the Gulf of Maine, herring spawn in October and November only (Scattergood, 1952; Bigelow and Schroeder, 1953). From a study of herring larvae, Merriman and Sclar (1952) concluded that Block Island Sound herring spawn in late summer and early fall. According to Breder (1929), herring spawn in the fall in the latitude of New York. Perlmutter (1939) found newly-

FIGURE 2. Spawning periods of herring in the Gulf of St. Lawrence, Rivière du Loup, 1953 and 1954 as indicated by the percentage, in daily samples, of fish at maturity stage IV. Black triangles indicate days when no sampling was done. Temperatures are surface temperatures taken daily at the Grande-Rivière wharf.

20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100

APRIL MAY JUNE JULY AUGUST SEPTEMBER

hatched larvae in October on the western shore of Long Island, New York.

The factors determining the number of spawning seasons of herring in an area are as yet unknown.

B. Composition of Spawning Populations

1. Degree of Maturity

A study of the composition as to degree of maturity of herring samples caught at Grande-Rivière indicates that the populations sampled inshore are primarily spawning populations. The proportion of herring at various stages of maturity caught inshore at Grande-Rivière from April to October is given in Fig. 3.

The fact that the first samples caught are made up of fish at stage III (ripe) in the proportion of about 90% indicates that adult herring approach the shore only when they are about to spawn. Nets set some two weeks before the estimated arrival of herring in 1953 and 1954 did not catch any herring.

As the season advances, herring at stage IV (spawning) become more and more abundant (Fig. 3). Later again, i. e., in July and early August spent (V) and recovering spent (VI) spring spawners predominate in the samples.

Herring present on the spawning grounds in the spring are practically all mature fish as indicated by the fact that very few herring at stages I and II are caught during the actual spawning season. Immatures or "small summer herring" (Tibbo, 1949) are caught in late June and July.

When spring spawning is completed some spent (V) and recovering (VI) herring remain along shore in July and early August, presumably feeding. This was particularly evident in 1954 (Fig. 3).

Fall spawners appear in mid-August and herring at stage IV again constitute the largest proportion, varying between 50% and 100%, of the samples (Fig. 3). In contrast to the behavior of spring spawners, fall spawners appear to move to deeper waters as soon as they have spawned. Few herring at stages V and VI

100 □ immature

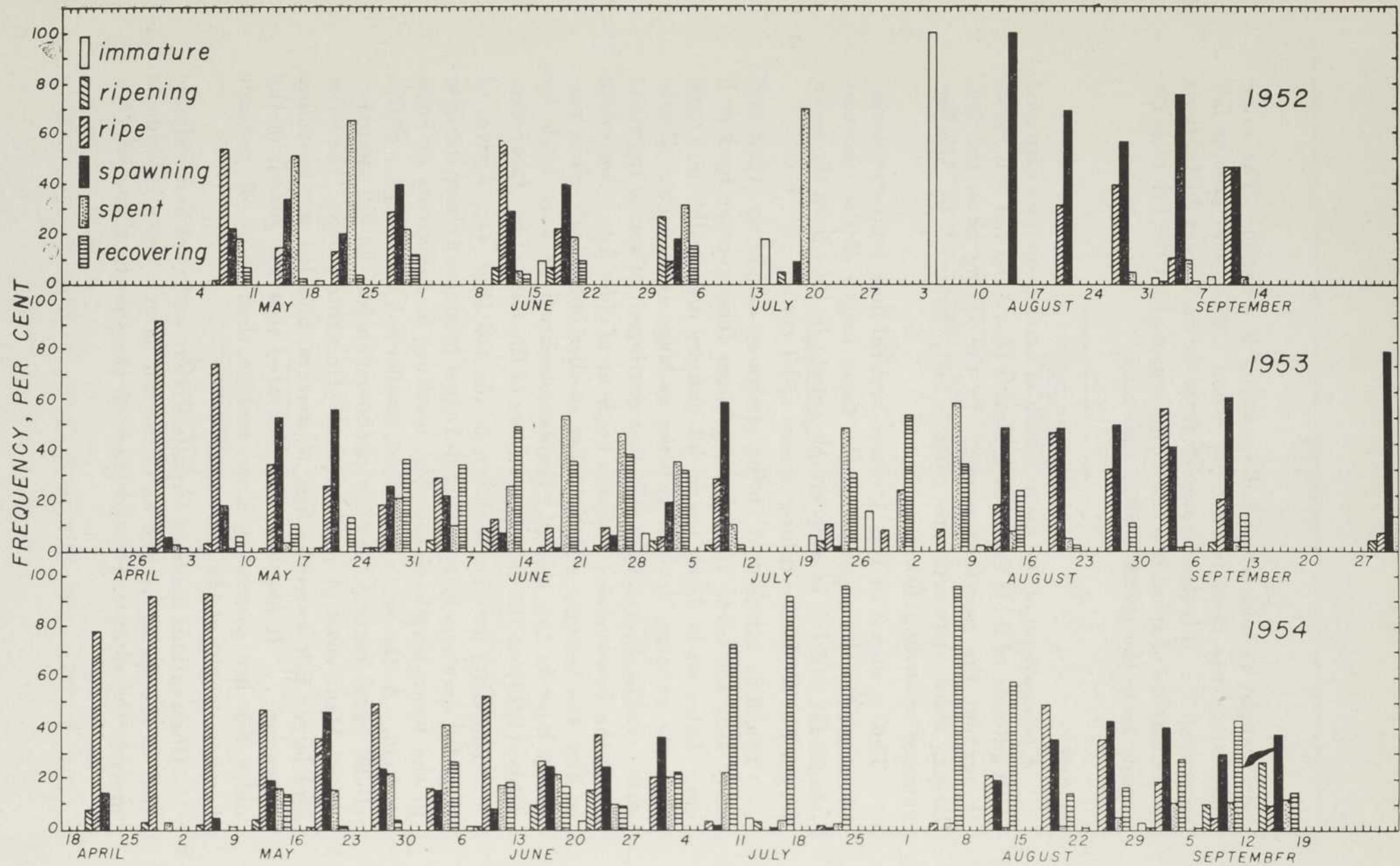


FIGURE 3.—Frequency distribution of maturity stages in weekly samples of herring caught at Grande-Rivière from April to September.

were caught inshore after fall spawning has begun. The same conclusions has been reached by Wood (1937) who said of fall spawners: ". . . it is clear, however, from the very great fluctuations in the catches of spent fish late in the season, that the fish disperse rapidly from the grounds after spawning."

2. *Size*

A comparison of the mean length of herring samples captured with gill-nets of 2 1/8 in. mesh indicates that length of fish varies throughout the spawning period. In the spring as in the fall, larger, older spawners are caught first, followed by smaller, younger spawning fish.

This is shown in Fig. 4 where vertical lines represent deviations, positive or negative, of the mean length of the spawners (stages III and IV) of each sample caught in 1954 from the mean length for the entire fishing season (30.3 cm.).

The first samples of spring spawners caught in April and early May are made up of herring larger than average by 2 or 3 cm. Later on in June, nearly all samples are smaller in length than the average, deviations being as large as — 4 cm. Runnström (1941) observed that the first contingent of spring spawners along the Norwegian coast was made up of older fish. According to him, the younger and therefore smaller individuals reach maturity later in the season. Similar observations were made by Tibbo (1949) on the spring spawners of the Gulf of St. Lawrence.

The same pattern is shown in the fall (Fig. 4). Arrival of large fall spawners inshore in mid-August produces a sharp increase in the mean length of samples, resulting in deviations as large as 5 cm. As the season advances, smaller fish are caught. Smith (1938, 1948) reported similar phenomenon for the fall spawners of the Manx coast of the Irish Sea. He wrote (1948) "the older and larger fish were the first to mature, and led the spawning migration. . . It has been demonstrated that the gonads of the older fish are somewhat more mature than those of younger herrings caught at the same time".

Observations made at Grande-Rivière and elsewhere indicate that in the spring as well as in the fall, larger, older individuals precede the smaller, younger ones on the spawning grounds.

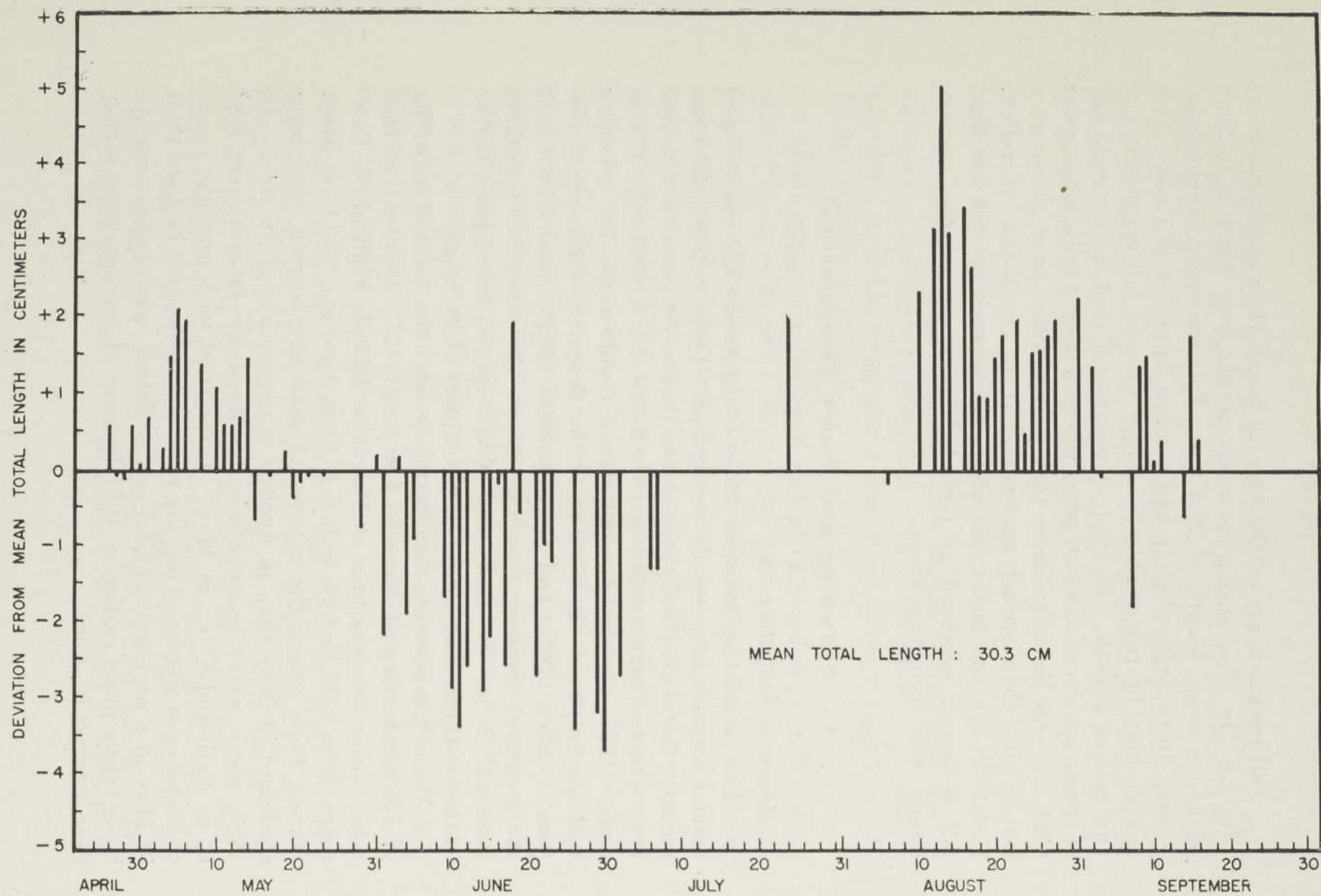


FIGURE 4.— Deviations of the means of individual samples from the mean length of all samples of herring collected at Grande-Rivière during the fishing season of 1954.

Fall spawners are on the average larger than spring spawners (Fig. 4). In 1954, spring spawners caught from April 23 to June 39 had a mean length of 29.3 cm. Fall spawners caught from August 10 to September 16 had a mean length of 32.1 cm. Two factors may be responsible for larger sizes in fall spawners: age and rate of growth. In 1954, it was found that the average age of spring spawners was 6.30 years whereas that of fall spawners was 6.98. It will be shown later that fall spawners have grown at a faster rate than spring spawners. It is concluded, therefore, that both age and faster rate of growth account for the fact that fall spawners captured at Grande-Rivière are on the average larger than spring spawners.

C. Spawning and Water Temperature

1. *Review of Literature*

The correlation between water temperature and spawning of marine animals is generally recognized. Orton (1919) and more recently Hutchins (1947) have shown that several species of marine invertebrates, spawn within narrow limits of temperature. Runnström (1927) correlated temperature requirements at spawning with geographical distribution of the flounder (*Pleuronectes platessa*). Allen (1897) and recently Sette (1950) have shown that the mackerel (*Scomber scombrus*) spawn at temperatures ranging from 12° to 15° C. Spawning of this species takes place earlier in the southern than in the northern part of its range.

Water temperature may hasten or delay the onset of spawning of Atlantic herring as shown by Lauzier (1952). He observed that mean water temperatures at Magdalen Islands, Gulf of St. Lawrence, from 1933 to 1950 were 0.3° C. in April and 4.5° C. in May. During these years, the catches of spawning herring were more abundant in May than in April in a proportion of 18 to 1. In 1951, mean water temperatures at Magdalen Islands were 3.8° C. in April and 6° C. in May. In contrast with previous years, the catches of spawning herring were more abundant in April than in May in a proportion of 4.5 to 1. Spring spawning appears to have taken place earlier in 1951 because of temperatures higher than normal in April.

A review of the literature, however, shows that herring spawn at a wide range of temperatures. This is indicated in Table I where data gathered from various authors are grouped according to localities; ranges of water temperature during spawning are those mentioned by the authors. Table I shows that water temperatures at which herring spawn range from 0° to 12° C. in the spring and from 8° to 15° C. in the fall.

2. *Water temperatures at Grande-Rivière*

A study of water temperatures at Grande-Rivière during spawning of the herring shows that in this locality as in the others mentioned in Table I eggs are deposited at lower temperatures in the spring than in the fall.

Herring eggs are demersal and after being deposited adhere firmly to seaweeds, rocks, etc., at the bottom. Bottom temperatures are therefore those at which development of eggs takes place. Temperatures on the Grande-Rivière spawning grounds were estimated from records of surface temperatures taken every morning at the Grande-Rivière wharf about one mile west of where the nets were anchored. In order to find out to what extent surface temperatures at the wharf differed from bottom (20 m.) temperatures on the spawning grounds, temperatures have been taken simultaneously at the two places from May to July 1953. The results are indicated in Table II which shows that during that period bottom temperatures on the spawning grounds were nearly always lower than surface temperatures at the wharf. From May to July 1953 bottom temperature was on the average 1.5° C. lower than surface temperature.

The temperatures mentioned in the following pages are surface temperatures at the Grande-Rivière wharf which, as seen in Table II, may have a somewhat higher value than the actual temperatures at which the eggs are deposited and develop. As the purpose of the present study is to compare temperatures at which development of herring eggs takes place in the spring and in the fall at Grande-Rivière, it is believed that surface temperatures at the wharf give sufficient indication to make such a comparison possible.

Daily surface temperatures at the Grande-Rivière wharf are plotted in Fig. 2.

TABLE I
WATER TEMPERATURES DURING SPAWNING OF HERRING
(*Clupea harengus*) IN DIFFERENT AREAS

<i>Locality</i>	<i>Season</i>	<i>Temperature °C</i>	<i>Authors</i>
<i>Norway</i>	February- March	3.0 — 7.0	Buch (1885) Johansen (1924) Runnström (1941)
<i>North Sea</i>	August- November	6.0 — 13.0 12.0 — 14.0	LeCall (1935) Johansen (1924)
<i>Kattegat</i>	January- June	4.0 — 12.0	Johansen (1924) LeGall (1935)
	September- October	11.0 — 13.0	Johansen (1924) LeGall (1935)
<i>Baltic</i>	April- June	6.0 — 11.0	Altnöder (1929) LeGall (1935) Cieglewicz & Posadzki (1947)
	September- October	11.0 — 14.0	Hessle (1925) Cieglewicz & Posadzki (1947)
<i>English Channel</i>	December- February	6.0 — 12.0	Fage (1920) Johansen (1924)
<i>Scotland</i>	February- March	3.9 — 7.1	Fulton (1906) Wood (1936)
	July- September	11.0 — 12.0	Fulton (1906) Fage (1920) Johansen (1924) Wood (1936)
<i>Barents Sea</i>	February- April	0.0 — 6.9	Rass (1936) Rass (1939) Manteufel & Marty (1939)
<i>Iceland</i>	Spring	5.0 — 9.0	Tåning (1936)
<i>Faeroes</i>	March- April	ca 3.0	Johansen (1921)
<i>Grand Manan</i>	Fall	8.0 — 11.0	Bigelow & Schroeder (1953)
<i>Cape Cod</i>	Fall	11.7 — 12.8	Bigelow & Schroeder (1953)
<i>Newfoundland</i>	Spring	8.0	Tibbo (1946)
<i>Block Island Sound</i>	Late summer	13.0 — 15.0	Merriman & Warfel (1948) Merriman & Sclar (1952)
<i>Magdalen Islands</i>	April- May	3.8 — 4.5	Lauzier (1952)

TABLE II

COMPARISON OF SURFACE TEMPERATURES AT THE WHARF
AND BOTTOM TEMPERATURES ON THE SPAWNING GROUNDS
AT GRANDE-RIVIÈRES IN 1953

<i>Date</i>	<i>Surface temp. Wharf °C.</i>	<i>Bottom temp. Spawning gr. °C.</i>	<i>Difference</i>
May 8	4.6	2.7	- 1.9
" 9	4.7	4.6	- 0.1
" 11	5.1	4.8	- 0.3
" 12	5.2	4.8	- 0.4
" 13	5.0	4.2	- 0.8
" 15	5.0	4.2	- 0.8
" 16	5.0	4.5	- 0.5
" 18	5.9	2.7	- 3.2
" 20	5.9	6.1	+ 0.2
" 21	6.2	0.8	- 5.4
" 23	6.2	0.9	- 5.3
" 26	4.2	3.8	- 0.4
" 27	5.0	4.2	- 0.8
" 28	7.0	3.2	- 3.8
" 29	6.5	5.9	- 0.6
" 30	6.5	5.8	- 0.7
June 1	6.3	6.2	- 0.1
" 3	6.8	6.6	- 0.2
" 4	6.8	6.8	- 0.0
" 5	7.5	6.8	- 0.7
" 8	8.1	7.2	- 0.9
" 11	6.2	6.5	+ 0.3
" 12	7.7	7.1	- 0.6
" 13	9.0	7.2	- 1.8
" 15	9.8	8.0	- 1.8
" 19	9.9	7.6	- 2.3
" 20	8.0	5.1	- 2.9
" 22	10.3	7.6	- 2.7
" 23	10.7	5.8	- 4.9
" 25	9.5	8.1	- 1.4
" 26	10.3	9.0	- 1.3
" 27	11.5	7.2	- 4.3
" 29	10.2	7.6	- 2.6
" 30	10.3	9.6	- 0.7
July 2	11.1	10.4	- 0.6
" 6	11.6	10.6	- 1.0
" 8	12.4	12.5	+ 0.1
" 9	13.5	12.6	- 0.9

In 1953 spring spawning started on May 1 at a temperature of 2.2° C. and ended on July 8 at a temperature of 12.4° C. In 1954 spring spawning began on April 23 at a temperature of 0.5° C. and ended on July 2 when water temperature at the wharf was

12.9° C. Sampling in the spring of 1952 was not started until May 9 when spawning was already under way (Fig. 2). Records of commercial catches indicated that the first herring were caught on April 28 of that year. That date presumably coincided with the beginning of spring spawning.

Mean surface temperatures at the wharf during the 1953 and 1954 spring spawning periods were 7.3° C. and 6.5° C. respectively. Mean temperature from May 5, 1952 (first date for which record of water temperature was available) to June 30 (estimated date of the end of the spawning period) was 7.4° C. These figures show that spawning in the spring at Grande-Rivière takes place at temperatures ranging from 0.5° to 12.9° C. and averaging about 7° C. As bottom temperature on the spawning grounds was found to be 1.5° C. lower on the average than surface temperature at the wharf, eggs of spring spawners are deposited at temperatures which are probably lower than the ones indicated here.

Only in 1953 was sampling continued long enough to ascertain the end of the fall spawning. That year, the last spawners were caught on September 29 when water temperature was 10° C. Mean water temperatures were calculated from the beginning of the fall spawning season in mid-August to the end of September and were found to be 13.6° C. in 1952, 11.6° C. in 1953 and 11.6° C. in 1954. Herring therefore spawn in the fall at Grande-Rivière at temperatures ranging from 16.6° to 10° C. and averaging between 11.6° and 13.6° C.

In conclusion, herring spawn at Grande-Rivière during a period of rising temperatures in the spring and of falling temperatures in the autumn. Mean water temperature is approximately 5° C. lower in the spring than it is in the fall.

DEVELOPMENT, ABUNDANCE AND GROWTH OF LARVAE

Water temperature during development and early life affects characters such as vertebral counts and scale pattern of herring. If spring and fall broods are exposed to different environmental

conditions, vertebrae are therefore likely to differ in number and scales in pattern.

A survey of herring larvae was made at Grande-Rivière in 1952, 1953 and 1954 with a view to determining periods of incubation in the spring and in the fall at Grande-Rivière, and temperature conditions during incubation of the eggs and early life of the larvae. Relative strengths of spring and fall broods were compared. Rate of growth and time of scale formation of spring and fall larvae were established. Finally, certain morphological characters of spring and fall larvae were studied.

A. Water Temperature During Development of Eggs

The majority of herring eggs deposited at Grande-Rivière in the spring are exposed to lower temperatures than the ones deposited in the fall. This is shown by a study of water temperatures during the interval of time separating the beginning of spawning and the appearance of the first larvae.

1. *Dates of first Capture of Larvae*

Larvae of the spring brood only were sampled in 1952 since plankton tows started on May 17, were discontinued after July 31. In 1953 and 1954, sampling began in mid-May and was continued until late September. Both spring and fall larvae were caught.

Plankton tows were started several days before the estimated date of first appearance of larvae. Among the first larvae caught, several were only 4 mm. long and had a full yolk sac. There is therefore good reason to believe that the first captures of larvae were made very soon after the onset of hatching. Dates of first capture of spring and fall larvae are given in Table III.

Observations made during these three years indicate that the date of appearance of herring larvae in the plankton is fairly constant, the end of May for spring larvae and the end of August for fall larvae.

TABLE III
 DATES OF FIRST CAPTURE OF HERRING LARVAE
 AT GRANDE-RIVIÈRE

	<i>Spring</i>	<i>Fall</i>
1952	May 29	—
1953	June 4	August 25
1954	May 28	August 31

2. Incubation Period

The incubation period of Atlantic herring eggs at various temperatures has been determined in nature or in the laboratory by many investigators (Kupffer, 1878a, 1878b; Meyer, 1878, 1880; Ljungman, 1880; Holt, 1889; MacIntosh and Prince, 1889; Dannevig, 1895; Fulton, 1906; Prince, 1907; Williamson, 1910; Johansen, 1923, 1927; Aurich and Stier, 1939; Kotthaus, 1939; Manteufel and Marty, 1939; Schach, 1939; Soleim, 1940; Dannevig, 1948; Jones, 1948; Jensen, 1950). Observations made by these investigators are summarized in Table IV.

TABLE IV
 INCUBATION PERIOD OF HERRING EGGS AT VARIOUS
 TEMPERATURES

From sources mentioned in text

<i>Temperature in °C.</i>	<i>Incubation period in days</i>
0.0.....	47
1.0 — 2.0.....	33 — 40
2.0.....	40 — 45
3.5 — 4.0.....	40
5.0.....	25
5.8 — 6.9.....	20
6.5 — 7.8.....	15
8.3.....	17 — 20
8.7.....	14 — 18
10.0.....	10
10.7.....	10 — 12
10.0 — 10.5.....	11
11.0 — 12.0.....	10 — 11
12.3.....	7 — 9
13.0.....	8 — 12
18.0 — 20.0.....	8 — 10
20.0.....	3

The age of herring larvae caught at Grande-Rivière is not known, but there is good reason to believe, as mentioned earlier, that they are captured by the tow-net soon after hatching.

The interval of time separating capture of first spawners and of first larvae is therefore a good indication of the incubation period of the first brood of each season.

Dates of capture of first spawners and first larvae at Grande-Rivière are given in Table V. From these the incubation period of spring and fall larvae was estimated.

TABLE V
PRESUMED INCUBATION PERIOD OF HERRING EGGS
AT GRANDE-RIVIÈRE

	<i>Spring</i>			<i>Fall</i>		
	<i>Date of capture</i>			<i>Date of capture</i>		
	<i>First spawners</i>	<i>First larvae</i>	<i>Incubation days</i>	<i>First spawners</i>	<i>First larvae</i>	<i>Incubation days</i>
1952	April 28	May 29	31	—	—	—
1953	May 1	June 4	33	Aug. 14	Aug. 25	11
1954	April 23	May 28	35	Aug. 10 (Aug. 16)	Aug. 31 Aug. 31	21 (15)

Observations recorded in Table V indicate that incubation takes from 31 to 35 days in the spring and from 11 to 21 days in the fall.

The incubation period appeared to be twice as long in the fall of 1954 (21 days) as in the fall of 1953 (11 days). The interval of 21 days in 1954 was calculated from August 10, date of capture of the first spawners. After that date, however, very few spawners were caught until August 16 (Fig. 2). If the larvae caught on August 31 resulted from the August 16 spawning, the actual incubation period would be 15 days as indicated in parentheses in Table V.

3. *Water Temperature during Incubation at Grande-Rivière*

Mean surface temperatures at the wharf between the dates of capture of first spawners and of first larvae at Grande-Rivière were calculated. The results are shown in Table VI.

TABLE VI
MEAN WATER TEMPERATURE DURING INCUBATION
OF HERRING EGGS AT GRANDE-RIVIÈRE

	<i>Spring</i>		<i>Fall</i>	
	<i>Temperature °C.</i>	<i>Incubation period in days</i>	<i>Temperature °C.</i>	<i>Incubation period in days</i>
1952	4.4	31	—	—
1953	5.3	33	13.0	11
1954	3.7	35	11.9 (11.7)	21 (15)

Table VI indicates that the first herring eggs deposited at Grande-Rivière take nearly five weeks to hatch at a temperature of about 4.5° C. in the spring and approximately two weeks in the fall at temperatures of 12° or 13° C. These observations are consistent with those of other investigators (Table IV).

It is concluded that larvae hatched early in the spawning period come from eggs which have developed at lower temperature in the spring than in the fall at Grande-Rivière. The difference is of the order of 7° or 8° C.

These figures, however, apply only to larvae hatched from eggs deposited at the beginning of the spawning seasons. Temperatures at which spawning ends in the spring (12° C.) (Fig. 2) approximate those at which spawning starts in the fall (12.9° to 16.6° C.). But the larger part of the spring spawned eggs develop at lower temperatures than the ones to which fall spawned eggs are exposed. Late spring spawning (June 10 to July 8) (Fig. 2) took place in 1953 at an average temperature of 10.9° C. Most of the spawning in the fall of that year took place between August 14 and September 11 at an average temperature of 13.0° C. Mean

temperatures during the corresponding periods of 1954 were 11.0° C. (June 10 to July 1) and 12.1° C. (August 15 to September 16).

It is therefore safe to state that herring eggs develop at temperatures which are from 1° to 8° C. lower in the spring than in the fall.

B. Abundance of Spring and Fall Larvae

Evidence seems to point toward larger spawning populations in the spring than in the fall at Grande-Rivière. Spring spawning (Fig. 2) extends over a period of two months, whereas most of the fall spawning, at least in 1953 when the entire spawning season was covered by the sampling, is completed one month after arrival of the first fall spawners.

Commercial landings of herring (not including New Brunswick sardines) along the Atlantic coast of Canada (exclusive of Newfoundland) for the period from January to June were 98 million pounds in 1952 and 86 million pounds in 1953 (*TradeNew*, Ottawa, 6 (2): : 8, 1953) as compared to 78 and 63 million pounds for the period July-December of the same years (*Ibid.*, 6 (8): 16, 1954). Fishing effort may not have been of the same magnitude during these two periods, but a difference of nearly 20 million pounds in the commercial landings seem to indicate that herring is more abundant during the first part of the year when spring spawning takes place, than during the second part when fall spawning occurs.

No data are available on the number of herring caught in the sampling nets anchored off Grande-Rivière during the years of this investigation. It was observed, however, that herring were always more plentiful in May and June than in any other month of the fishing season.

Yet it appears that the production of larvae, as indicated by the number of larvae per tow is larger, or at least more concentrated in the fall than in the spring. This is shown in Fig. 5 where the mean numbers of larvae per daily tow are plotted, and in Table VII where the means for the whole seasons are given.

TABLE VII
NUMBER OF HERRING LARVAE PER 20-MIN. TOW IN THE
SPRING AND IN THE FALL AT GRANDE-RIVIÈRE

	<i>Spring</i>			<i>Fall</i>		
	<i>Total no. larvae</i>	<i>No. of tows</i>	<i>Mean no. larvae</i>	<i>Total no. larvae</i>	<i>No. of tows</i>	<i>Mean no. larvae</i>
1952	13,591	59	230.4	—	—	—
1953	1,982	40	49.6	8,462	20	423.1
1954	1,228	93	13.2	5,674	16	354.6

Fraser (1949) found that spring and fall broods were to equal strength in northern North Sea. According to Jensen (1950) fall larvae are more numerous than spring larvae in the Skagerrak and Kattegat. This is not due, according to Jensen, to a greater production of larvae in the fall but rather to the fact that spawning in the spring extends over a longer period: spring larvae are more scattered. Jensen (1950) also thought that larvae grew more rapidly in the spring and reached sooner a stage when they could escape the net.

A greater concentration of larvae in the fall at Grande-Rivière may be due to a larger number of eggs being deposited per unit of time in the fall than in the spring. No data are available on the number of eggs of spring and fall spawners of Bay of Chaleur. Farran (1938) on the other hand has shown that larger fish had more eggs than smaller fish, the number of eggs being roughly equal to $L^{4.5}$. As mentioned previously, fall spawners caught at Grande-Rivière are on the average 2 cm. larger than spring spawners. It is therefore possible that egg deposition in a given time is more abundant in the fall than in the spring. This would account for a larger number of larvae per tow in the fall than in the spring.

Fig. 5 and Table VII also show that the number of larvae caught at Grande-Rivière was much larger in the spring of 1952 than in the spring of the two following years: 230.4 larvae per tow in 1952 as compared to 49.6 in 1953 and 13.2 in 1954.

Records of commercial landings of herring given previously indicated that the catches of January-June, 1952, were some 10 million pounds larger than those of the corresponding period of 1953. If commercial landings reflect abundance, these figures would indicate larger spring spawning populations in 1952 than in 1953, thus accounting for a larger number of larvae captured in the spring of 1952 than in the spring of 1953. Records of herring catches for the January-June period of 1954 include Newfoundland and therefore are not comparable to those of the two previous years.

C. Morphological Characters of Spring and Fall Larvae

Martin (1949) studied the mechanics of environmental control of body form in fishes and stated: « Many facts have been discovered which point to a close correlation between rate of development and the relative size of many body parts of fishes. » He also wrote: « . . . in general, decreasing the rate of development increases the numbers of meristic parts ».

Heincke (1898) stated that spring spawned herring larvae differed from fall larvae in non-meristic characters such as length of head, position of anal and dorsal fins and general body shape. Fage (1920) found that the head was larger in larvae hatched off northern Scotland at temperatures of 11°-12° C. than in larvae hatched in the English Channel at temperatures of 7°-8° C. Martin (1949) found the same difference in rainbow trout (*Salmo gairdnerii*) hatched in the laboratory at different temperatures.

Very few racial studies of herring larvae based on meristic characters such as number of myotomes, vertebrae, etc., have been made.

Myotome counts are useful in distinguishing larvae of different species of clupeoids (Lebour, 1921), but cannot be made with enough accuracy to be of any use in racial studies. This decision was reached by Kotthaus (1939) and confirmed in the present study. Trunk myotomes, defined by Lebour (1921) as those located between operculum and anus, were counted in several spring and fall larvae captured at Grande-Rivière. These counts

were later discarded as unreliable because of the difficulty in identifying the first two or three anterior myotomes.

Vertebral counts, most generally used in racial studies of adults, cannot be made in herring larvae smaller than 35 mm. in length (Tesch, 1937). Larvae larger than 35 mm. as mentioned previously, are difficult to catch with ordinary plankton nets. On the other hand, post-larvae 50 or 60 mm. long on which vertebrae can be counted are too large to be ascribed with certainty to either fall or spring brood.

In spite of these difficulties, Tesch (1937) has counted the vertebrae of herring larvae collected from weirs of the southwestern inlets of Holland. Larvae of this area are believed to be a mixture of fall spawned larvae from the North Sea and winter spawned larvae from the English Channel. Larvae ranging in size from 35 to 45 mm. could be separated on the basis of length and vertebral count. Larvae from the English Channel, hatched at low temperature, occupied the lowest portion of the size range and had a mean vertebral count of 56.73. Larvae from the North Sea hatched at higher temperature were larger and had a mean vertebral count of 56.57. Tesch (1937) found that at larger sizes there was a considerable degree of mixing and the two groups could no longer be separated.

Vertebral counts were also used successfully by Clark (1933) in separating spring and fall spawned larvae in Scottish waters. Frequency distributions of vertebrae in samples considered by Clark as pure spring and pure fall spawned larvae are given in Fig. 6. Mean vertebral counts, as seen in Fig 6, are higher in spring spawned (upper two polygons) than in fall spawned larvae (lower three polygons).

It will be shown later that the polygons representing vertebral distribution of adult herring caught at Grand-Rivière and believed to have been hatched in the spring on the one hand and in the fall on the other closely resemble those given by Clark for larvae of Scotland.

Length of Head of Spring and Fall Larvae

Length of head of herring larvae caught at Grande-Rivière in the spring and in the fall of 1953 and 1954 has been measured

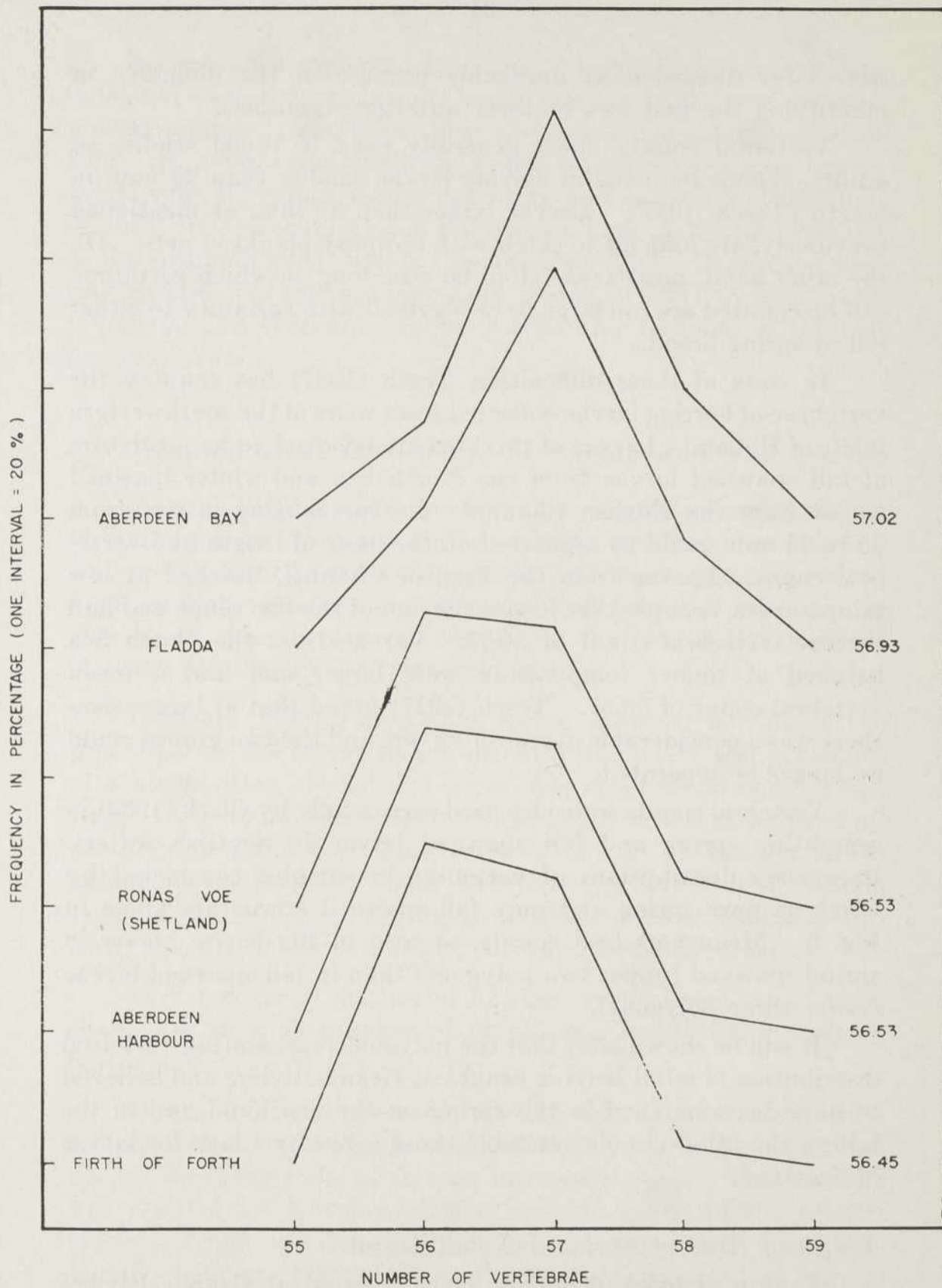


FIGURE 6.— Frequency distribution of vertebrae of spring (upper two polygons) and fall (lower three polygons) herring larvae from Scottish waters. (Clark, 1933).

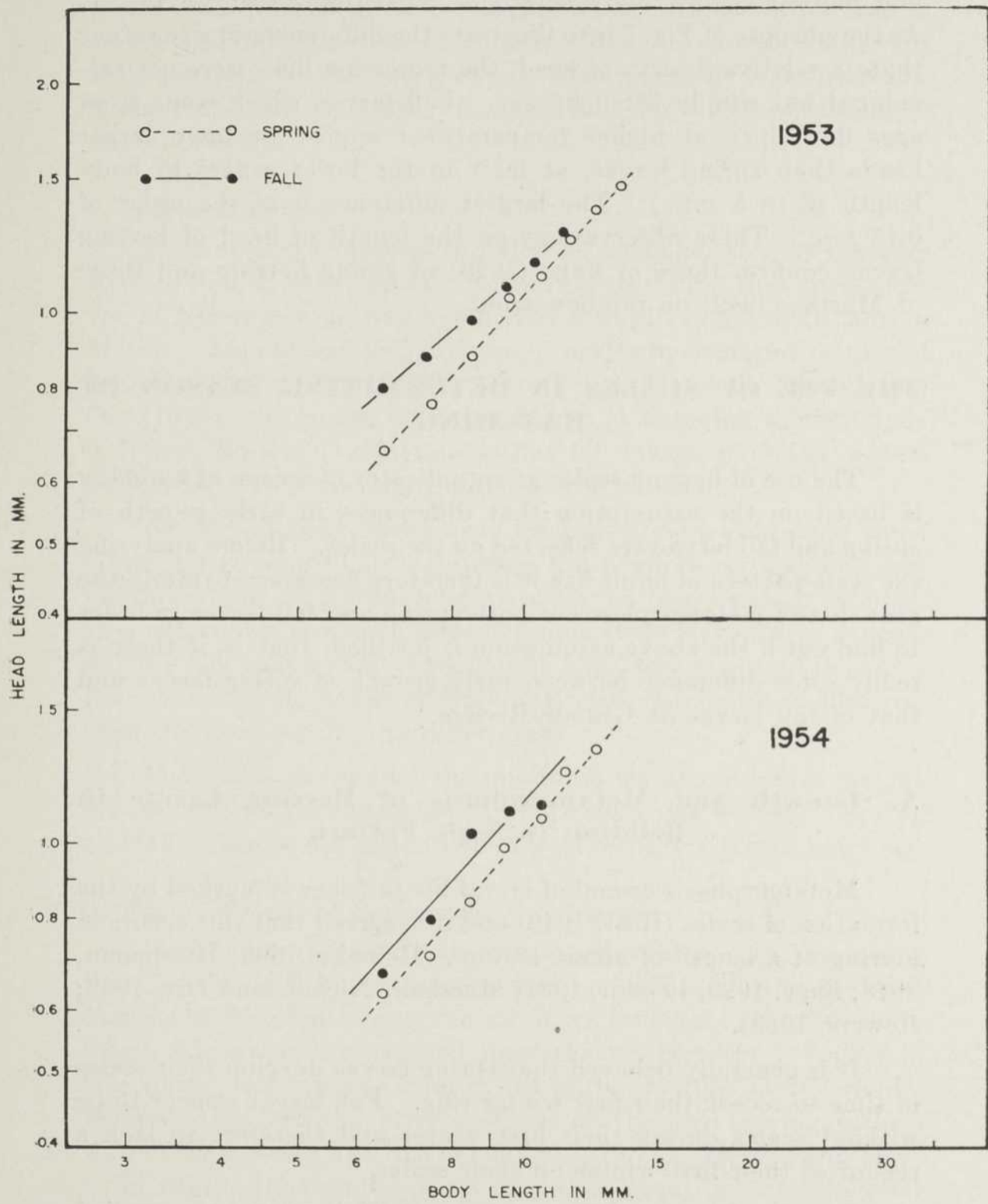


FIGURE 7.— Comparison of head length of spring and fall larvae caught at Grande-Rivière in 1953 and 1954.

and plotted against body length on logarithmic scale in Fig. 7. As the purpose of Fig. 7 is to illustrate the differences in size rather than in relative growth of head, the regression lines were not calculated but simply fitted by eye. Fall larvae which come from eggs developed at higher temperatures appear to have larger heads than spring larvae, at least in the lower ranges of body length (6 to 8 mm.). The largest difference is of the order of 0.13 mm. These observations on the length of head of herring larvae confirm those of Fage (1920) of young herring and those of Martin (1949) on rainbow trout.

THE USE OF SCALES IN DETERMINING SEASON OF HATCHING

The use of herring scales as an indicator of season of hatching is based on the assumption that differences in early growth of spring and fall larvae are reflected on the scales. Before analysing the scale pattern of adult fish it is therefore necessary to study the growth and metamorphosis of both spring and fall larvae in order to find out if the above assumption is justified, that is, if there is really some difference between early growth of spring larvae and that of fall larvae at Grande-Rivière.

A. Growth and Metamorphosis of Herring Larvae in Relation to Scale Pattern

Metamorphosis or end of larval life in fishes is marked by the formation of scales (Rass, 1946) and it is agreed that this occurs in herring at a length of about 40 mm. (Heincke, 1898; Huntsman, 1918; Fage, 1920; Lebour, 1921; Marshall, Nichols and Orr, 1937; Bowers, 1952).

It is generally believed that spring larvae develop their scales in time to record their first winter ring. Fall larvae appear to be without scales during their first winter and therefore to lack a record of their first winter on their scales.

Growth of herring larvae at Grande-Rivière has been studied mainly with a view to determining the time of the year at which scales are formed in spring and fall larvae. Differences in the ti-

me of scale formation and of laying down of first winter ring in spring and fall spawned herring are likely to produce different scale patterns in the two groups. Differences in scale patterns, if detectable in adult fish, may possibly allow determination of season of origin.

1. *Size at Hatching*

Herring larvae appear to hatch at a smaller size at Grande-Rivière than in other areas. Soleim (1940) found that spring larvae of Norwegian herring hatched at a length of 6.5 to 10 mm. in March. Larvae hatched in June in northern Scotland measured from 6 to 8 mm. (Fage, 1920). According to Marshall, Nicholls and Orr (1937), the length of spring larvae at hatching in the Clyde is 7 mm. Bowers (1952) found that fall larvae in Manx waters were from 6 to 9 mm. long when newly hatched.

Nearly all tows made near Grande-Rivière contained some larvae 4 mm. long. This is shown in Fig. 8 where vertical lines join minimum and maximum lengths of larvae of each daily sample. It is not known how soon after hatching these larvae were caught, but the fact that larvae as small as 4 mm. were captured indicates that some herring larvae at Grande-Rivière hatch at a smaller size than the ones reported in other areas.

Fig. 8 also shows that the minimum lengths of larvae caught are rather constant throughout the two spawning seasons. Spring and fall larvae do not seem to differ with respect to size at hatching.

2. *Rate of Growth of Spring and Fall Larvae*

Herring larvae hatch at colder temperatures in the spring than in the fall, but environmental conditions during the first months of life of spring larvae are more favourable than those to which fall larvae are exposed since the temperature is higher in late spring and summer than in the fall. On July 31 at Grande-Rivière, two months after capture of the first spring larvae, water temperature was 16.8° C. in 1952, 12.7° C. in 1953 and 13.9° C. in 1954. On October 31 on the other hand, two months after appearance of the first fall larvae, the water temperature was 4.5° C. in 1952 and 6.3° C. in 1954. (Records are incomplete in October 1953). Spring larvae being exposed to higher tempera-

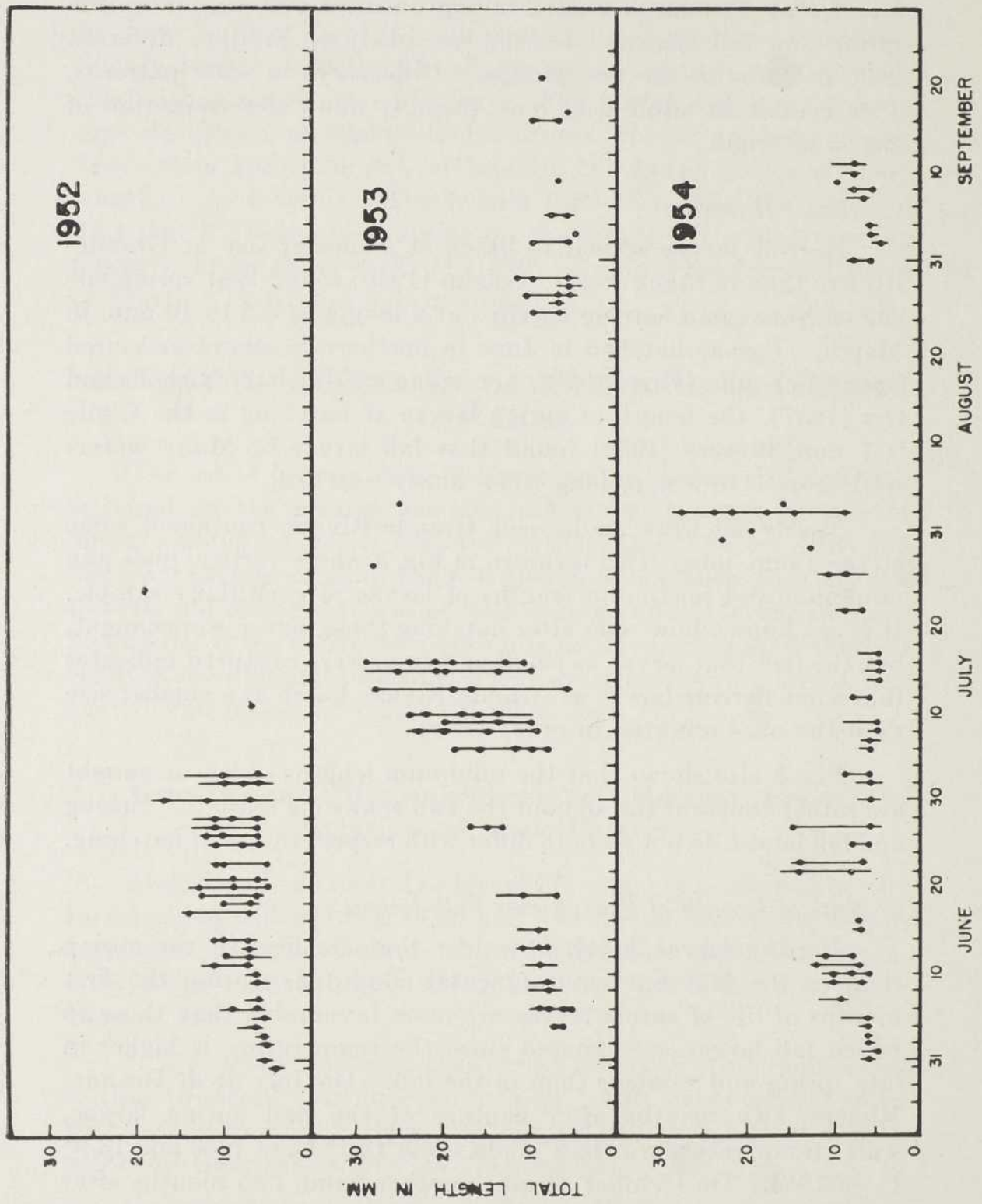


FIGURE 8.— Length of herring larvae caught at Grande-Rivière in 1952, 1953 and 1954. Vertical lines denote range in length, circles denote modal length.

tures than fall larvae during the first months of their lives are likely to grow at a faster rate.

Since larvae collected at any one time especially as the season advances include individuals of different ages, the estimation of rate of growth is rendered difficult. Newly hatched larvae are constantly being added to the stock of older, larger larvae (Fig. 8). Mean lengths of individual samples, therefore, do not provide a method for estimating rate of growth. Marshall, Nicholls and Orr (1937) preferred to use the median or mid-point between minimum and maximum sizes in estimating rate of growth. Bowers (1952) suggested that modal lengths gave a better indication of rate of growth than mean or median.

The best available means of estimating rate of growth of Grande-Rivière larvae appears to be the size of the largest specimens at successive dates. If the largest specimens in each sample are those which have hatched first and had the longest growing period, then their size gives a measure of rate of growth. Some, of course, may be faster growing individuals of later spawning. However, in spite of this limitation, maximum size of successive samples seems to be the best measure of rate of growth.

Maximum sizes of larvae of each sample are indicated in Fig. 8 by the upper limits of the vertical lines. Modal lengths are also plotted, in order to give an idea of the size composition of each sample.

Fig. 8 indicates that no larvae larger than 30 mm. were caught in the tow-net. Larger larvae became progressively fewer in the samples owing to their ability to escape the net in daytime. This means that the method suggested above cannot be used in estimating rate of growth of larvae larger than 30 mm. Other investigators (Mielck, 1929; Marshall, Nicholls and Orr, 1937; Clark 1934 1939; Bückmann, 1938; Taning, 1948; Simpson, 1949; Jensen, 1950; Bowers, 1952; Tibbo, 1954) have encountered similar difficulties in sampling larval populations of herring with an ordinary plankton net.

Fig. 8 indicates that the longest spring larvae collected at Grande-Rivière were between 15 and 18 mm. at the end of June, one month after appearance of the first spring larvae and about

30 mm. at the end of July, two months after appearance of the first larvae in the plankton.

Data on the rate of growth of spring and fall larvae in areas for which figures are available are given in Fig. 9. Three points representing the maximum lengths of spring spawned larvae captured at Grande-Rivière 30 and 60 days after appearance of the first larvae in the plankton are included for comparison.

A comparison of the growth rate of spring larvae in the Clyde and Bay of Chaleur areas indicates a very similar rate of growth. This is probably due to the similarity of the temperatures at which they hatch and grow. Marshall, Nicholls and Orr (1937) estimated that hatching in the Clyde in 1934 took place chiefly between March 16 and March 24. On March 19 in the area investigated by these authors, bottom temperature was 6.88° C. In Grande-Rivière, hatching of spring larvae began at the end of May when surface temperatures were between 5.8° C. and 6.1° C. during the years 1952, 1953 and 1954.

According to Marshall, Nicholls and Orr (1937) spring larvae in the Clyde reach a length of 40 mm. and metamorphose when three months old. If Grande-Rivière larvae grow at a similar rate, as seems to be indicated by their lengths at one and two months of age, they would attain a length of 40 mm., i.e., deposit their scales at the end of August.

Data on the growth of fall larvae at Grande-Rivière are rather scanty. In 1953, sampling was continued until the end of September, yet very few larvae were caught after August 29 (Fig. 5). Data for this year indicate that the few larvae caught nearly one month after the first appearance were only 10 mm. long. This points toward a slower growth of larvae in the fall than in the spring at Grande-Rivière.

Growth of fall larvae is indicated in Fig. 9 for the Manx coast, Dogger Bank and Jutland Reef. The growth curve based on Manx larvae indicates that fall larvae grow at a much slower rate than spring larvae.

The temperatures to which Manx larvae are exposed during their first months of life (Bowers, 1952) are not greatly different from those at which fall hatched young develop at Grande-Rivière.

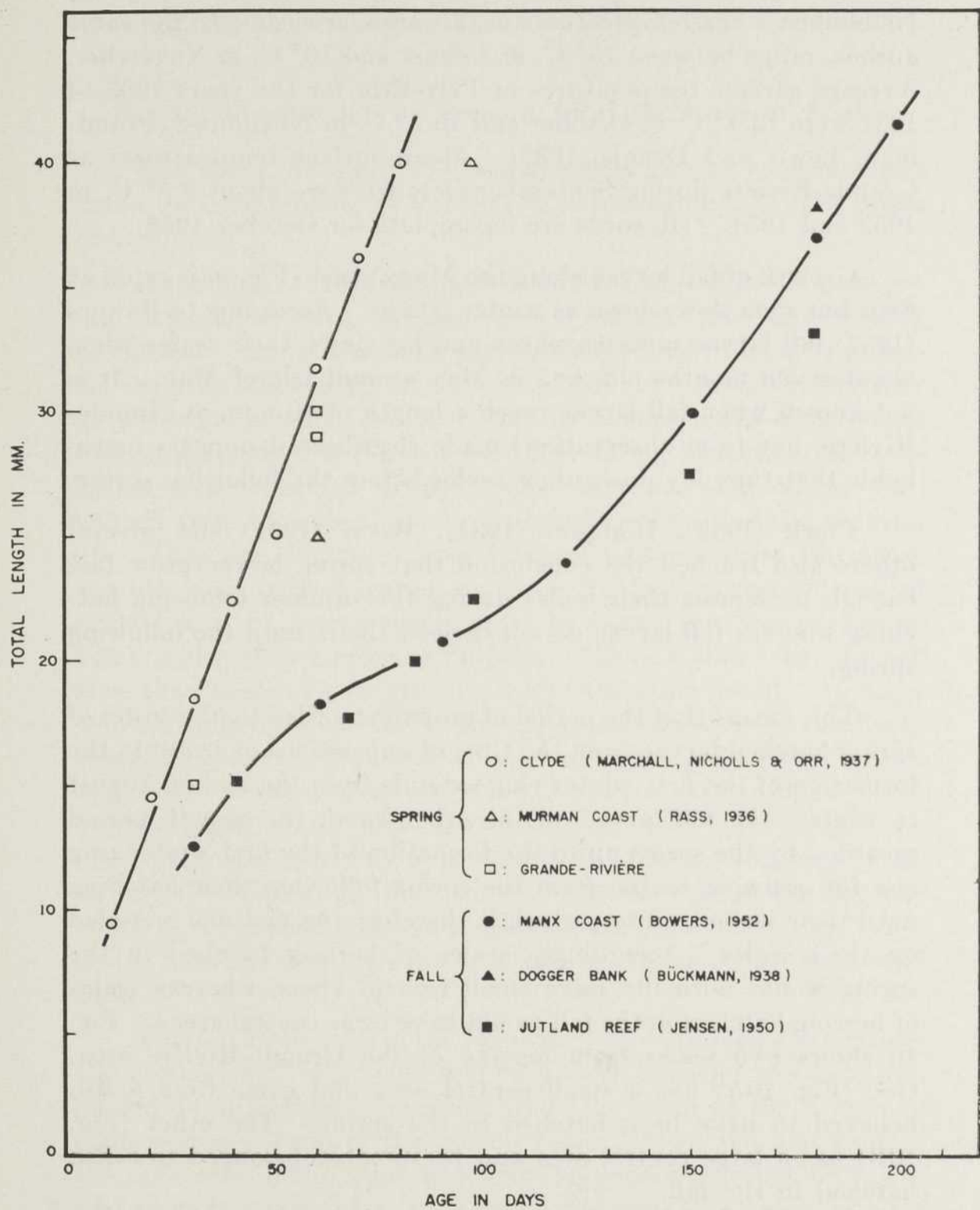


FIGURE 9.— Growth rate of spring and fall larvae. Data from various authors.

Manx larvae according to Bowers (1952) hatch in October and November. Sea temperatures in this area, according to the same author, range between 15° C. in August and 10° C. in November. Average surface temperatures at Port-Erin for the years 1903 to 1931 were 12.4° C. in October and 10.7° C. in November (Proudman, Lewis and Dennis, 1937). Mean surface temperatures at Grande-Rivière during September-October were about 9.5° C. in 1952 and 1954. (Records are incomplete for October 1953).

Growth of fall larvae along the Manx coast (Fig. 9) is rapid at first, but soon slows down as winter sets in. According to Bowers (1952) fall larvae metamorphose and lay down their scales when about seven months old, i.e., in May around Isle of Man. It is not known when fall larvae reach a length of 40 mm. at Grande-Rivière, but from observations made elsewhere it appears improbable that they lay down their scales before the following spring.

Clark (1933), Hodgson (1934), Wood (1951) and several others also reached the conclusion that spring larvae grow fast enough to deposit their scales during the summer following hatching whereas fall larvae do not deposit theirs until the following spring.

This means that the period of growth recorded by the scales of spring hatched larvae from the time of appearance of scales to the formation of the first winter ring extends from the end of August to winter. In fall larvae on the other hand, the growth period recorded by the scales up to the formation of the first winter ring is a full growing season from the spring following their hatching until their second winter, which is therefore the first one recorded on their scales. Accordingly scales of herring hatched in the spring would normally have small central areas, whereas scales of herring hatched in the fall would have large central areas. Fig. 10 shows two scales from herring of the Grande-Rivière area. One (Fig. 10A) has a small central area and came from a fish believed to have been hatched in the spring. The other (Fig. 10B) has a large central area and presumably belonged to a fish hatched in the fall.

A study of the central zone of scales of adult herring caught at Grande-Rivière was therefore undertaken with a view to determ-

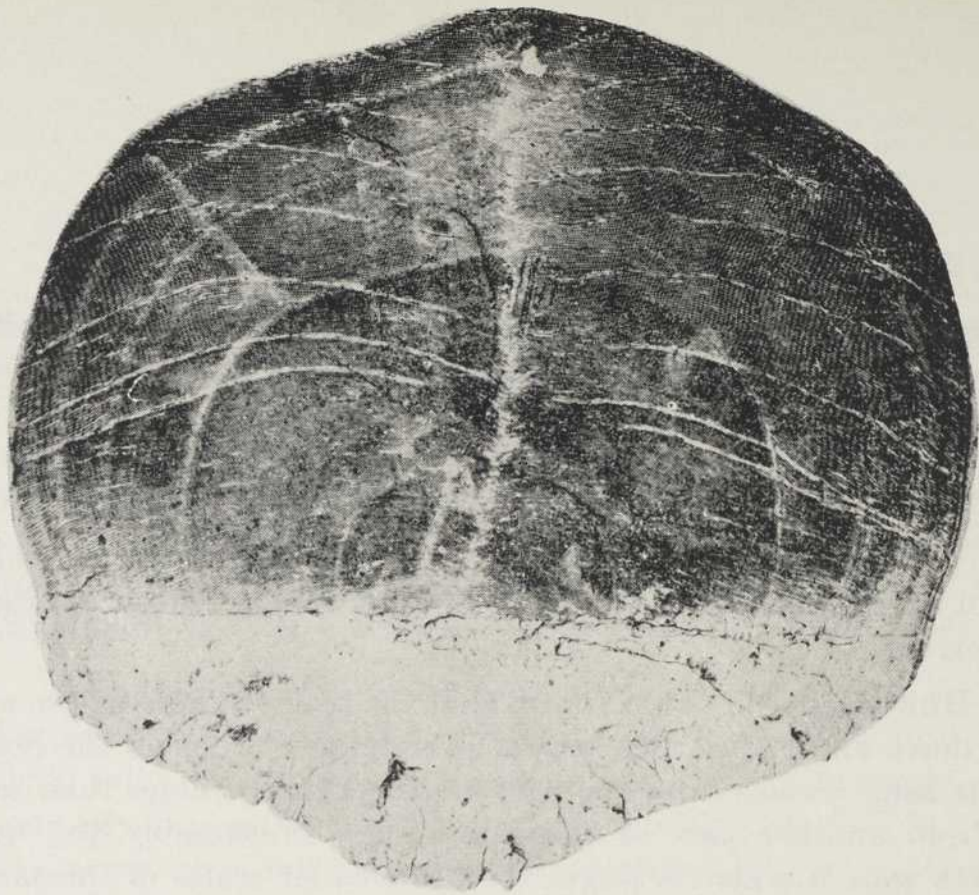
ining season of hatching and to finding out whether or not herring spawn at the same season as the one at which they were hatched.

B. Ratio of First to Second Growth Zone of Scales

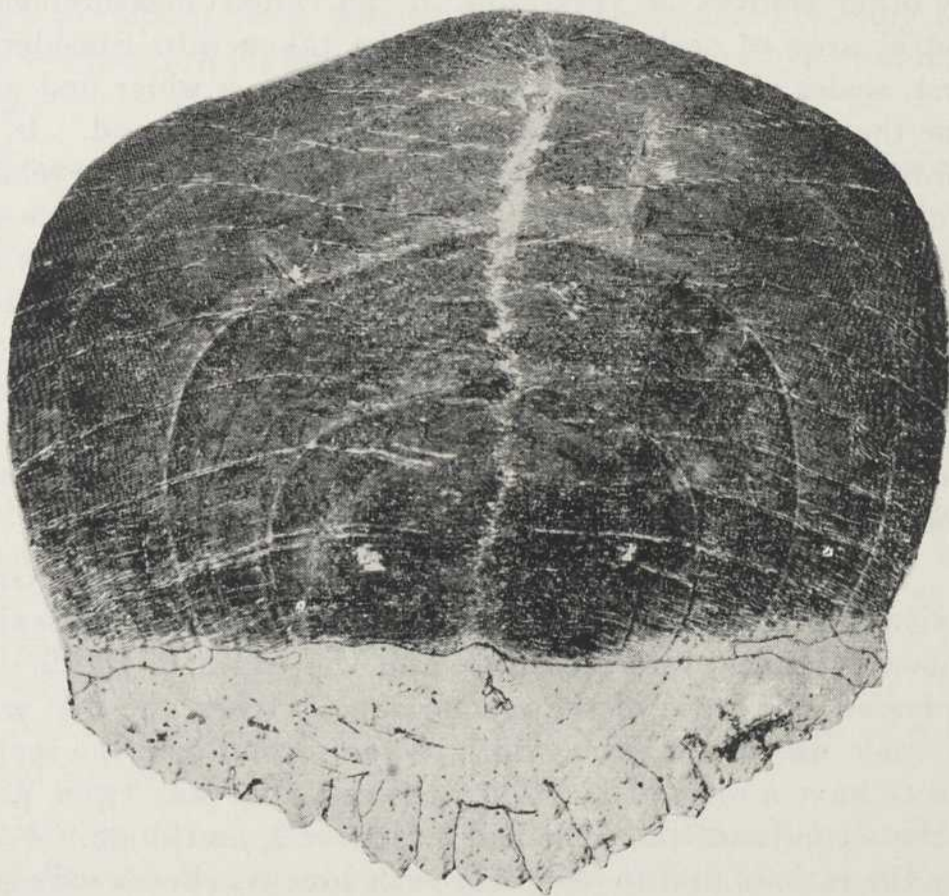
The use of absolute width of the first growth zone of scales is not entirely reliable as a means of determining season of origin of herring.

Huntsman (1918) has shown that the scales of herring are not laid down all at once, but appear in a definite order on the body of the fish. Scales from one part are accordingly larger than scales from another part of the same fish. Presumably the first growth zone is wider in larger than in smaller scales of the same individual. Most of the scales studied during the present investigation were collected always from the same area of the fish, namely from the side of the body, opposite the tip of the pectoral fin. They are therefore comparable in that respect. But there are other sources of variations in individual measurements of central area of scales which must be taken into consideration. First, scales of fast growing individuals have a wider first growth zone than those of slow growing fish of the same brood. In other words, two herring hatched in the spring may have, one a relatively small central area, the other a large one because they have grown at a different rate. Second, it is not always easy to draw a line between narrow and wide first growth zones. What seems narrow to one observer may appear large to another, and vice versa. In order to minimize these sources of error in interpreting the width of the central zones of herring scales, Andersson (1947) suggested that the first zone of the scales be compared to the second zone.

This has been done in the following way with scales of Grande-Rivière herring. First and second growth zones of the scale magnified 14 times were measured and the width of the first zone expressed as a ratio of the second zone. When the first zone of the scale was of the same width as the second one, the scale was said to have a ratio of 1. When the first zone was twice as wide as the second one, the scale had a ratio of 2, and so on. For brevity the ratio of first to second growth zone is called « *scale ratio* ».



A



B

FIGURE 10.—Scales of herring from Grande-Rivière. Scale A has a narrow central area and came from a fish presumably hatched in the spring. Scale B has a wide central area and came from a fish presumably hatched in the fall.

« *Proportion Board* » used in Determining Scale Ratio

A method was devised whereby scale ratio was calculated in one operation. The method makes use of a board called here « *proportion board* » (Fig. 11).

The data card with a magnified image of the scale is placed on the board with D, center of the scale, on line AB. The card is then moved along AB until E (first winter ring) coincides with line AC. Arm AN, made of cellulose acetate, and fixed at the end A, is then moved until line AN is on F, position of second winter ring.

The point N where line AN meets the curve MNO is the value of the ratio sought, read on the logarithmic scale at right. In the example chosen (Fig. 11) point is on the horizontal line corresponding to 1 on the logarithmic scale. Ratio of this particular herring scale is 1.

The curve MNO was determined empirically. It is the central portion of a curve of equation¹:

$$X = \frac{\log_{10} y^{-3}}{m \left(1 \times \frac{100}{y}\right)}$$

in which $m = -\text{tang. } \theta$
 $\theta = \text{angle BAC, constant}$

C. Scale Ratios of Grande-Rivière Herring

The study, reported in a previous section, of the time of the year at which scales are laid down and begin to record growth of the fish has led to the conclusion that a narrow central area of scales is characteristic of spring hatched herring and a wide one, characteristic of fall spawned herring. For reasons given previously, scale ratio is considered the best measure of width of central zone of the scales. Scale ratio therefore is an indicator of season of hatching.

1. We are indebted to Dr D. W. Allan, Department of Applied Mathematics, University of Toronto, who worked out this equation.

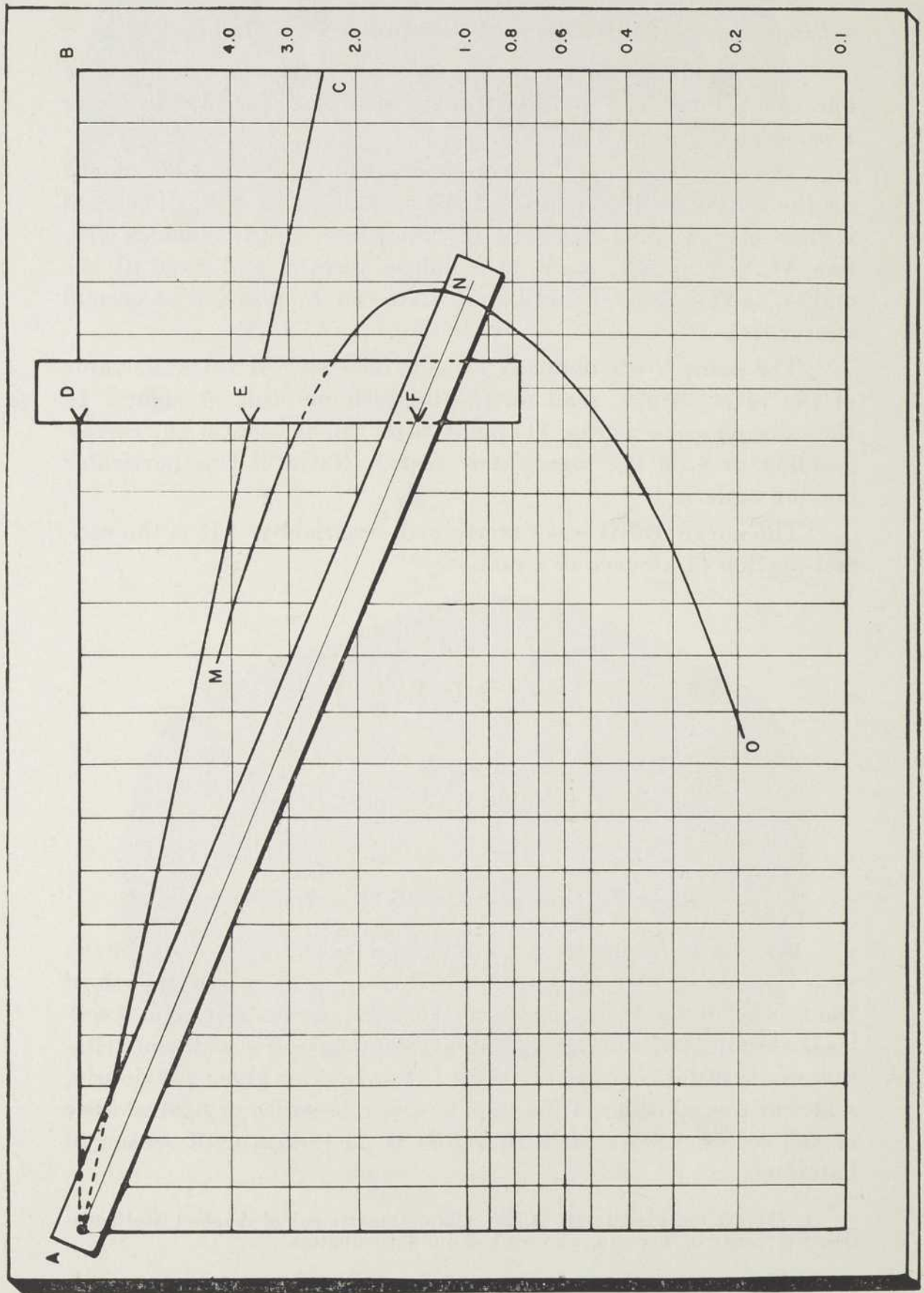


FIGURE 11.—“Proportion board” used in determining scale ratio of herring.

In order to find which values of scale ratio should be ascribed to spring hatched fish and which ones to autumn hatched herring, three steps were taken. First, the frequency distribution of scale ratios of spring and fall spawners at Grand-Rivière was studied. Second, scale ratios of herring from Grande-Rivière where two spawning seasons occur were compared with those of herring from areas where only one spawning season is present. Third, frequency distribution of scale ratios of both spring and fall spawners combined were analysed by means of probability paper.

1. *Comparison of Scale Ratios of Spring and Fall Spawners*

Scale ratios of 5,601 spring spawners and 1,379 fall spawners captured at Grande-Rivière during the fishing seasons of 1952, 1953 and 1954 were calculated. Frequency distributions of these ratios in spring and fall spawners are given in Fig. 12 A and B.

Scale ratios of spring spawners (Fig. 12A) range from .2 in scales with narrow central zone to 3.1 in scales whose first zone is more than 3 times as wide as the second zone. Two specimens with scale ratios of 3.3 and 3.5 respectively were not included in Fig. 12A. Scale ratios of fall spawners (Fig. 12B) have approximately the same range as those of spring spawners: .2 to 2.9.

Frequency distribution of scale ratios of spring and fall spawners were compared by means of analysis of variance (Snedecor, 1946). F. value of 1.11 falls below 3.84, F. value at the 0.5 probability level. Distributions of scale ratios of spring and fallspawners, therefore, do not differ. Both spring and fall spawners possess scales with narrow and scales with wide central areas in sensibly the same proportions.

2. *Comparison of Scale Ratios of Grande-Rivière Herring with those of Herring from other Areas*

It was mentioned previously that in some areas there is only one spawning season of the herring. A comparison of scale ratios of herring from Grande-Rivière where two spawning seasons occur with those of herring from areas where there is only one spawning season is likely to bring out differences which may help in ascribing values to scale ratios of fish hatched in the spring or in the fall at Grande-Rivière.

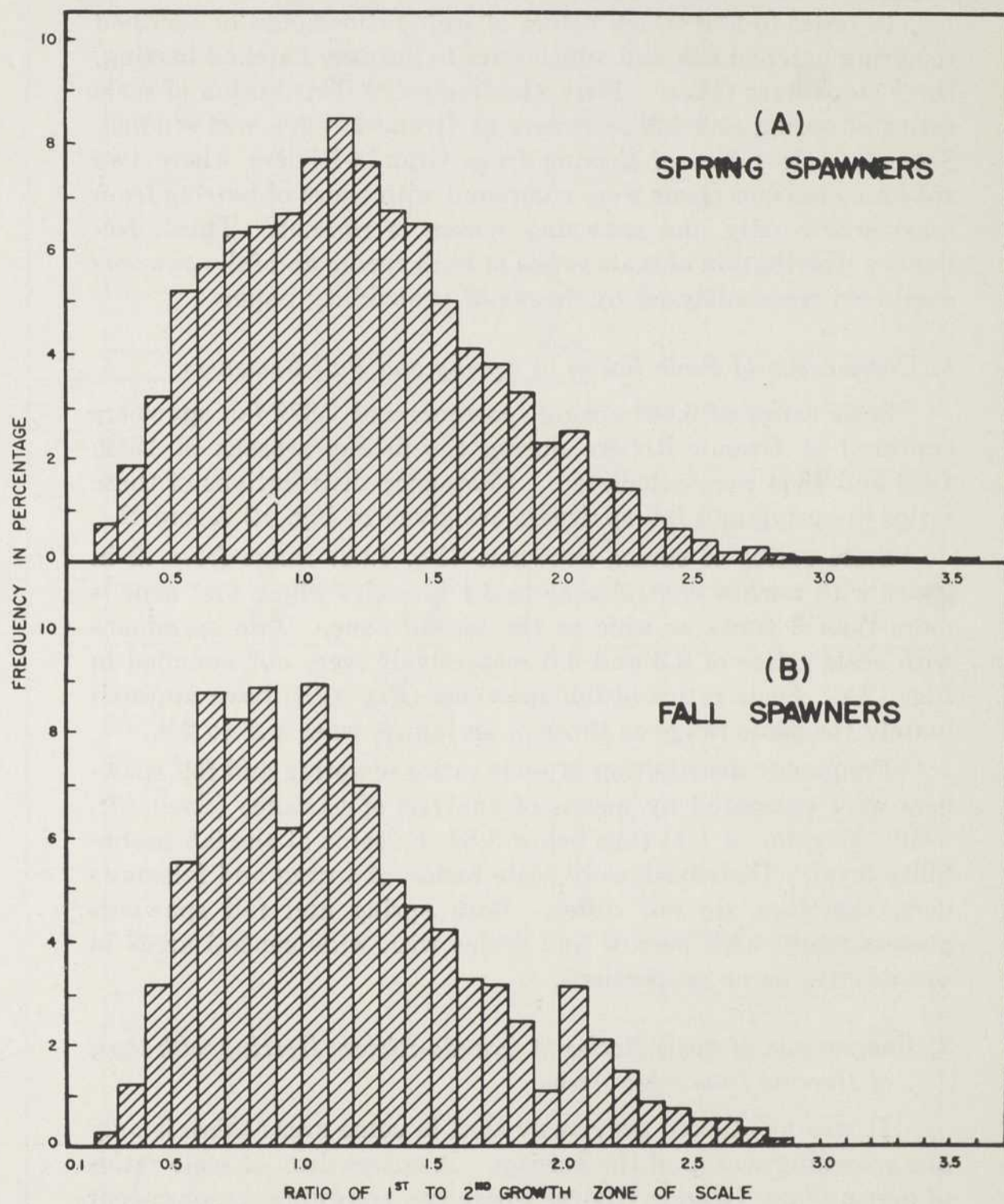


FIGURE 12.— Frequency distribution of scale ratios of spring and fall spawners at Grande-Rivière.

Among the localities with one spawning season only are Newfoundland (May-June), Norway (February-March) and Isle of Man (September-November). If, as generally agreed, herring populations are discrete units which do not mix to any great extent with other populations, herring spawning in the spring along the Newfoundland coast were themselves hatched in the spring, those caught in Norway were hatched in early spring and those caught along the Manx coast were hatched late in the fall. Herring from Bay of Chaleur on the other hand include fish hatched both in the spring and in the fall.

Scale ratios of 209 scales from Bay of Islands, Newfoundland (Jean, 1945) were determined. Similar ratios were calculated from Birtwistle's (1921) data on 54 herring of the Manx coast and from Hjort's (1910) data on 212 herring from the coast of Norway. The frequency distribution of these ratios, together with those of Grande-Rivière herring (spring and fall spawners combined) are given in Fig. 13.

Fig. 13 shows that scale ratios of Newfoundland, Norway and Manx herring hatched at one season of the year only are contained within much narrower limits than those of herring from Grande-Rivière hatched at two seasons, spring and fall. This indicates that scale ratio is a reliable indicator of growth of fish during their first year. Growth of fish hatched at one time of the year only would be included within a much narrower range than that of a mixture of fish hatched at two different times.

Fig. 13 also shows different modal values in distribution of scale ratios of herring from these areas. The modes are observed to move gradually to the right, i.e., to correspond to higher scale ratios in histograms A, B and C of Fig. 13. This is expected on the basis of season of hatching of these three groups of herring.

Newfoundland herring were hatched probably in June. Scales of these fish accordingly record growth from late summer until winter. Their scale ratios are relatively small and grouped about a mode of .8.

Norwegian herring being hatched earlier in the spring (eggs deposited in February-March) than Newfoundland herring, have a longer growing season before laying their first winter ring. Ac-

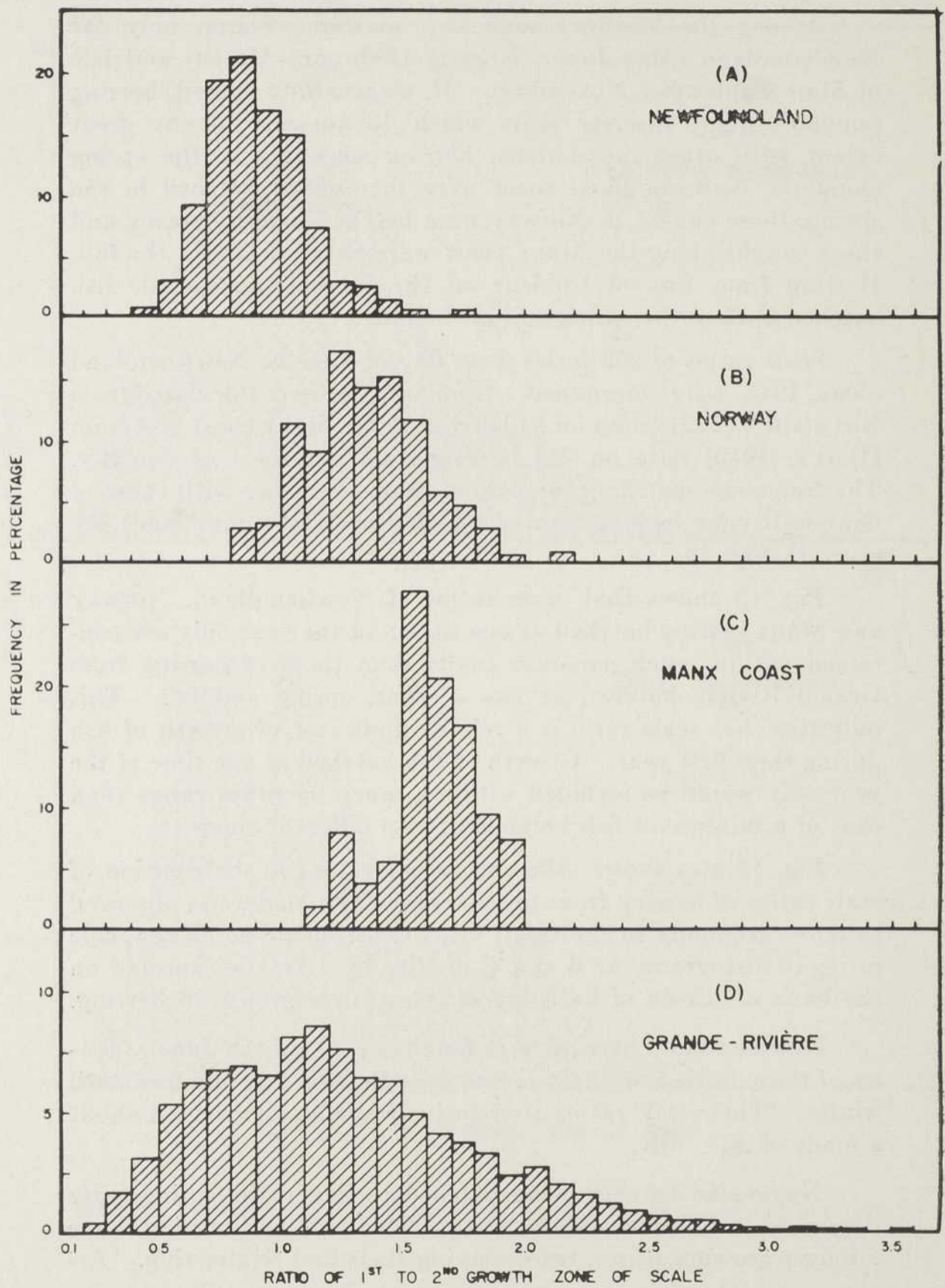


FIGURE 13.— Frequency distribution of scale ratios of herring from Newfoundland (Jean, 1945), Norway (Hjort, 1910), Isle of Man (Birtwistle, 1921) and Grande-Rivière.

Accordingly, scales from Norway herring (Fig. 13B) have wider central zones or larger scale ratios (mode at 1.2) than Newfoundland herring scales.

Manx herring being hatched late in autumn do not record their first winter on their scales (p. 34). The first growth zones of these scales represent a full growing season of the fish, from the spring following their hatching until their second winter of life. This longer growing season is reflected in a still larger scale ratio (mode at 1.5, (Fig. 13C) than either Newfoundland or Norwegian herring scales.

A study of scale ratios of Newfoundland, Norway and Isle of Man herring therefore shows that the longer the growing season before formation of first winter ring, the wider is the central zone of scales or the larger the scale ratio.

Scales of Grande-Rivière herring (Fig. 13D) belong to fish hatched both in the spring and in the fall. Distribution of scale ratios shows modes at .8, 1.1 and 2. As spawning takes place in the spring at the same time in Grande-Rivière as in Newfoundland (May-June), the growth period from hatching to formation of the first winter ring is comparable in spring spawned herring from Grande-Rivière and in herring from Newfoundland. Accordingly it is believed that the modal value of .8 observed in scale ratios of Grande-Rivière herring corresponds to the scale ratios of fish hatched in the spring.

Turning back to fall spawned herring from the Manx coast (Fig. 13C), it was found that their scale ratios were grouped about a mode of 1.5. Modes were observed at values of 1.1 and 2 (Fig. 13D) in Grande-Rivière scale ratios. Before ascribing any one of these modes to scales of herring hatched in the fall at Grande-Rivière, further analysis of the frequency distribution of scale ratios of these herring was made.

3. Analysis of Scale Ratios by means of Probability Paper

In order to be able to ascribe values to scale ratios of herring hatched in the spring and of herring hatched in the fall at Grande-Rivière, the frequency distribution of scale ratios (of spring and fall spawners combined) was analysed with probability paper (Fig.

14). The method was described in detail by Harding (1949) and will not be dealt with here.

As pointed out by Harding (1949) unimodal frequency distributions when plotted on probability paper result in a straight line, bimodal distributions in a sigmoid curve with one point of inflexion, and trimodal distributions in a double sigmoid curve with two points of inflection.

The sigmoid curve obtained in Fig. 14 with a point of inflexion corresponding to a value of about 80% on the abscissa would indicate that frequency distribution of scale ratios of Grande-Rivière herring is not trimodal but bimodal. According to this analysis histogram D of Fig. 13 is the resultant of two overlapping histograms. Means and standard deviations corresponding to the two parts of histogram D (Fig. 13) were determined graphically (Harding, 1949). Scale ratios of the left portion of histogram D, representing herring spawned in the spring, have a mean of $.92 \pm .33$. Ratios making the right portion of the histogram, representing herring spawned in the fall, have a mean value of $1.83 \pm .40$. This would indicate that the mode of 2 rather than of 1.1 belongs to scales of fall spawned herring.

When mean scale ratio of Newfoundland herring hatched in the spring is calculated by the ordinary method, a value of $.86 \pm .20$ is obtained. Manx herring hatched in the fall have a mean scale ratio of $1.56 \pm .19$. These values are close to the ones found by probability paper in Grande-Rivière herring scales.

D. Scale Ratios of Spring and Fall Hatched Herring

A comparison of scale ratios of herring from Grande-Rivière where two spawning seasons occur with those of herring from areas where only one spawning season is present, and an analysis by means of probability paper show that scale pattern is an indication of season of hatching.

Grande-Rivière herring scales with small central areas-mean ratio of .8 — .9, belong to fish hatched in the spring. Scales with large central areas-mean ratio of approximately 1.8, belong to fish hatched in the fall.

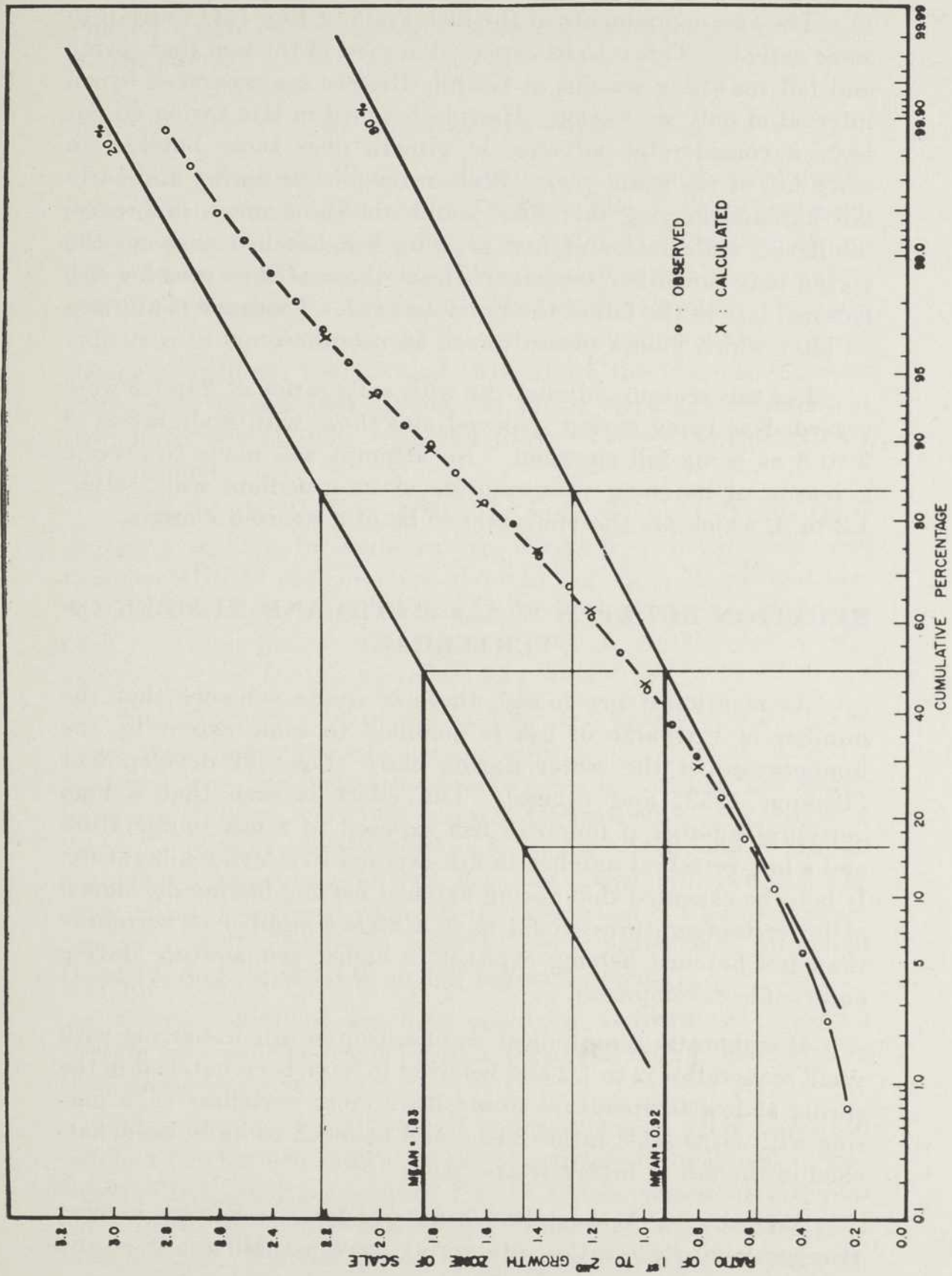


FIGURE 14.— Analysis of frequency distribution of scale ratios of Grande-Rivière herring by means of probability paper.

The two components of the histogram of Fig. 13D overlap to some extent. This is to be expected in view of the fact that spring and fall spawning seasons at Grande-Rivière are separated by an interval of only six weeks. Herring hatched in late spring do not have a considerable advance in growth over those hatched in early fall of the same year. Scale ratios of late spring and early fall hatched herring therefore would not show much difference. Similarly, scale ratios of fast growing fish hatched early in the spring may not differ very much from those of slow growing fish hatched late in the fall of the previous year. Evidence is presented later which points towards such an occurrence.

For this reason, only herring with scale ratios of .2 to 1.2 were regarded as being spring spawned and those with scale ratios of 2 to 3 as being fall spawned. No attempt was made to ascribe a season of hatching to specimens of intermediate scale ratios, 1.2 to 2, which are therefore said to be of a « mixed » origin.

RELATION BETWEEN SCALE RATIO AND NUMBER OF VERTEBRAE

As mentioned previously, there is ample evidence that the number of vertebrae of fish is modified to some extent by the temperature of the water during early stages of development (Taning, 1952, and others). The effect is such that a high vertebral number is found in fish exposed to a low temperature and a low vertebral number in fish exposed to a high temperature. It is to be expected that spring hatched herring having developed at lower temperatures would have a higher number of vertebrae than fall hatched herring exposed to higher temperature during embryonic development.

If scale ratio is an indication of season of origin, herring with small scale ratios .2 to 1.2 and believed to have been hatched in the spring at low temperature would have more vertebrae than herring with large scale ratios 2 to 3 and believed to have been hatched in the fall at higher temperature.

Accordingly the vertebral counts of Grande-Rivière herring grouped from scale ratios into spring spawned, fall spawned and

« mixed » were determined first in spring spawners and second in fall spawners.

A. Spring Spawners

Since vertebral number is influenced by temperature during early development and since the temperature under which each class develops is almost certain to be different from that of any other year-class (Tester, 1938), it is necessary to compare vertebral counts only among individuals of the same year-class, i.e., individuals with equal number of winter rings on their scales. Year-classes of 1946-47, 1947-48 and 1949-50 are the year-classes most abundantly represented among the spring spawners captured at Grande-Rivière in 1952, 1953 and 1954. These year-classes only were studied.

Each of the three year-classes were subdivided into three groups according to scale ratio. Frequency distribution and mean number of vertebrae are given in Fig. 15. Means and percentage frequencies are given separately for yearly samples of each year-class (i.e., 4 winter rings in 1952, 5 winter rings in 1953 and so on), and for the year-class as a whole.

Fig. 15 shows that in the case of each yearly sample of the three year-classes studied, herring with scale ratios of .2 to 1.2 (stippled line) and believed to have been hatched in the spring have a high mean vertebral count. Herring with scale ratios of 2 to 3 (solid line) and regarded as having been hatched in the fall at higher temperature have a low mean vertebral count. The same result is obtained when all the specimens of a year-class are grouped (56.61, 56.67 and 56.68 in spring hatched as compared to 56.17, 56.58 and 56.48 in fall hatched herring).

As no season of hatching could be ascribed to « mixed » herring with scale ratios of 1.2 to 2, these will not be dealt with in this comparison.

The differences in vertebral counts between spring and fall hatched herring are shown by the shapes of the polygons. The shape of frequency polygons of Fig. 15 shows consistent differences between spring spawned (stippled line) and fall spawned (solid line) herring. Fig. 15 shows that the proportion of herring with

FREQUENCY, PER CENT (1 INTERVAL = 20%)

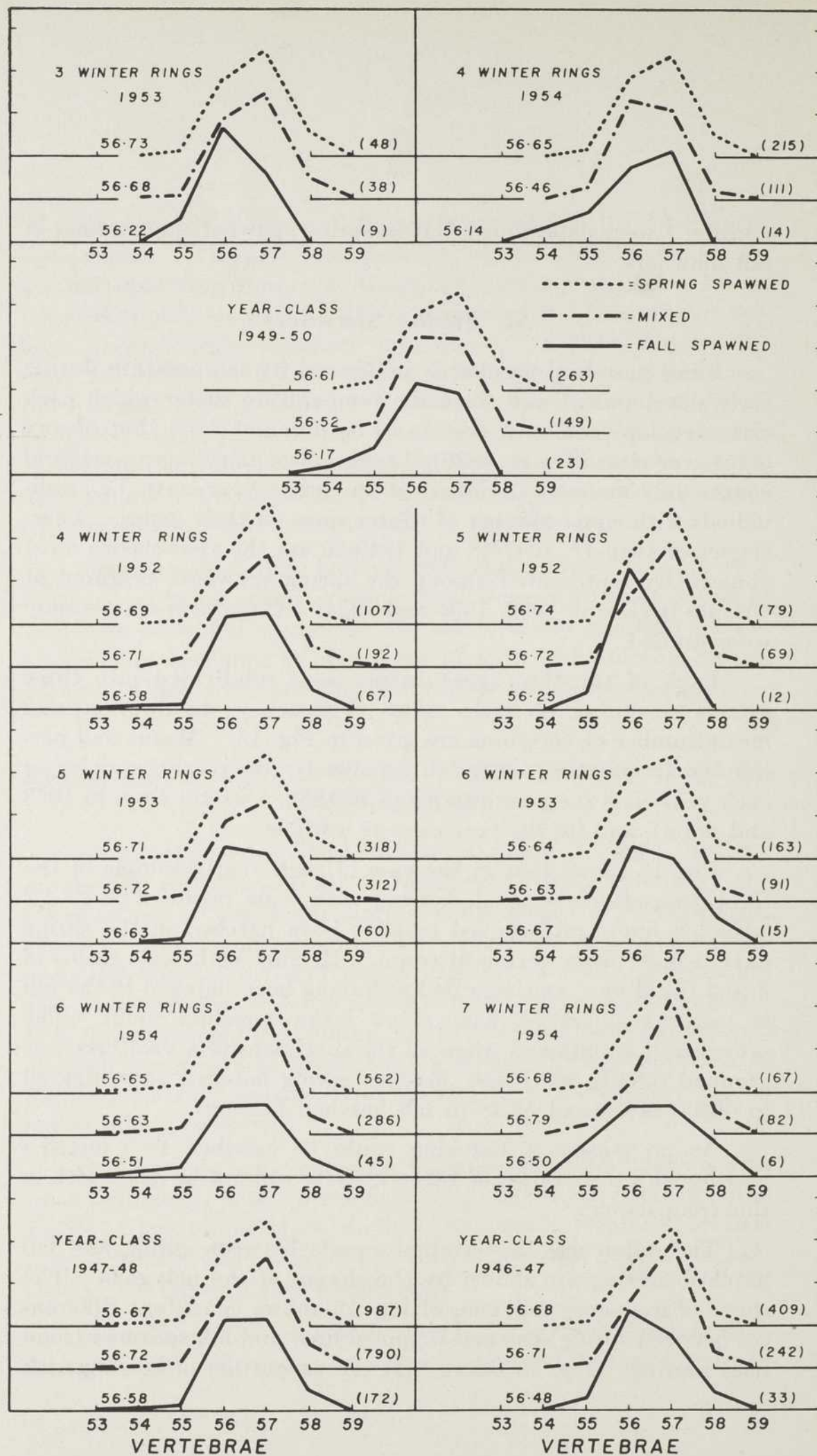


FIGURE 15.—Frequency distribution of vertebral counts of spring spawners grouped according to season of hatching. (Stippled line: spring spawned; solid line: fall spawned; broken line: "mixed").

56 and with 57 vertebrae is responsible for the shape of the polygons. Among herring hatched in the spring, more individuals with 57 than with 56 vertebrae are found. In herring hatched in the fall, the frequencies of 56 and 57 vertebrae are about the same: there are as many individuals with 56 as there are with 57 vertebrae in fall spawned herring of the year-classes considered. For this reason, differences in frequencies of 56 and 57 vertebrae, rather than mean vertebral counts, were analysed statistically by means of X^2 . The probability that differences of this order in the vertebral count of spring and fall hatched herring are due to chance is less than 1%

Two conclusions, at this point, are drawn from the foregoing analysis of spring spawners. First, it appears that season of hatching of herring can be determined from the scales. Vertebral counts confirm the deductions made from scale ratios as to season of hatching of herring. Second, spring spawning populations are composed of fish hatched both in the spring and in the fall. A study of the frequency distribution of scale ratios in spring spawners, made in a previous section (Fig. 12A), had also indicated that this was the case. Scales with small as well as large central areas were found among spring spawners.

Cumulative percentages of frequency distribution of scale ratios in spring spawners indicate that about 52% of spring spawners have a scale ratio of .2 to 1.2 (spring hatched) and 8% have a scale ratio of 2 to 3 (fall hatched), the remaining 40% belonging to fish of « mixed » origin. It therefore appears that at least 8% of the spring spawners were hatched in the fall and that herring do not necessarily spawn at the same season as the one at which they were hatched.

B. Fall Spawners

In order to make the comparison between spring and fall spawners uniform, the same year-classes of 1946-47, 1947-48 were studied in the fall spawners. The year-class of 1949-50 considered in the previous section was not represented among the fall spawners in large enough numbers to make it worth including here.

As in the case of spring spawners, scale ratios of fall spawners were subdivided into three groups: small, intermediate and large. Frequency distribution and mean number of vertebrae were established for each category. The results are represented graphically in Fig. 16.

The lower part of Fig. 16 referring to year-classes as a whole indicates that fish with small central area of scales (stippled lines) and believed to have been hatched in the spring have the same vertebral means (56.66 and 56.62) when found among fall spawners (Fig. 16) as when found among spring spawners (56.61, 56.67 and 56.68) (Fig. 15). Frequencies of 56 and 57 vertebrae in spring spawned herring spawning in the spring was compared by means of X^2 to those of spring spawned herring spawning in the fall and found to be identical.

This means that spring spawned herring characterized by a small scale ratio and a high vertebral count are found among fall spawners as well as among spring spawners. This supports the conclusion reached on the basis of the study of both scales and vertebrae that herring hatched in the spring do not necessarily spawn in the spring, but that some of them may also spawn in the fall.

Herring with wide central areas of scales of large scale ratios (solid lines, lower polygons of Fig. 16) have higher vertebral means (56.80 and 56.79) when found among fall spawners (Fig. 16) than when found among spring spawners (56.17, 56.58 and 56.48) (Fig. 15). Frequencies of 56 and 57 vertebrae in fish with large central areas of scales differ significantly in fall spawners and in spring spawners.

This anomaly observed in herring with large scale ratios and spawning in the fall may be due to sampling error, but since it is repeated in three out of six yearly samples (Fig. 16), a real difference is likely to exist.

The finding of fall spawning fish with large scale ratios and high vertebral counts may be explained on the basis that at least some had been hatched very early in the spring when water temperature was at its lowest, thus resulting in high vertebral counts. It is possible that some fish hatched early in the spring grow at

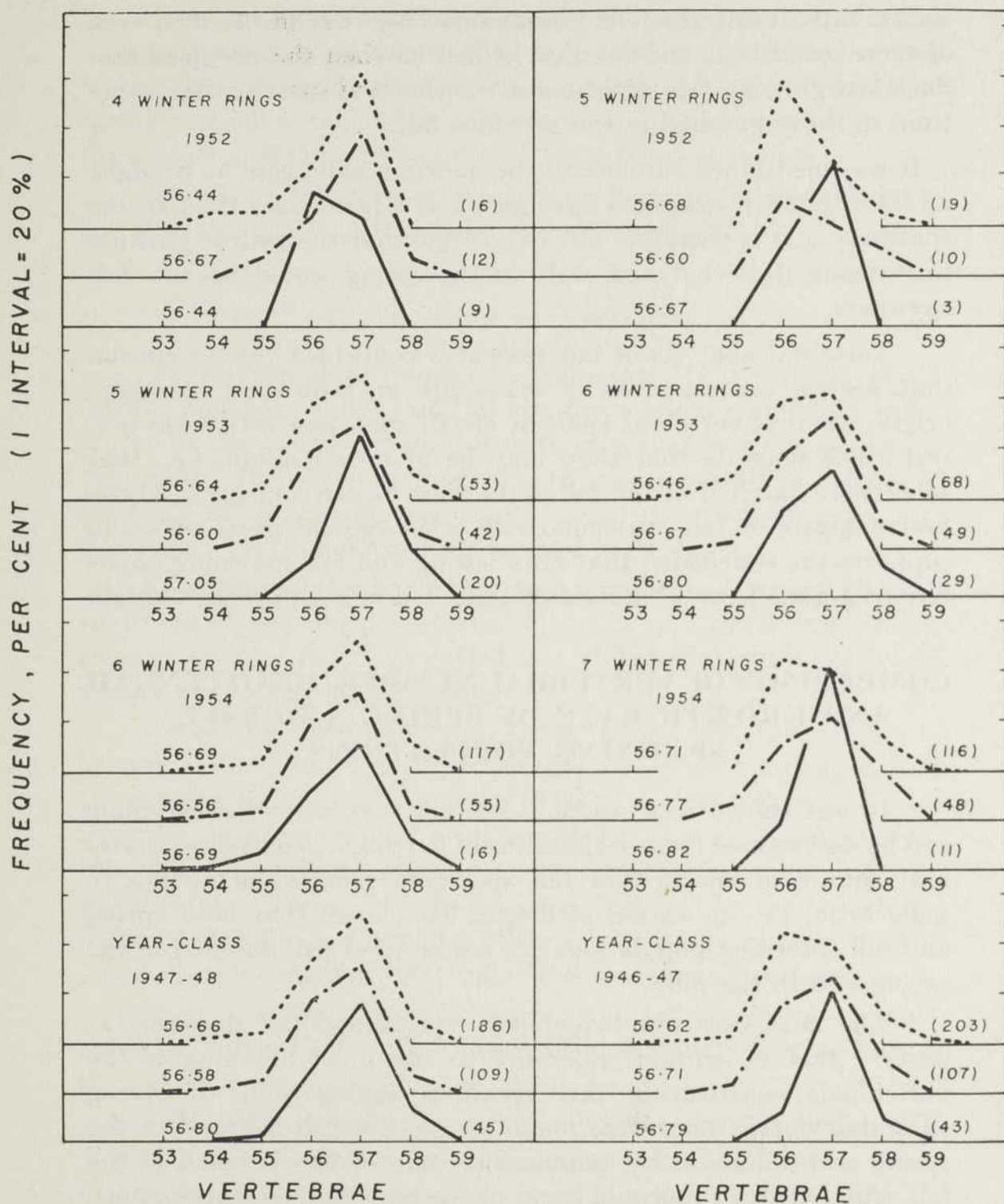


FIGURE 16.— Frequency distribution of vertebral counts of fall spawners grouped according to season of hatching. (Stippled line: spring spawned; solid line: fall (?) spawned; broken line: "mixed").

such a rate during their first summer of life that the central area of their scales is as wide as that of fish hatched the previous fall. Such fast growing fish might mature earlier and spawn at the same time as those hatched in the previous fall.

It was mentioned earlier and the question will again be brought up later that fall spawners have grown at a faster rate than spring spawners. It is therefore not impossible that the fastest growing fish among those hatched early in the spring would become fall spawners.

Vertebral analysis of fall spawners confirmed the conclusion that narrow central areas of scales are an indication of spring origin, whereas vertebral analysis of fall spawners with wide central areas suggests that they may be of mixed origin, i.e., that some were hatched in the fall and others in early spring. Vertebral analysis of fall spawners with wide central areas of scales supports the conclusion that both spring and fall spawning populations are made up of individuals hatched in both spring and fall.

COMPARISON OF VERTEBRAL NUMBER, HEAD LENGTH AND GROWTH RATE OF SPRING AND FALL SPAWNING POPULATIONS

It was shown in a previous section that season of hatching can be determined from scale ratios of herring. Analysis of vertebral counts of spring and fall spawners grouped according to scale ratio, i.e., to season of origin, has shown that both spring and fall spawning populations are made up of fish hatched in the spring and in the fall.

The next step was to compare spring and fall spawners as units — that is, without reference to season of hatching of the individuals constituting the spawning aggregation. If spring spawning populations were made up only of fish hatched in the spring and fall spawning populations only of fish hatched in the fall, differences in morphological characters like vertebral count, head length and rate of growth would be expected. The two groups, spring and fall spawners, would have then developed at different times of the year and under different conditions of water temperature.

If on the other hand spring and fall spawning populations were both made up of fish hatched in the spring and of fish hatched in the fall, their differences would be less marked, especially if spring and fall hatched fish are present in about the same proportions among spring spawners and among fall spawners.

Spring and fall spawners were therefore compared as to number of vertebrae, length of head and rate of growth.

A. Number of Vertebrae

Several European workers, Einarsson (1951, 1952), Wood (1936), Johansen (1924) and others have found significant differences in the mean vertebral counts of spring and fall spawners. Einarsson (1952) for instance found mean vertebral counts of about 57.22 in several samples of spring spawners and of 56.95 in autumn (July) spawners of Iceland in 1950.

An extensive study of vertebral numbers of spring and fall spawners of Bay of Chaleur by Tibbo et al. (1954) and by the present author, failed to reveal any difference in the vertebral means of the two populations.

For reasons mentioned previously (p. 53) vertebral counts of herring from Grande-Rivière were compared only among fish of the same year-classes. Since the 1947-48 and 1946-47 year-classes were the most abundant of those sampled at Grande-Rivière during this study, vertebral counts were compared within these two year-classes only. These year-classes were identified by the occurrence respectively of 4 and 5 winter rings in specimens caught in 1952, 5 and 6 winter rings in 1953 and 6 and 7 winter rings in 1954.

Mean vertebral counts of spring and fall spawners are compared in Table VIII. The means of each yearly sample and of the year-classes as a whole are given.

Table VIII indicates very little difference in vertebral counts of spring spawners as compared to those of fall spawners, either in the yearly samples or in the year-classes as a whole. It is seen that the means of the whole year-classes are close to 56.67 in all cases. Analysis of variance (Snedecor, 1946) shows that spring and fall spawners when considered as units without reference to season of hatching do not differ with respect to vertebral counts.

Tibbo et al (1954) counted vertebrae of some five thousand spring and fall spawners of Bay of Chaleurs during the years 1946 to 1948 and they also came to the conclusion that spring and fall spawners did not differ in mean vertebral count.

As vertebral count is considered by most students of herring as the most reliable character in identifying herring populations, the similarity of vertebral counts of spring and fall spawners of Bay of Chaleurs indicates that the two populations are of similar composition.

This similarity can only be explained on the basis that both spring and fall spawning aggregations are a mixture of fish hatched in the spring and in the fall in a proportion which is about the same in spring and fall spawners.

B. Head Length

Heincke (1898) distinguished herring populations on the basis of head length among other characters. Somov (1938) subdivided herring of the Barents Sea into three groups differing in length of head and structure of opercular bones. Jean (1945) has shown

TABLE VIII
MEAN VERTEBRAL COUNTS OF SPRING AND FALL SPAWNERS
OF THE 1947-48 AND 1946-47 YEAR-CLASSES, WITHOUT
REFERENCE TO SEASON OF HATCHING

Number of specimens in parentheses

	<i>Spring spawners</i>	<i>Fall spawners</i>
<i>1947-48 year-class</i>		
1952 — 4 winter rings	56.68 (366)	56.51 (37)
1953 — 5 “ “	56.71 (690)	56.70 (115)
1954 — 6 “ “	56.66 (893)	56.65 (188)
Whole year-class	56.68 (1949)	56.65 (340)
<i>1946-47 year-class</i>		
1952 — 5 winter rings	56.71 (160)	56.66 (32)
1953 — 6 “ “	56.64 (269)	56.60 (146)
1954 — 7 “ “	56.71 (255)	56.73 (175)
Whole year-class	56.68 (684)	56.67 (353)

that spring spawners from the estuary of the St. Lawrence had smaller heads than spring spawners from Bay of Chaleur. He related these differences to water temperatures in the two areas.

Head length was compared, without reference to year-classes, in spring and fall spawners caught at Grande-Rivière in 1952 (Jean, 1953). Measurements are given in Table IX.

TABLE IX
COMPARISON OF HEAD LENGTH OF SPRING AND FALL SPAWNERS
CAUGHT AT GRANDE-RIVIÈRE IN 1952 (From Jean, 1953)

Number of specimens in parentheses

<i>Total length cm.</i>	<i>Mean head length, mm.</i>	
	<i>Spring spawners</i>	<i>Fall spawners</i>
23 — 23.9	46 (6)	45 (2)
24 — 24.9	47 (7)	46 (2)
25 — 25.9	49 (22)	48 (2)
26 — 26.9	51 (63)	—
27 — 27.9	52 (198)	51 (2)
28 — 28.9	53 (143)	53 (3)
29 — 29.9	55 (70)	55 (19)
30 — 30.9	57 (92)	56 (36)
31 — 31.9	58 (127)	57 (36)
32 — 32.9	59 (92)	58 (17)
33 — 33.9	62 (24)	61 (11)
34 — 34.9	63 (5)	63 (13)
35 — 35.9	64 (1)	65 (10)
36 — 36.9	67 (3)	65 (15)

These results were not submitted to statistical analysis because it was felt that the similarity in head length was close enough to justify the conclusion that spring and fall spawners did not differ with respect to head length within the range of body length studied. Head length data therefore support the conclusion based on vertebral counts that spring and fall spawners are of identical composition.

C. Growth Rate

Although spring and fall spawners at Grande-Rivière are identical with respect to vertebral count and relative length of

head, they differ in rate of growth, fall spawners having grown at a faster rate than spring spawners.

Cieglewicz and Posadzki (1947) have shown that fall spawners of the Baltic Sea were on the average more than 2 cm. longer than spring spawners of the same age. Tibbo and Day (1948) found that fall spawners of Bay of Chaleur were larger (in some cases by 3 cm.) than spring spawners of the same age. They concluded that fall spawners have grown at a faster rate than spring spawners.

The mean total length of spring and fall spawners from 2 to 14 years of age caught at Grande-Rivière in 1952 (Jean, 1953) were compared. The results are given in Table X. Table X shows that fall spawners at Grande-Rivière are larger than spring spawners of the same age. In the case of 3- and 4- year old fish, this difference amounts to 3 cm. In older fish, differences are not so large but still remain of the order of 2 cm. This indicates that the difference in growth rate is more pronounced in younger than in older fish and that the advance in growth of fall spawners is acquired during their first years. This was also Cieglewicz and Posadzki's (1947) opinion. They wrote: « the greatest difference (in growth of spring and fall spawners of the Baltic) is to be observed in the first year of life amounting to 2.8 cm.»

As mentioned previously, these authors were of the opinion that fall spawners have been hatched in the fall and spring spawners in the spring. They explained the larger size of fall spawners on the basis of season of hatching: fall spawners have had a longer growing period than spring spawners before the first winter ring is laid down.

Evidence gathered during the present investigation indicates that this argument is not valid. Another explanation has to be sought. Because fall spawners are caught later in the season than spring spawners, some difference in size is to be expected. Fall spawners at Grande-Rivière are caught in August and September. They have an advance of nearly a complete growing season over spring spawners caught the previous May or June. Herring with 4 winter rings, as an example, are expected to be larger in August than fish with the same number of winter rings were in May or

TABLE X

RATE OF CROWTH OF SPRING AND FALL SPAWNERS CAUGHT
AT GRANDE-RIVIÈRE IN 1952 (From Jean, 1953)

Number of specimens in parentheses

Age years	Total length, cm.			
	Spring spawners		Fall spawners	
2	18.8	(18)	24.4	(4)
3	24.5	(41)	27.4	(5)
4	27.4	(510)	30.5	(54)
5	28.7	(211)	31.1	(43)
6	30.5	(93)	31.8	(17)
7	31.3	(136)	33.4	(13)
8	31.7	(140)	34.9	(6)
9	32.9	(36)	35.6	(14)
10	33.8	(9)	34.2	(7)
11	34.7	(5)	35.9	(8)
12	35.7	(1)	37.3	(3)
13	36.2	(2)	37.1	(1)
14	36.3	(1)	—	—

June. Differences of 2 cm. in size of spring and fall spawners, however, are larger than those expected on the basis of differences in time of capture since, from the fifth year on, herring grow at a rate of about 1 cm. per year (Table X).

The only explanation left to account for larger size of fall spawners is that season of spawning in herring is determined largely by the rate at which herring grow during the first year of their lives. Fast growing fish either of the spring or of the fall brood would become fall spawners, whereas slow growing fish would become spring spawners. This hypothesis would account for the faster rate of growth observed in fall spawners. The vertebral analysis of fall spawners with wide central areas of their scales had already indicated that fast growing fish hatched in the spring may become fall spawners.

In conclusion, a study of spring and fall spawners at Grande-Rivière has shown that these two populations are identical with respect to vertebral count and length of head, two characters of recognized value in separating herring populations. Differences

in size of spring and fall spawners are explained on the basis that rate of growth during early life may determine season of spawning.

Similarity of the two populations excludes the possibility of spring spawning aggregations being made up exclusively of fish hatched in the spring, and fall spawning populations being made up of fish hatched in the fall.

Instead, the two spawning populations are each a mixture of fish hatched in the spring and of fish hatched in the fall.

DISCUSSION AND CONCLUSIONS

A study of water temperature at Grande-Rivière has shown that herring eggs deposited in the spring develop at lower temperature than eggs deposited in the fall. As a result, a higher vertebral count is expected in spring than in fall hatched herring.

Spring larvae on the other hand are exposed to higher temperatures than fall larvae during the first months of their lives, resulting during the first year in faster growth in spring than in fall larvae. It is believed that herring hatched in the spring lay down their scales in time to record their first winter on their scales, whereas herring hatched in the fall do not form their scales until the following spring, so that the first winter recorded on their scales is in reality their second winter of life.

The central area of scales is an indication of the growth of the fish up to the formation of the first winter ring. Scales with narrow central area are therefore considered to belong to spring hatched fish, and scales with wide central areas belong to fall hatched fish. This conclusion was confirmed by the fact that, at least in spring spawners of the Grande-Rivière area, fish with narrow central zones of scales believed to have been hatched in the spring at low temperature have more vertebrae than fish with large central zones believed to have been hatched in the fall at higher temperature.

Cumulative percentages of frequency distribution of scale ratios in spring spawners indicate that some 52% of spring spawners had been hatched in the spring and about 8% had been hat-

ched in the fall. These are minimum figures. The remaining 40% were ascribed to herring of « mixed » origin whose season of hatching could not be definitely determined from the scales.

Evidence based on the relative number of spawners caught in the spring and in the fall at Grande-Rivière and on the records of commercial landings of herring led to the belief that total production of larvae is larger in the spring than in the fall even if production per unit of time appears to be larger in the fall than in the spring. Greater production of larvae in the spring would account for a larger number of spring hatched fish on the spawning grounds. No data are available on differential rate of mortality of spring and fall larvae at Grande-Rivière. It was shown, however, that water temperatures were decreasing at the time fall larvae hatched. Food in the fall is becoming less abundant and winter sets in before the larvae have time to grow appreciably. Environmental conditions are therefore less favourable to survival in the fall than in the spring. A larger number of spring than fall hatched larvae would therefore reach maturity and spawn.

Analysis of season of origin of fall spawners appeared to yield somewhat contradictory results from those obtained from an analysis of season of origin of spring spawners. However, this difference can be explained if it is assumed that some of the fish with wide central areas on their scales were hatched from eggs spawned very early in the spring, and therefore had a full summer's growth before their first winter ring is laid down. This would explain the combination of wide central zone with high vertebral number. This explanation would also account in part for the fact that rate of growth is faster in fall spawners than in spring spawners. It is not impossible that rate of growth during the first year determines to some extent whether a fish becomes a spring or a fall spawner.

That herring may spawn at a different season than the one at which they had been hatched is further substantiated by the fact that spring and fall spawners at Grande-Rivière cannot be separated on the basis of morphological characters such as vertebral count and length of head. In view of the influence of temperature during development and early life on these characters, if spring spawning populations were made out entirely of spring spawned

fish, they would differ in these respects from fall spawning populations made out exclusively of fall spawned fish.

The similarity of morphological characters in the two spawning populations can be achieved only if the two have similar composition, that is, if both spring and fall spawning populations are made up of fish hatched in the spring and of fish hatched in the fall.

It can therefore be concluded that in spite of the fact that the two units making up Bay of Chaleur herring population spawn at different times of the year, they are not reproductively isolated since spring spawned and fall spawned fish mix freely on the spawning grounds.

SUMMARY

1. Two spawning seasons of the herring occur at Grande-Rivière, Bay of Chaleur, Que., one in the spring from May 1 to June 30, the other in the fall from August 15 to September 30. Water temperature during spawning range from 5° to 12.9° C. (mean around 7.5° C.) in the spring and from 16.6° to 10° C. (mean around 12.5° C.) in the fall.

2. Development of the first eggs deposited takes place in the spring at temperatures averaging from 3.7° to 5.3° C., and in the fall at an average temperature of about 12° C. Incubation takes from 32 to 35 days in early spring and from 10 to 15 days in early fall.

3. It was shown for other areas where temperature conditions appear to be similar to the ones observed at Grande-Rivière, that spring larvae grow at a faster rate than fall larvae. As a result, spring larvae at Grande-Rivière are believed to reach a length of 40 mm. and lay down their scales in August and record their first winter ring on their scales. Fall larvae do not form their scales until the spring of the following year and do not record their first winter on their scales.

4. The amount of growth before formation of the first winter ring is greater in fall spawned than in spring spawned herring resulting in large central areas on scales of fall spawned fish and

in small central areas on scales of spring spawned fish. By comparing width of first and second growth zones of scales, the « scale ratio » was determined and used as an indication of season of origin of adult fish.

5. The time of hatching determined from the scales was further confirmed by a study of vertebral numbers. Among spring spawners, fish with narrow central areas of scales and believed to have been hatched in the spring have a high vertebral count. Herring with wide central areas of scales and believed to have been hatched in the fall have a low vertebral count.

6. Among fall spawners, fish with wide central areas of scales have more vertebrae than fish with small central areas, a condition opposite to the one observed in spring spawners. This condition is believed to characterize fish hatched from eggs spawned very early in the spring when the water temperature was low. They would have a full summer's growth before recording their first winter ring.

7. Herring therefore do not necessarily spawn at the same season as the one at which they have been hatched. As a result, both spring and fall spawning populations are made up of fish hatched in the spring and of fish hatched in the fall.

8. The spring spawning populations at Grande-Rivière are composed of approximately 52% of herring hatched in the spring and of at least 8% of herring hatched in the fall. The remaining 40% are said to be of « mixed » origin, since no season of hatching could be ascribed to them.

9. Spring and fall spawning populations at Grande-Rivière have identical mean vertebral counts and similar relative length of head. This similarity in morphological characters of the two populations confirms the belief that both spring and fall spawners are of mixed origin — some hatched in the spring and some in the fall.

10. It is concluded that spring and fall spawning populations at Grande-Rivière are not two reproductively isolated populations, but are parts of one and the same population.

REFERENCES

- AASEN, O.
1952 The Lusterfjord herring and its environment. Rep. Norweg. Fish. Invest., 10(2): 1-63.
- ALLEN, E. J.
1897 Reports on the present state of knowledge with regard to the habits and migrations of the mackerel (*Scomber scomber*). J. Mar. biol. Ass. U. K., n. s. 5: 1-40.
- ANDERSSON, K. A.
1947 Some remarks on the fluctuations of the herring fishing on the west coast of Sweden. Rapp. Cons. Explor. Mer, 118: 31-39.
- AURICH, H. J., and A. STIER
1939 Über das Vorkommen von Heringslaich im Magen von Schellfischen aus dem Gebiet der norwegischen Nordwest-Küste. J. Cons. int. Explor. Mer, 14: 385-392.
- BIGELOW, H. B., and W. C. SCHROEDER.
1953 Fishes of the Gulf of Maine. Fish. Bull. Fish and Wildl. Serv., 53, Fish. Bull. no. 74: 88-100.
- BIRTWISTLE, W.
1921 Biometric investigations on the herring. Proc. Lpool. biol. Soc., 25: 116-126.
- BOWERS, A. B.
1952 Studies on the herring (*Clupea harengus* L.) in Manx waters: — The autumn spawning, and the larval and post-larval stages. Proc. Lpool. biol. Soc., 58: 47-74.
- BREDER, C. M.
1929 Field Book of Marine Fishes of the Atlantic Coast from Labrador to Texas. G. P. Putman's Sons, New-York. 332 pp.
- *BROCH, H.
1908 Forteckning ofver Goteborgs museums sillsamlingarmed en kort vagledning i fjallundersokningsmetoden. Svenska hydrogr-biol. Komm. Skr. 3: 1-8.
- BUCH, S. A.
1885 Spawning of spring herring near Norway. U. S. Comm. Fish. Fish., Bull. 5 (1885): 297-300.
- BÜCKMANN, A.
1938 Über das Wachstum der Nutzfische im gebiet der sudlichen Nordsee. Rapp. Cons. Explor. Mer, 108, app. 12: 73-84.
- CIEGLEWICZ, W., and K. POSADZKI.
1947 Comparative studies on the spring and autumn spawning herring of the Bay of Danzig. Ann. biol., Copenhagen, 2: 159-165.

* Original not consulted.

- CLARK, R. S.
1933 Herring larvae. The mixing of the broods in Scottish waters. Rapp. Cons. Explor. Mer, 83: 11-18.
1934 Herring larvae in Faroese waters. Rapp. Cons. Explor. Mer. 89: 23.
1939 Movement of herring larvae. Advanc. Sci., Lond., 1: 44.
- DAHL, K.
1907 The scales of the herring as a means of determining age, growth and migration. Rep. Norweg. Fish. Invest., 2(6): 1-36.
- DANNEVIG, A.
1948 Rearing experiments at the Flødevigen seafish hatchery 1943-46. J. Cons. int. Explor. Mer, 15: 277-283.
- DANNEVIG, H.
1895 The influence of temperature on the development of the eggs of fishes. Thirteenth Ann. Rep. Fish. Bd. Scot. part III: 149.
- DAVIS, F. M.
1936 A contribution to the "race question". Rapp. Cons. Explor. Mer, 100(2): 12-13.
- DICE, L. R.
1940 Ecologic and genetic variability within species of *Peromyscus*. Amer. Nat., 74 (752): 212-221.
- EINARSSON, H.
1949 The beginning of spring-spawning in Faxa Bay and southern coastal waters. Ann. biol., Copenhagen, 4: 34-35.
1951 Racial analysis of Icelandic herring by means of otoliths. Rapp. Cons. Explor. Mer, 128: 55-74.
1952 Analysis of the Icelandic herring during the year 1950. J. Cons. int. Explor. Mer, 18: 172-186.
- FAGE, L.
1920 Engraulidae. Clupeidae. Rep. Danish oceanogr. Exp. Mediter. and adjacent Seas, 2, Biol. A 9: 1-140.
- FARRAN, G. P.
1938 On the size and number of the ova of Irish herrings. J. Cons. int. Explor. Mer, 13: 91-100.
- FRASER, J. H.
1949 Eggs and larvae. Annual brood values of fish larvae. Ann. biol., Copenhagen, 4: 67-68.
- FULTON, T. W.
1906 On the growth and age of the herring (*Clupea harengus*). Twenty-fourth Ann. Rep. Fish. Bd Scot., part III, Sci. Invest. no. 12: 293-342.
- GABRIEL, M. L.
1944 Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. J. Exp. Zool., 95: 105-147.

- HARDING, J. P.
1949 The use of probability paper for the graphical analysis of poly-modal frequency distributions. *J. Mar. biol. Ass. U. K.*, n. s. 28: 141-153.
- HEINCKE, F.
1898 Naturgeschichte des Herings. I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren. *Abh. deutsch. Seefisher.*, 2: 1-223.
- HESSLE, C.
1925 The herrings along the Baltic coast of Sweden. *Publ. Circ. Cons. Explor. Mer*, no. 89: 1-55.
- HEUTS, M. J.
1947 Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. *Evolution*, 1: 89-102.
- HICKLING, C. F., and E. RUTENBERG.
1936 The ovary as an indicator of the spawning period in fishes. *J. Mar. biol. Ass. U. K.*, n. s. 21: 311-317.
- HJORT, J.
1910 Report on herring-investigations until January 1910. *Publ. Circ. Cons. Explor. Mer*, no. 53: 1-174.
1915 Investigations into the natural history of the herring in the Atlantic waters of Canada, 1914. Preliminary Report no. 1. Canada, Dept. Naval Service, Supp. Fifth Ann. Rep.: 1-38.
- HODGSON, W. C.
1925 Investigations into the age, length and maturity of the herring of the southern North Sea. Part II. The composition of the catches in 1922-24. *Min. Agric. Fish., Fish. Inv.*, ser. 2, 8(5): 1-47.
1928 Some spawning places of the herring of the southern North Sea. *J. Cons. int. Explor. Mer*, 3: 224-230.
1929 Investigations into the age, length and maturity of the herring of the southern North Sea. Part III. The composition of the catches from 1923 to 1928. *Min. Agr. Fish., Fish. Invest.*, ser. 2, 11(7): 1-71.
1934 *The Natural History of the Herring of the Southern North Sea*. London. 120 pp.
- HOLT, E. W. L.
1889 Notes on the early life-history of the herring. *Ann. Mag. nat. Hist.*, 6th ser., 4: 368-372.
- HSÜEH, F.
1939 A study of Manx herring shoals. I. Study of shoaling in Manx herring. *Rapp. Cons. Explor. Mer*, III: 55-73.
- HUBBS, C. L.
1926 The structural consequence of modifications of the developmental rate in fishes. *Amer. Nat.*, 60: 57-81.

- 1934 Racial and individual variations in animals, especially fishes. Amer. Nat., 68: 115-128.
- 1940 Speciation in fishes. Amer. Nat., 74: 198-211.
- HUNTSMAN, A. G.
1918 The growth of scales in fish. Trans. roy. Can. Inst., 12(27), part I: 61-101.
- HUTCHINS, L. W.
1947 The bases for temperature zonation in geographical distribution. Ecol. Monogr., 17(3): 325-335.
- JEAN, Y.
1945 A comparative study of herring (*Clupea harengus*, L.) from the Estuary and the Gulf of St. Lawrence. MA thesis, University of Toronto.
1953 Recherches sur le Hareng. Rapp. Sta. Biol. mar., Québec, 1952, App. II: 19-46.
- JENSEN, A. J. C.
1950 Amount and growth of herring fry in the Danish waters. Rep. Danish biol. Sta., 51: 19-48.
- JENSEN, A. S.
1939 Concerning a change of climate during recent decades in the arctic and subarctic regions, from Groenland in the west of Eurasea in the east, and contemporary biological and geophysical changes. K. danske Selsk., Biol. Meddel., 14(8): 1-75.
- JOHANSEN, A. C.
1919 On the large spring-spawning sea herring (*Clupea harengus* L.) in the north-west European waters. Medd. Komm. Havundersøg Kbh., ser. Fisk., 5(8): 1-56.
- JOHANSEN, A. C.
1921 On the summer-spawning herring (*Clupea harengus* L.) of Iceland. Medd. Komm. Havundersøg, Kbh., ser. Fisk., 6(3): 1-40.
1923 Über die Winterherings des Kattegats. Wiss. Meeresuntersuch., Kiel, n. F. 15(12): 1-59.
1924 On the summer — and autumn — spawning herrings of the North Sea. Medd. Komm. Havundersøg, Kbh., ser. Fisk., 7(5): 1-119.
1927 On a spawning place for winter spawning herring in the northern part of the Belt Sea. Rep. Danish biol. Sta., no. 33: 17-24.
- JONES, R.
1948 An artificial fertilisation of herring off Laxey Bay, Isle of Man. Rep. Mar. biol. Sta. Pt Erin, 58-60: 38.
- KOTTHAUS, A.
1939 Zuchtversuche mit Heringslarven (*Clupea harengus* L.). Wiss. Meeresuntersuch., Helgoland, 1(3): 349-358.

- KUPFFER, C.
1878a Ueber Laichen und Entwicklung des Herings in der westlichen Ostsee. *Wiss. Meeresuntersuch.*, Kiel, 1874-76, IV-VI: 23-25.
1878b Die Entwicklung des Herings im Ei. *Wiss. Meeresuntersuch.*, Kiel, Jahresb. 1874-76, IV-VI: 175-226.
- LAUZIER, L.
1952 Recent water temperatures along the Canadian Atlantic coast *Progr. Rep. Atl. biol. Sta.*, no. 53: 5-7.
- LEA, E.
1929a The Herring's scale as a certificate of origin. Its applicability to race investigations. *Rapp. Cons. Explor. Mer*, 54: 21-34.
1929b The oceanic stage in the life history of the Norwegian herring. *J. Cons. int. Explor. Mer*, 4: 3-42.
- LEBOUR, M. V.
1921 The larval and post-larval stages of the pilchard sprat and herring from Plymouth district. *J. Mar. biol. Ass. U. K.*, n. s. 12: 427-457.
- LEGAL, J.
1935 Le hareng *Clupea harengus* Linnée. I. Les populations de l'Atlantique Nord-Est. *Ann. Inst. oceanogr. Monaco*, 15: 1-125.
- LINDSEY, C. C.
1953 Variation in anal fin ray count of the reidside shiner *Richardsonius balteatus* (Richardson). *Can. J. Zool.*, 31: 211-225.
1954 Temperature-controlled meristic variation in the paradise fish *Macropodus opercularis* (L.). *Can. J. Zool.*, 32: 87-98.
- LJUNGMAN, A. V.
1880 The propagation and growth of the herring and small-herring, with special regard to the coast of Bohuslan. *U. S. Comm. Rep. for 1878*: 639-659.
- MACINTOSH, W. C., and E. E. PRINCE.
1889 On the development and life-histories of the teleostean food — and other fishes. *Trans. roy. Soc. Edinb.*, 35: 665-946.
- MANTEUFEL, B. P. and J. J. MARTY.
1939 The study of the spawning of the Murman herring. *Trans. Knipovich polyar. sci. Inst.*, 4: 41-94.
- MARSHALL, S. M., A. G. NICHOLLS, and A. P. ORR.
1937 On the growth and feeding of the larval and post-larval stages of the Clyde herring. *J. Mar. biol. Ass. U. K.*, n. s., 22: 245-267.
- MARTIN, W. R.
1949 The mechanics of environmental control of body form in fishes. *Univ. Toronto Studies, Biol. Ser. no. 58. Publ. Ont. Fish. Res. Lab. no. LXX*: 1-91.
- MAYR, E.
1942 *Systematics and the Origin of Species*. New York, 334 pp.

MERRIMAN, D., and R. SCLAR.

1952 The pelagic fish eggs and larvae of Block Island Sound. Bull. Bingham oceanogr. Coll., 13, art. 3: 165-220.

MERRIMAN, D. and H. E. WARFEL.

1948 Studies on the marine resources of southern New England. VII. Analysis of a fish population. Bull. Bingham oceanogr. Coll., 11, art. 4(5): 131-146.

MEYER, H. A.

1878 Beobachtungen über das Wachstum des Herings im westlichen Theile der Ostsee. Wiss. Meeresuntersuch., Kiel, Jahresb. 1874-76, IV-VI: 227-252.

1880 Biological observations made during the artificial raising of herrings in the western Baltic. U. S. Comm. Fish Fish., Comm. Rep. 1878: 629-638.

MIELCK, W.

1925 Heringslarven, Eier und Larven anderer Fische und Nahrung der Larven in der westlichen Nordsee im Oktober 1922. Ber. dtsh. Komm. Meeresforsch. n. F. 1: 209-246.

MOLANDER, A. R.

1918 Studies in the growth of the herring, especially with regard to the examination of the scales for determining its growth. Svenska hydrogr.-biol. Komm. Skr., 6: 1-16.

MOTTLEY, C. M.

1934 The effect of temperature during development on the number of scales in the Kamloops trout, *Salmo kamloops* Jordan. Contr. Can. Biol., 8: 254-263.

ORTON, J. H.

1919 Sea-temperature, breeding and distribution in marine animals. J. Mar. biol. Ass. U. K., n. s. 12: 339-366.

PERLEY, M. H.

1852 Reports on the Sea and River Fisheries of New Brunswick. 2d ed. Fredericton. 294 pp.

PERLMETTER, A.

1939 A biological survey of the salt water of Long Island, 1938. I. An ecological survey of young fish and eggs identified from tow net collections. Suppl. 28th Rep. N. Y. Cons. Dept., part 2: 11-71.

PRINCE, E. E.

1907 The eggs and early life-history of the herring, gaspareau, shad and other clupeoids. Ottawa, Dept. Marine Fish., Fish. Branch, 39th Rep. Sessional Paper no. 22a: 95-110.

PROUDMAN, J., H. M. LEWIS and A. L. DENNIS.

1937 On the temperature of the surface waters of the Irish Sea. Phil. Trans., ser. A, 236(8): 261-302.

RASS, T. S.

- 1936 Spawning, eggs and fry of the food-fishes of the Barents-Sea. Breeding and development of fish in subarctic. *Int. Rev. Hydrobiol.*, 33: 250-270.
- 1939 On the life-history of the Murman herring. *Trans. Knipovich polyar. sci. Inst.*, 6: 93-164. (In Russian with English summary).
- 1946 Phases and stages in the ontogenesis of teleostean fishes. *Zool. Zh. (Moscow)*, 25: 137-148. (In Russian with English summary).

ROUNSEFELL, H. A.

- 1939 Contribution to the biology of the Pacific herring, (*Clupea pallasii*), and the condition of the fishery in Alaska. *Bull. U. S. Bur. Fish.*, 45, (1080): 227-320.

RUNNSTROM, S.

- 1927 Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. *Bergens Mus. Aarb.*, 1927, no. 2: 1-67.
- 1941 Racial analysis of the herring in Norwegian waters. *Rep. Norweg. Fish. Invest.*, 6(7): 6-110.

SCATTERGOOD, L. W.

- 1952 The maturity of the Maine herring (*Clupea harengus*). *Maine Dept. Sea Shore Fish., Res. Bull.* no. 7: 1-11.

SCHACH, V. H.

- 1939 Die kunstliche Aufzucht von *Clupea harengus* L. *Wiss. Meeresuntersuch., Helgoland*, 1(3): 359-372.

SCHMIDT, J.

- 1919a Racial studies in fish. II. Experimental investigations with *Lebistes reticulatus* (Peters) Regan. *J. Genet.*, 8: 147-153.
- 1919b Racial investigations. III. Investigations with *Lebistes reticulatus* (Peters) Regan. *C. R. Trav. Lab. Carlsberg*, 14(5): 1-8.

SCHNAKENBECK, W.

- 1931 Zum Rassenproblem bei den Fischen. *J. Cons. int. Explor. Mer*, 6: 28-40.

SETTE, O. E.

- 1950 Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II. Migrations and habits. *Fish. Bull. Fish Wildl. Serv.*, 51, *Fish. Bull.* no. 49: 251-358.

SIMPSON, A. C.

- 1949 Notes on the occurrence of fish eggs and larvae in the southern Bight of the North Sea during the winter of 1947-48. *Ann. biol., Copenhagen*, 5: 90-97.

SMITH, W. C.

- 1924 A study of the composition of the Manx herring shoals during the season of 1923. *Proc. Lpool. biol. Soc.*, 38: 120-135.
- 1938 The Manx herring shoals. *Proc. Lpool. biol. Soc.*, 51: 22-70.

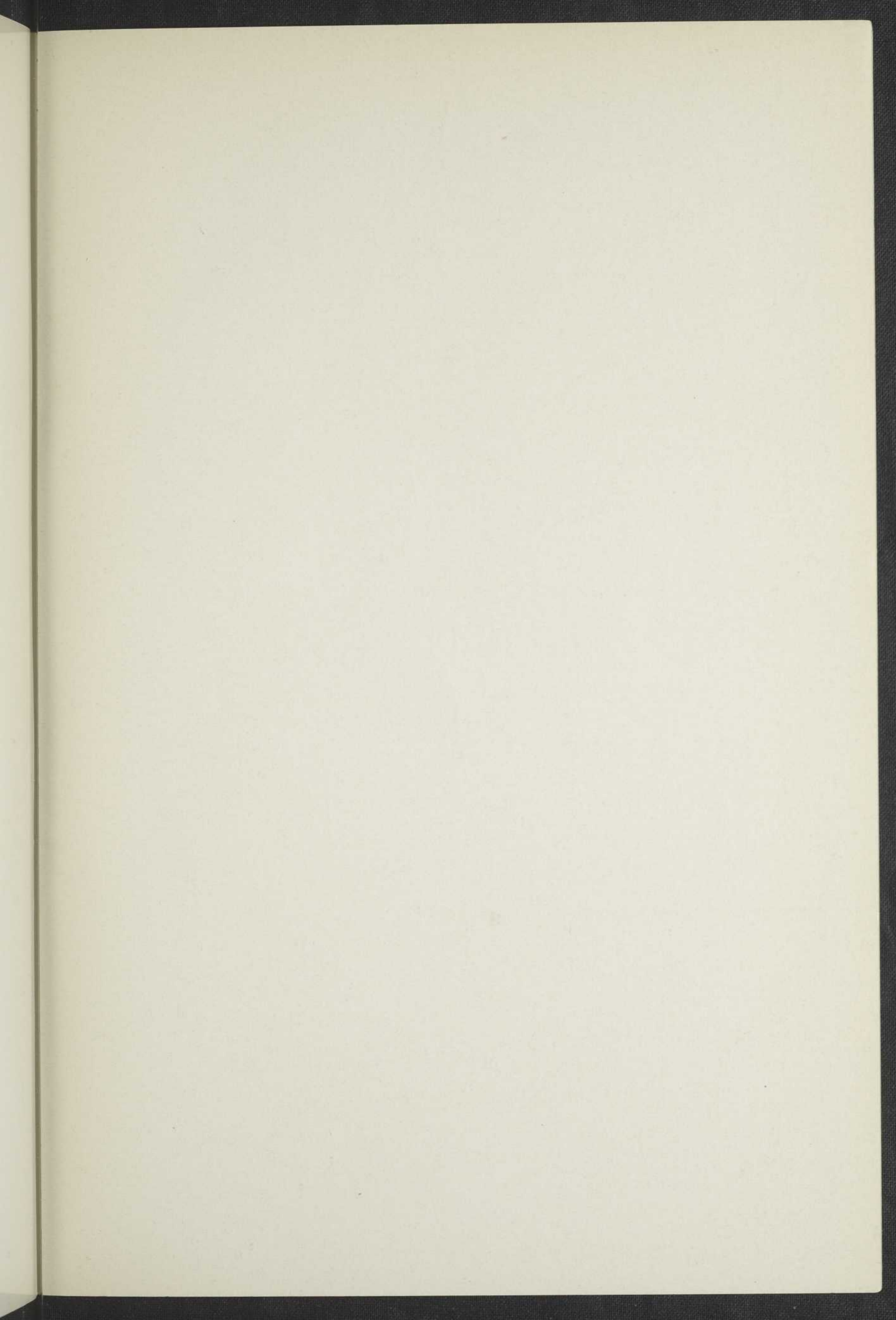
- 1948 Behaviour in shoals and growth of Manx herring. Proc. Lpool. biol. Soc., 56: 29-59.
- SNEDECOR, G. W.
1946 Statistical Methods. 4th ed. Iowa. 485 pp.
- SOLEIM, A. P.
1940 Herring larvae from the spring herring area. Rep. Norweg. Fish. Invest., (6(4): 38-55. (In Norwegian with English summary).
- SOMOV, M. P.
1938 Morphological characteristics of the populations of the Barents Sea herring (*Clupea harengus harengus* L.). Trans. Knipovich polyar sci. Inst., 1: 59-73. (In Russian with English summary).
- STORROW, B.
1920 Herring investigations, I. Herring shoals. Rep. Dove Mar. Lab., n. s. 9: 8-94.
- SUND, O.
1940 Herring investigations in 1939. Rep. Norweg. Fish. Invest., 6(4): 12-18.
- TANING, A. V.
1936 Herring larvae in Icelandic waters 1924-1934. Rapp. Cons. Explor. Mer, 99, part 6: 1-20.
1948 Larval herring. Iceland, 1946. Ann. biol., Copenhagen, 3: 25.
1952 Experimental study of meristic characters in fishes. Biol. Rev., 27: 169-193.
- TESCH, J. J.
1937 Racial investigations of herring larvae in the south-western inlets of Holland. Rapp. Cons. Explor. Mer, 6, 105: 7-9.
- TESTER, A. L.
1938 Variation in the mean vertebral count of herring (*Clupea pallasii*) with water temperature. J. Cons. int. Explor. Mer, 13: 71-75.
- TIBBO, S. N.
1946 Populations of herring (*Cluprs arengus* L.) in Newfoundland waters. MA thesis, University of Toronto.
1949 Atlantic Herring Investigation Committee, Rept. Inv. March 1948 to March 1949, ser B. Herring population studies. Mim. Rept.
- TIBBO, S. N.
1954 Personal communication.
- TIBBO, S. N. and L. R. DAY.
1948 Atlantic Herring Investigation Committee, Rep. Inv. March 1947-March 1948, sec. B, Herring populations, p. B-24.
- TIBBO, S. N., L. R. DAY and A. H. LEIM.
1954 Atlantic Herring Investigation Committee. Final Report, vol. 2, 101 pp. Mim. Rept.

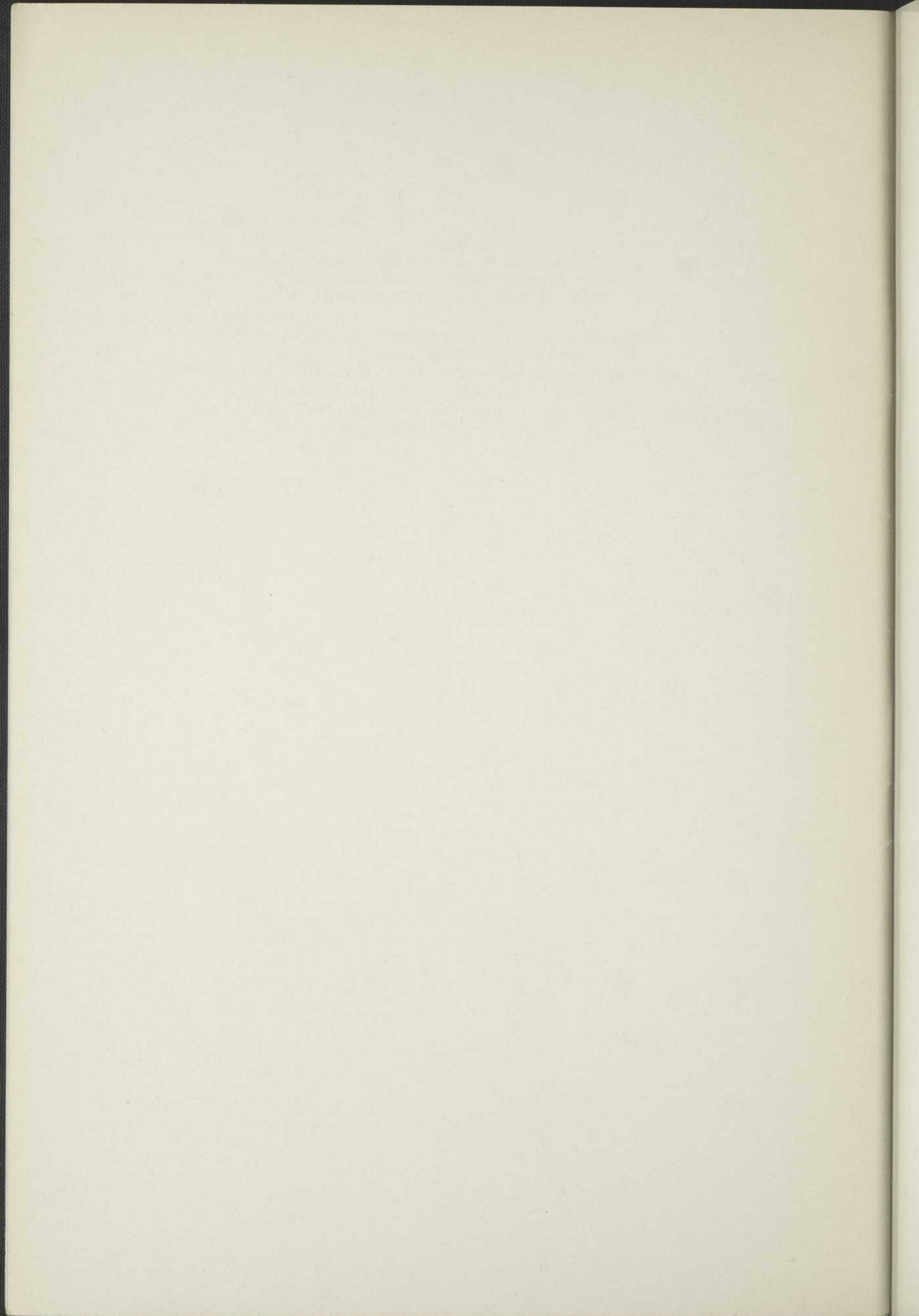
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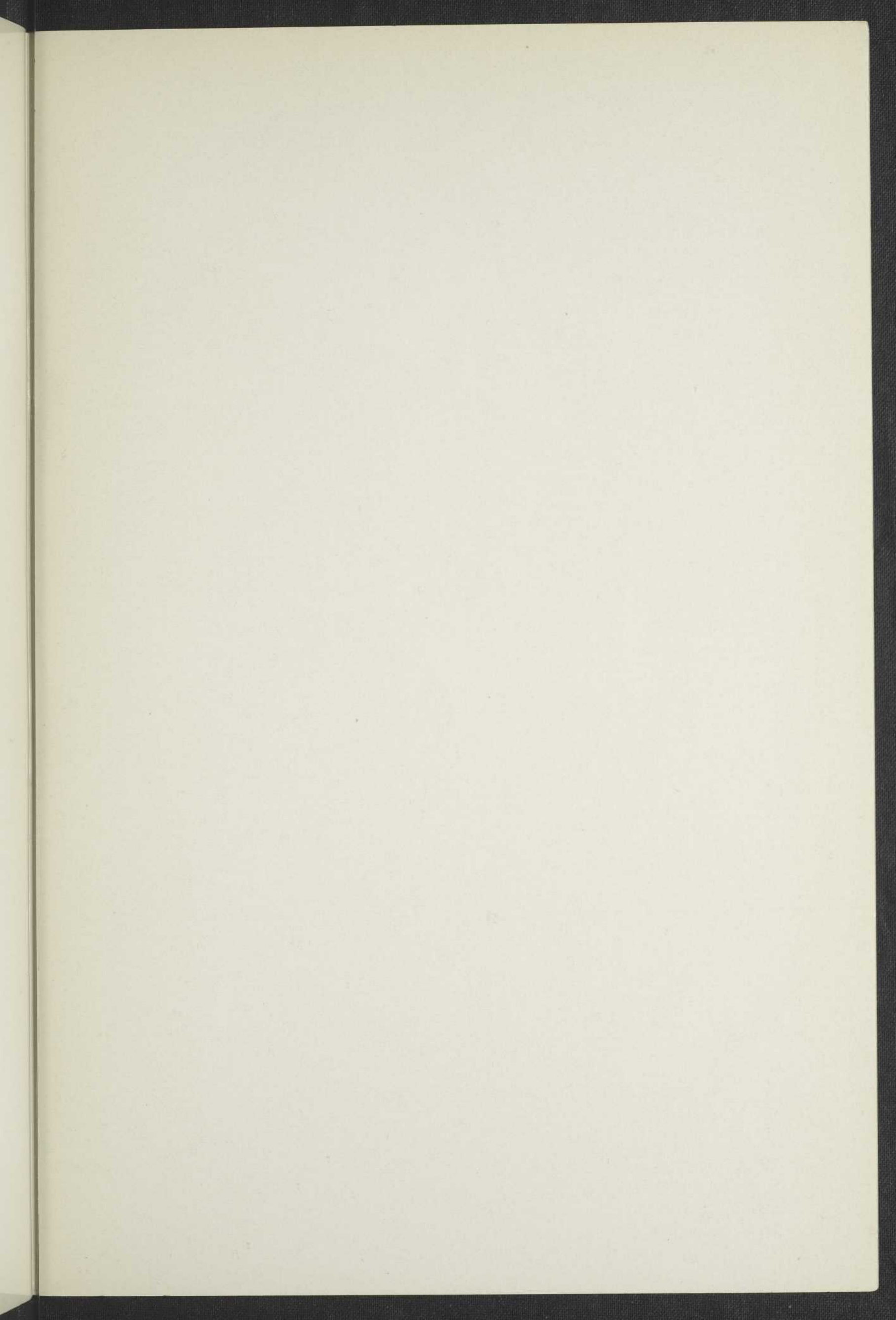
- 1910 Experiments to show the influence of cold in retarding the development of the eggs of the herring (*Clupea harengus*, L.), plaice (*Pleuronectes platessa*, L.), and haddock (*Gadus aeglefinus* L.). Twenty-seventh Rep. Fish. Bd. Scot.,: 120-128.

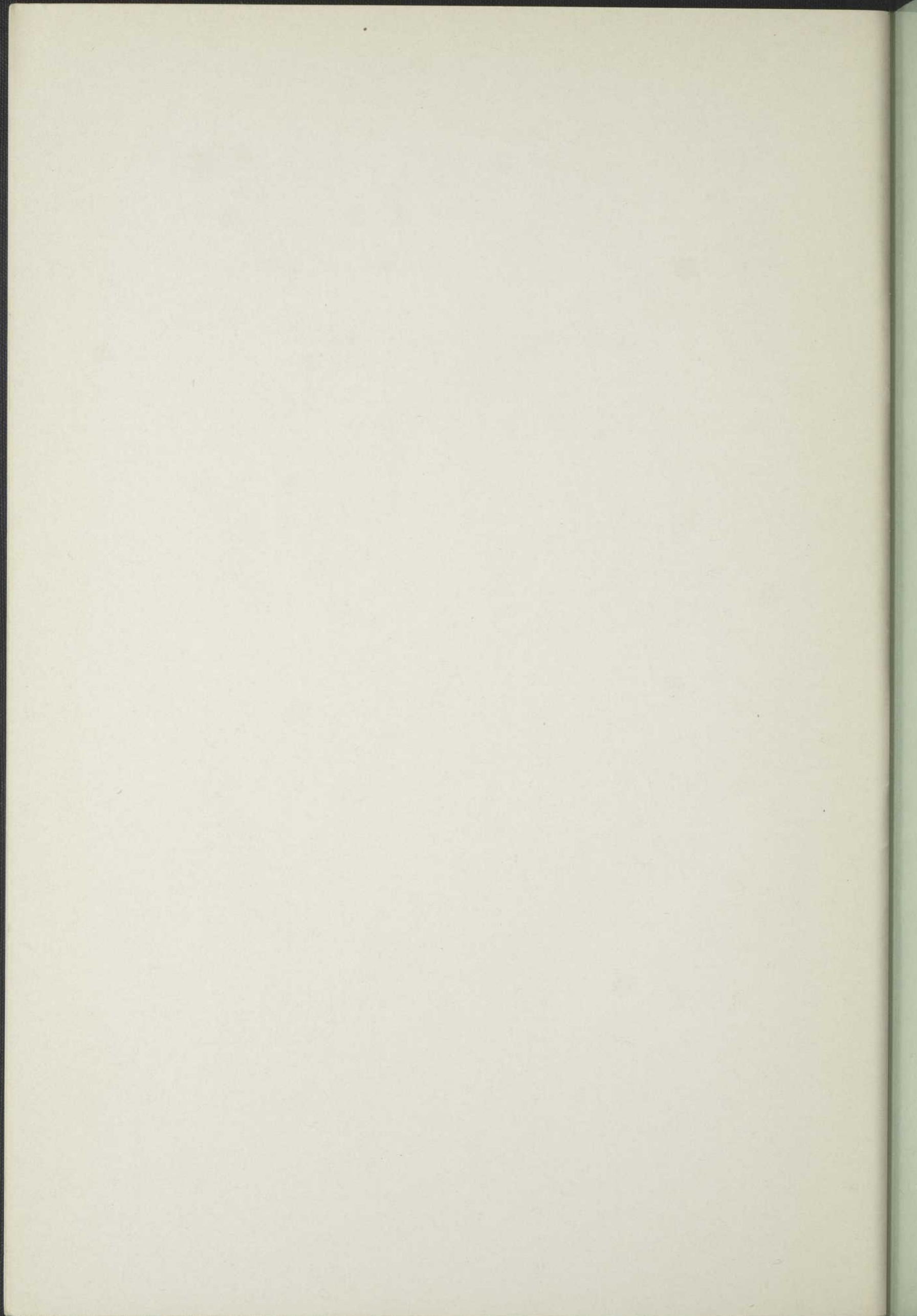
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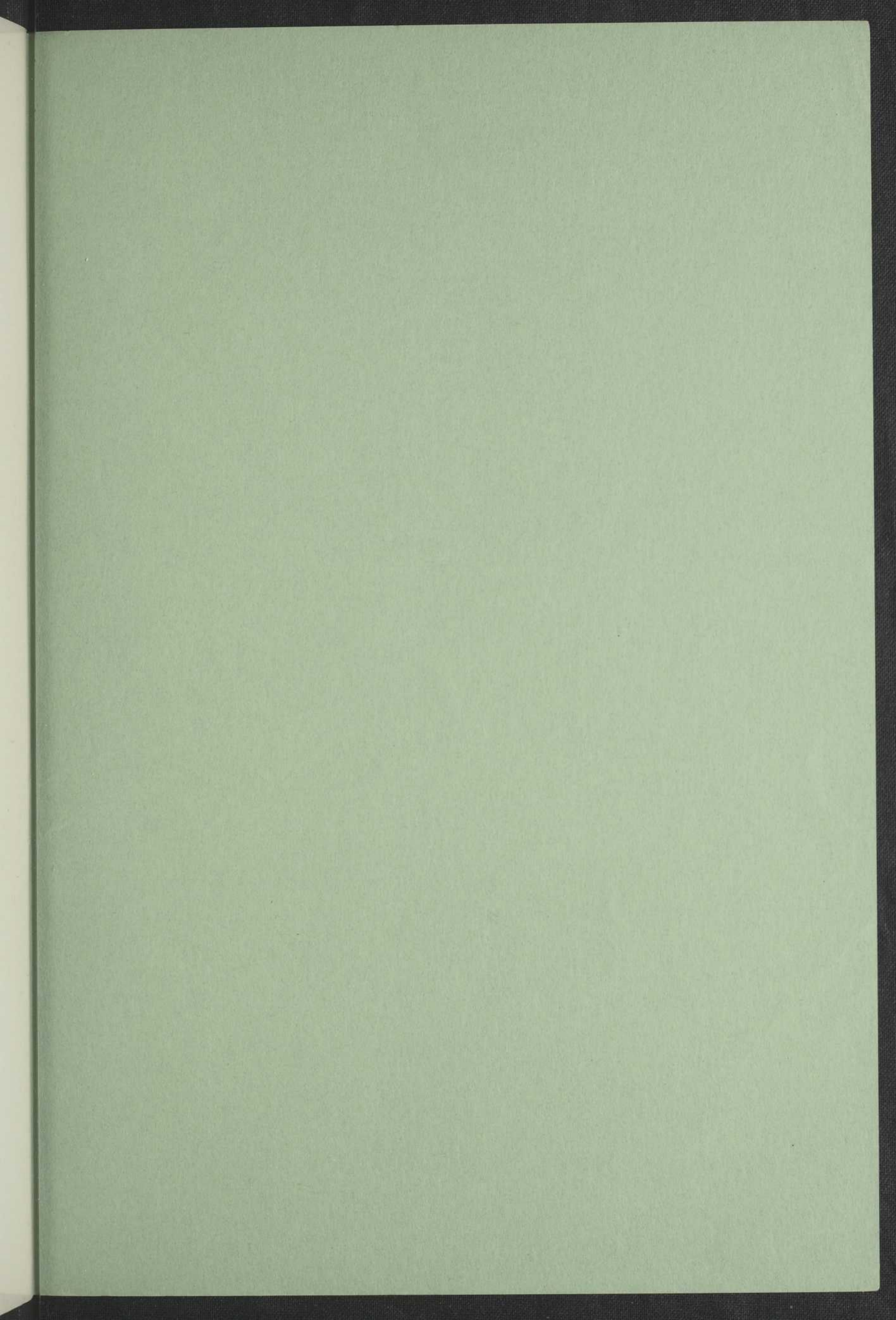
- 1936 Race investigations of the herring population of Scottish waters. Fisheries, Scotland, Sci. Invest., 1936, no. 3: 1-52.
1937 Movements of Herring in the northern North Sea. Fisheries, Scotland, Sci. Invest., 1937, no. 3: 1-49.
1951 Observations on the value of l_1 , in herring investigations. Rapp. Cons. Explor. Mer, 128: 39-46.











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