EFFECT OF CURRENTS ON DISTRIBUTION AND SURVIVAL OF THE EGGS AND LARVAE OF THE HADDOCK (*MELANOGRAMMUS ÆGLEFINUS*) ON GEORGES BANK [1]

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CONTENTS

INTRODUCTION [2]

The problem of fluctuating abundance.—It is a fact of common knowledge to fishermen as well as to marine biologists that the American haddock, like many other animal populations, fluctuates in abundance from year to year. This is a matter of great economic importance, not only because it prevents the trade from reckoning in advance its yearly take but also because it complicates considerably the task of conservation. It is obviously desirable, therefore, to learn as much as possible about these fluctuations, and about the nature of the elements causing them.

Judging from present studies of the Bureau of Fisheries, natural fluctuations in abundance of the American haddock over a wide area are due not to migrations of the adult population away from the fishing grounds but to actual changes in the number of fish. Furthermore, these changes do not usually affect the population as a whole but rather individual year broods, which, during the first year of their life, are subject to varying fortunes that determine their success or failure. It is believed

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[2] This is a contribution from a comprehensive study on the life history and abundance of the American haddock conducted by a staff of the U. S. Bureau of Fisheries under the direction of William C. Herrington. The collection of hydrographic and biological field data interpreted herewith was planned and executed by William Herrington and John R. Webster and later given the author for study at Harvard University. It is anticipated that detailed papers on the hydrography will be presented later. The author is greatly indebted to members of the Department of Biology at Harvard University, especially to Professor Henry B. Bigelow, for helpful advice, suggestions, and criticisms.

to be true for haddock, as it certainly is for many other kinds of fishes, that the critical time when the success or failure of a year brood is determined occurs during the period of the embryonic, larval, and post-larval stages; in other words, from the time the eggs are deposited until the young fish are strong enough to go to the bottom to live a self-directed existence. It is to be expected, therefore, that causes of fluctuations in abundance can be found by intensively studying the biology of these early stages in the field and at the same time by observing changes in the environmental elements.

The geographic distribution of the haddock is peculiarly suited to a study of this sort, being confined as it is to the continental shelf, and, more particularly, to the coastal and offshore banks of the Atlantic coast between New Jersey and Cabot Strait. Probably the most important area of its distribution in this range, however, is Georges Bank, which supplies at least three-fourths of the total commercial catch. Here resides a very dense haddock population, more or less imprisoned by natural barriers; by high temperatures to the southwest; by oceanic depths along the southern edge; and by deep water and muddy bottom along the northern edge. On the eastern edge is a deep channel separating Georges from Browns Bank, which probably forms at least a partial barrier on that side.

It has long been known that the haddock spawns on Georges Bank and that its eggs are more or less buoyant, drifting passively wherever the currents carry them. Even after hatching, the larvae and young fish continue to drift until they become strong enough to direct their own movements effectively and go to bottom. With such a picture in mind, it can be reasonably supposed that the currents might carry at least some, if not all, of the drifting stages away from the bank. Furthermore, if the brood produced on the Bank always drifted away in wholesale fashion, then there must be an immigration from other nursery grounds to Georges Bank in order to sustain the large population there. Finally, if the maintenance of this population is dependent on the action of the currents, then changes in the currents might somehow influence the abundance of the population.

This paper is concerned specifically with events on Georges Bank during two spawning seasons, those of 1931 and 1932. From data collected during those periods, we shall endeavor to answer the following questions:

1. Where did the haddock of Georges Bank spawn in 1931 and 1932?
2. Where, or in what direction, and with what speed did the newly spawned eggs drift after deposition?
3. Was there immigration from other breeding grounds? If so, from what direction did this occur?
4. How did fluctuations in the currents affect the success of the broods?

Brief summary of the findings of this study.—Perhaps the most important discovery made in this study is that the events connected with the spawning season change from month to month and from year to year. Although the spawning of the haddock may occur over the entire bank, it tends to be concentrated in certain definite areas, the location of which may change from to time.

In 1931, spawning seems to have been concentrated on the eastern part of the bank, whence the eggs drifted in a clockwise direction around the bank. Although some of the young drifted toward Nantucket Shoals, many of them were evidently carried northward to Georges Shoals, where they were able to settle to bottom and establish a year class. There was no evidence that in 1931 there was any immigration from other breeding grounds. Thus, in that year Georges Bank seems to have supplied its own brood, and apparently without a significant loss to other regions.

In 1932, however, the situation was quite different. There were now two important separate breeding centers on Georges Bank, one on the eastern part of the bank, the other in the South Channel. The system of currents that year was evidently also different, being such that large numbers of young seem to have been carried off the northern and southern edges of the bank into deep water where conditions were presumably unfavorable for their possible continued existence. As in the year before, there was no evidence of immigration from other breeding grounds, consequently the loss of eggs due to the change in currents was probably disastrous to that year's brood. It is thus apparent that there may be an important connection between the success of a given year brood, consequently between the ultimate fortunes of commercial fishermen, and the system of currents. The need for a continued, permanent study of currents and the relation to the distribution of young fish is therefore obvious.

The balance of this paper gives a detailed description of the evidence supporting the conclusions. The methods of collecting the material and of preparing the data for interpretation are described in the appendix. Readers unfamiliar with the methods used in ordinary plankton research are advised to read the appendix before beginning the argument.

THE SPAWNING AREAS OF HADDOCK ON GEORGES BANK

There are two standard methods by which the spawning areas of a fish population can be located; first, by determining the regions where sexually mature, market-size fish of the species in question are taken in quantity by commercial fishermen during the breeding season; second, by mapping the regions where newly spawned eggs are taken in plankton hauls. It has long been known from these sources that in general haddock spawn all along the New England coastal belt from Cape Cod to the entrance of the Bay of Fundy, on Georges Bank, and on the banks in the Nova Scotia region, chiefly Browns and Sable Island Banks (Bigelow and Welsh, 1925; A. B. Needler, 1931). Further, Thompson (1932) found evidence of some spawning on the banks to the south of Newfoundland. Georges Bank, itself, the most productive breeding ground for haddock in American waters (Bigelow and Welsh, 1925), thus forms the southern boundary of significant haddock spawning. To its northwest lie the less productive grounds inshore along the coast; to its northeast lie the Nova Scotia Banks.

Beyond the general conclusion reached by Bigelow and Welsh (1925) from material collected in 1913, 1915, and 1920, that the principal spawning grounds on Georges Bank occur on the level bottom of the eastern portion, the precise location of spawning has not previously been determined.

Spawning grounds indicated by commercial records.—The regions where fish were taken commercially during the spawning seasons of 1931 and 1932 have been determined from the records of a fleet of 12 fishing vessels. For the purposes of statistical analysis, the positions where these ships made catches during the period studied were grouped by areas of which the dimensions were 20 minutes of latitude and of longitude. In the center of each of these areas represented on a chart, a point was plotted to which was attributed all the catches (in hundredweights) taken in the square during the entire period by all the boats which operated there. Such a plot was made for each of the spawning months of 1931, and for those of 1932, up to May. From these data isometric charts were constructed in the manner described on page 65.

During the entire spawning season of 1931, viz, from February through May (figs. 1 and 2), fish were caught over a large area of the bank; but the greatest catches were made—and, therefore, presumably the greatest abundance of fish occurred—in the northeastern region, just east of Georges Shoals. In March (fig. 1–B), judging from the catch, there was some indication of a second region of abundance in the southern part of the South Channel, just west of Georges Shoals. A fishing center is to be seen also on Browns Bank, developing in February (fig. 1–A) and March (fig. 1–B), reaching its greatest production in April (fig. 2–A), and declining in May (fig. 2–B).

Limitation in catch records as evidence of spawning grounds.—Since fishermen naturally operate where they can get the most fish for the least expenditure of effort, that is, where the population is concentrated, these charts are useful as positive evidence that there were concentrations of fish in the regions indicated by the high contours. On the other hand, since fishermen probably do not sample every part of the bank during the course of a month, the charts are not necessarily representative of the population abundance in regions where the vessels failed to fish. Also, the presence of fish during the spawning season does not necessarily indicate they are spawning at that place. Because of these limitations in the catch charts, it is necessary to examine the distribution of the newly spawned eggs to determine the boundaries of the spawning season for the entire population.

Spawning grounds indicated by distribution of newly spawned eggs.—It is to be observed in figures 7–A and 13–A that during March and April the principal concentration centers of newly spawned haddock eggs agree in the main with those of adult fish. There are, to be sure, discrepancies between the two classes of observations.

Comparison of two methods.—First, the population center which developed in the South Channel from February to March, and persisted to some extent in April (figs. 1 and 2), was not reflected by a corresponding egg center (figs. 7–A, 13–A, and 21–A). The apparent absence of eggs in that region may be due to an insufficient number of stations there. The number of eggs found around the periphery of the Channel, however, is much less than in 1932 (p. 37), suggesting that relatively little spawning took place there in 1931.

Second, according to the egg chart for March (fig. 7–A), considerable quantities of eggs were found south of the parallel of 41° and westward, outlining a second center of egg abundance which is not reflected on the corresponding catch charts. According to W. C. Herrington, who has made an extensive study of the sizes and ages of haddock, more small haddock of unmarketable size are found in that part of the bank than elsewhere. Between September 1930 and May 1931 the percentages of undersized haddock [3] in the various regions of the bank were as follows:

	Percent
South Channel	50
Northern part of Georges	67
Southeastern Georges	75

It is therefore possible that the fishermen did not operate on the southern part of the bank because of a preponderance of fish below market size there.

In any case the catch records are not indicative of spawning in that particular region in 1931. Fortunately, however, the egg charts are based on samples distributed over the entire bank, and the presence in the southeastern region of an

[3] "Undersized" in this sense means below marketable size.

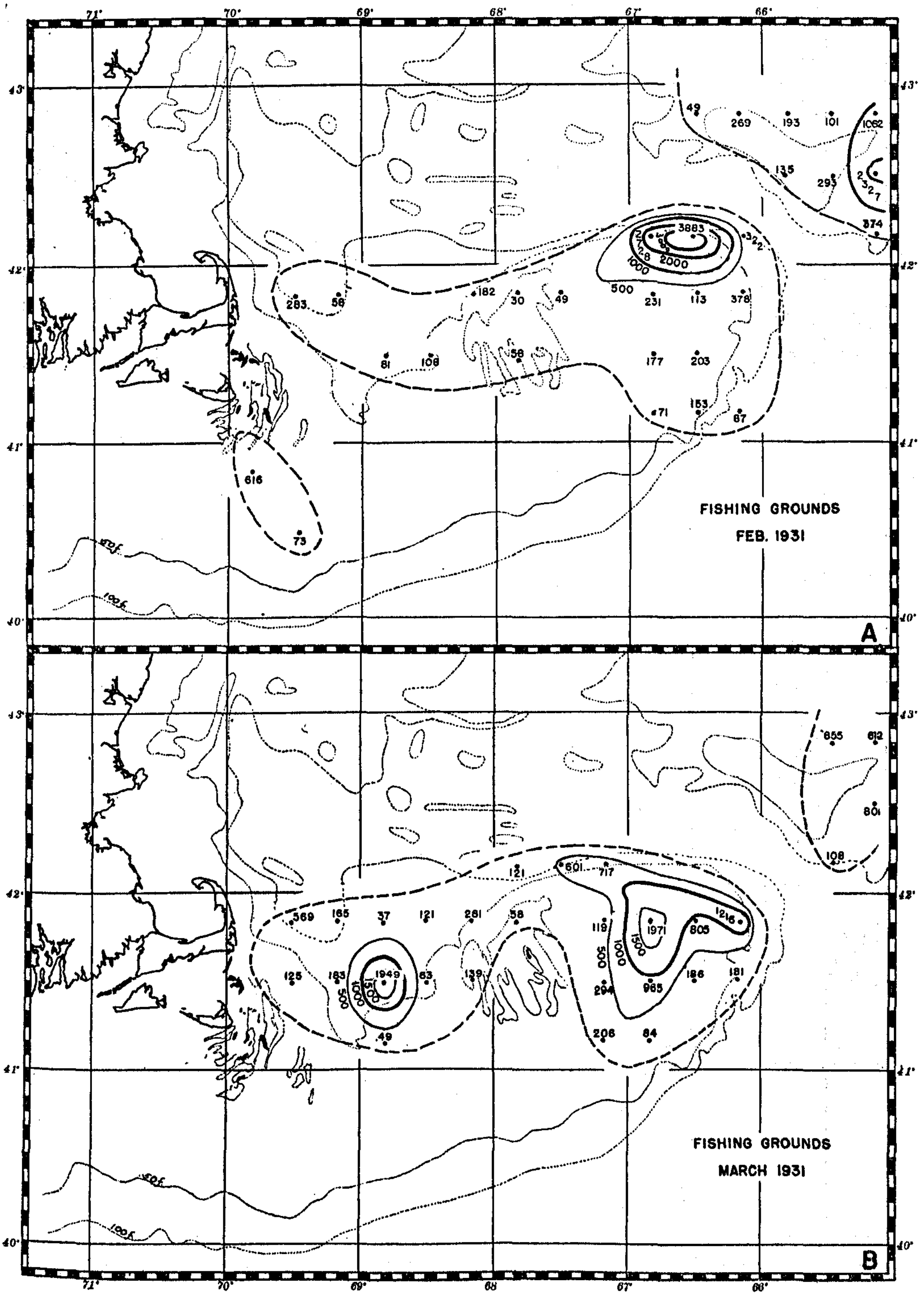

FIGURE 1.—Isometric chart showing the population centers for adult haddock in February (A) and March (B) 1931, as indicated by the positions where fishermen made successful catches during the month. The numbers represent hundredweights.

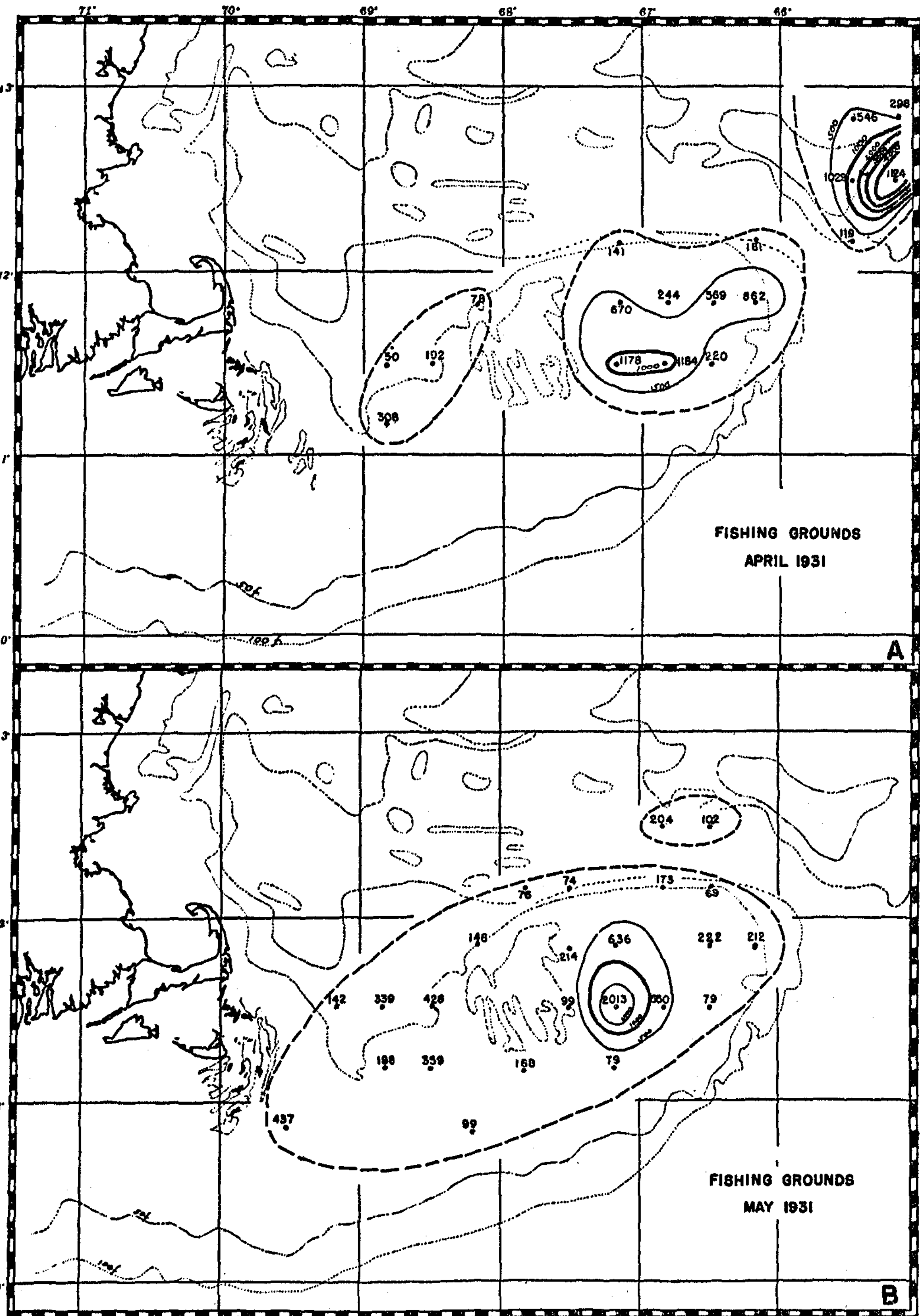

FIGURE 2.—Isometric chart showing the population centers for adult haddock in April (A) and May (B) 1931, as indicated by the positions where fishermen made successful catches during the month. The numbers represent hundredweights.

abundance of young eggs which were from 0 to 6 days old is sufficient evidence that there was actually considerable spawning there.

Third, although a fishing center occurred on the northeastern part of the bank in May (fig. 2–B), stage I eggs [4] were found only near the coast, in the vicinity of Cape Cod and south of Nantucket Shoals during that month. It is evident from the egg charts that spawning had ceased in the northeastern center, but persisted in the western region, where the population was perhaps too sparse to repay the fishermen's efforts to exploit it. Consequently, the catch chart for May is not indicative of the spawning grounds.

From the above considerations it is apparent that the catch charts are useful to indicate the presence of population concentrations only in localities where it is known the fishermen sampled. Furthermore, they indicate the presence of spawning populations only when and where the fish are mature, or when and where newly spawned eggs are found. Thus the catch charts without the egg charts are insufficient evidence for the location of breeding grounds.

Effect of the presence of cod eggs on the accuracy of the isometric charts.—As the spawning seasons of cod and of haddock overlap, the egg charts include some cod eggs, which in the first three stages of development are indistinguishable from those of haddock.[5] If there were an appreciable difference between the location of the spawning grounds of cod and those of haddock, the paths of dispersion would presumably differ for the two species and the distributional pictures for haddock eggs alone would no doubt be seriously distorted. But since the eggs are separable when in stage IV, we have a basis for judging the possible extent of differences in the initial distribution.

In figure 3–A which represents the distribution of stage IV cod eggs in March, the centers of abundance occur in precisely the same regions as those in the corresponding haddock egg chart (fig. 3–B). Further, the market-size cod in February and March (fig. 4) appear to have had essentially the same distribution as the market-size haddock (fig. 1). Therefore, it may be concluded that the charts presented in the present paper for March may be used to indicate the distribution and drift of haddock eggs despite the presence of cod eggs.

THE SPAWNING GROUNDS IN 1932

1. *From the commercial catch.*—In 1932, judging from the catch records (figs. 5 and 6), an important fishing center again occurred on the northeastern part of Georges Bank following the same trend of production as in 1931; that is, the catches were highest there in February and gradually declined through March and April. Again the catch of fish on Browns Bank reached its peak in April. This is consistent with the fact observed by Bureau of Fisheries investigators, that spawning normally occurs later on Browns Bank than on Georges, reaching a period of greatest production in April.

2. *From distribution of newly spawned eggs.*—Although the *Albatross II* was not available during most of the 1932 season, it was fortunately secured for one cruise in April, thus permitting a comparison between the 2 years. The isometric egg chart for the group I eggs taken on this cruise (fig. 26–A) agrees very well with the commercial catch charts as to the location of the centers of abundance, which in

[4] Page 66.
[5] Page 66.

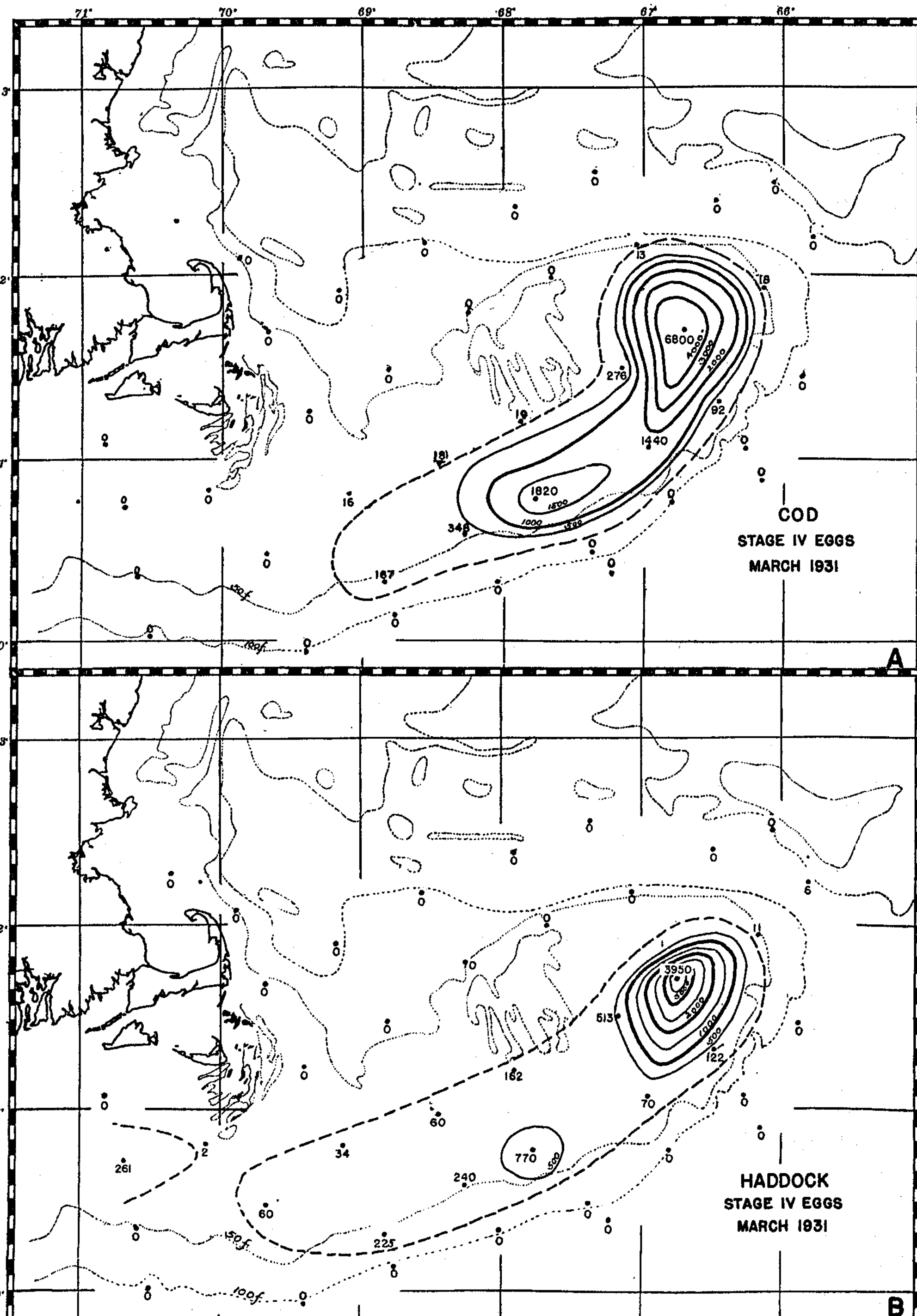

FIGURE 3.—Isometric chart showing the distribution of (A) stage IV cod eggs, and (B) stage IV haddock eggs, in March 1931. The numbers are population indices (p. 61).

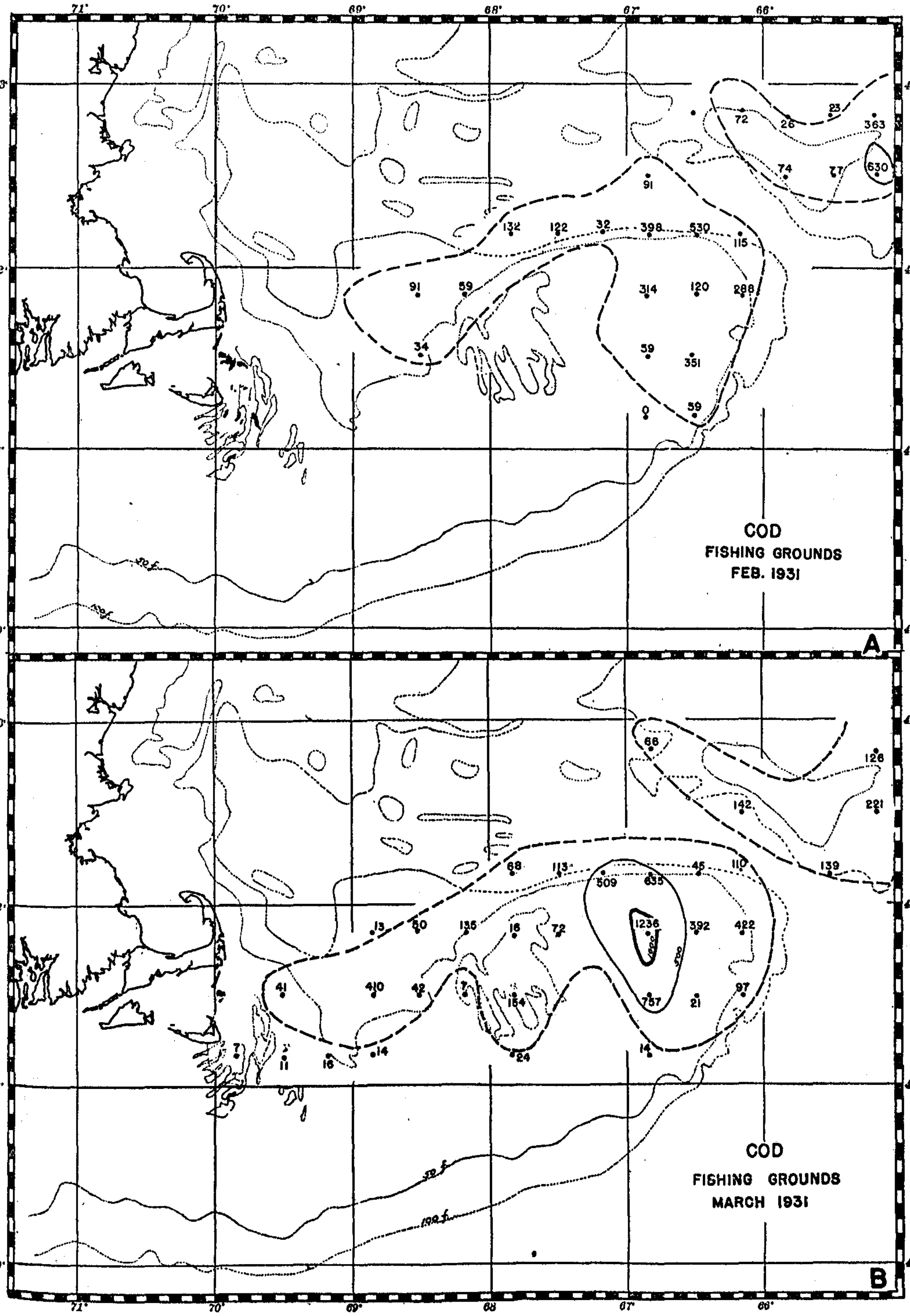

FIGURE 4.—Showing the population centers for adult cod in February (A) and March (B) 1931, as indicated by the positions where fishermen made successful catches during the month. The numbers are in hundredweights.

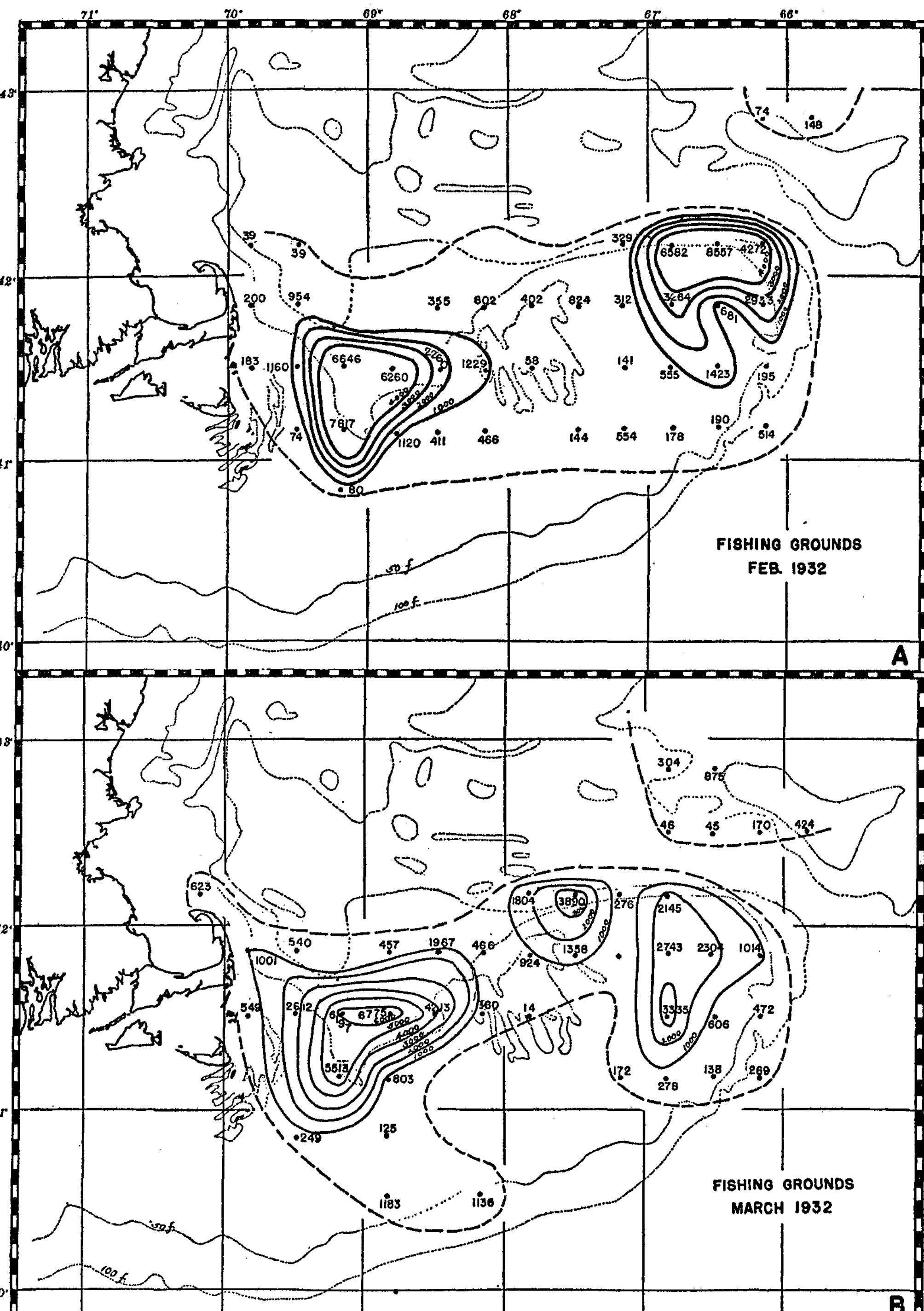

FIGURE 5.—Showing the population centers for adult haddock in February (A) and March (B) 1932, as indicated by the positions where fishermen made successful catches during the month. The numbers are in hundredweights.

both charts (figs. 6 and 26–A) occur in the South Channel, the eastern portion of Georges, and on Browns Bank.

Comparison of spawning grounds for 1931 and 1932.—The two chief differences between the spawning charts for 1932 and those for 1931 are these; first, there was in 1932 a rather large spawning center in the South Channel, which may have been represented in 1931 only to a very slight degree if at all in April; second, the total population seems to have been distributed over a broader area in 1932 than in 1931. These differences, however, are not widely significant, being no greater than one would expect from ordinary environmental differences between any 2 years. We may, therefore, draw the following general conclusions:

General conclusions about the spawning grounds.—

1. Spawning may occur at one time or another over the whole of Georges Bank from Nantucket Shoals and Cape Cod eastward, with the exception of the region of Georges Shoals. That spawning does not occur in the latter place is deduced from

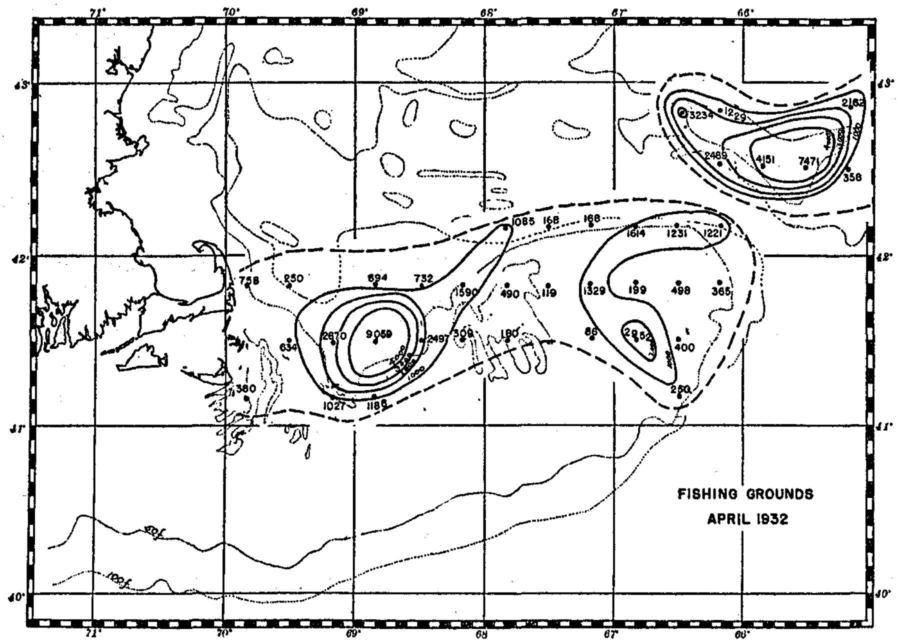

FIGURE 6.—Showing the population centers for adult haddock in April 1932, as indicated by the positions where fishermen made successful catches during the month. The numbers represent hundredweights.

the fact that haddock do not frequent water of much less than 25 fathoms during the spawning season (Goode and others, 1884; Bigelow and Welsh, 1925). Observe also in the catch charts that adult fish were not taken in significant quantity on the shoals as far as commercial fishermen were able to take their vessels. Furthermore, relatively few eggs were found around the edges of the shoals.

2. Spawning tends to be concentrated in certain definitely delimitable areas.

3. In both years there was a definite spawning center on the northeastern part of Georges Bank just east of Georges Shoals; and a concentration of eggs was described for the same general locality by Bigelow and Welsh (1925) from *Albatross* collections made in 1920.

4. In April 1932 there was a second spawning center in the South Channel. In 1931, on the other hand, there seems to have been little spawning there.

5. A spawning center occurred on Browns Bank in both years, reaching its greatest magnitude in April.

6. Spawning evidently began in the northeastern region of abundance, occurred later in western and southern centers, and was completed by a diffuse, scanty population on the westernmost part of the bank.[6]

7. Sudden and radical changes in the location of the spawning centers did not occur within either of the 2 years studied. This is an important point upon which the whole following argument rests. In neither of the 2 years studied was there any evidence that spawning occurred in small isolated regions, here and there on the bank, at haphazard times during the season. It is, therefore, reasonable to infer that the older eggs originated from the regions where the young eggs were taken, not from other unknown centers of abundance which had existed previously elsewhere.

8. In general, the 100-fathom contour marks the limits of spawning. Where eggs were taken in deeper water, they probably had drifted there with currents from shallower regions.[7] In March and April 1931 eggs were taken along the southern edge of the bank beyond the 100-fathom contour. In April 1932 stage I eggs occurred in deep water off the northern edge and in the Fundian Channel. The significance of this distribution and the origin of these eggs will be considered later.[8]

9. The limit of the spawning grounds in the waters south and west of Cape Cod is not precisely known. Although it is true that no stations were made west of the 71st meridian, it is well known to both biologists and commercial fishermen that the haddock which inhabit those waters are not abundant.

Conditions necessary for spawning.—The elements which attract haddock to certain definite regions to spawn are at present unknown. Of the three known hydrographic variables which may influence spawning—depth, temperature, and density—no one seems clearly to be a determining factor. Whatever combination of these factors which may obtain in regions where young eggs are abundant, can also be found in regions of scarcity. This problem, therefore, cannot be solved with the data at hand.

DISPERSAL OF THE EGGS FROM THE SPAWNING AREAS

I. VERTICAL DISPERSAL

Evidence that haddock spawn on the bottom.—It is a generally accepted fact that haddock normally spawn on or near the bottom (Goode and others, 1884; Bigelow and Welsh, 1925; Needler, 1931). The kind of gear which fishermen must use to catch haddock during the breeding season is sufficient evidence to support such a conclusion. For the most part, these gear consist of otter trawls, line trawls, which are set on the bottom, and bottom gill nets. If haddock frequented the upper strata at any season, the fishermen would be obliged to modify their fishing technique during that period by using surface instead of bottom gear. But fishermen do not find it necessary to change their apparatus seasonally. There is only one reference in the literature (Bigelow and Welsh, 1925) of spawning haddock being taken by gill nets which were set near the surface. That was in Boothbay Harbor in 1912, and there is no record of its having occurred since. There is, therefore, no reason to doubt that the bottom is the normal place of haddock spawning activity.

[6] See also p. 29.
[7] Page 19.
[8] Page 19, ff.

The eggs rise toward the surface after being spawned.—According to Needler (1931), haddock eggs rise in the water after they are spawned and float either at or near the surface. Bigelow and Welsh (1925, p. 443) hypothesize that "* * * in whatever part of the Gulf (of Maine) haddock eggs are deposited they will rise from the bottom; and if they fail to reach the surface locally because of its low density, they will merely float, balanced in the water, a few fathoms down."

During the cruises made for the present study, relatively few eggs were taken on the bottom with the sled net.[9] In 29 unselected stations where the sled net was used the several nets collected eggs as follows:

The top net collected more than the bottom net in 16 hauls; the same as the bottom net in 6 hauls; less than the bottom net in 5 hauls; more than the sled net in 27 hauls; and less than the sled net in 2 hauls.

It is thus evident that eggs do tend to rise toward the surface after being spawned; but there are apparently exceptions to this rule. That these exceptions were not due to age is evidenced by the fact that at each station all stages of development were distributed at the same general levels in approximately the same proportions.

Dependence of vertical distribution on specific gravity.—From purely physical considerations, the eggs must finally become suspended in water having the same specific gravity as their own. Apart from turbulence of the water, which tends to cause a dissemination of the eggs from bottom to top, the chief property which determines the vertical distribution is thus presumably the specific gravity.

While the problem of when and how the specific gravity of pelagic eggs is determined has been given some attention by biologists, no one has yet clarified the various questions which arise from it in the detail which it deserves.[10] Although this detail is beyond the scope of the present paper, some light may be thrown upon the general subject of the passive vertical distribution of haddock from the data at hand.

Fortunately, not only was the plankton sampled on the stations made during the *Albatross II* cruises, but also the temperatures and samples of the water were taken at several depths, including the top and bottom.[11] From the latter the salinity was determined and the specific gravity calculated.

Definition of terms.—The specific gravity of sea water differs from that of distilled water only in the second and subsequent decimal places. In oceanographic work, however, it is commonly contracted into the form designated σ in order to avoid the use of long decimal fractions. This is obtained from the formula

$$\sigma_0 = 1{,}000\ (S_0 - 1)$$

where S_0 is the specific gravity of sea water at 0° C. referred to distilled water at 4°. Given the salinities, the values for σ_0 were obtained directly from Knudsen's tables (1901). We are interested, however, in the specific gravity which the water in question actually possessed at the temperature prevailing at the time of the sample. Given, therefore, the temperature (t) and σ_0, values for σ_t were obtained directly from Matthew's tables (1932). The term "density" is applied to σ_t usually in place of "specific gravity", and will be so hereafter in this paper.

Variation in the specific gravity of haddock eggs.—If haddock eggs had a uniform specific gravity, one should expect to find them always suspended, if they are suspended, in water of a uniform density. But judging from figures 18, 19, and 35, for example, there was in 1931 and 1932 actually no uniformity of the water in which the eggs were found.

[9] Page 60.

[10] For a review of the early literature on the subject, see Jacobsen and Johansen (1908).

[11] Water samples and temperatures were obtained with a Greene-Bigelow water bottle and reversing thermometer.

Bigelow and Welsh (1925), balanced artificially fertilized eggs in sea water having a σ_0 value of 23.2. In one experiment of my own, eggs from a female caught off Cape Ann were artificially fertilized in water of $\sigma_0=22.79$. The fertilized eggs remained suspended and evenly distributed in this water until they hatched. A few transferred into water having a σ_0 value of 23.13 promptly rose to the surface and floated there until they became adjusted to the new density. Another group of eggs from a fish caught in the same region a month later was fertilized and remained suspended in water having a σ_0 value of 23.79. When placed in water of $\sigma_0=23.43$, they sank to the bottom. It thus appears as if the eggs adopt within limits the specific gravity of the surrounding water in which they are fertilized and that they tend to distribute themselves and remain suspended in this stratum. This is in agreement with the conclusion of Ehrenbaum and Strodtmann (1904) based on observations of several North Sea and Baltic species.

If the stratum in which the eggs are suspended drifts into a region where there is a layer of lighter water above and one of heavier below, the eggs appear to be kept from rising to the surface by the water which is lighter than themselves, and from sinking to the bottom by the water which is heavier. This argument is supported by the fact that at stations where eggs predominated at the surface, they were consistently separated from the bottom by strata of dense water (fig. 11); and where eggs were concentrated near the bottom, they were always separated from the top by strata of light water (fig. 35).

Effect of changing the density of the water.—If the stratum in which the eggs are suspended mixes with lighter or heavier water, so that its own density is affected, one should expect the eggs either to change levels or to change specific gravity to correspond with the density of the new water. This effect has been discussed in detail for cod eggs by Jacobsen and Johansen (1908), who found experimentally that cod eggs tend to alter their specific gravity to conform to the density of the water into which they have been transferred.

In order to test the same point for haddock eggs, the following experiments were performed: Eggs which had been artificially fertilized in water having a density of 22.69 were placed in lots of about 300 into glass cylinders of sea water of different densities ranging from 22.33 to 26.43. These were then observed at intervals of 12 hours for 3 days. The following table records the results of these observations.

TABLE 1.—*Effect of changing the density of the water on the vertical distribution of haddock eggs*

σt	First reaction on adding eggs to new water	Second day	Third day
22.69 (Control)	Remain suspended and distributed through the water.	Same	Same.
22.33	All sank to bottom	do	Do.
22.78	About 75 percent float on top of water; about 25 percent suspended.	About 30 percent on top; 70 percent suspended.	Do.
23.08	About 95 percent on top; 5 percent suspended.	do	Do.
23.61	do	About 90 percent on top; 10 percent suspended.	Do.
23.98	do	do	Do.
25.18	100 percent on top	About 95 percent on top; 5 percent suspended.	About 90 percent on top; 10 percent suspended.
26.43	do	do	Do.

On the third day, samples of eggs from each cylinder were placed in a cylinder of water having the density of that in which they had been fertilized. In all cases where eggs had been transferred to heavier water, they sank when returned to their original water. Because the specimens which had been placed into light water had died, this experiment was not possible with them.

It is evident from these results that haddock eggs do change their specific gravity, at least to conform partially to changes in the density of the water in which they drift. With increases of less than about 2 percent of the original density of the water, the majority of the eggs can alter their specific gravity enough to remain suspended. With greater increase, the majority of eggs seems to be unable to make sufficient adjustment, and rise to the surface to remain there. As the amount of change increases, the percentage of eggs which remain floating seems also to increase in a relationship which cannot be given mathematically from these qualitative observations. If the density of the water to which the eggs have been transferred is sufficiently less than the original, as in the single instance here given, the eggs remain sunk, unable to make the necessary adjustment to buoy them. Under such circumstances, they die.[12]

The foregoing facts have proved a useful tool in tracing the sources of eggs taken in our tow nets. If in one station, for example, most of the eggs are taken by the top net in water which is separated from the bottom by a dense stratum, the source of the eggs can be found by tracing the isopycnics [13] to the bottom. This will be illustrated incidentally during the following discussion.

II. HORIZONTAL DISPERSAL

MARCH, 1931

Cruise of March 19–31.—There were two important spawning centers on Georges Bank in March 1931,[14] northeastern and southeastern. For the sake of clarity in the following discussion, these two centers will be referred to as *A* and *B*, respectively (fig. 7).

Newly spawned eggs (stage I) were found abundant in both regions in March. The eggs in stages II, III, and IV [15] (fig. 7 ff.) also were concentrated at *A* and *B* in essentially the same areas as were the young eggs. It is, therefore, evident that at least since the eggs then in stage IV had been spawned, viz, since about the first of March,[16] there had been no drift away from those spawning grounds. In other words, there had been no current on the eastern part of Georges Bank to carry the eggs deposited there into distant regions.

Evidence from isopycnics.—Further evidence of this lack of a directional drift away from the abundance centers is to be seen in a longitudinal section through those centers (fig. 9) showing the relation between the vertical distribution of the eggs and the isopycnics.

Between stations C–7 and B–5 (figs. 8, 9) there was a homogeneous water mass, which may consequently be assumed to have been a relatively inactive one. The eggs in that area, as indicated at stations B–5 and B–6 (fig. 9), were apparently

[12] It is the usual experience of hatchery men that haddock eggs die when they sink to the bottom because of a low density of the water.

[13] Isopycnics are lines passing through points at which the density is equal.

[14] Page 12 ff.

[15] See page 66 for definition of the stages.

[16] The approximate incubation period at 3.97° C., the average prevailing temperature in the abundance centers during the March cruise, is about 21 days (p. 67).

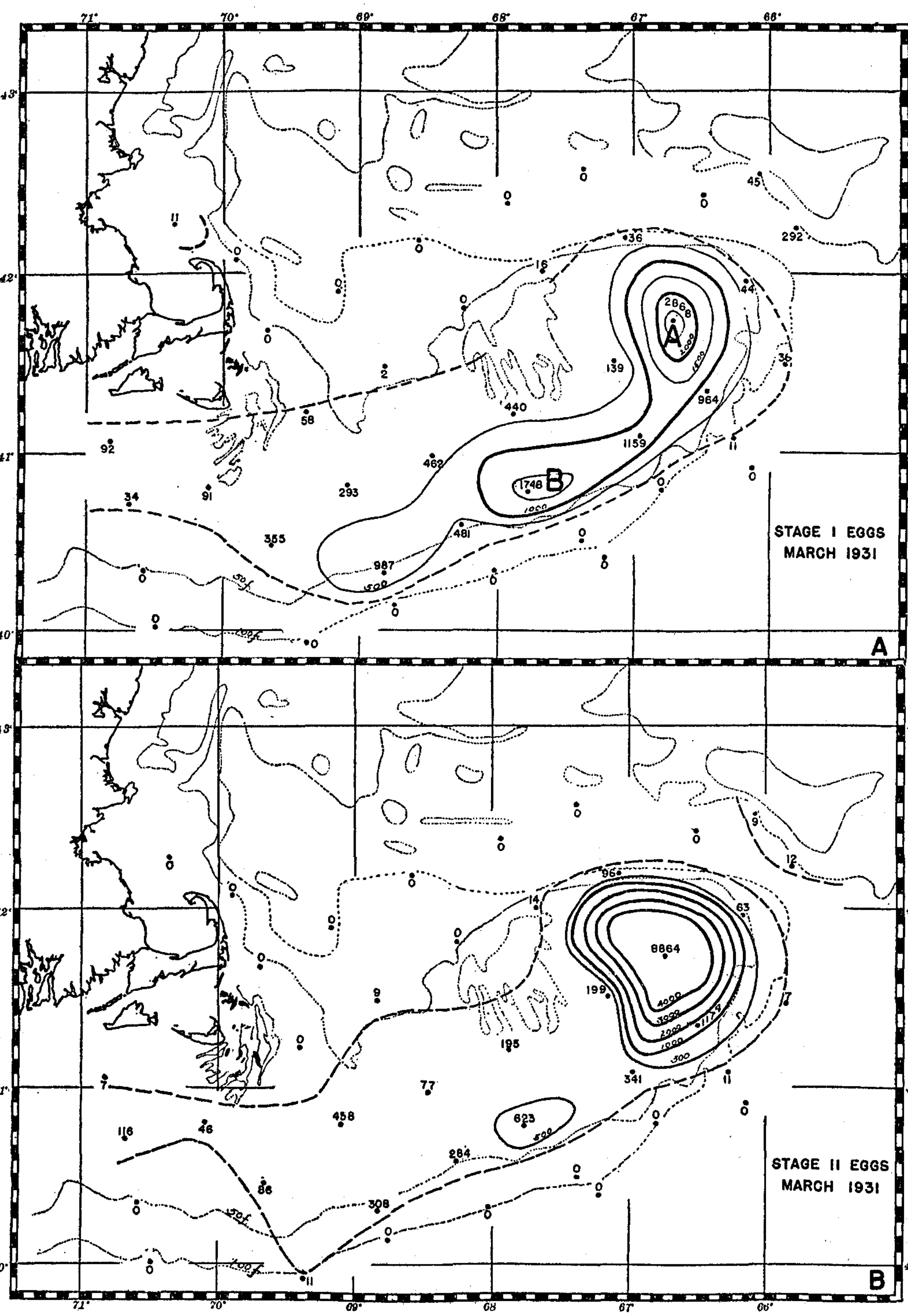

FIGURE 7.—Isometric chart showing the distribution of stage I (A) and II (B) cod-haddock eggs in March 1931.

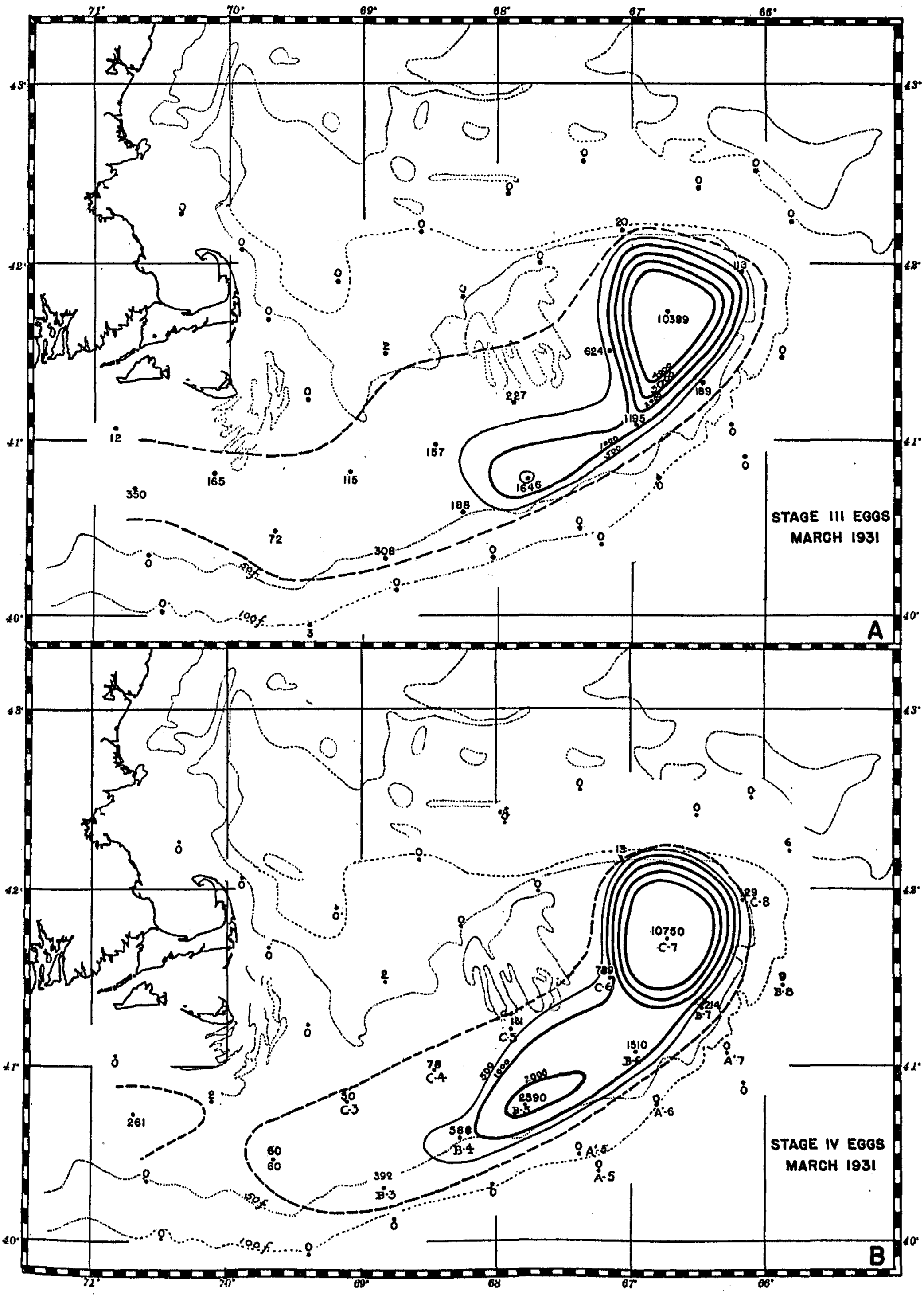

FIGURE 8.—Isometric chart showing the distribution of stage III (A) and IV (B) cod-haddock eggs in March 1931.

fairly evenly distributed from surface to bottom, and probably had been spawned in water of similar density, viz., within the area enclosed by the 26.00 isopycnic in figure 10.

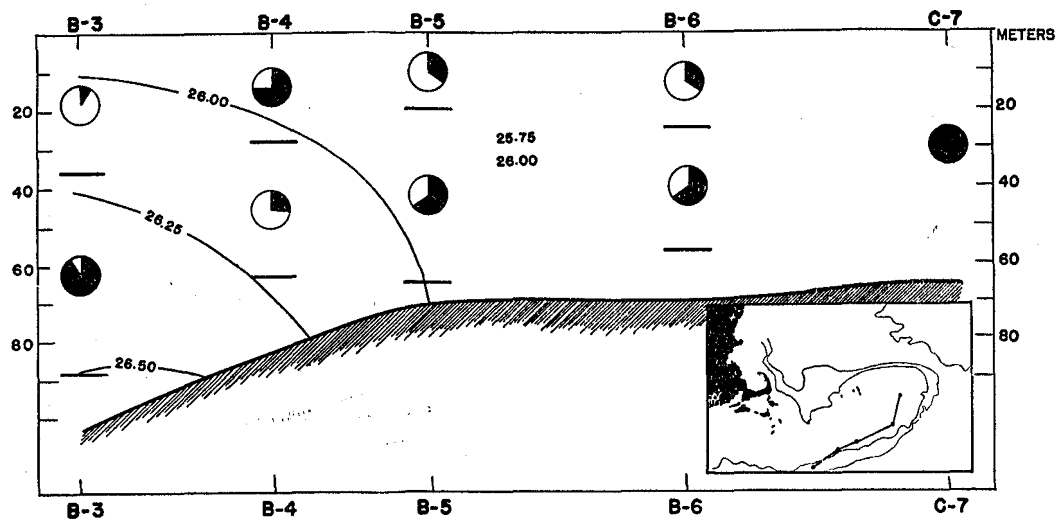

FIGURE 9.—Relation between the vertical distribution and the isopycnics along the southern edge of Georges Bank in March 1931. The curved lines are isopycnics (lines connecting points of equal density); the short horizontal lines represent the upper and lower boundaries of strata fished; the circles at each station express, by the percentage of black, the relative number of eggs found in the indicated levels. Inset shows the course of the section.

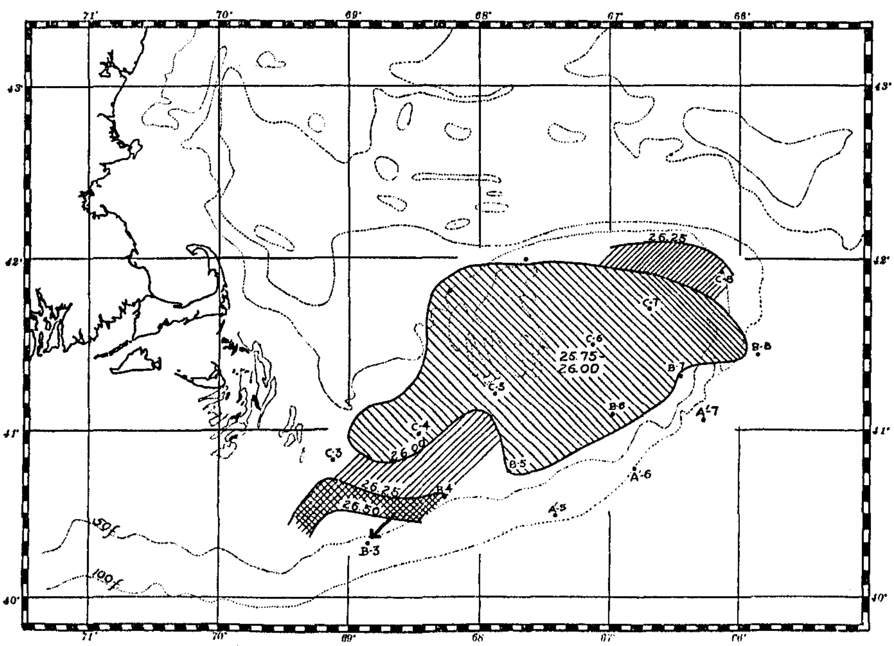

FIGURE 10.—Bottom isopycnics (lines of equal density) on Georges Bank in March 1931. Areas of equal density are indicated by characteristic shading.

At stations B-3 and B-4 (fig. 9), on the other hand, the obliquity of the isopycnics indicates a horizontally unstable water mass. Eggs found at station B-4 may have come from either of two sources: those above the 26.00 isopycnic from the area shaded with northwest lines in figure 10; those below, from the area shaded with northeast lines in figure 10, where water of density 26.00 to 26.25 prevailed on the bottom.

At station B–3, the majority of the eggs were found in the lower strata in water which, judging from its density, may have originated in the region between the 26.25 and 26.50 bottom isopycnics indicated in figure 10 (cross-hatched).

Origin of eggs found in deep water.—Some eggs were found off the edge of the bank, e. g., at station B–8 (fig. 7) over a depth of 1,000 meters. Since haddock do not occur in such depths, much less spawn there, these eggs probably drifted from the bank. In figure 11, they are shown concentrated near the top in water having a density of 26.00 to 26.25. They seem, therefore, to have been deposited on the northeastern part of Georges Bank, where such water was in contact with the bottom.

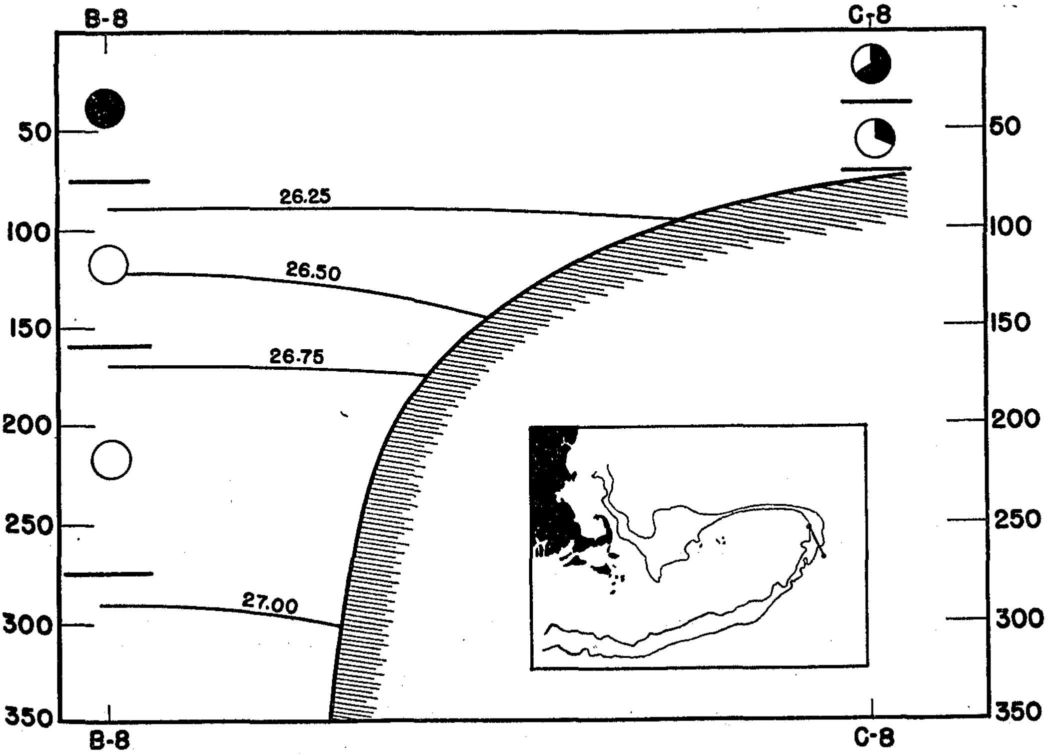

FIGURE 11.—Relation between the vertical distribution and the isopycnics on the southeastern slope of Georges Bank in March 1931. Explanation as in Figure 9.

There is thus evidence of some water movements which, however, did not affect the regions where the bulk of eggs was concentrated, and therefore did not essentially change the distributional picture as discussed on page 15.

Origin of eggs found off Browns Bank and north of Cape Cod.—Although both young and old eggs were found on the slope of Browns Bank, and stage I eggs were taken north of Cape Cod, there were not enough of them to indicate the presence of spawning centers in either of those regions. Furthermore, there is no evidence that eggs migrated from these grounds to Georges Bank in March 1931.

Distribution of the larvae.—The larvae taken on the March cruise were all 2 to 3 millimeters long, that is, recently hatched, and therefore the product of early March or late February spawning (fig. 12). Because no cruise was made in February, the significance of this distribution cannot be interpreted with assurance.

The fact that larvae were found concentrated nearer the center of the bank than were the eggs suggests either: (1) that there may have been an earlier westward drift which carried the eggs from the northeastern center (*A*) slightly westward, or from the southeastern (*B*) center northward; or (2) that these larvae had hatched from eggs produced in the same region and were the first on the bank to appear that season. Since the average prevailing temperature was higher in the larval zone than in the egg zone, viz., 4.17° C., as compared with 3.97° C. at the time of the cruise, the incubation period may have been a day or two shorter.[17] Consequently, larvae would be expected to appear there a day or two earlier.

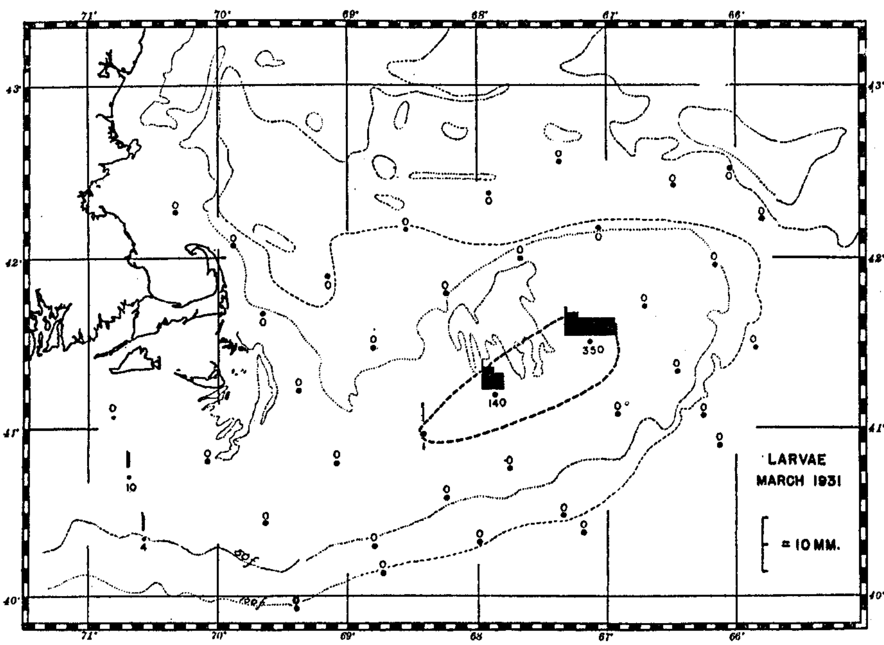

FIGURE 12.—Showing the distribution of larvae in March 1931. The vertical dimension of the black figures represents the total lengths of larvae found at the indicated stations; the horizontal dimension, the number of specimens. The total number of specimens taken is indicated by the figures at each station.

Whichever of these two suppositions be correct, conclusions as to the fate of eggs hatched in March or earlier, as derived from data collected in the April and May cruises, would be unaffected.[18]

APRIL 1931

Cruise of April 16–29.—In the last half of March, as seen, there were two important concentration centers for newly spawned eggs east of the 68° meridian, a northeastern and a southeastern, which we called *A* and *B*, respectively.

In the last half of April there was only one concentration center on the eastern part of the bank for stage I eggs, that at region *A* (fig. 13–A), the only trace of the center formerly existing at *B* being an extension from *A* of the 500-egg contour.

One may reasonably assume from the above that no shift had occurred in the location of the spawning center at *A* during the interval between the March and April

[17] Page 67 ff.
[18] Page 29 ff.

cruises; that spawning at the *B* center had practically ceased meantime; and that no new spawning centers had developed.

Figure 28 shows the course of the cod-haddock spawning season through March and April (1931) in the eastern part of the bank as it is reflected by the relative quantities of the four stages of eggs collected in these months. Likewise, the estimated trend of the cod season is shown. By subtracting the latter curve from the former, the haddock spawning season has been obtained. The following conclusions about that part of the spawning season covered by these studies are evident:

1. In 1931 haddock spawning had probably been maximal the first week of March or earlier.

2. There seem to have been at least two distinct peaks of egg production of almost equal intensity, a greater one in March and a slightly lesser one in April.

3. The general trend of both cod and haddock seasons between March and April was downward.

4. Haddock spawning had probably started, at the latest, early in Febraury.

Distribution of the older stages.—In March, it will be recalled, the three oldest stages of eggs were concentrated in the same regions in which they had been produced, i. e., at *A* and at *B*, where the stage I eggs were also most abundant.

By the last half of April, on the other hand, the situation had changed (figs. 13 and 14). The three oldest classes of eggs were now no longer abundant at *A*; but they were very abundant at *B*, and also at a new region, southwest of *B*, which will henceforth be called *C*.

Since spawning had evidently been continuous at *A* through March and April, and since the only other significant spawning center on Georges Bank seems to have been at *B*, the eggs found at *B* and *C* probably had originated at *A* and *B* respectively, and had been carried by a current moving southwest parallel with the edge of the bank.

Evidence from vertical distribution.—Another line of evidence to support these arguments is to be seen in figures 15 and 16. According to figure 15, the eggs found in April in the *A* center (station C–7), in the *B* center (stations B–6 and B–5), and apparently even a few in the *C* center (stations B–4 and B–3), were suspended in water having a density of 25.75 to 26.00,[19] and hence may be assumed to have originated in a region where such water was in contact with the bottom, namely within the area delimited by the 26.00 isopycnic in figure 16 (shaded with northeast lines), which corresponds roughly in area and position with the spawning center at *A* (figs. 7 and 13).

On the other hand, the majority of eggs found at *C* in April (stations B–4 and B–3, fig. 15) seem to have been suspended in water having a density of 26.00 to 26.25, hence were probably spawned within the area so designated in figure 16, which corresponds in position with the *B* center of egg production in March (fig. 7).

If such a current as is necessary to carry the eggs from *A* and *B* to *B* and *C* had been in existence throughout the period during which those eggs were in the water, then the eggs in each succeeding stage of development should be found concentrated in a region farther away from the spawning ground than the next earlier stage. But in April, the three oldest classes of eggs were concentrated in essentially identical centers (viz, at *B* and *C*). Also, although situated close together, these two concentration centers remained completely separated from each other. Furthermore, they retained about the same spacial relations one to the other as their corresponding centers had in

[19] Page 13.

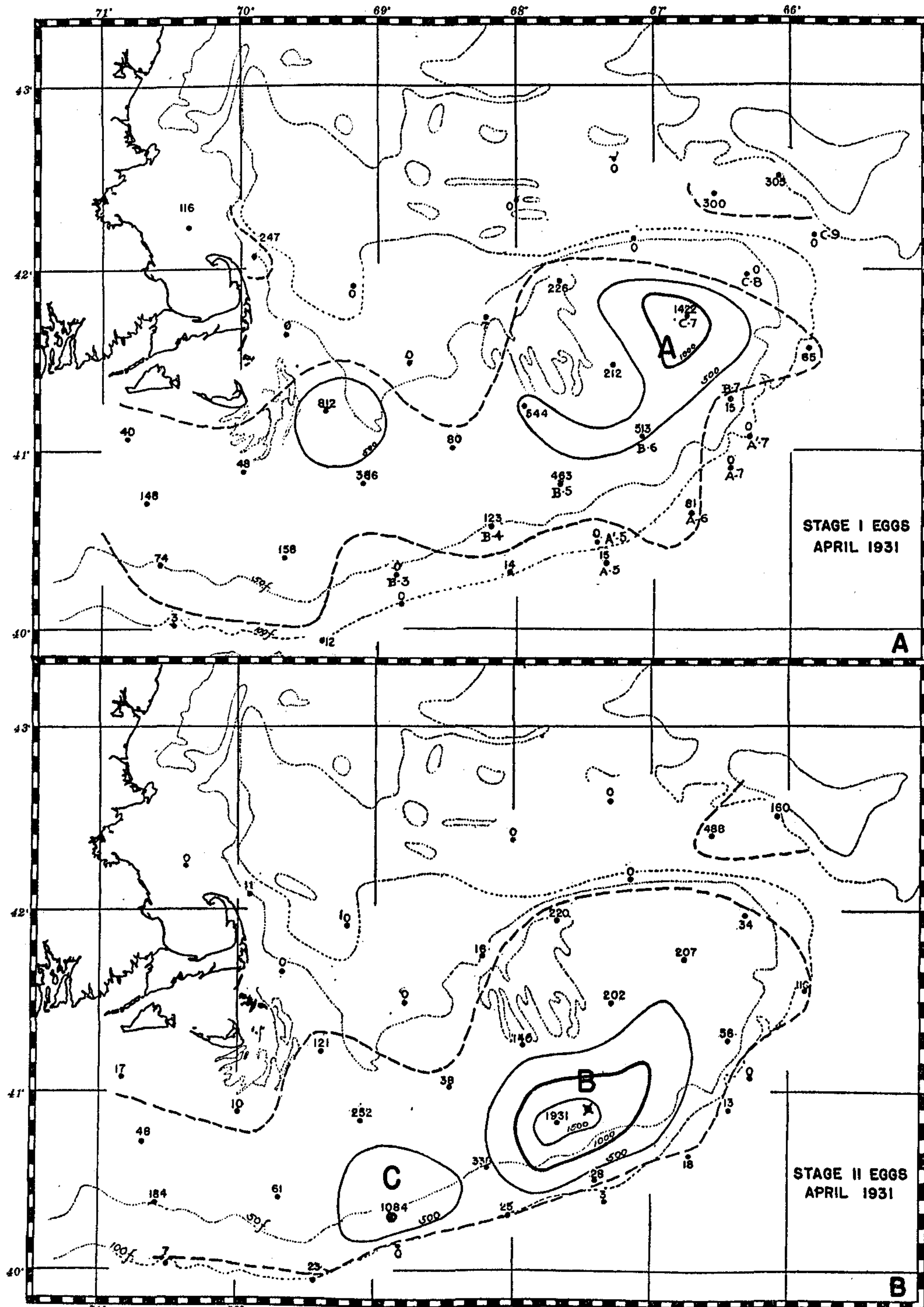

FIGURE 13.—Distribution of stage I (A) and II (B) eggs, April 1931. The letters in heavy print indicate the location of concentration centers A, B, and C. The cross gives the location of the reference point (see p. 25) in the B center.

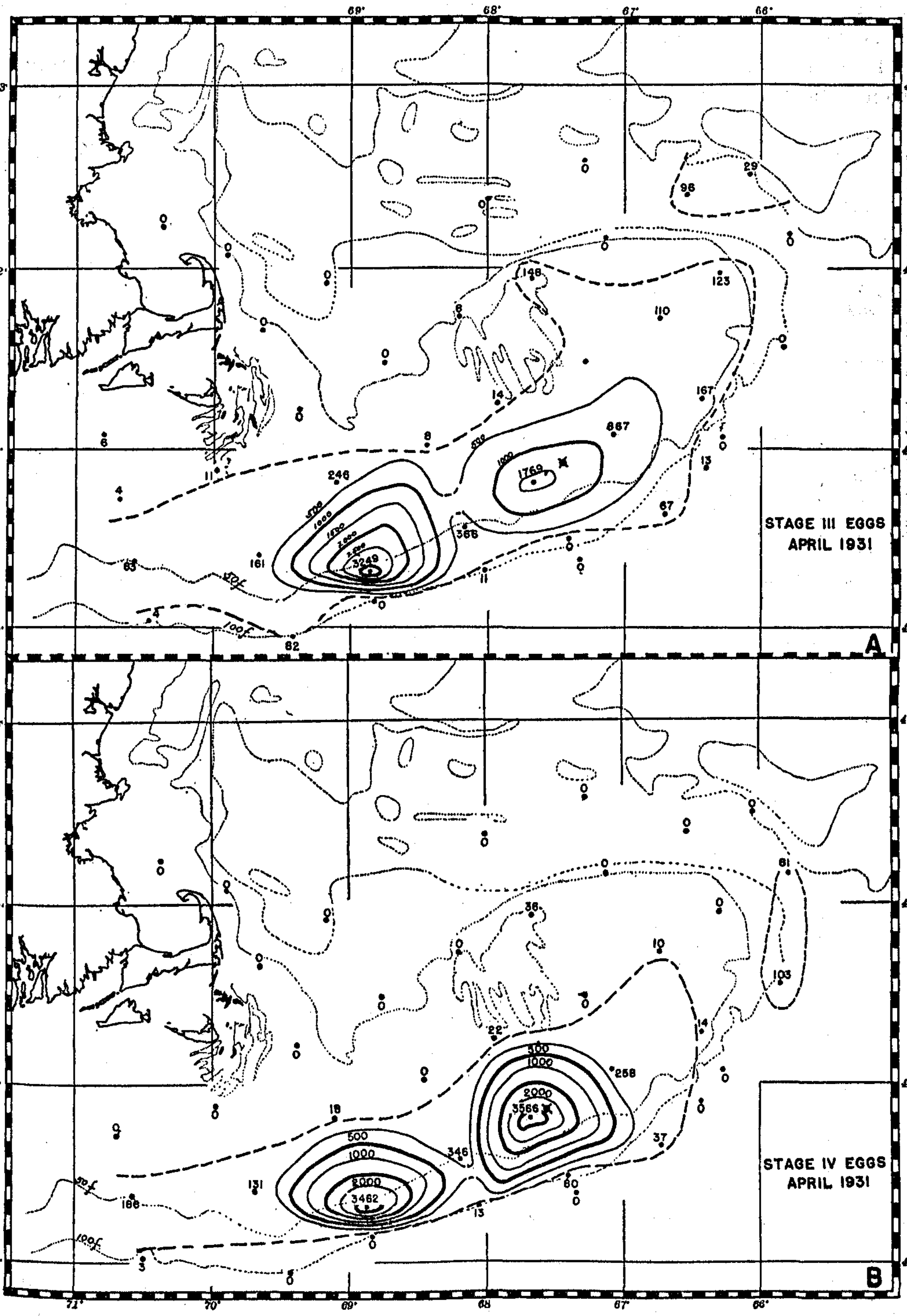

FIGURE 14.—Distribution of stage III (A) and IV (B) eggs, April 1931. The cross indicates the location of the reference point in the B concentration zone (p. 25).

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March (fig. 7), as one can verify by superimposing figure 7–A upon figure 14–A and rotating the former clockwise so as to bring the corresponding egg centers together. This is shown completed in figure 17.

From the facts given by the April charts and what has been learned from the March data, the course of events on the bank can now be interpreted as follows:

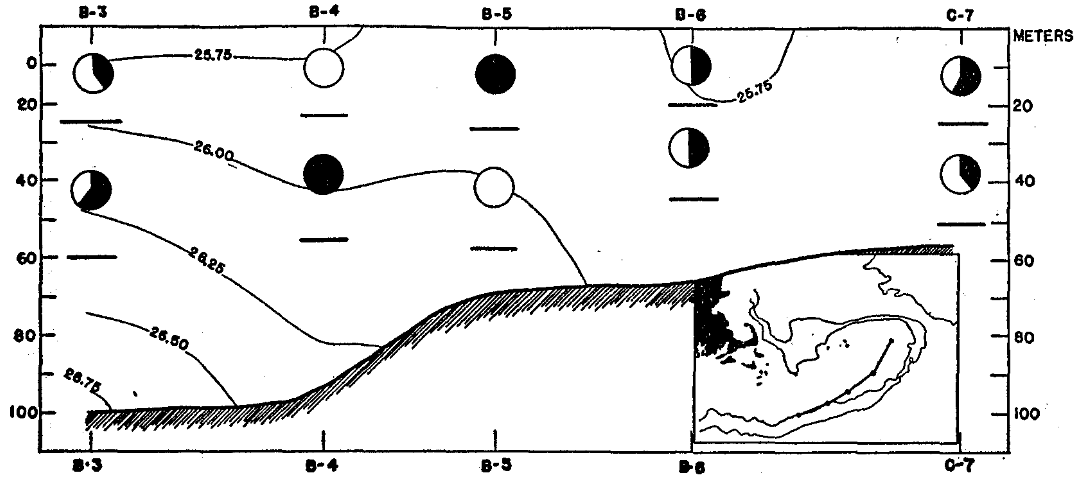

FIGURE 15.—Showing the relation between the vertical distribution and the density in a region through the centers of abundance, April 1931. Explanation as in Figure 9.

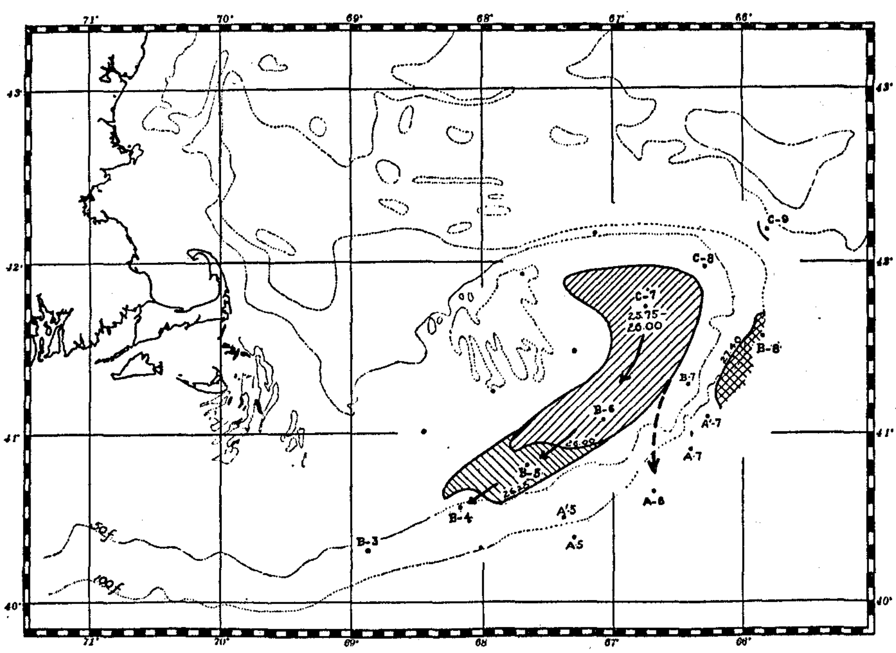

FIGURE 16.—Showing bottom isopycnics on Georges Bank in April 1931. Areas of equal density are indicated by distinctive shading.

During March and the first part of April the water mass in the region of the eastern centers of abundance (*A* and *B*) exhibited no definitive drift; consequently eggs in all stages of abundance accumulated there in the regions where they had been spawned.

The changes in the distribution from March to April are best explained on the assumption that rather suddenly, during the first 2 weeks of April, a current developed on the eastern part of Georges Bank which had a resultant path toward the southwest, parallel with the edge of the bank. Perhaps this current moved slowly at first, as we may judge from the slight difference between the positions of the reference point [20] in the *B* center for the group IV and that for the group III egg charts, and between that for the group III and that for the group II egg charts (figs. 13 and 14). The current seems to have gathered momentum very swiftly about the time the eggs that were in stage II during the April cruise had been spawned. This is indicated by the considerable distance—about 60 miles—between the reference point in the abundance zone at *B* for the group II chart, and that in the corresponding zone at *A* for the group I chart. This may be taken to represent the distance which the eggs

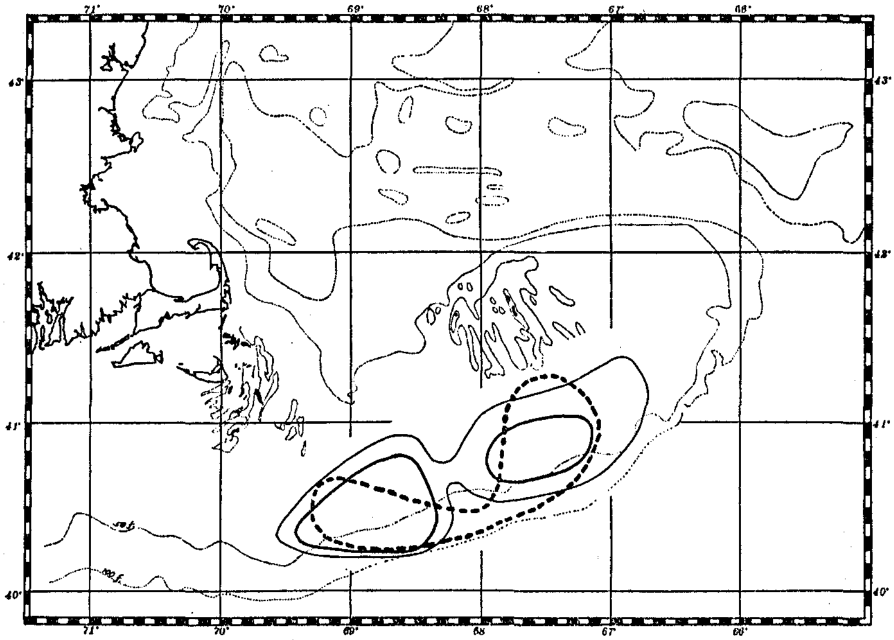

FIGURE 17.—The solid lines represent the 500 and 1,000 contours from the stage III egg chart for April 1931 (fig. 14-A). The dotted line represents the position which the 1,000 egg contour for March 1931 (fig. 7-A) would have were it moved around the bank from its original location.

drifted during the time interval covered by their development from the middle of stage I to the middle of stage II.

The approximate average temperature prevailing in the region traversed by the eggs in this period was 5.5° C. At this temperature, according to figure 48, the age of group I eggs averaged about 2 days; the age of group II eggs about 6½ days.[21] The indicated average speed of the current, by this reasoning, would be of the order of 13 miles per 24 hours.

[20] Because the location of the isolines is at best a rough approximation of the true distribution of the eggs, and because changes in the abundance of the organisms during the course of the spawning season frequently preclude using the same contours for making comparisons between the location of the centers, it is more instructive to reckon the distance of drift from some central point. Such a point, analogous to the location of the center of gravity that the concentration zone would have were it a solid mass of eggs, can be conveniently located as follows: Cardboard figures of the size and shape of the contours in the concentration zone in question are cut out, one for each 500 egg line. These are then glued together, one on top of the other so as to build up figures like those indicated in the isometric charts. The center of gravity of such a figure is then determined as the point at which the figure will balance on the flat end of a match. This position will be referred to hereafter as the reference point.

[21] Page 67.

Origin of eggs found in deep water.—In April, as in March, eggs were found off the bank outside the 100-fathom contour at various points along the southern edge. The origin of these eggs can best be deduced from distribution-isopycnic charts. In figure 18, which gives a profile through the southern stations, the eggs are shown everywhere separated from the bottom by strata of dense water. It seems unlikely, therefore, that they originated on the bottom at these localities. At B–8 about 200 eggs were taken by the net used deepest, in water having a density of 27.40 to 27.60,

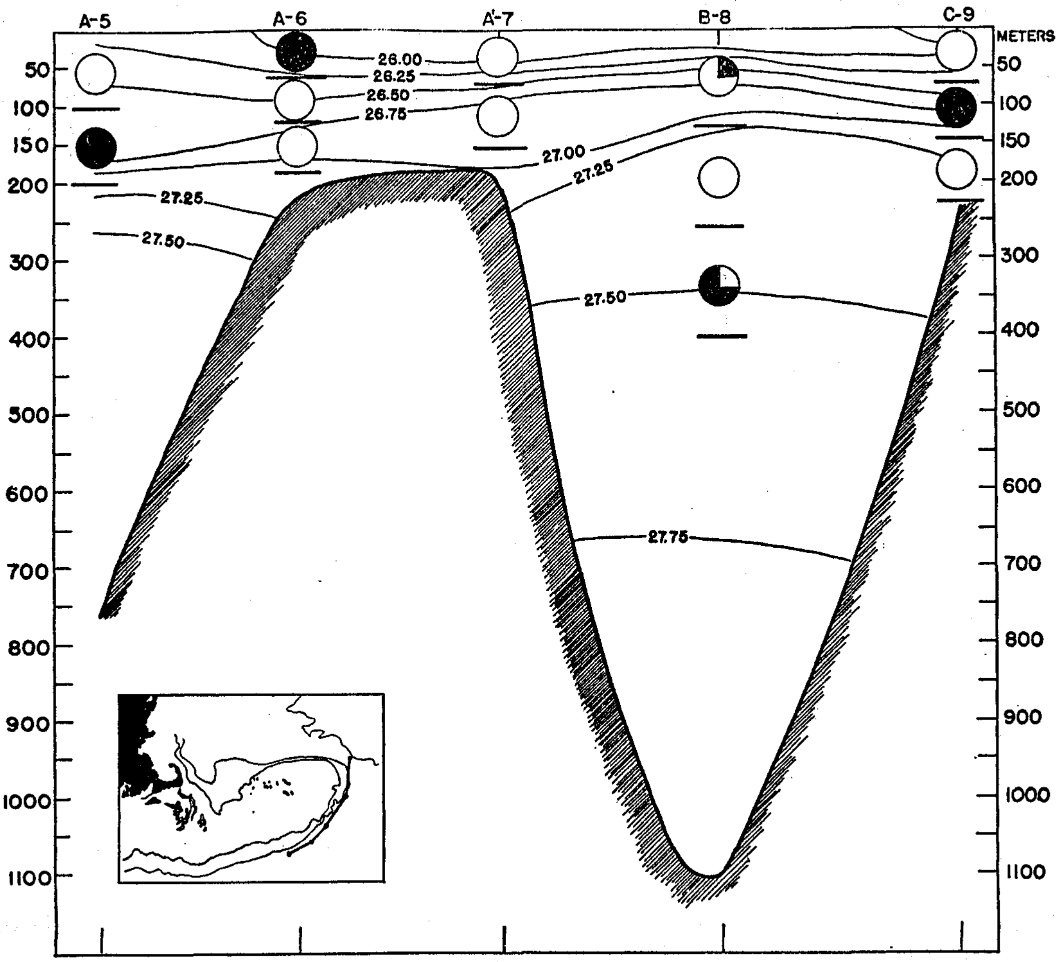

FIGURE 18.—Showing the relation between vertical distribution and the density in deep water along the southern edge in April 1931. Explanation as in Figure 9.

which could have originated either on the steep slope of Browns Bank near C–9 (fig. 16), or on the southern slope of Georges in the area to the west of B–8 delimited by the 27.40 isopycnic (cross-hatched in fig. 16).

At station A–6 (figs. 18 and 19) the eggs were all found in water having a density of 26.00 to 26.25, which touched bottom on the plateau of the bank within the area circumscribed by the 26.00 to 26.25 isopycnic in figure 16 (shaded with northeast lines). There seems, therefore, to have been a slight seaward drift from the southern edge of the centers of abundance. Because no stations were made on Browns Bank, the data do not permit interpretation of the origin of eggs collected in the Fundian Channel.

Distribution of the larvae.—The distribution of the larvae in April was consistent with such a sequence of events as that described above. The regions where the larvae were most abundant correspond with the concentration centers for eggs in late stages of incubation, which further supports the conclusion that the water mass on the eastern and southern parts of the bank started its southwest course so short a time before

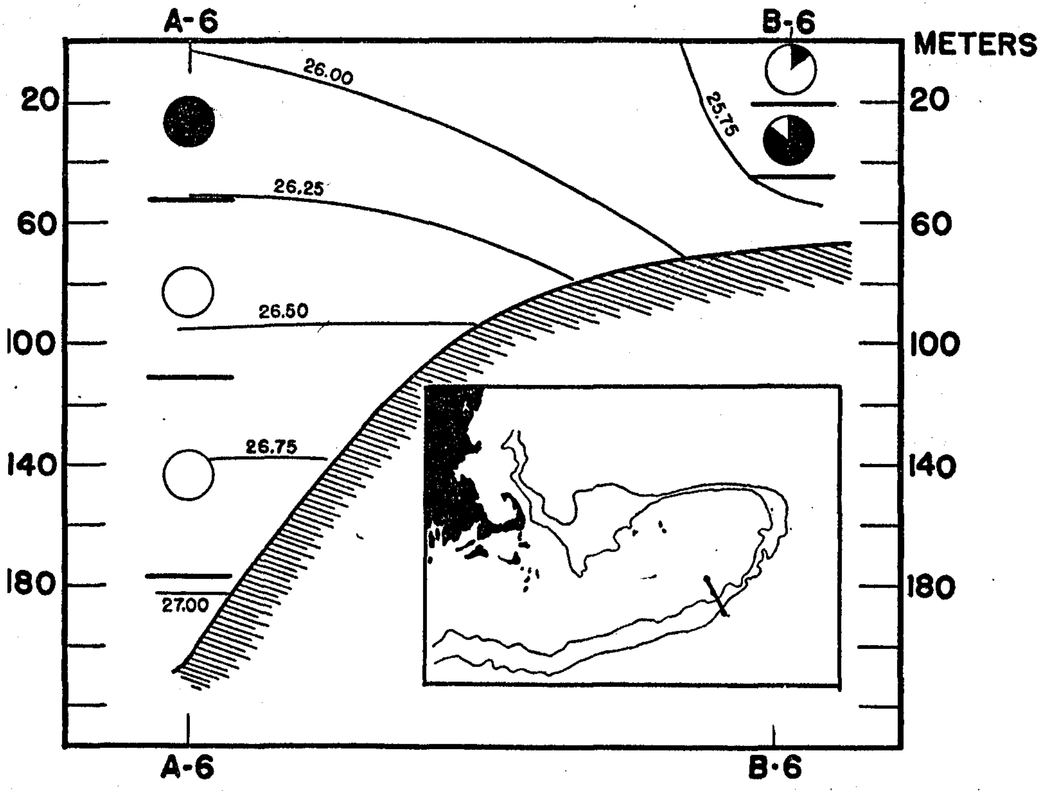

FIGURE 10.—Showing the relation between the vertical distribution and the isopycnics on the southern slope of Georges Bank in April 1931. Explanation as in Figure 9.

the region was sampled that the main body of larvae had not yet drifted beyond the 69° meridian. With the exception of a single specimen found on Browns Bank, all the larvae were taken along the southern edge of Georges. All were recently hatched; therefore, the product of eggs spawned about the end of March or the beginning of April. There were no larger larvae—no trace of those which had been hatched earlier in March, samples of which had been collected during the March cruise.

Possible reasons why larvae hatched in March were not taken in April are the following:

1. They may have already grown strong enough to direct their own movements actively and thus elude the meshes of the tow net. This argument, however, is

refuted by the fact that large larvae as old as 3 months were taken near the surface in relatively appreciable quantity in May, June, and July.[22]

2. They might have become large enough to descend to the bottom. That this argument is unfounded is evidenced by the fact that the sled net, which fishes on the bottom,[23] did not take any large larvae. Furthermore, larvae as old as 3 and 4 months were found near the surface in May 1931, and even as late as June and July in 1932.

3. They might have been destroyed by natural enemies or by unfavorable physical conditions. There is no information available either to defend or to refute this argument. It is known, however, that abnormal physical conditions did not prevail in March or April of that year.

4. Perhaps they had drifted off the bank. The same current which carried the

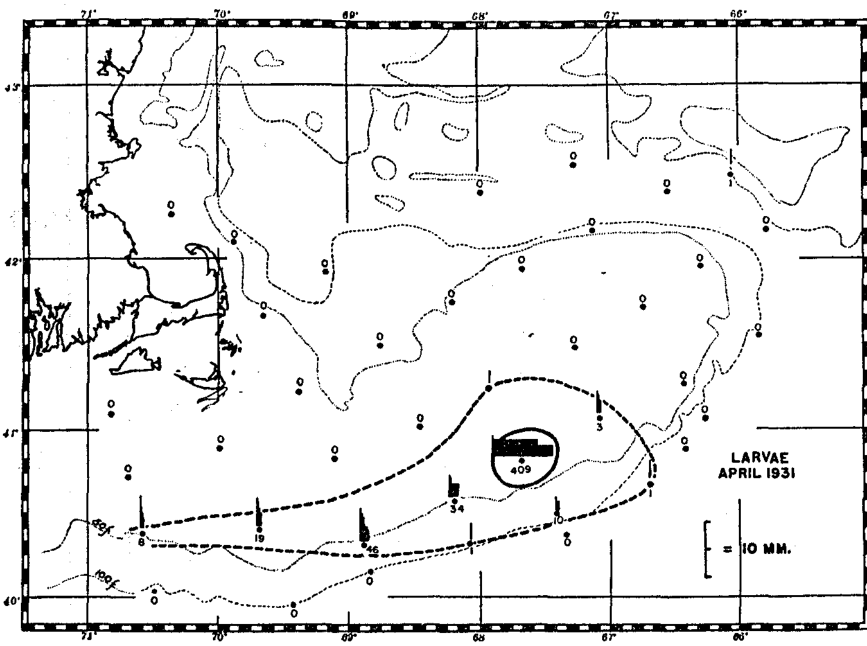

FIGURE 20.—Distribution of larvae in April 1931. The vertical dimensions of the black figures represent total lengths of fish, the horizontal dimensions, number of specimens.

eggs produced in the *A* center toward the southwest also could have borne the March larvae westward. But it is doubtful that this current started early enough to carry the larvae past Nantucket Shoals, and there is no evidence that a dominant drift occurred directly southward off the bank in March or April.

5. Possibly they drifted into Georges Shoals where our vessel did not sample. It will be recalled (fig. 12) that in March they had been concentrated just south of the Shoals. Furthermore, March larvae were found in the vicinity of Georges Shoals at the end of May.[24] This possibility will be considered later.

[22] Page 29 ff.
[23] Page 60.
[24] Page 32.

MAY–JUNE 1931

Cruise of May 26–June 9, 1931.—Up to this point, the discussion has focused upon what we have been calling centers of abundance. Such centers were so conspicuous during March and April on the eastern and southern parts of Georges Bank at regions *A*, *B*, or *C*,[25] that the abundance of haddock eggs west of the 69° meridian in the region of Cape Cod and of Nantucket Shoals, seems insignificant by comparison. The largest quantity of newly spawned eggs found in the latter region during any of the three cruises of 1931 was 812 (in April, see fig. 13), as compared with 10,750 for the eastern production centers (in March, see fig. 8). It appears, therefore, as if the fish in the western region produced but a small fraction of the total number of eggs deposited on Georges Bank during that year.

By the end of May (figs. 21 and 22) there were no abundance centers found anywhere on the bank, and save for scattered spots here and there, the only region where spawning seems to have persisted is the western part of the bank, south of Cape Cod and in the vicinity of Nantucket Shoals. Judging from the quantities of eggs taken there during the three cruises, spawning began and ended later there than on the eastern part of the bank, not reaching its peak until about the end of April (see fig. 13–A) and declining by the end of May.

Spawning apparently had practically ceased at *A* and at *B* (fig. 21-A), at least by the time the eggs then in stage IV had been deposited, viz, shortly after the middle of May. This estimate is based on the average prevailing temperature (8° C.) at which haddock eggs develop from stage I to stage IV in about 12 days.[26]

The quantity of eggs in all stages of incubation taken at the end of May 1931, was so small as compared with that taken earlier, it is reasonably certain that relatively few larvae were to be hatched out later in June that year. In other words, the larvae present in the last week of May and the first week of June presumably constituted the bulk of the contribution to the total haddock population of Georges Bank by that year's breeding season. For that reason, their distribution (fig. 23) is especially interesting.

Anticipated distribution of larvae.—Evidence has been presented leading to the conclusion that the only significant regions of production in 1931 were at *A* and at *B*,[27] that the larvae hatched in March from eggs produced there had possibly disappeared from the bank, for the most part, by the last half of April; and that larvae hatched in April were drifting westward at the time of the April cruise toward Nantucket Shoals to regions unfavorable to haddock development.

If this drift continued through May, and if there were no immigration from other spawning grounds, larvae hatched in April or earlier presumably should be carried away by the end of May, and one would expect to find only recently hatched specimens on the bank at that time. Furthermore, one should expect to find these larvae concentrated somewhere along the southern edge of the bank, whither the current had carried the eggs up to the time of hatching.

Actual distribution of larvae in May.—The distribution of larvae at the end of May as it was actually found, however, was quite different from the above expectation. Larvae were found at nearly all stations on the bank, and in quantities not significantly less than were found earlier.[28] Furthermore, they were of all ages,

[25] Page 15 ff.
[26] Page 67 ff.
[27] Page 20 ff.
[28] Pages 20, 28.

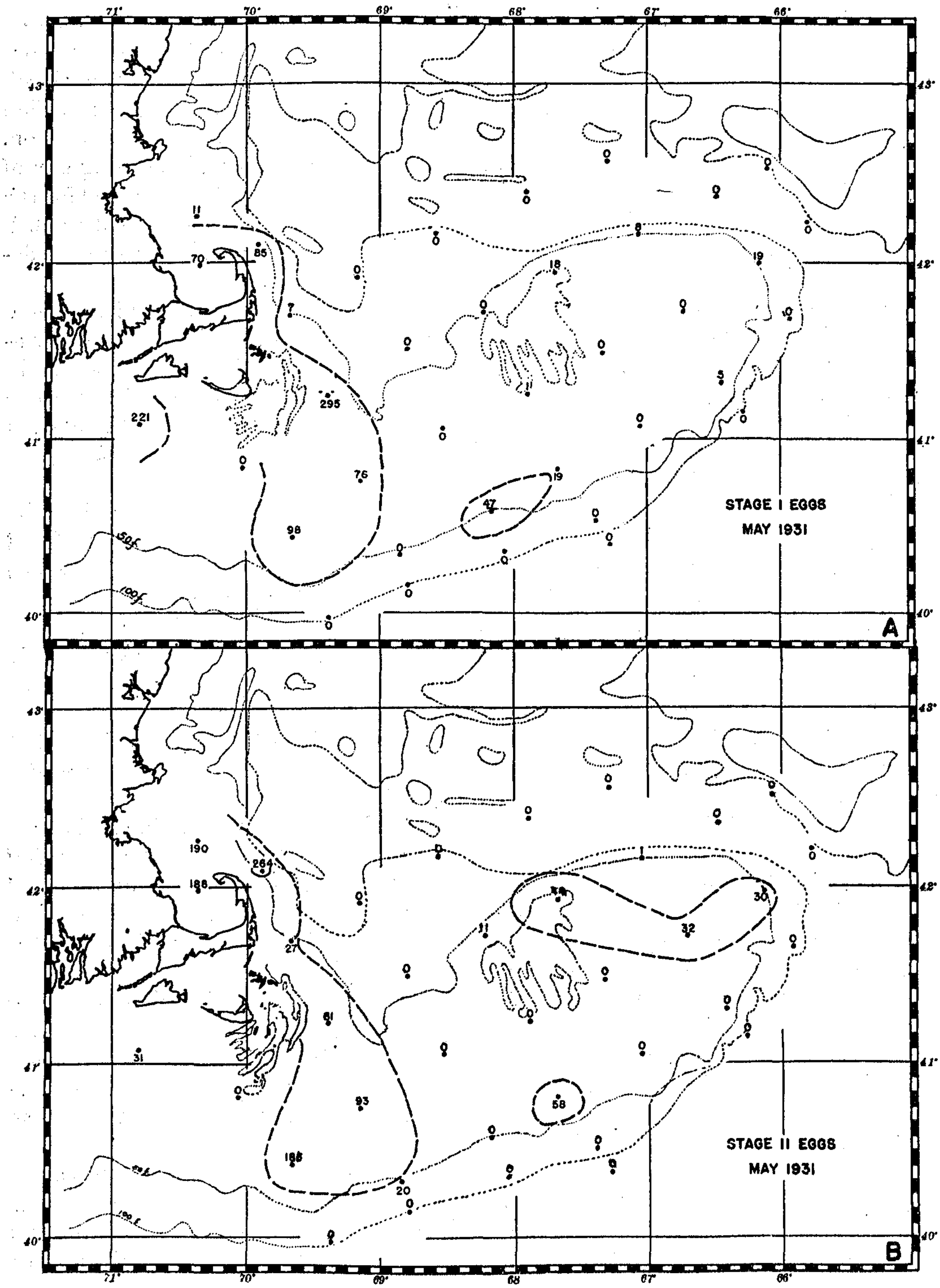

FIGURE 21.—Distribution of stage I (A) and II (B) eggs in May 1931.

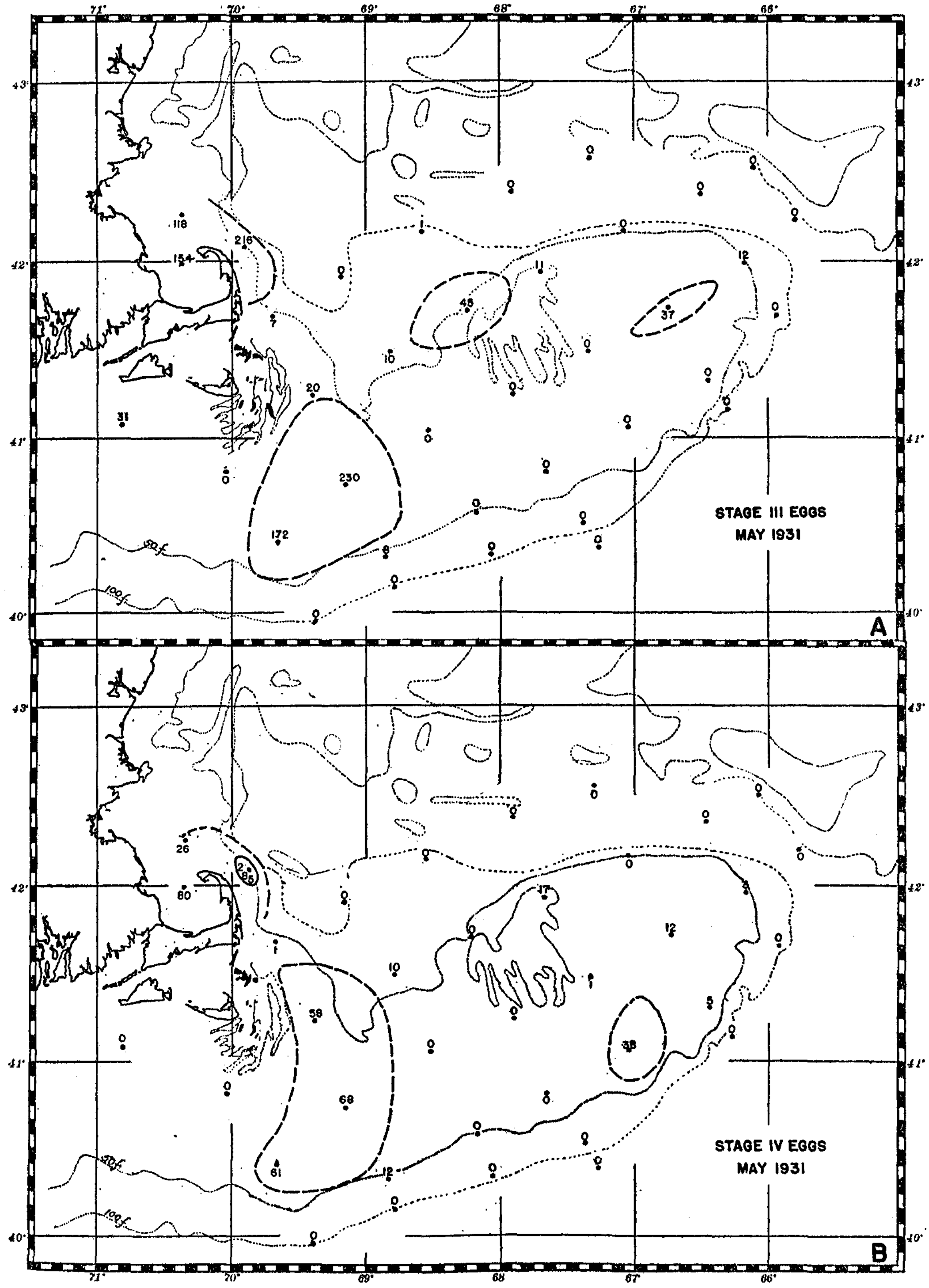

FIGURE 22.—Distribution of stage III (A) and IV (B) eggs in May 1931.

judging from their size,[29] from recently hatched to 2 months. Finally, they were most numerous in the vicinity of Georges Shoals, where no spawning center seems to have existed that year.

Source of these larvae.—Provided it can be shown that the drift indicated in April continued in the same direction through May; [30] that the larvae swept off the bank as a consequence of this drift had not returned; and that spawning on the western part of the bank earlier in the season had been too insignificant to supply the larvae found on the bank in May, it must then be concluded that the latter had immigrated there from outside breeding grounds. Assuming for the moment that these conditions have

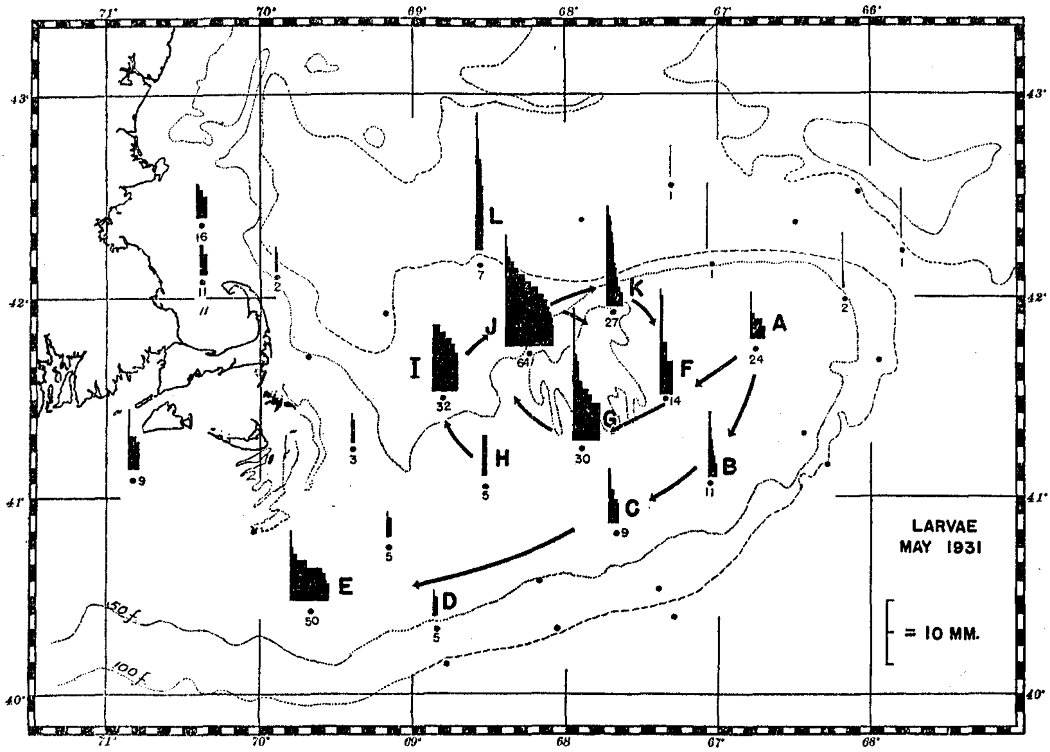

FIGURE 23.—Distribution of larvae in May 1931. Vertical dimensions of the black figures indicate length of larvae in millimeters (see scale); horizontal dimensions, the number of specimens, which are also indicated for each station by numbers.

been satisfied, we shall consider the possibility of such an immigration actually occurring during that year.

Evidence of immigration.—If there had been immigration during March and April, we probably would have detected it in the course of our analysis of the data collected in those months. Since stations were made completely around the periphery of the bank in deep water just off the edge, all regions were sampled through which significant masses of eggs would have had to pass in order to reach the bank. None of the outside stations yielded significant quantities of eggs during any of the three cruises of 1931. Therefore, according to this line of evidence, any immigration which may have occurred that year must have done so sometime between the cruises. If it had occurred between the March and April cruises, its effect should have been detected during

[29] Pages 69, 70.
[30] Page 25.

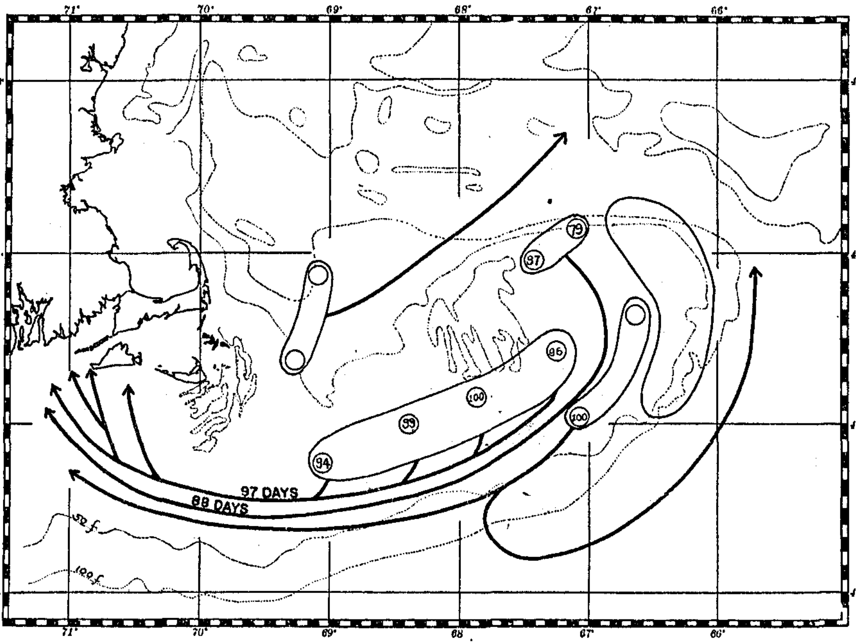

FIGURE 24.—In April 1931 drift bottles were liberated in the regions marked by circles. The numbers in the circles represent days later that the bottles were recovered. The arrows point the direction of recovery.

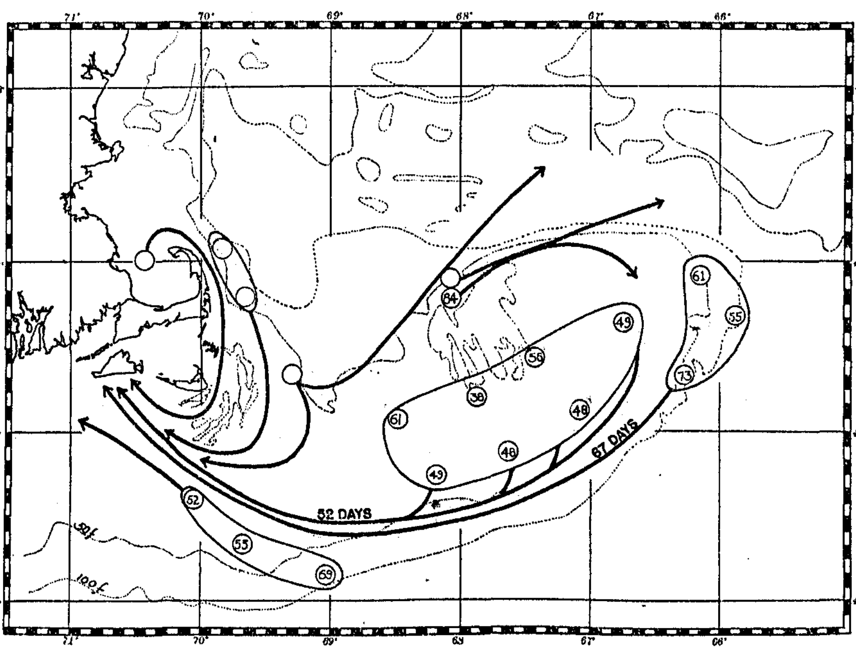

FIGURE 25.—In May 1931 drift bottles were liberated in the regions marked by circles. The numbers in the circles represent days later that the bottles were recovered. The arrows point the direction of recovery.

the latter cruise. No such effect was found. There is left, then, the period of about 40 days between the April and May cruises, during which an immigration may have occurred.

From what direction could such an immigration have taken place? The bank is bounded on the west by land; therefore, it could not have been from that direction. There are no known spawning grounds for haddock south of Georges Bank; and even if there were, there is no record of a drift ever having occurred onto the bank from that direction. To the east is Browns Bank, a known breeding ground for haddock, which may be considered a possible source of supply for Georges Bank. However, many of the larvae found on Georges in May were a month old or more. A month before the May cruise [31] there seems to have been one current carrying newly spawned eggs away from Browns Bank in a northwesterly direction, and perhaps another [32] carrying some to the southwest, just off the southern edge of Georges. Neither of these currents flowed in such a direction as to be likely to carry eggs or larvae onto Georges Bank. Therefore, evidently, month-old larvae could not have drifted directly to Georges Bank from Browns in May. This conclusion is substantiated by the results of the drift bottle experiments.[33]

There is left, then, only the spawning grounds to the north of Georges Bank whence immigration may have occurred. The most extensive grounds known in that direction are those along the coast north of Cape Cod. According to United States Bureau of Fisheries records, the haddock population in that region is relatively scanty and presumably, therefore, could produce relatively few eggs. Furthermore, drift bottle experiments carried on that year [34] did not indicate a drift on to Georges Bank proper from the northwest in May, or thereafter.

It may reasonably be concluded from the above that in 1931 there was no immigration of eggs or larvae on to Georges Bank from outside breeding grounds, and consequently, that Georges Bank supplied its own stock that year.

How Georges Bank could have supplied its own stock in 1931.—It can be interpreted how this could be accomplished by the following facts, which have already been established:

1. The larvae found on the bank in May were concentrated about the vicinity of Georges Shoals.

2. At no time during the season had there been evidence of a spawning center in that region, the only important breeding grounds being those on the eastern part of the bank at regions *A* and *B*.[35]

3. The small spawning center on the western part of the bank found in April (fig. 13–A) seems by comparison to have been of slight significance. Furthermore, drift bottle experiments indicated a southwest drift from that region around Nantucket Shoals into the region south of Cape Cod.

It is reasonable to conclude, therefore, that the bulk of the larvae found on the bank in May had been supplied by the breeding grounds at *A* and *B*. It will be remembered,[36] however, that at the end of April, when the fish in those breeding grounds were a little beyond the peak of their spawning season, a current was apparently carrying the eggs produced there along the southern edge of the bank toward Nantucket Shoals.

[31] Figs. 13, 14.
[32] Page 26.
[33] Page 35.
[34] Page 35.
[35] Page 15.
[36] Page 20 ff.

Since some of the eggs produced at A and B seem not to have been lost from the bank, there must then have been a change in the current between the date of the April cruise (April 16–29), and that of the May–June cruise (May 26–June 9). The dominant group of larvae found during the latter cruise, judging from the size composition, had been spawned from 30 to 40 days previously,[37] in other words, about the time of the April cruise. At that time (fig. 14) there was a concentration of the three older classes of eggs at B, which is situated just south of Georges Shoals, and it is reasonable to suppose that some of these eggs were carried northward into the shoals.

Further evidence of a change in the current system during May is the fact that larvae were found at region A in May (fig. 23), whence in April the eggs had been carried away long before hatching. It appears either that these larvae had hatched from eggs spawned in that region, or that they had drifted there from the northern edge of the bank, possibly from the South Channel in the direction suggested in figure 23.

Increase in the size of the larvae in May progressively from A to F to G (fig. 23)[38] suggest a slow drift from A to Georges Shoals; and a general increase in the size of larvae from H to I to J[39] further suggests an eddy tendency from the southern part of the bank toward Georges Shoals. A slight progression in size from A to B to C[40] also suggests a drift from A toward Nantucket Shoals. The rather large number of larvae at E suggests that in that region there may have been a meeting of currents bearing larvae from the north and from the east.

It appears, therefore, as if the rapid southwest current which developed on the eastern part of the bank in April had become considerably modified by the last week in May, splitting in the north-eastern region to produce an outer current which proceeded in the direction of Nantucket Shoals, and an inner, which formed an eddy in the region of Georges Shoals. These supposed movements are indicated by arrows in figure 23.

These interpretations explain the presence and origin of larvae spawned in April or later. They fail to explain, however, the presence of the largest larvae at stations I, J, and L, which may be estimated from figure 50 to be 60 to 70 days old; therefore, the product of March spawning. It will be recalled[41] that in April no larvae which had been hatched in March were found. It was suggested among other things that this may have meant that March larvae had disappeared from the bank, or that they had drifted into the region of Georges Shoals where no sample was taken. The fact that specimens were found in June favors the latter of the two suggestions.

Evidence from drift bottle experiments.—It is fortunate that additional evidence of a more direct nature is available from which the complex water movements operating between April and June may be deduced in another way, viz., from drift bottle returns.

At the time of the April and May cruises, 800 surface drift bottles were put out at the stations where plankton hauls were made. Since then, 13 percent of these bottles have been found and returned. Although the Bureau has not yet completed a detailed study of the currents on the basis of these returns, it has, nevertheless, been possible to determine the main courses of drift from them (figs. 24 and 25).

Since the bottles were found from 35 to 100 days after being set adrift, water movements inferred from the differences in the locations of the places where they were put out and the places where they were found, necessarily occurred after the times of the April and May cruises. Nevertheless, assuming the bottles drifted in the same cur-

[37] Page 67 ff.

[38] The average sizes of specimens at these stations were 3.0, 7.9, and 8.7 millimeters, respectively.

[39] The average sizes of specimens at these stations were 6.1, 8.7, and 9.9 millimeters, respectively.

[40] The average sizes of specimens at these stations were 3.0, 4.2, and 4.7 millimeters, respectively.

[41] Page 27.

rents as the eggs, the time required by the former to drift from Georges Bank to the shore where they were picked up can be used to reflect the maximum time which the larvae could have spent upon the bank.

Bottles liberated in April (fig. 24) south of Georges Shoals, viz, in the same general area where eggs in late stages of incubation were concentrated at that time (at *B*, see fig. 13), drifted to the shore south of Cape Cod in an average of 97 days. Those liberated in the same region in May (fig. 25), on the other hand, drifted to the same general destination in an average of only 52 days. The difference in time could be explained by an absence of water movements in that region during the intervening time. It could also be explained by the existence of an eddy into which the April bottles were caught for a period of about 45 days. At the end of that period they presumably were released into the southwest current.

Such an eddy is characteristic of the region of Georges Shoals (Bigelow, 1927), and in view of the fact that the larvae were apparently concentrated about the shoals in May, it is reasonable to conclude that the bottles also drifted into the same region. During the 45-day period which the larvae are thought to have spent in the neighborhood of the shoals, they could possibly have grown large and strong enough to descend to the bottom, and thus remain unaffected by the change in the currents which apparently occurred after the May cruise.

The drift bottle data, therefore, support the interpretation that some of the eggs produced in the eastern centers of abundance in April and earlier drifted into the region of Georges Shoals. These data further add to the evidence that Browns Bank did not supply a population to Georges, since the system of currents did not favor a drift in that direction. Thus, by what is of necessity a circuitous argument, we arrive at the conclusion that Georges Bank in 1931 supplied its own brood of young fish. That the brood was a relatively successful one has been indicated by subsequent studies.

Summary of the 1931 Studies

Something of the order of 90 percent of the haddock spawning on Georges Bank in 1931 apparently occurred in the two regions on the eastern part of the bank which we have designated *A* and *B*. Although there was a small spawning center just north of Nantucket Shoals and east of Cape Cod, this seems to have contributed less than 10 percent of the total number of eggs produced on the bank that year.

During March there was no directive drift, consequently no dispersal of the eggs from the spawning place. In April a current developed, carrying the eggs from the centers of abundance at *A* and *B* around the southern edge of the bank. A portion of this current seems to have moved into an eddy during May, into the region of Georges Shoals, carrying some of the eggs with it. In this way enough eggs spawned at *A* and *B* were kept on Georges Bank to contribute a relatively abundant year class to the haddock population in 1931.

April 1932

Cruise of April 1–15.—While in March and April 1931, there were two spawning centers on the eastern part of Georges Bank, at *A* and at *B*, there was only one such center during the first 2 weeks of April 1932, that at *A* (fig. 26–A). On the western part of the bank, in the South Channel, on the other hand, where no significant volume of spawning was indicated in 1931, there was a rather important center in April 1932.

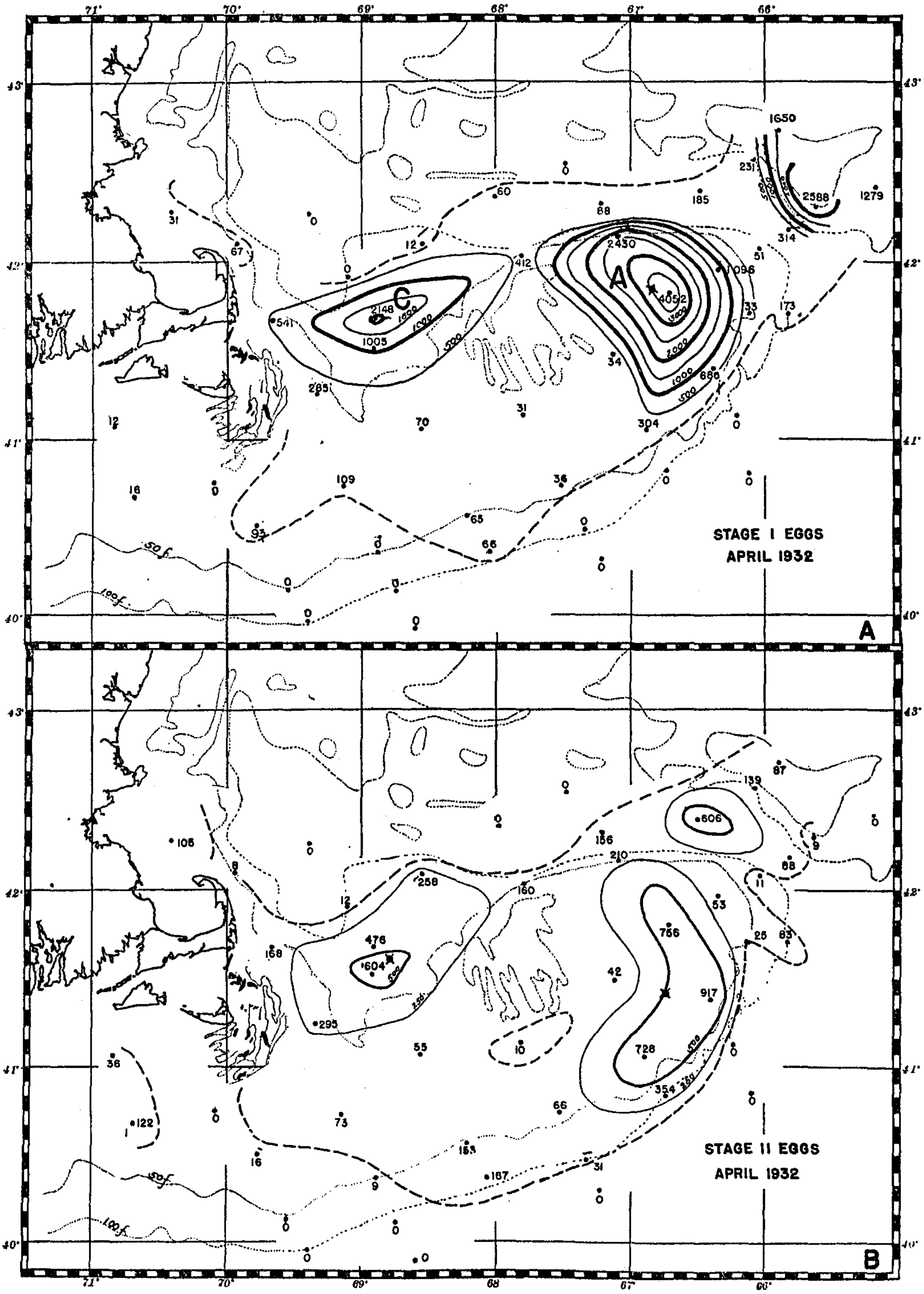

FIGURE 26.—Distribution of stage I (A), and II (B), eggs in April 1932. The crosses indicate the location of the reference points.

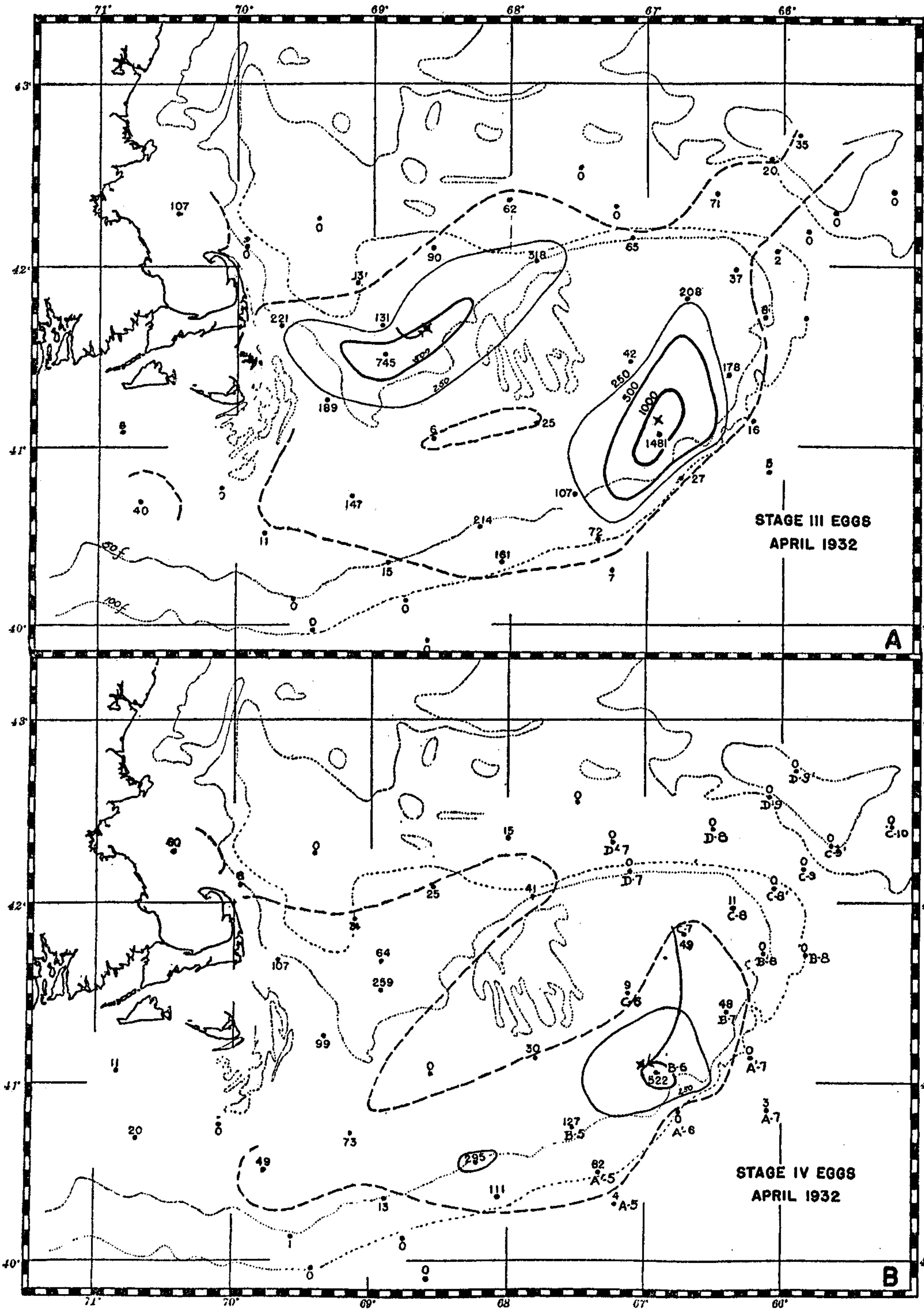

FIGURE 27.—Distribution of stage III (A), and IV (B), eggs in April 1932. The crosses indicate the location of the reference points. The arrow gives the direction of the supposed drift from the spawning ground shown in Figure 26-A.

The most interesting difference between the 2 years' data, however, is in the quantity of eggs in the older stages. The 1932 cruise was made from April 1 to 15, a period corresponding to the interval between the March and April cruises of the previous year. It will be recalled (p. 21) that in that period of 1931 the spawning season had been apparently on the decline, having been at its climax sometime before the March cruise. This conclusion was supported by the preponderance of older eggs over younger ones in both March and April.

In April 1932, on the other hand, the situation was reversed, the youngest eggs being far in excess of the older ones (figs. 26 and 27). This situation may be interpreted in at least two ways: either the spawning season at *A* had started considerably later in 1932 than it had in 1931, and at the time of the April cruise was approaching its peak rather than receding from it; or, its occurrence had been essentially the same as in the preceding year and there had been, for one reason or another, a heavy mortality of eggs older than stage I.

Unfortunately, our knowledge of the American haddock spawning season is very scanty, based as it is on scattered data. Some notion of the normal onset and decline

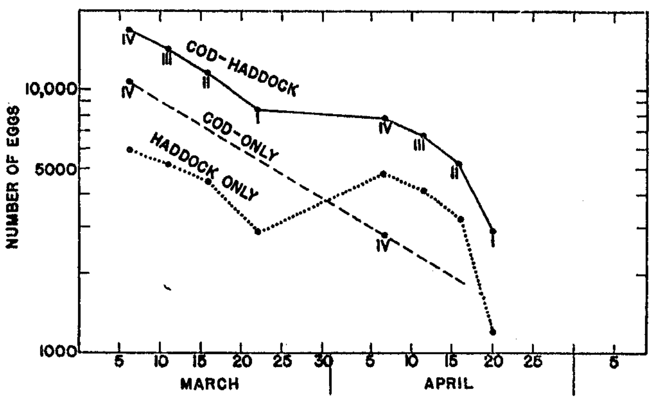

FIGURE 28.—The numbers of cod-haddock eggs in each of the four stages of development taken on the eastern part of Georges Bank during the 1931 cruise are plotted to indicate the approximate average time when they were produced. The cod spawning season, as estimated from the number of eggs in stage IV, is indicated by dotted line. The haddock season has been given by subtracting the estimated number of cod eggs from the actual number of cod-haddock eggs.

of the season may be obtained by the dates when the Gloucester Hatchery began and ended its annual stripping of mature haddock. For the 5-year period 1917 to 1921, the average date when this work began was February 23; the average date when it ended was April 28. Bigelow and Welsh (1925, p. 442) write:

> The spawning season is apparently the same on Georges Bank as in the inner waters of the Gulf, for we found cod-haddock eggs in moderate numbers across the western end late in February, great numbers of them (and took ripe haddock in the trawl) on the eastern end on March 11 and 12, and they were still plentiful there on April 16 and 17. Similarly, Mr. Douthart, of the Bureau of Fisheries, towed haddock eggs over the north-central portion of the bank on April 14 and again on the 26th and 27th, in 1913, but the *Albatross* found none on the western part of the bank on May 17 in 1920.

Likewise, in the North Sea, haddock normally spawn from January to May, and most intensively in February, March, and April (Damas, 1909).

From these scattered data it may be inferred that the 1931 spawning season as graphed in figure 28 was approximately a normal one, for it had evidently started early in February or earlier, was going strong in March and April, and was practically complete before the end of May (cf. figs. 21 and 22). Likewise, it may be inferred that something was abnormal about the 1932 season; for judging wholly from figure 29, it seems to have started late in February, to have been relatively insignificant in March, and to have reached its peak not before the first week of April, i. e., a whole month later than in the previous year. What could have caused such a delay? From the fact that haddock usually spawns progressively later toward the northern regions of its range,[42] it may reasonably be supposed that temperature is one of the most important elements influencing that process. Thus, a striking difference between the bottom temperatures for the 2 years might explain the apparent difference in the onset of the spawning season. The estimated trend of bottom temperature in the *A* abundance center during 1931, based on the average temperature of stations

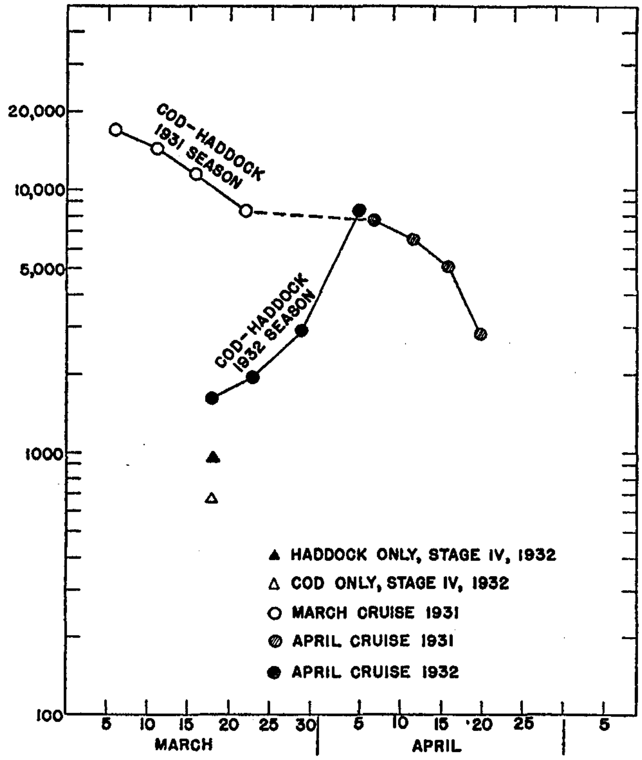

FIGURE 29.—The numbers of cod-haddock eggs in each of the four stages of development taken on the eastern part of Georges Bank during the 1931 and 1932 cruises are plotted to indicate the approximate average time when they were produced. The number of identifiable cod eggs taken on the 1932 cruise in that region is also indicated, along with the number of stage IV haddock eggs.

sampled there, is shown in figure 30. The average for the April 1932 cruise, 4.3° C., was slightly less than 0.3° lower than the estimated average for the corresponding period of 1931; and its range extended beyond the estimated range for the same period of 1931 (fig. 30). Thus, there seems to have been insufficient difference between the bottom temperatures for the 2 years to cause the great delay in the 1932 season suggested by figure 29.

If some unknown elements did cause a delay of a month in the 1932 spawning season, it is not unreasonable to expect the cod spawning season to be also affected. It is known that the cod season normally begins sooner than the haddock season, and

[42] Off Nova Scotia haddock spawning extends well into July; around Iceland the peak of egg production comes in June as compared to February, March, and April in the North Sea. (cf. Bigelow and Welsh, 1925; Damas, 1909.)

lasts longer (Bigelow and Welsh, 1925). The estimated trend of the 1931 cod season, based on the number of eggs in identifiable stages collected, is shown in figure 28 to be declining between the March and April cruises. If the cod season were delayed, then it should be expected that more eggs would be found in April 1932 than in a corresponding period of the previous year, for it should be nearer to the peak rather than to the end of the season. Actually, however, only about one-ninth as many cod eggs were found. This condition might be due to either of two causes. Either the cod spawning had run its course considerably sooner than in the previous year, or there had been a heavy mortality of cod eggs. An advancement of the cod season, however, seems hardly consistent with a retarding of the haddock season.

Another line of evidence bearing on the spawning season is to be obtained from the quantity of larvae. During the April cruise no more than one-half as many larvae were collected as in either the March or April cruises of the previous year.

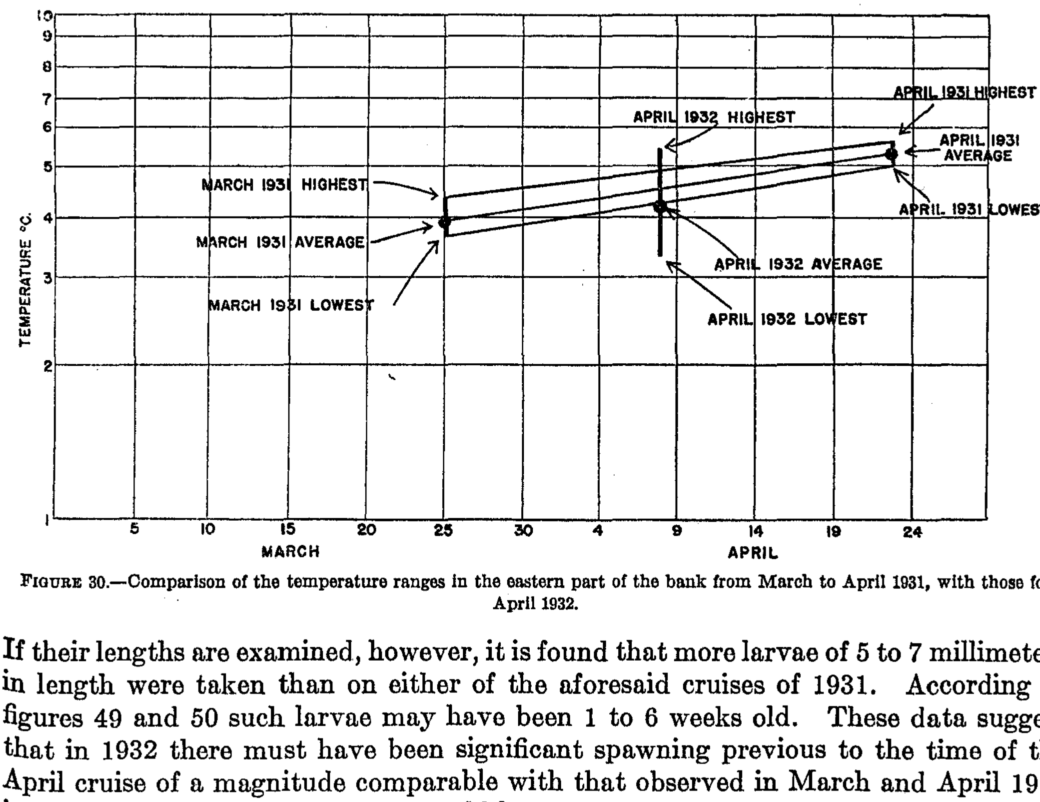

FIGURE 30.—Comparison of the temperature ranges in the eastern part of the bank from March to April 1931, with those for April 1932.

If their lengths are examined, however, it is found that more larvae of 5 to 7 millimeters in length were taken than on either of the aforesaid cruises of 1931. According to figures 49 and 50 such larvae may have been 1 to 6 weeks old. These data suggest that in 1932 there must have been significant spawning previous to the time of the April cruise of a magnitude comparable with that observed in March and April 1931 in order to produce the quantity of old larvae found.

TABLE 2.—*Length-frequencies of larvae taken during the March and April cruises of 1931 and the April cruise of 1932*

Cruise	Lengths of larvae in millimeters					
	2	3	4	5	6	7
March 1931	8	278	137	17		
April 1931	123	377	28	3	2	
April 1932	17	170	63	24	4	1

These points of evidence suggest, at least tentatively, that in 1932 haddock spawning started not later than it did in 1931, and that somehow a large number of eggs had been removed from the bank. The fact that more older larvae and fewer younger larvae were found in April 1932 than in either March or April of 1931, suggests that whatever may have befallen the egg and larval population probably occurred sometime since the production of those oldest larvae, viz, since about the first week of March. What could have happened?

1. The eggs could have been killed by enemies, disease, or accident. In the absence of any evidence suggesting such an event, however, or even any accounts in

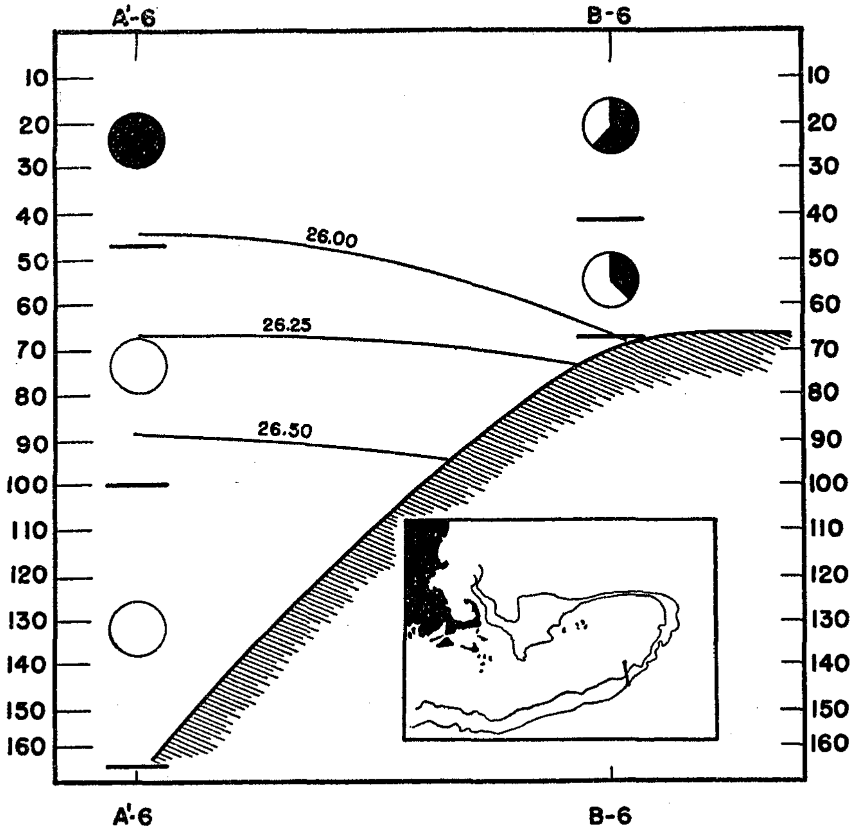

FIGURE 31.—Relation between the vertical distribution of cod-haddock eggs and the density of the water on the southeastern part of Georges Bank in April 1932. The inset gives the location of the stations; Figure 9 the explanation of the symbols.

literature of such a catastrophe having occurred in previous years on any species in the open sea, this possibility is merely suggested.

2. They might have been carried away from the bank by currents. Such a thing has happened before. Bigelow (1926, p. 77) writes:

> * * * at the time of our March and April visits (to the northeastern part of Georges Bank) in 1920 the presence of newly spawned eggs in abundance right out to the 1,000-meter contour proved that a drift out to sea was then taking place from the southern point of the bank.

In 1931 evidence indicated that a few eggs had drifted off the southeastern edge of the bank. In 1932 a larger number of eggs (354, all in stage II) was found at station A′6 in deep water off the southern edge of the bank than had been found at any one station in that locality the previous year. These eggs, as well as those at station A′7 (figs. 31 and 32), were all found suspended in water having a density of 25.75 to 26.00, and supposedly were produced on the bank where such water prevailed and where spawning was concentrated (fig. 34). Likewise, at station A′5 (fig. 33), and perhaps also at station A–5, the bulk of the eggs had a specific gravity of 26.25 to 26.50 and could therefore have been spawned somewhere along the southern part

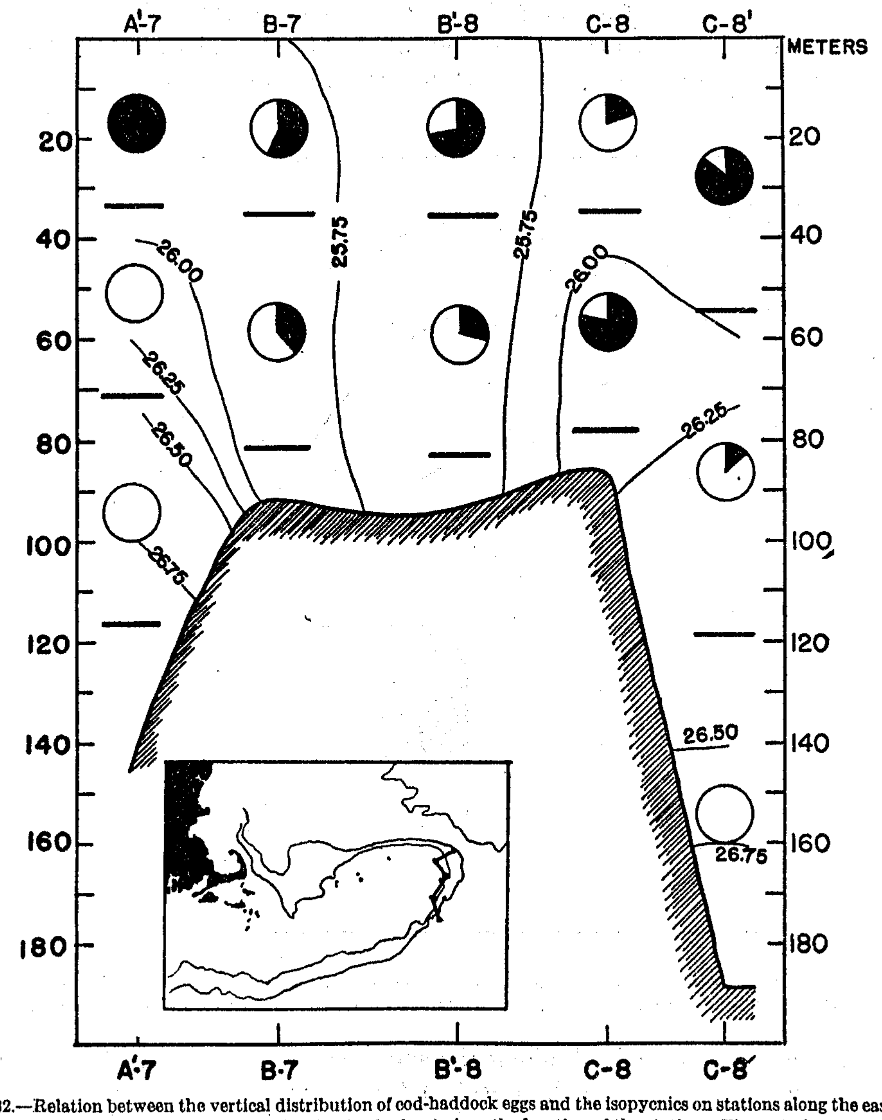

FIGURE 32.—Relation between the vertical distribution of cod-haddock eggs and the isopycnics on stations along the eastern edge of Georges Bank in April 1932. The solid line in the inset gives the location of the stations; Figure 9 gives an explanation of the symbols.

of the bank where water of this density prevailed on the bottom. Thus there is evidence that eggs had drifted off the southern edge of the bank in 1932.

On the northeastern part of the bank, at station D–7 (fig. 27), more than 2,000 eggs were collected, about one-sixth of them from strata having a density of 26.00 to 26.25, and, therefore, presumably originating farther south on the bank where spawning was fairly concentrated. Also at station D′7 eggs were found near the surface in water of density 25.75 to 26.00, and, therefore, probably had their origin on the bank where such water touched bottom. Since only stage I and stage II eggs were found there, they probably could not have originated on Browns Bank, not having had time to come that far. At both stations D′7 and D–7 most of the eggs were found in lower strata, of density 26.25 to 26.50, and, therefore, probably originated on the northern edge of the bank. It this appears from these evidences that there was a tendency to a drift of eggs off the northern edge in 1932.

There are, then, reasons to believe that in late March and early April 1932, viz, during what may have been a very important period of the spawning season, Georges

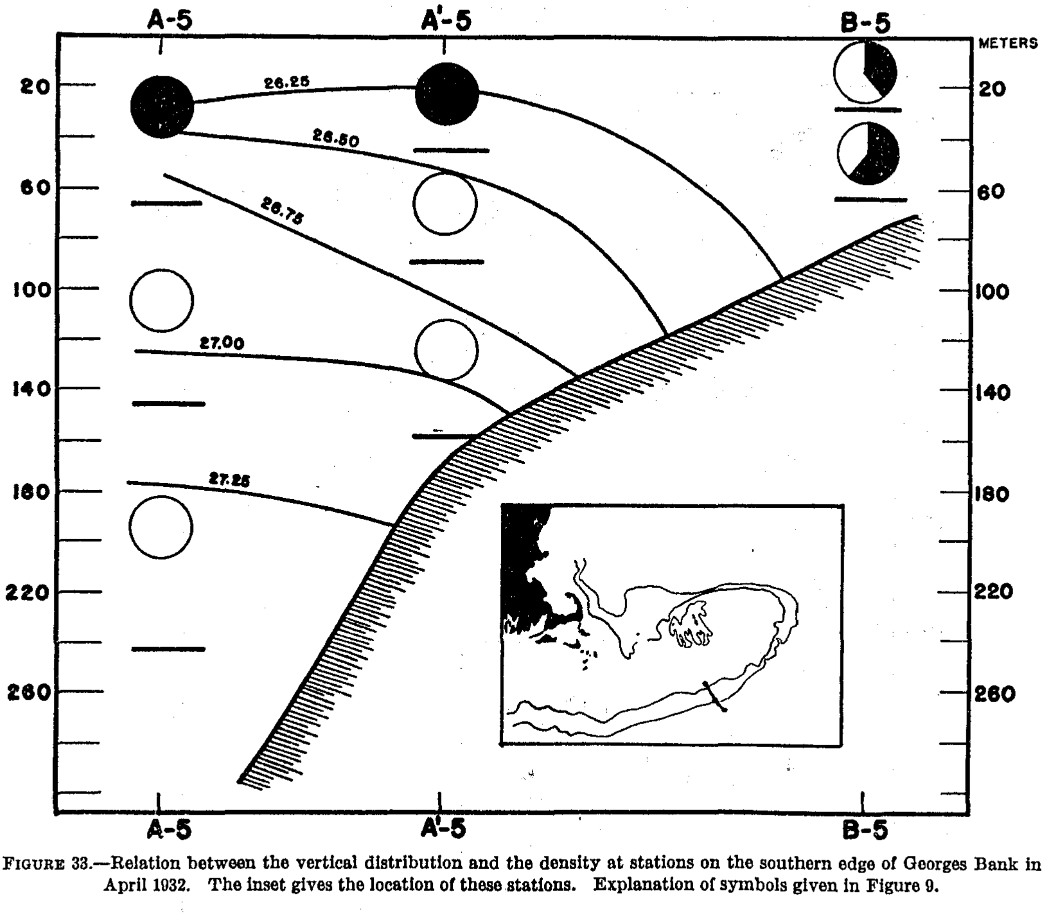

FIGURE 33.—Relation between the vertical distribution and the density at stations on the southern edge of Georges Bank in April 1932. The inset gives the location of these stations. Explanation of symbols given in Figure 9.

Bank suffered a loss of eggs both along the southeastern and the northeastern edges. Owing to the uncertainty as to the onset of the spawning season, it cannot be told how long this seaward drift had been going on before the April cruise nor to what extent it had already affected the quantity of eggs produced on the bank. But drift bottles liberated at the time of the April cruise in the South Channel, along the northern edge of Georges Bank, on the eastern part in the region of the *A* production center, and along the southern edge were recovered not along the American coast as in 1931, but in northern Europe or in the Azores (fig. 36). Only bottles liberated in the central part of the bank were picked up along the shore south of Cape Cod. There is thus evidence of a very direct nature that a dominant drift from Georges Bank out to sea obtained after the April cruise. Regardless of whether spawning was climactic before, during, or after the April cruise, such a drift was probably inimical to the accumulation of old eggs and subsequently of young fish on the bank. Consequently, it is reasonable to expect the 1932 year class to be seriously affected thereby. Actually, Mr. Herrington's studies have indicated that the 1932 brood of haddock during subsequent years was less abundant on Georges Bank than either the 1931 or the 1933 broods, being, apparently, a relatively poor one.

It is obvious from figures 26 and 27 that even though a large number of eggs may have gone off the bank by one route or another, all produced on the eastern spawning

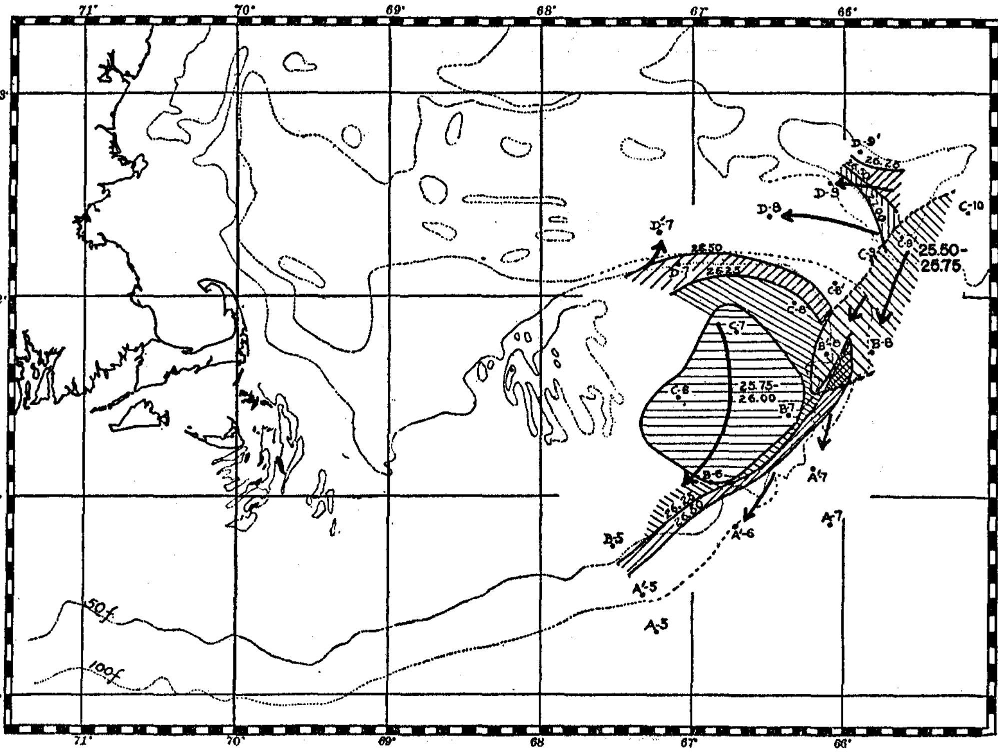

FIGURE 34.—Bottom isopycnics on the eastern part of Georges Bank in April 1932. Areas of equal density are represented by distinctive patterns of shading. The area where water of density 25.50 to 25.75 touched bottom is bound by solid lines. The area where this water occupied intermediate strata only is bound by dotted lines. Arrows indicate the direction of drift.

ground did not so drift away. If the argument be correct that spawning had been at its climax there before the time of the April cruise, then something of the order of 10 percent of the eggs seem to have been able to remain on the bank long enough to reach stage IV. During this period they seem to have drifted in a southwest direction from the spawning ground, as indicated by a progressive shift in the distribution of stage II, III, and IV eggs. Therefore, presumably, there may have been two currents, one carrying eggs out to sea from the eastern end of the bank, the other retaining some eggs on the bank and carrying them clockwise in the general direction of Nantucket Shoals.

Spawning in the South Channel.—It has been seen (figs. 26, 27) that in 1932 apparently more spawning occurred in the South Channel than in 1931. Eggs in all stages of development were found in about the same region, the distances between the reference points being 6 to 7 miles apart. It may be estimated from these distances and the average prevailing temperature (4.75° C.) that the velocity of drift was something of the order of less than 1 mile per 24 hours. The fact that larvae which were several days old were found in the station where the stage I eggs were most abundant further minimizes the importance of a directive drift of the water mass in the South Channel during the last half of March and the first half of April.

Since in that region the newly spawned eggs far outnumbered the eggs in the older stages of development, and since there was no indication of a mass drift away from this region at that time, it may be reasonably concluded that by the time of the April cruise spawning in the South Channel had not yet passed its peak for the year.[43]

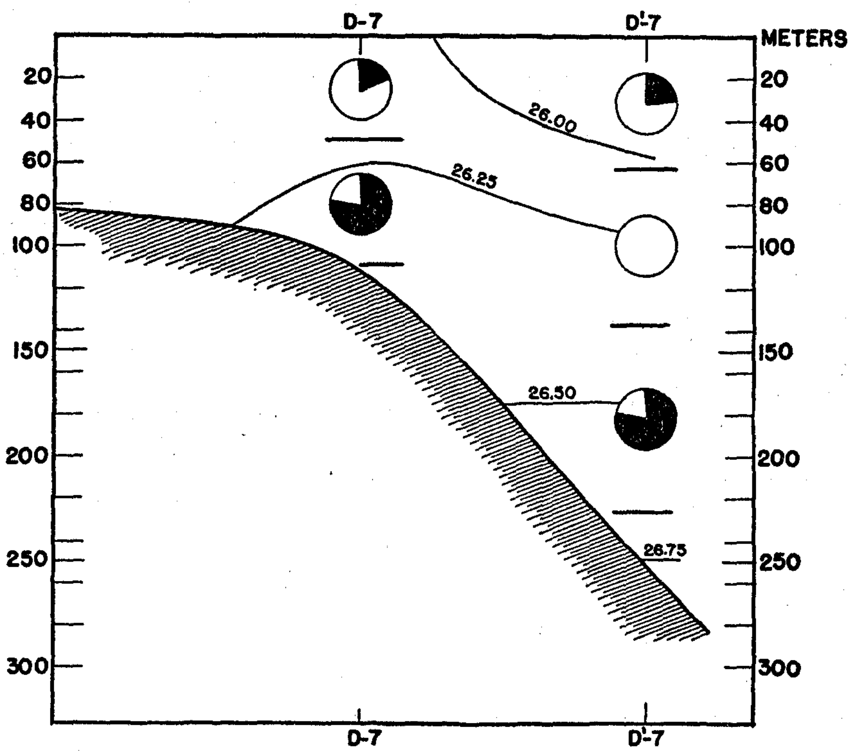

FIGURE 35.—Relation between the vertical distribution of cod-haddock eggs and the isopycnics at stations on the northern edge of Georges Bank in April 1932. See Figure 34 for location of these stations and Figure 9 for explanation of the symbols.

Drift from Browns Bank.—Although the plateau of Browns Bank was not sampled during the cruises of 1931, enough stations were made between Browns and Georges Banks to intercept any significant mass movement of eggs from one region to the other. No such movement was indicated in 1931.

In April 1932, additional stations were made upon the plateau of Browns Bank where a concentration of stage I eggs was found (fig. 26–A), but apparently there were not many eggs in older stages of incubation there. This may mean either that spawning on Browns Bank had started not long before the time of the April cruise

[43] It will be remembered that in 1931, what little spawning was indicated there seems not to have been at its peak before the April cruise. Thus, spawning may normally occur later there than on the eastern part of the bank. In any case, the water is warmer and saltier in the South Channel, and the depths greater. Hence, it has seemed most advisable to treat the two regions separately in this analysis.

or that the bulk of the eggs deposited there had drifted away. The presence of a concentration center for stage II eggs at station D–8, where the water is too deep for spawning (292 meters), suggests that there may have been a westerly drift from Browns Bank in that direction. Additional evidence in this respect results from a study of the vertical distribution and the specific gravity of the eggs.

At station D–8 (fig. 37) the bulk of all stages of eggs was obtained in lower strata of water having a density of 26.50 to 27.25 and could have originated on the western edge of Browns Bank (cf. fig. 34) where water of this density prevailed on the bottom, probably not on Georges Bank where such water was not present. Some of the eggs found at station D–8 were suspended in the upper strata of lighter water and might equally have been spawned on the northern edge of Georges Bank or on Browns.

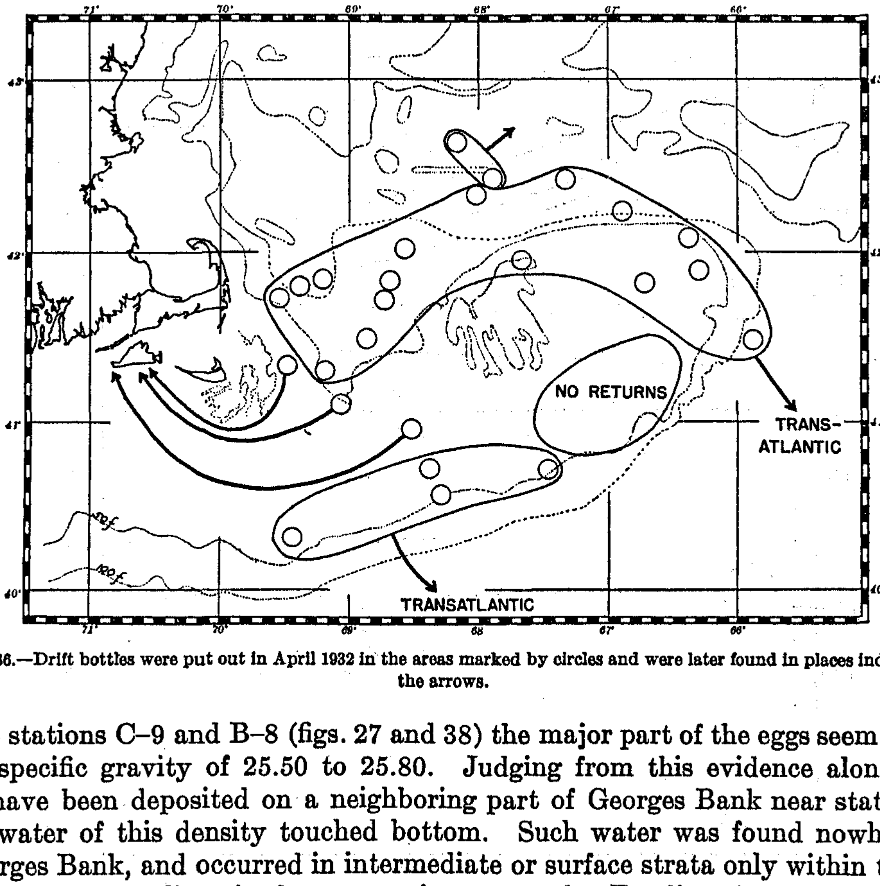

FIGURE 36.—Drift bottles were put out in April 1932 in the areas marked by circles and were later found in places indicated by the arrows.

At stations C–9 and B–8 (figs. 27 and 38) the major part of the eggs seem to have had a specific gravity of 25.50 to 25.80. Judging from this evidence alone, these could have been deposited on a neighboring part of Georges Bank near station B′8 where water of this density touched bottom. Such water was found nowhere else on Georges Bank, and occurred in intermediate or surface strata only within the area enclosed by dotted lines in figure 34, viz, across the Fundian Channel to Browns Bank. It is therefore also possible that eggs found at stations B–8, C–9, and B′8 could have drifted from Browns Bank. Of the two alternatives, the latter is more in accord with the normal circulation, a drift from Georges to Browns never, to our knowledge, having been recorded in that region. Since there was evidently a seaward drift from the southeastern edge of Georges,[44] eggs carried in this current were presumably borne off to sea, and consequently were probably lost. Thus there seems to have been no immigration of eggs from Browns Bank to Georges during

[44] Page 44.

either 1931 or 1932. This conclusion is consistent with the results of the drift bottle experiments.[45]

Distribution of the larvae in April 1932.—While the larvae found in April 1931 were all recently hatched, those taken in April 1932 ranged in age from recently hatched to about a month old (reckoned from the time of spawning). They were, therefore, larvae which had been produced from eggs spawned as early as the first week of March. Fewer than one-half as many larvae were found in April 1932 as

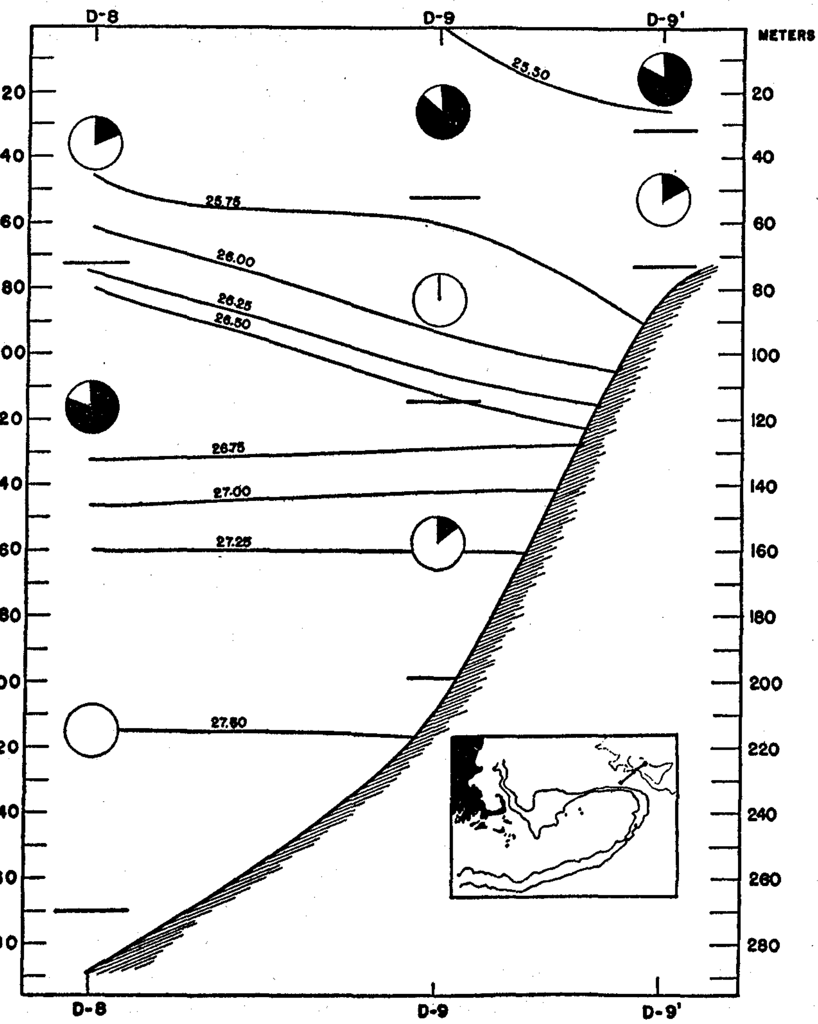

FIGURE 37.—Relation between the vertical distribution of cod-haddock eggs and the isopycnics on Browns Bank and in the Fundian Channel in April 1932. The inset gives the location of the stations, Figure 9 an explanation of the symbols.

in either March or April 1931, thus further substantiating the argument that either spawning was delayed in 1932 or there was a loss of young stages from the bank. It will be recalled [46] that the greater part of the surviving larvae found in May 1931 had been spawned in April, indicating thereby the importance of the April larvae to

[45] Pages 35, 44.
[46] Page 29.

the year brood. It is interesting that while no larvae were found in the South Channel in March or April 1931, several were found there in 1932, evidently the product of eggs produced in the spawning center indicated there. This further supports the argument that considerably more spawning occurred in that region in 1932 than in 1931.

The larvae along the southern edge show a slight tendency to increase in age composition westward. This, along with the additional fact that most larvae were found in stations 35 to 65 miles west of the eastern concentration zone of stage IV eggs (fig. 27–B) suggests a westward drift from the latter region in the direction of Nantucket Shoals.

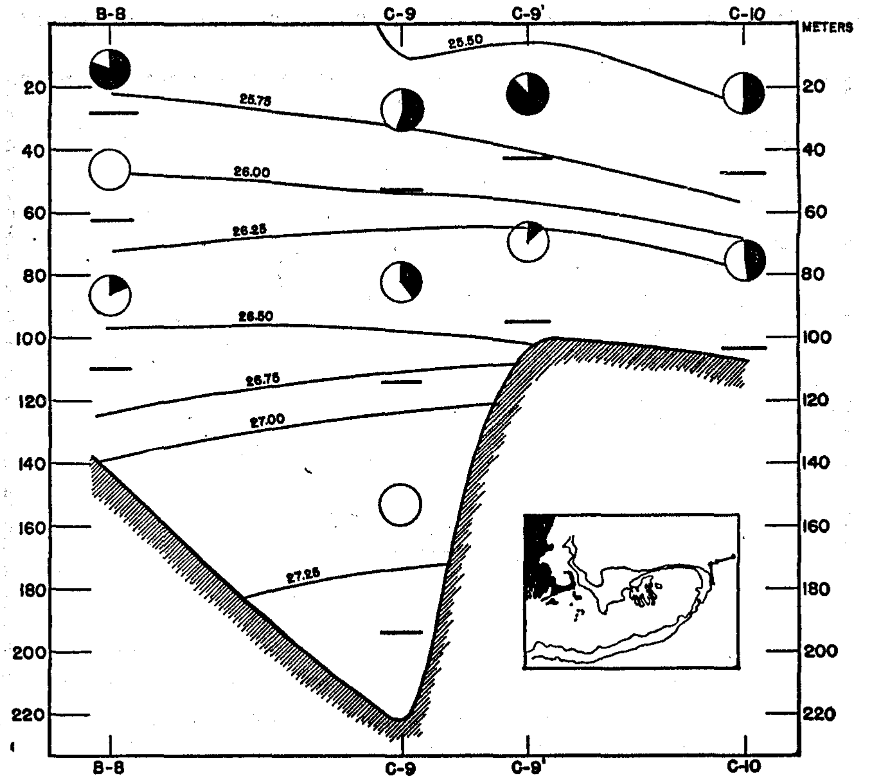

FIGURE 38.—Relation between the vertical distribution of the eggs and the isopycnics at stations between Georges and Browns Banks in April 1932. The inset gives the location of the stations; Figure 9 an explanation of the symbols.

The specimens found off the southern edge near the 100-fathom contour, where spawning did not occur, were probably drifting seaward in the water movements indicated by other data.

It is evident from the above discussion that there was a very important difference between the circulatory picture in the season of 1932 and that of the corresponding period in 1931. While in 1931 the water movements were such as to permit the bulk of the eggs to remain on the bank and hatch there, in 1932 there were currents carrying eggs off the northern and southern edges into deep water where they were probably lost to Georges Bank.

Summary of the 1932 Studies

During the last half of March and the first half of April 1932, spawning on Georges Bank was concentrated in two centers: in the region which we have been calling *A* [47] and in the South Channel. The distribution in the latter region indicated no directional drift, consequently a relatively inactive water mass in the channel. The distribution of eggs produced at *A*, however, indicated a southwesterly current around the southern edge of the bank, which seems to have split, forming two streams, one continuing in the direction of Nantucket Shoals, the other apparently moving off the southern edge of the bank out to sea. The latter stream apparently bore a significant part of the eggs which had been produced at *A*. Also, there was evidence that eggs drifted away from the bank off the northern edge. This situation seems

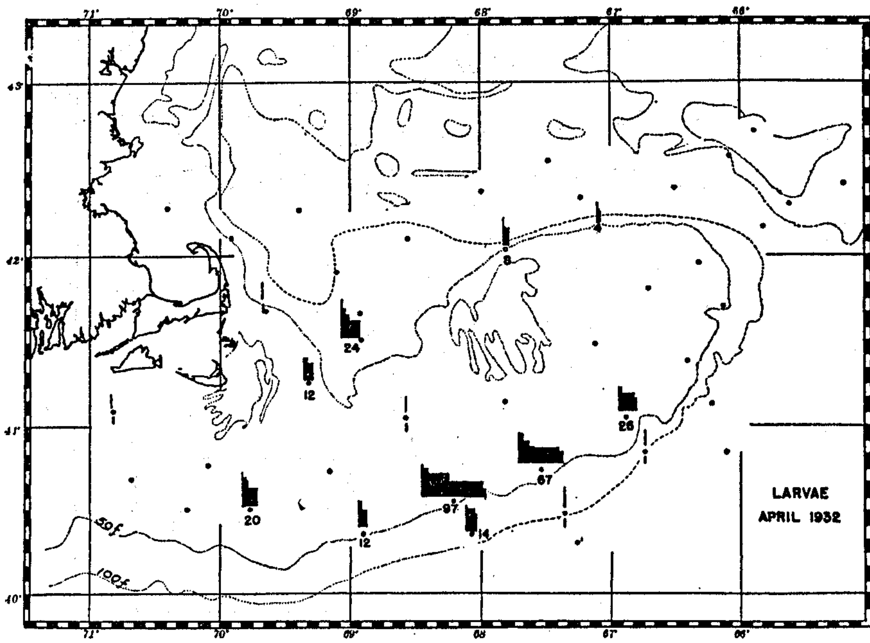

FIGURE 39.—Distribution of larvae in April 1932. The vertical dimensions of the black figures represent lengths of the larvae in millimeters; the horizontal dimensions, numbers of specimens. Scale as in Figure 24.

to have lasted at least as long as the eggs then in stage IV had been in the water, viz, about 20 days. This estimate was based on the rate of incubation at 4.3° *C.*, the approximate average prevailing temperature.[48] The argument that a large part of the eggs was lost from the bank depends, of course, on the premise that the spawning season followed essentially the same course in 1932 as it had in 1931. Even if this were untrue, the evidence from drift bottle experiments points to an unmistakable and dominant drift from the bank following the April cruise.

DISTRIBUTION OF LARVAE SOUTH OF NANTUCKET SHOALS

In both 1931 and 1932 there was some spawning west of Nantucket Shoals (fig. 7 ff.), the volume of which, however, evidently was not of great importance in

[47] Page 15.
[48] Page 67.

comparison with that in the spawning centers of Georges Bank proper. Although only two or three stations were explored west of the shoals, there is no reason to believe that there were important spawning grounds there or farther south which were overlooked. Fishing boats rarely if ever make more than incidental catches of haddock west of Nantucket Shoals, from which point the haddock population becomes increasingly sparser southward.

Nevertheless, in both 1931 and 1932 the currents on Georges Bank were such that some eggs and larvae may have drifted westward from the plateau of the bank past Nantucket Shoals to augment the small population of eggs and larvae produced in the relatively warm water south of Cape Cod. It is desirable to know the fate of the young which drifted into these southern waters in order further to complete the story

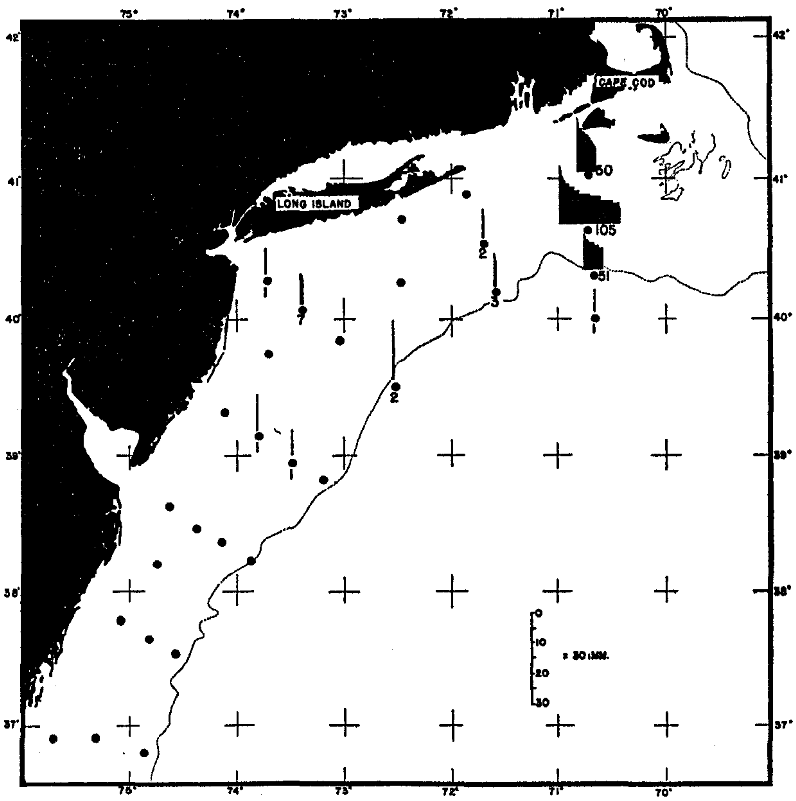

FIGURE 40.—Distribution of haddock larvae south of Cape Cod in May 1932. The vertical dimensions of the black figures represent lengths of larvae in millimeters (see scale); the horizontal dimensions, number of specimens.

of the 1931 and 1932 year broods. If a significant proportion of these young survived, for example, it would then be necessary to investigate the possibility of their return, as adults, to Georges Bank. It is fortunate, therefore, that data for this region have been made available by O. E. Sette, who made hauls with tow nets as far south as Chesapeake Bay in the course of his investigations on the movements of mackerel larvae, and who has contributed the haddock material which he collected during those years. Since these data are more complete for 1932 than for 1931, we shall consider that year first.

Distribution during 1932.—

1. *May.*—In 1932 southern cruises were made during May, June, and July. In May larvae ranging in age from less than a month to about 2 months after spawning were taken as far south as latitude 39° (fig. 40). The bulk of the larvae, however, appeared to be concentrated south and slightly west of Cape Cod, only a few specimens being found south of this region of accumulation.

2. *June.*—In June (fig. 41) larvae ranging in age from about 1½ to about 3 months after spawning were found from Nantucket to as far south as latitude 38°, viz, about 55 miles farther south than the May southern extreme. Also, the region where the largest catches were made lay between 50 and 75 miles farther southwest

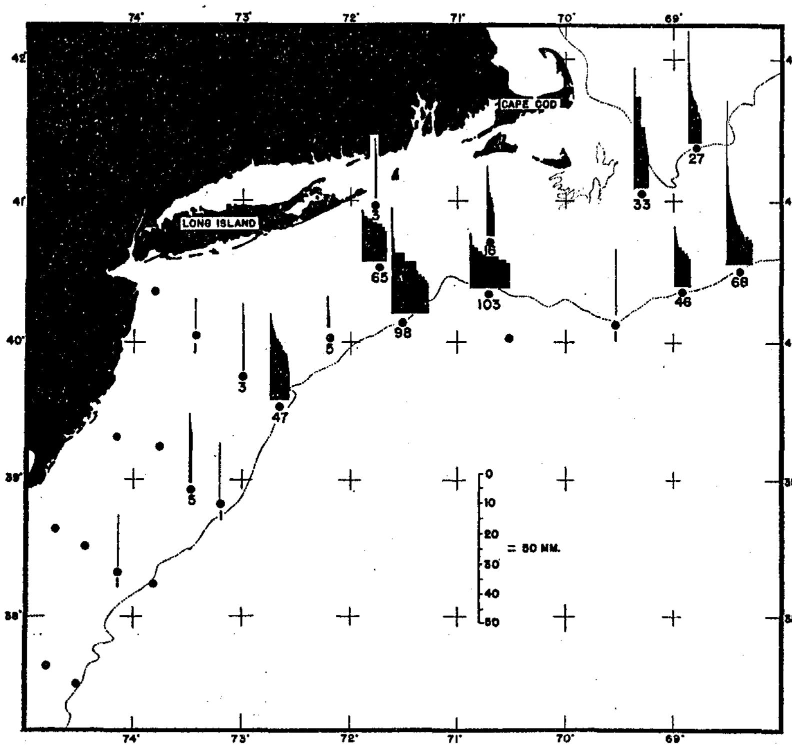

FIGURE 41.—Distribution of haddock larvae south of Cape Cod in June 1932. The vertical dimensions of the black figures represent lengths of larvae in millimeters (see scale); the horizontal dimensions, number of specimens.

of the region of greatest abundance for May (fig. 40). This may be interpreted to mean that between May and June 1932 there was a slow southward drift of the order of about 2 miles per 24 hours.[49]

3. *July.*—Since as many as 250 specimens of larvae 1 to 2 months old were found south of Nantucket Shoals in May and 300 from 1½ to 3 months were found in June, one would reasonably expect to find a number of specimens from 2 to 4 months old there in July. As a matter of fact, however, less than 2 dozen specimens ranging in age from 2 to 3 months old were found there during that month (fig. 42). This may be interpreted to mean one of at least two things: either that between June and July the bulk

[49] Several stations east of Nantucket Shoals also were sampled in June: two in the South Channel and four on the southwestern part of Georges Bank. Specimens taken at these stations ranged in age from about a month to about 3 months. Owing to insufficient data, the source of these specimens and the direction of their drift cannot be judged.

of the larvae south of Nantucket Shoals had been destroyed, leaving few survivors, or that they had taken to bottom and escaped the tow nets. Since the hauls were made from the bottom to top during the July cruise, and with a net four times the ordinary size, viz, one having a mouth opening of 2 meters instead of 1, there is no reason to believe that the water near the bottom was not adequately sampled during that cruise. Also, very large specimens of about 4 months old were taken north of Cape Cod showing that all young haddock had not yet taken to bottom. It is thus reasonable to suppose the former of the two alternatives to be the correct one.[50]

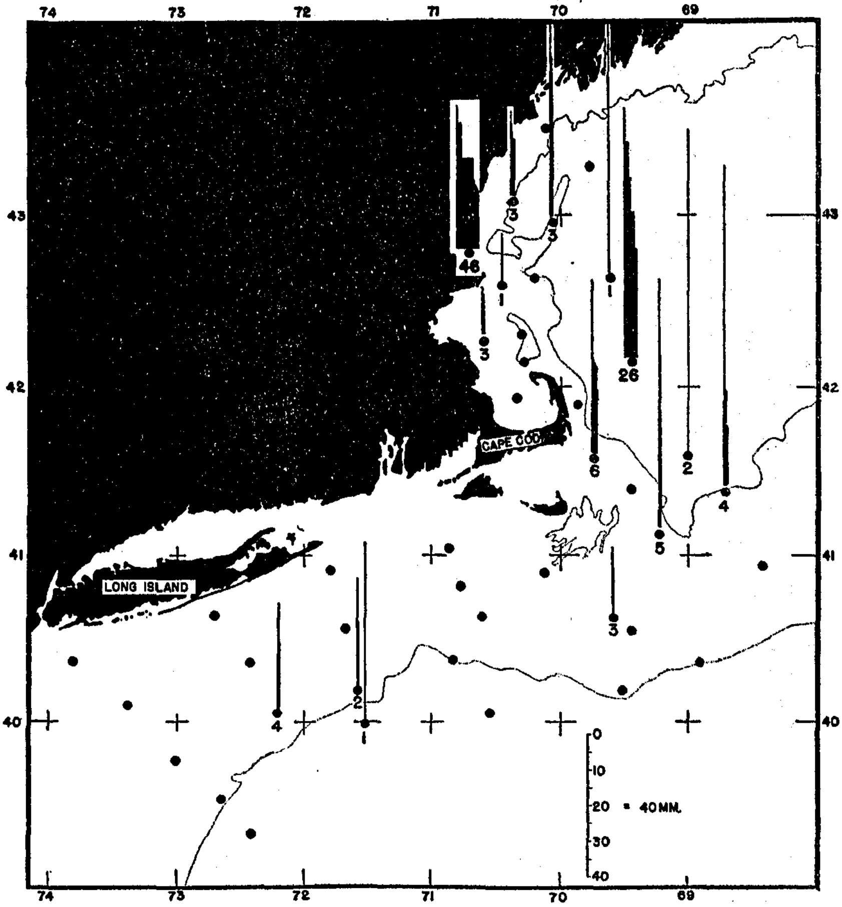

FIGURE 42.—Distribution of haddock larvae along the coast south of Cape Cod in July 1932. The vertical dimensions of the black figures represent lengths of larvae in millimeters (see scale); the horizontal dimensions, number of specimens.

From the above discussion it appears that the larvae moving south and west of Cape Cod in 1932 continued to drift slowly southward, and that the bulk of them was destroyed. The possibility of an important northward migration back to Georges Bank thus seems to be slight.

In June 1931 (fig. 43) the larvae south of Cape Cod were evidently distributed in essentially the same way as were those in June 1932 (fig. 41), the only important

[50] A number of stations sampled east and north of Cape Cod yielded specimens ranging in age from 2 to 4 months. Many of these, particularly the larger ones, occurred near the surface in deep stations where spawning probably did not occur. This distribution seems to suggest a drift in the direction of the South Channel from the northern coast.

difference being that they seemed to be less abundant.[51] Where over 300 larvae were found in June 1932 only 60 were found the previous year. This difference may mean that in 1931 fewer larvae drifted off the bank in a southwesterly direction than in 1932. If this supposition be correct, we then have a further reason for explaining why the year class of 1931 should have exceeded in abundance that of 1932. In any case, this evidence is highly suggestive that the character of the southwesterly drift changes from year to year in such a way as to affect more or less significantly the Georges Bank population of young haddock.

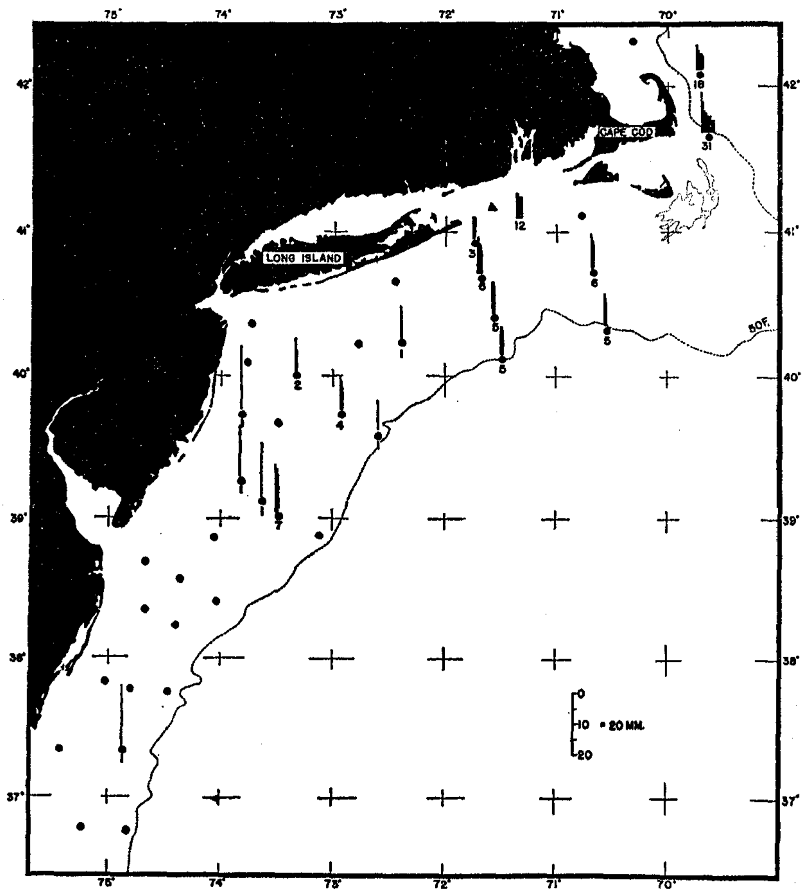

FIGURE 43.—Distribution of haddock larvae along the coast south of Cape Cod in June 1931. The vertical dimensions of the black figures represent lengths of larvae in millimeters (see scale); the horizontal dimensions, number of specimens.

RESULTS

The evidence presented in the foregoing pages has demonstrated with a high degree of certainty that spawning of the haddock on Georges Bank during any year is concentrated in certain definite areas. This is a point of primary importance, for any event occurring in those areas must affect a large proportion of the population.

It seems well established by all the evidence at our disposal that in both 1931 and 1932 Georges Bank not merely supplied its own brood but received no significant

[51] Although the largest specimens found in 1932 were larger than those taken the previous year, the difference was not sufficient to warrant an interpretation of its significance.

quantity of recruits from other breeding grounds. Therefore, should the eggs in one of the spawning centers be destroyed by any unusual condition in that area during those years, there was apparently little probability that the loss could be replaced.

While the conclusions from the 2 years' data agreed in these respects, they differed widely in certain other respects. There is evidence that the circulatory picture on Georges Bank was different in 1932 from that of 1931. It is reasonable then to suppose *a priori* that the ultimate distribution of the young which were borne by that circulation consequently differed for the two years.

By following the process step by step it has been seen that significant quantities of eggs produced in 1931 drifted from the spawning grounds into the safe waters of Georges Shoals where they could develop; and by indirect evidence it is believed that many of the eggs in 1932 drifted off the bank into the deep ocean toward destruction.

Evidence has thus been found that a change in the drift may be disastrous to the brood, and consequently may be an important cause of fluctuations in abundance. It may be argued that fluctuations in the success of year classes cannot be confidently explained without studying data over a long series of years and obtaining during that period a continuous high correlation between the supposed cause and the observed effect. But such a requirement implies that it is always the same causes which produce fluctuations, that even if there is a multiplicity of causes, these all bear a constant relation to each other.

If, as is generally believed, the causes of fluctuations are multiple, then it is reasonable to expect the controlling factor might change from year to year, and that therefore under some circumstances, it would not be possible to produce a continuous positive correlation between the abundance of surviving larvae and the known environmental physical factors.

SUMMARY

1. The aims of this study were to chart the spawning grounds of the American haddock on Georges Bank in 1931 and 1932; to trace the drift of the eggs and larvae; to find whether Georges Bank was supplied with young haddock from other breeding grounds; and to learn the effect on the brood of changes in the direction of drift.

2. These purposes were met adequately by a study of the vertical and horizontal distribution of different ages of eggs and larvae.

3. Although spawning of the haddock may occur over the whole of Georges Bank, it tends to be concentrated in certain definite areas. It is probable that the eastern part of the bank may normally be such an area, and that other regions, for example, the South Channel or the southern part of the bank, may or may not become important breeding grounds during any year.

4. At spawning, haddock eggs seem to adopt the specific gravity of the water into which they are deposited, and in general, to remain suspended in the same stratum until hatched. This fact has proved useful in tracing the origin of eggs in the later stages of development.

5. In March 1931 the eggs were spawned mostly on the eastern and southeastern parts of the bank. Since the water there exhibited no directional drift, the eggs remained on the spawning grounds throughout development.

6. In April 1931 spawning continued in the same grounds on a smaller scale; and the eggs were carried southwest by a current which moved toward Nantucket Shoals around the southern edge of the bank. Some of these eggs evidently drifted into the region of Georges Shoals.

7. By the end of May 1931 spawning had practically ceased on the bank.

8. Georges Bank seems to have supplied its own brood during the 1931 spawning season, receiving no recruits of young from outside breeding grounds.

9. In April 1932 spawning occurred on the eastern part of the bank and in the South Channel.

10. Although there was at that time a southwest drift comparable to that of the previous year, there were also evidently important drifts southward and northward off the edge of the bank, which seem to have carried significant quantities of eggs away.

11. The resulting loss of young evidently seriously affected the success of the 1932 year brood, which appears to have been a relatively small one.

12. There was no evidence that young haddock immigrated from other breeding grounds in 1932.

13. Although some larvae drifted past Nantucket Shoals southward during both years, apparently their mortality was too great to permit them to establish an important haddock population in those waters.

APPENDIX

METHODS USED IN THIS STUDY

Working assumption.—The methods by which the drift of eggs and larvae are traced are based on these two assumptions:

First, that pelagic eggs and larvae are carried altogether passively by the ocean currents from the spawning place to wherever they may be when, as young fish, they become able to take up an autonomous life.

Second, that the distance between the distributional boundaries of the newly spawned eggs and those of the oldest planktonic stages corresponds to the least distance which the eggs and larvae have drifted during the intervening developmental period.

Literature.—Both assumptions are supported by abundant evidence. The pelagic character of haddock eggs, with which hatchery workers are quite familiar, was first observed and recorded scientifically by G. O. Sars in 1864 (1869). The passive character of its drift was established by Fulton (1897), who found that on the east coast of the British Isles the haddock spawns in offshore waters beyond the 3-mile limit. Although newly spawned eggs were not found inshore, old eggs, larval, and post-larval forms, as well as young fish occur there in abundance. They are carried thither in a southerly direction by the currents, which Fulton charted with the aid of drift bottles and floats.

Damas (1909) and Schmidt (1909) traced the movements of several gadoids, including haddock, in the seas of northern Europe in a more quantitative way than did earlier workers. The drift of eggs and larvae in Icelandic waters is particularly spectacular (Schmidt, 1909). The eggs of cod and haddock, which are deposited off the south and west coasts, were found to be carried around the island during the course of their development and actually to reach the east coast by the time they are ready to take to bottom, a distance of over 700 miles. The existence of the cyclonic current responsible for this involuntary migration was independently determined hydrographically by Nielsen (1905), who found that the speed of the current agrees with that at which the eggs and young drift, as determined by the distribution at different ages.

Damas (1909) traced the drift of young haddock in the current which enters the North Sea to the west of Shetland, descends toward the Doggerbank, circles into the Skagerak and the Norwegian deep to lose itself toward the north along the Norwegian coast. Along this path, Damas obtained planktonic stages of haddock which were progressively larger. He showed, further, the influence of changing currents, by observing that in 1900 planktonic haddock were taken in abundance as far as 240 miles from the coast. In 1904 and 1906, on the other hand, only isolated specimens were taken far from the coast, the concentration of the population being found inshore.

In this country the only study made to date on gadoid eggs is that of Fish (1929), who followed the drift of cod eggs from the spawning center off Plymouth down into the lower arm of Massachusetts Bay and directly eastward across the bay. No larval or post-larval stages were taken; and this was accepted as evidence of the passage of these young out of the bay beyond Cape Cod.

Method of determining distribution.—The standard method of determining the distributional boundaries of eggs and larvae in an area of the sea, and the method used in the above studies, is to measure somehow the population abundance at several points spaced more or less widely over the area, and to construct from these sample measurements the total distributional picture. The representativeness of this picture depends on a satisfactory distribution of the stations, on an accurate sampling technique, and on a rational and proper interpretation of the collected data.

Location of the stations.—In the present study there were no preconceptions about the distribution of haddock eggs and larvae on Georges Bank; hence there was no reason for concentrating the stations about any particular region. Since it was necessary to ascertain positively both the regions where there were numerous eggs and larvae and those where there were few or none, stations were so located as to sample all parts of the bank equally; that is, at equidistant points on the plan of a checkerboard.

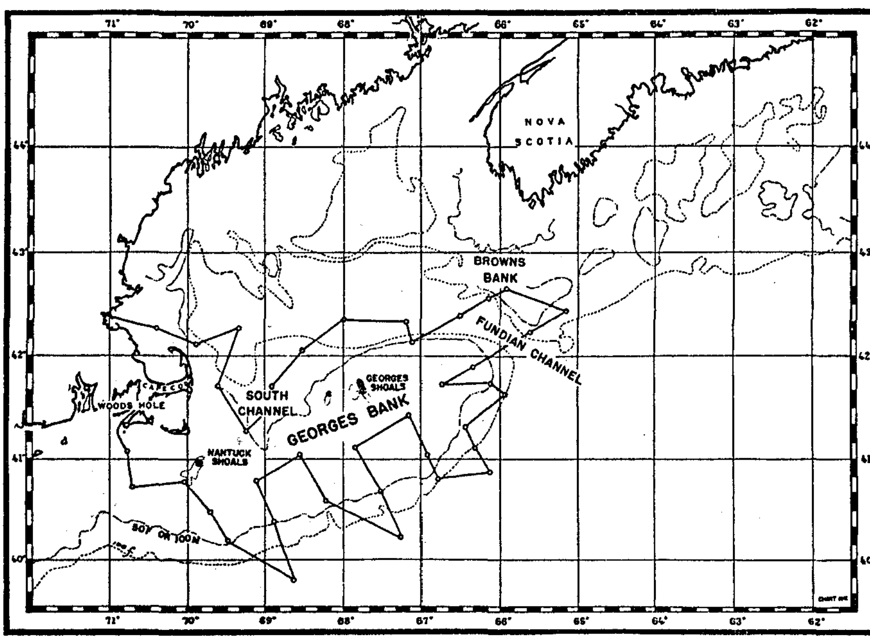

FIGURE 44.—Course followed by the *Albatross II* on the April 1932 cruise.

Only one ship was available for this work, the *Albatross II*, which had a cruising radius of about 15 days. This period gave enough time to work about 50 stations; that is, to cover the whole of Georges Bank and a fringe of deep water around the bank with points so spaced that each represents an average area of 400 to 500 square miles. Is this sampling adequate to give a true picture of the distribution? There are several arguments to support the conclusion that it is.

To begin with, many successful distributional studies, for example, those of Hensen (1890) in the eastern Baltic, Ehrenbaum (1897) in the German Bight, Damas (1909) in the North Sea, Schmidt (1909) in Iceland, have been made from samples spaced all the way from 15 to 100 miles apart.

As for the present study on Georges Bank, there are the following arguments to justify the distribution of the stations:

Spawning occurs mostly in certain definite regions of large area—of the order of 5,000 square miles—and the bulk of the eggs are dispersed from these great spawning centers, not from small, widely scattered, and isolated localities (p. 15 ff). The quantity of eggs produced in the spawning centers is enormous, as one may deduce from the following facts:

The total catch of large haddock on Georges Bank in 1932, for example, was 59,400,000 pounds, and of small haddock 26,100,000 pounds (Fiedler, 1933). The fish averaged for that year 3.6 and 1.85 pounds, respectively, and the total catch therefore, amounted to roughly 30,000,000 fish. On the basis of current research at the United States Bureau of Fisheries, this sum may be estimated at about 30 to 40 percent of the total population of commercial-sized fish on Georges Bank, which was therefore, roughly, 87,000,000 fish. Presumably about half these fish were females, some of which, throughout the spawning season, were giving off eggs into the water. The number of eggs produced by each female in a season ranges from 12,000 to 1,800,000 (Earll, 1880; Raitt, 1932), and the total number of eggs deposited on the bank in 1932 was therefore of the order of eight million millions.

Since the water of Georges Bank is characteristically in continual motion, being kept so by strong tides and currents (Bigelow, 1927), the eggs remain neither clumped together in little batches after extrusion nor do they stay near the bottom where they have been deposited.[52] Being absolutely inert, they are mixed through the churning water and carried along in the currents. Such a combination of conditions may be reasonably expected to produce a smooth gradation in abundance away from the great spawning centers.

The most significant argument, however, is given by the results themselves. The series of distributional pictures drawn from data gathered at 30-mile intervals has proved to be consistent; and this fact alone justifies the location of the stations.

Method of making the samples.—At each of the stations a column of water was strained approximately from bottom to top with ordinary plankton nets.[53] In order to strain as much water as possible, hence, to obtain a maximum number of organisms, and also in order to be able to control the path of the net effectively in the rough seas characteristic of Georges Bank, approximately oblique hauls were made rather than vertical ones. That is to say, the net was raised at regular intervals in equal steps, in such a way that the vertical part of the steps was very short in proportion to the horizontal. Thus, the hauls were so nearly oblique that for practical purposes they can be considered to be completely so.

Number of nets used at each station.—In order to learn something of the vertical distribution of the eggs, two and sometimes three of these nets were used in series. In depths of less than 50 fathoms, two nets were used, one to strain water from bottom to middepth, the other from middepth to surface. Depths of 50 fathoms or more were divided into three parts, and three nets were used. The nets were fastened to a wire cable which was weighted by a heavy iron ball. The lower net was attached 5 meters above the weight to keep it off the bottom in case of uneven ground or error in measuring the depth. To minimize the effect of the ship's heavy rolling, the nets

[52] Page 13.

[53] The type of net used was one meter in diameter at the mouth and 4 meters long. The first meter of its length was a cylinder having the same diameter as the mouth; the last 3 meters formed a truncated cone, of which the smaller base was 5 inches in diameter. To this end was fastened a detachable bag 14 inches long—the cod-end—into which the collected material drained.

The first meter of the net was constructed of No. 0-XX bolting silk (38 threads to the inch) the last 3 meters of No. 2-XX silk (54 threads to the inch); the cod-end of No. 6-XX silk (74 threads to the inch). The mouth of the net was provided with a 4-inch canvas hem which was buttoned to a metal hoop one meter in diameter.

were attached by their bridles to ropes 25 to 30 feet long, which connected with the cable.

In order to collect any young fish which had taken to the bottom, or any eggs or larvae which had remained there, in certain stations on the plateau of the bank a tow net was mounted on heavy metal runners and dragged along the bottom for a period of 30 minutes. This apparatus is referred to in this paper as the "sled net."

Description of the procedure.—After being fastened to the cable, the nets were payed out to their maximum depths, the ship proceeding at a speed of about 1½ knots. Then during a measured period of about 30 minutes, they were hauled in equal steps at regular intervals toward the upper limits of their levels, the ship continuing at an unchanged rate. The length of the intervals was adjusted for different hauls according to depth. The sled net was sent vertically to the bottom after the other nets had completed their hauls, dragged along the sea floor for 30 minutes, then hauled vertically aboard as quickly as possible.

Sources of error.—In this study, particular effort was made to minimize the various errors which are met with in all tow-net work, and which at times might seriously modify the representativeness of the samples.

1. *Clogging.*—Clogging of the nets with phytoplankton was largely prevented by using No. 2–XX mesh, with which the effect of clogging is not serious except when phytoplankton is unusually abundant.

2. *Variations in the speed of the vessel.*—It is obvious that whether or not diagonal hauls made with the same net are comparable depends on whether the average volume of water strained per unit of fishing time is the same at all stations. Provided it is, the data collected in hauls of different duration can be adjusted later to a common basis. Within limits the volume of water per unit of fishing time depends on the speed with which the net is pulled through the water, consequently, on the speed of the vessel. If the latter varies at different stations, the volume of water strained per unit of fishing time must also vary, and the hauls are not comparable.

In calm weather, with no subsurface currents, the speed of the haul can be measured with reasonable accuracy from the speed of the ship. In rough weather, or where there are differences between the current speed at the surface and that at lower depths, however, the measurement of speeds becomes more difficult.

The best method yet devised for controlling the speed of the net through the water, and that used universally, is so to control the speed of the ship as to maintain a desired angle of stray, viz, the angle which the cable makes with the vertical. The weight and dimensions of sinker, nets, and cable being constant, there are in this case two variables—the speed of the ship and the force of the currents. The cable is so slender that in the relatively shallow depths found on Georges Bank its resistance to the water is too slight to cause significant changes in its angle. The net is so large by comparison that variations in the pull on it alone cause significant differences in the angle of stray. Thus, one can hold the angle of stray constant—therefore the speed of the net—by controlling the speed of the ship.

3. *Variations in the speed of hauling in the net.*—The speed of hauling back the nets varied slightly according to the depth of the station. However, since the rate of the haul-back, which on the bank averaged 1.5 meters per minute, was slight compared with the speed of the boat, which averaged 45.7 meters per minute, errors due to variations in the former may be neglected. The resultant incoming speed of the net varied between 46.5 and 48.2 meters per minute, a greatest percentage difference

of 3.7 percent. This quantity, in a study in which errors are of large magnitude, is presumably of no consequence.

4. *Contamination.*—To learn something of the vertical distribution, two or sometimes three nets were used as described above (p. 59). Although self-closing nets are the ideal apparatus for this purpose, there were at the time of this study none which could be practically operated in series in the severe winter and early spring weather characteristic of the Gulf of Maine. Therefore, open nets were used. As a consequence, the bottom two nets and the sled net spent a period in strata in which they were not intended to fish (fig. 45). This period was short in comparison with the total fishing time, and has been corrected for in a manner which will be described and discussed below.

Magnitude of the sampling errors.—In spite of efforts to minimize the causes of sampling errors, it is obvious from the above discussion that many elements interoperate in a complex way to raise these errors above those obtained under the more easily controlled conditions of the laboratory.

We are not concerned in this study with absolute quantities of haddock eggs at each station, but with relative quantities. In order to delineate the boundaries of a spawning center, comparisons must be made between stations which yield numerous eggs and those which yield only a few. It is the relation between the size of these differences and that of the probable deviations of the individual catches from the greatest possible accuracy which will determine the significance of the former. Suppose, for example, that the extremes in the range of the catches made in a series of hauls from two stations were 100 percent of the mean. Then even though twice as many eggs are taken at station A as at station B, the difference of 100 percent may be of slight significance. If, on the other hand, station B yields 100 times as many eggs, it is reasonable to consider the difference a significant one. It matters not whether station A yields 1, 2, or 4 eggs, and station B 5,000, 10,000, or 20,000 eggs, station B is still a region of great abundance as compared with station A. As may be seen by examining the distributional pictures (fig. 7 ff.), we are dealing with such great differences in quantity between stations, that we can draw valid conclusions in spite of variations which are of high magnitude.[54]

Treatment of data.—We are interested in this study in the relative total population under unit surface area. This is here expressed by the population index (I), which is given by the formula:

$$I=\frac{N}{T}D$$

where N is the number of eggs taken (corrected for contamination, see p. 63), T the duration of the haul in minutes, and D the depth of the station. In cases where two or three nets towed in series, the population index for each stratum fished was calculated separately, and the sum of the indices for the group gave the total I for the station.

Calculation of the vertical depth.—For calculating the vertical depths of the strata fished, viz, the values for D, there were three known quantities: (1) The length of the cable put out between the nets; (2) the slope of the cable extending from the pulley to the water—the "angle of stray"; (3) the relation between this slope and the slopes below the surface produced by the pull of the nets. This relation, obtained empiri-

[54] See Winsor and Walford (1936) for a discussion of sampling variations in the use of plankton nets.

cally with a model, and also calculated from a consideration of the known forces, is as follows: At a fixed speed, three nets on the cable normally bend the latter to three different slopes from the vertical, which bear approximately the ratio of 30°: 50°: 60°; two nets bend the cable to slopes having approximately the ratio 30°: 50°. The length of wire to be put out was determined at each station from the formula:

$$L = D\,\frac{1}{\cos\alpha}$$

where L is the length of cable, D the depth of the stratum, and α the angle of stray. Likewise,

$$D = L\cos\alpha.$$

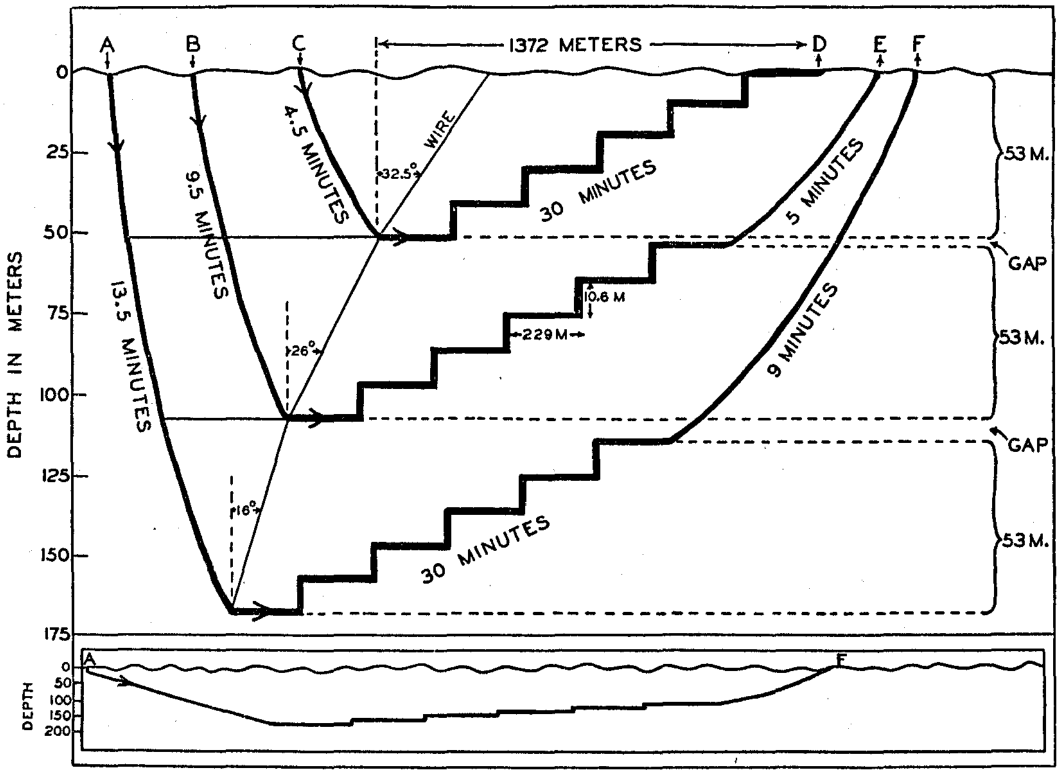

FIGURE 45.—Showing diagrammatically the path of the nets in the water. For the sake of clarity, the upper drawing is not to scale. In the inset below is shown the actual distance relation between the horizontal and vertical steps in the path of the bottom net. The nets are put into the water at the points marked A, B, and C, and are hauled out at the points marked D, E, and F. The arrows indicate the paths.

Since the angle of stray changed more or less during a haul, the depth fished was calculated from the initial and the final angles, giving thereby the depth at which the haul started and that at which it was completed.

As a consequence of the differences in the angles, there was from top to bottom an increasing vertical distance between the levels at which the nets were fishing. As soon as the top net was hauled aboard, however, the other nets were quickly raised and there was thus a space between strata (labeled "gap" in fig. 45) through which nets were drawn more rapidly than the normal fishing rate. In order to give due weight to these "gaps" in the calculation for the values for I, the population indices in these strata were interpolated by allotting half this distance to the upper net, half to the lower.

Correction for contamination.—Since we did not use closing nets, the catches of the lower two nets were contaminated by the plankton in the upper strata through which they passed on their way to and from the levels at which they were designed to tow. Thus, the catch of the bottom net, passing through the strata of the first and second nets both on the way down and on the way back, was contaminated during an average total of 17 minutes. The catch in the second net, passing only through the top stratum, was contaminated during an average total of 7 minutes. This error was corrected for by the formula:

$$N_L = n - \frac{Nu}{T} C$$

where N_L is the corrected number of eggs and larvae in the lower haul; n the number actually taken; $\frac{Nu}{T}$ the corrected number of eggs per minute in the upper haul, viz, from the stratum in which the lower net was contaminated; and C is the duration of the contamination in minutes. The effect of this correction is shown in table 3.

TABLE 3.—*Average number of eggs taken in nets Nos. 2 and 3 (when 3 nets are used), with and without correction for contamination*

Cruise	Number of eggs in—			
	Net No. 2		Net No. 3	
	Uncorrected	Corrected	Uncorrected	Corrected
March 1931	530	386	20	4
May 1931	70	40		
April 1932	345	270	130	40

The correction consistently diminished and sometimes eliminated the catches made by the lower nets. In most cases where three nets fished, the catches of the lowermost were so small as practically to be eliminated by the correction. In other words, the eggs collected in this net had been suspended in strata through which the net had to pass while being lowered and raised. The effect of the correction on the total distributional picture is slight.

Failure of the nets to reach the bottom, and the effect thereof.—In sampling an oblique column of water, it is presupposed that the entire column extends from the surface to a point as close to the bottom as can be safely reached without injuring the net. It transpired from the calculations, however, that the lower net frequently failed to reach the desired proximity to the bottom, there being an average unfished bottom stratum of 22 meters. It is necessary, therefore, to consider whether this has seriously affected the distributional picture resulting from the data at hand. Fortunately, we have at our disposal in this respect two items of evidence: first, there are the catches taken by the sled net;[55] second, there are those taken by the deepest net when three were used in series. If the numbers of eggs and larvae taken by either of these apparatus were high in places where the quantities taken by the upper nets were low, we would be forced to consider the failure to fish the stratum near the bottom a serious hindrance to obtaining a true picture of the distribution.

[55] Page 60.

Although the sled net tows horizontally along the bottom, there is no reason to believe the population density (viz, eggs per minute of tow) calculated from its catch is not comparable with that of the other nets, since its dimensions and the material comprising the bag are the same. Its only difference—an insignificant one in this case—is that it is mounted on runners. Table 4 compares the catch per minute made by the top two nets with that made by the sled net in all stations where the latter was operated. These stations are situated largely on the bank in regions of various degrees of abundance, and probably give a representative basis for judging the relative densities of the population near the bottom.

Judging from the 42 cases given, no generalizations can be drawn about the relation between the population on the bottom and that in the upper strata. In most of these stations the bottom stratum has yielded a relatively insignificnat quantity of eggs. Where low numbers obtain in the upper strata, the effect of this bottom stratum on the total population would be important only if eggs occurred there in such numbers as to alter materially the distributional picture. There are no such cases in the table. Where high numbers obtain in the top layers, the effect of failing to fish near the bottom, at least in the examples given in table 4, is to render the populaton index somewhat less, but not significantly less than its true value.

TABLE 4.—*Catch per minute for nets Nos. 1 and 2, and the sled net*

Cruise	Eggs per minute in—				Cruise	Eggs per minute in—			
	Station	Net No. 1	Net No. 2	Sled net		Station	Net No. 1	Net No. 2	Sled net
March 1931	B-1	0	0	0.14	May-June 1931—Continued.	D-9	0	0	0
	B-3	4.8	27.8	1.8		E-3	.88	.18	.67
	C-3	15.9	15.2	15.0		F-2	12.1	11.4	0
April 1931	A'7	0	0	.33		F-3	21.8	0	0
	B-3	77.2	78.4	4.0	April 1932	A'7	.5	0	0
	B-5	271.0	0	26.8		B-3	.3	.4	1.4
	B-7	7.2	0	2.9		B-5	3.9	4.6	2.3
	C-7	39.2	25.4	25.9		B-6	45.3	----------	26.1
	D-7	0	0	0		B-7	20.1	19.7	.9
May-June 1931	A'7	.07	0	0		C-2	2.9	1.9	0
	B-3	.89	0	0		C-3	9.7	2.8	7.1
	B-4	.25	.72	1.4		C-5	3.0	----------	11.8
	B-5	2.16	.24	0		C-7	51.6	96.5	10.6
	B-6	1.29	0	0		C-9	4.3	2.0	0
	C-2	20.67	.73	0		C-9'	43.5	8.8	0
	C-3	15.3	3.6	17.0		D-3	20.0	6.7	0
	C-7	1.9	1.58	.19		D-6	6.6	14.2	4.4
	D-1	8.6	----------	0		E-4	1.1	0	.9
	D-2	0	----------	.1		F-3	1.4	0	3.5
	D-4	.18	.12	0		G-2	3.0	3.1	.6
	D-5	.38	1.08	.4					
	D-7	.18	.09	0	Average	----------	17.12	7.79	3.96

The catches of the lowest net when three nets were used in series, given in table 5, show the lower distribution in the deeper stations. Among the 36 stations where this net was used, there is no example where significant quantities of eggs were taken in the lowest stratum. In the few cases where more eggs were taken in the lowest net than in those above it, the quantities were insufficient to alter the fact that the stations concerned were not in regions of abundance.

The lack of samples from the bottom layers in this case evidently will not distort significantly the distributional pictures. In order to compensate for this lack, however, the population index for the bottom unsampled stratum has been calculated on the basis of the index of the lowest stratum sampled.

Effect of the corrections.—The various corrections given in the above paragraphs might conceivably in some instances change completely the distributional picture.

In the present study, however, charts made with and without the corrections are essentially identical. The effect of the corrections in this case, therefore, has been to alter the numbers on the charts rather than the shape or location of the contours. This is a strong argument in support of the reliability of the data.

TABLE 5.—*Catch per minute for nets Nos. 1, 2, and 3*

Cruise	Eggs per minute in—				Cruise	Eggs per minute in—			
	Station	Net No. 1	Net No. 2	Net No. 3		Station	Net No. 1	Net No. 2	Net No. 3
March 1931	B-8	0.53	0	0	May-June 1931—Continued.	D-9	0	0	0
	C-9	4.5	0	0		E-5	.03	0	0
	D-4	.4	0	0		E-6	0	0	0
	D-7	1.6	1.6	.55		E-7	0	0	0
	D-8	0	0	0	April 1932	A-3	0	0	0
	D-9	.9	.03	.03		A-5	.14	0	0
	E-4	0	0	0		A-7	.09	0	.03
	E-5	0	0	0		A'2	0	0	0
	E-6	0	0	0		A'3	0	0	0
	E-7	0	0	0		A'4	9.1	0	0
April 1931	A-6	3.5	0	0		A'5	3.7	0	0
	A-7	0	.29	0		A'6	7.7	0	0
	A'1	.16	.12	0		A'7	.5	0	0
	B-8	.62	0	1.54		B-8	6.1	0	1.0
	F-3	5.3	.9	.07		D'7	.3	0	1.4
May-June 1931	A-5	0	0	0		E-4	1.1	0	0
	A'4	0	0	0		E-7	0	0	0
	A'5	0	0	0					
	D-8	0	0	0	Average		1.29	.08	.12

Method of graphic interpretation.—The distribution of the eggs and larvae is here represented graphically by isometric charts. This is a method analogous to that used in topographical work to illustrate slopes, and has been described by Buchanan-Wollaston (1915, 1923). The position of the contours was determined objectively so far as possible by simple proportion.

Vectors were drawn between all adjacent stations unless there were intervening physical barriers such as shoals. Wherever there was no basis for placing a contour objectively, as, for example, wherever the quantity of eggs at one of the stations was equal to 0, the line has been drawn in as seemed best to fit the facts at hand. The 25-egg contour, drawn to suggest the limits of distribution, has been broken throughout to indicate that its position has been determined altogether by inspection. It is a significant fact that the location of such lines has no bearing on the interpretation of the charts in this study. Furthermore, there is no case where the shape of a contour is made the basis for extensive interpretations.

IDENTIFICATION AND DEVELOPMENTAL STAGES OF THE EGGS

Eggs of the American haddock, described by Bigelow and Welsh (1925), have not been found to differ from those of the European haddock, described by earlier authors. They have a perfectly homogeneous yolk, no oil globule or other distinctive structure, and a narrow perivitelline space which is filled with a clear liquid. They measure 1.19 to 1.72 millimeters in diameter.

These characters distinguish the young haddock egg from all others known except that of the cod (*Gadus callarias*) and of the witch flounder (*Glyptocephalus cynoglossus*). Although the sizes of these species differ slightly—cod eggs measuring 1.16 to 1.82 millimeters; haddock, 1.19 to 1.72 millimeters; witch flounder, 1.07 to 1.25 millimeters—they overlap and hence are not useful for identification. As soon as black pigment appears in the haddock and cod embryos, however, viz, 5 to 8 days after they have been spawned, they may be separated from the flounder embryos which are pigmented only with faint yellowish. Since the quantity of witch flounder larvae and eggs in identifiable stages was negligible in the present material, the influence of this species may be forthwith disregarded.

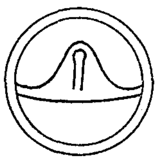

FIGURE 46.

In the case of cod and haddock eggs, however, for which the spawning seasons overlap, and which both possess black pigment, it is not until a few days before hatching, when the pigment pattern characteristic of the larva develops, that these species may be distinguished from each other. But since the distribution of cod eggs on Georges Bank essentially coincides with that of haddock eggs (p. 8), the account of haddock egg distribution is not significantly altered by the confusion of the two species.

Stages of development.—Because the embryonic development of the haddock egg is similar to that of the cod, which has been described by Ryder (1884) and by Meek (1924), it is unnecessary here to do more than define the stages which are used in this paper as landmarks to estimate ages of eggs taken in the ocean. The principal requisite of this arbitrary division of the incubation period is that the distinctions drawn must be easily recognizable in spite of the opacity and shrinkage caused by the preservative. We have specified four stages, separated by almost equal periods of time:

Stage I. From deposition of the unfertilized egg up to, but not including, the first appearance of the embryonic axis.

Stage II. From the appearance of the embryonic axis (see fig. 46) to the formation of the tail bud.

Stage III. From the formation of the tail bud until the chromatophores distribute themselves in the pattern characteristic of the larva.

Stage IV. From the formation of the characteristic pigment pattern to hatching,

The larvae and young fish agree with those stages for the European haddock. which have been described and figured by McIntosh (1897), Schmidt (1906), Ehrenbaum (1909), and others. In this study, relative stage of growth has been measured by total body length, which was recorded to the nearest millimeter below; e. g., all individuals between 3.0 and 3.99 millimeters were recorded as 3.0 millimeters. Measurements of the larvae and very small fish were made with an eyepiece micrometer, and of the larger specimens with dividers and a millimeter rule.

RELATION BETWEEN RATE OF DEVELOPMENT AND TEMPERATURE

As has been shown, the haddock eggs which the *Albatross II* took in the plankton hauls on George Bank were in all stages of development from newly-spawned to ready-to-hatch. To provide a basis for judging the length of time these eggs had been in the water, and hence the distance which they had moved from their supposed spawning place to the place where they were taken by the plankton nets, the rate of embryonic development must be learned. This is a function of the temperature.

The relation between the rate of development and temperature has been studied in a number of fishes, for example in several of the flounders (Pleuronectidae) and in the cod (*Gadus callarias*), by Dannevig (1895), Reibisch (1902), Apstein (1909), and by Johansen and Krogh (1914). Worley (1933), in a detailed study of the rate of development in mackerel eggs (*Scomber scombrus*), found that in this case, the relation follows the Arrhenius formula. As for the haddock, developmental rates at two temperatures given by Brice (1898) in America, and several more temperatures given by Harold Dannevig (1895) in Europe, indicate definitely that this fish exhibits essentially the same behavior as the others.

In order to obtain the rate of development from fertilization up to the several stages arbitrarily chosen as age boundaries in this paper, eggs collected and fertilized from spawning individuals caught by fishing boats offshore from Gloucester were hatched in my laboratory at different temperatures.

Description of apparatus.—The hatching apparatus consisted of two series thermostats essentially of the type described by Johansen and Krogh (1914). Each was a wooden box of the dimensions 30 by 6 by 8 inches, divided by celluloid partitions into five compartments, of which the dimensions are shown in longitudinal section in the diagram below. These compartments were filled with water and 250 cubic centimeter beakers inserted in the top through a lid. The experiment was performed in a cold room maintained at minus 1° C.

The temperatures in the compartments of each box were controlled as follows: At each end of the box were immersed a mercury thermoregulator and an electric

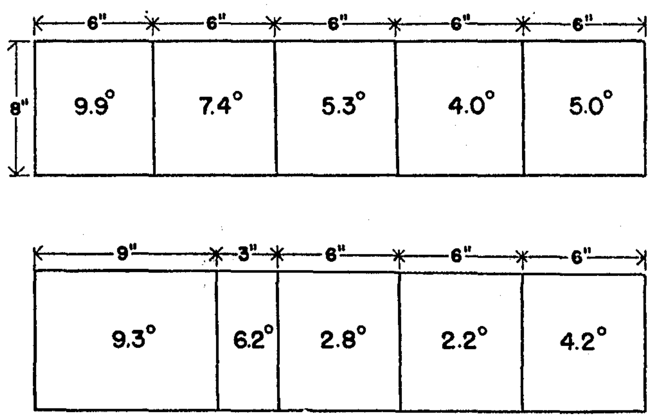

FIGURE 47.—Showing the arrangement of compartments in the series thermostats, the dimensions, and the average temperature in each.

light globe of the showcase type which the regulator controlled through a relay. At one end of the box the maximal temperature of the experiment was maintained; at the other end, the minimal temperature, which, nevertheless, was higher than the temperature of the room. Between these two controlled extremes, an irregular gradient of temperatures in the intervening compartments was established. During the entire course of the experiment the temperatures in the compartments fluctuated through mean deviations of ± 0.38° to 0.88° C.

Description of the procedure.—Two lots of eggs were studied. The first, in which data for only two temperatures were obtained, was maintained between April 23 and May 5; the second between May 9 and June 2. The material was collected from the U. S. Fisheries Station, Gloucester, Mass., by one of the hatchery operatives from fish caught at sea. The eggs for the first experiment were taken April 23, at 8 a. m., 8 miles ESE. of Eastern Point from fish caught in 35 fathoms depth. The surface temperature was 3.3° C. Those for the second were taken May 9, at 7:30 a. m., 10 miles N. by E. of Annisquam Light from fish caught in 35 fathoms. The surface temperature was 7.7° C. In both cases, the eggs were mixed with sperm in water collected at the surface in so-called vacuum jugs, which were immediately sealed.

The jugs were delivered to the laboratory in Cambridge and the eggs distributed in the beakers in approximately 15 cubic centimeter lots by 6 p. m.

The following procedure was pursued daily in the course of this work: Temperatures were taken at 10 a. m., at 5:30 p.m., and at 10 p.m.; an average of 5 eggs was examined

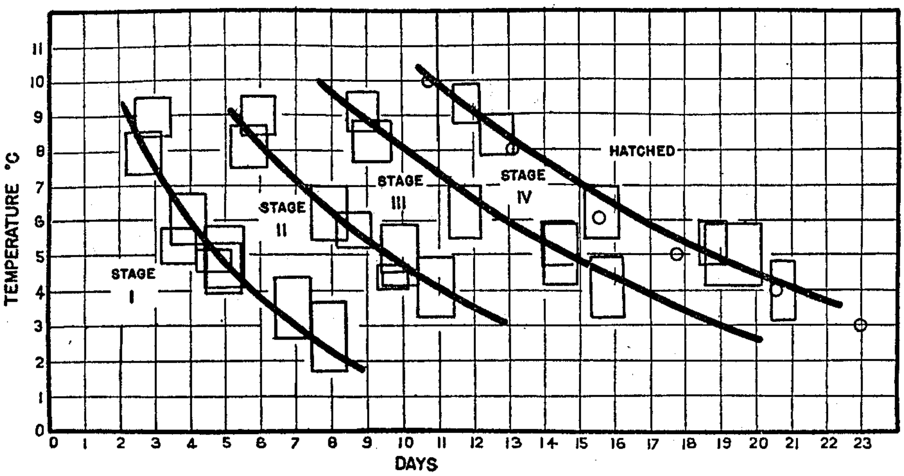

FIGURE 48.—Showing the relation between the temperature and the rate of embryonic development for haddock eggs. The circles represent data for the European haddock from Dannevig (1895).

from each container and the stages of development recorded between 5 and 6 o'clock; the water in each container was stirred gently when the temperatures were taken to prevent a constant gradient from being permanently established in any beaker; dead eggs were removed with a pipette when the temperatures were taken; the eggs in each

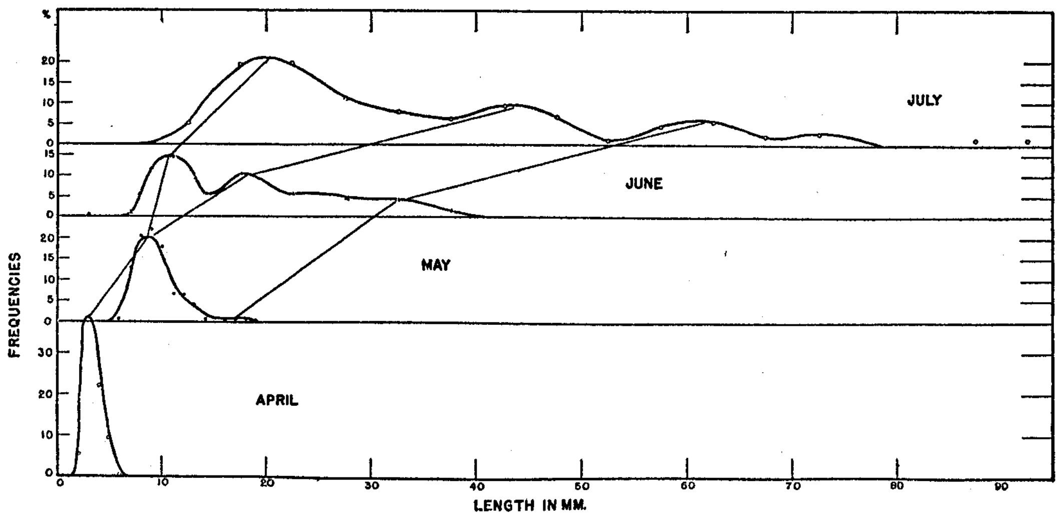

FIGURE 49.—Length frequency curves for larvae taken from April to July 1932.

beaker were transferred with a wire nickel gauze scoop to clean vessels filled with fresh sea water.

In figure 48 the time when each of the four stages of development passed into the succeeding one is plotted against the temperature. The left-hand boundary of the squares in the figure represents the last time, measured from fertilization, that the majority of the eggs in the sample was observed to be in the earlier stage. The right-hand boundary represents the first time when the majority of the eggs of the sample was first observed to be in the succeeding phase. The depth of the squares is equal to the mean deviation in temperature. The hatching time is taken as that when half the eggs were hatched.

The fact that the centers of the rectangles fall along smooth curves as well as the fairly close agreement between Dannevig's results and the data obtained in the experiment here described, is evidence of the representativeness of our observations. Assuming the developmental rate to be the same in the hatchery as in the ocean, it seems valid to use these curves for estimating the ages of eggs collected in the ocean.

AGE OF THE LARVAE

Since facilities were not available to permit raising young haddock in captivity after hatching, it was not possible to observe the growth rate directly. Some basis for

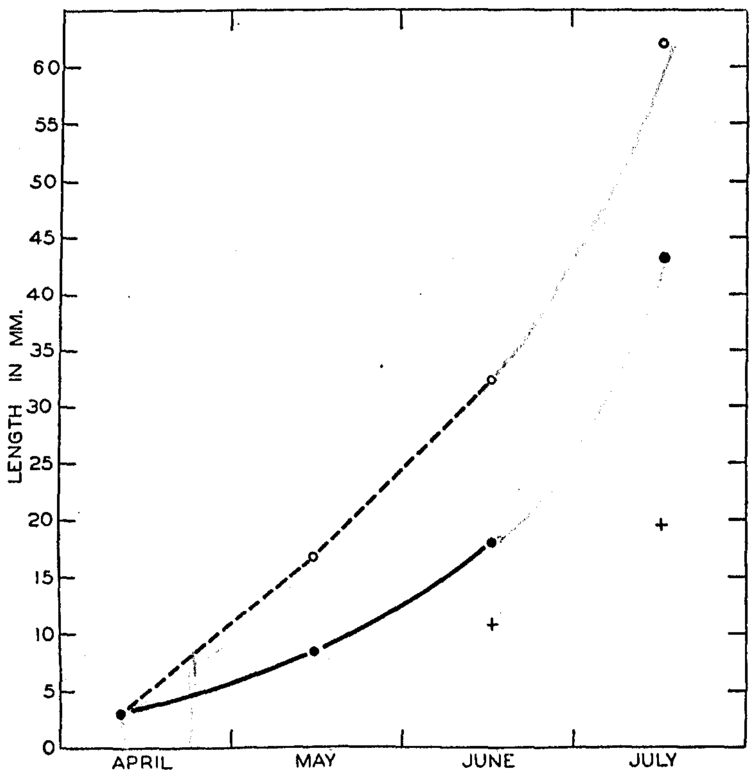

FIGURE 50.—Possible growth curves for larvae represented in Figure 49. See text for explanation.

determining roughly the larval growth rate, and consequently for estimating the age of a larva of given size, however, is furnished by the progressive increase in the size of specimens taken from May to July, 1932.

Both in 1931 and 1932 the smallest specimens obtained were 2 to 3 millimeters long. This is known from hatchery experience to be the size range of newly hatched larvae. Therefore, the length-frequency curve for April 1932 (fig. 49) may be taken as representing essentially a group of recently hatched individuals. The point plotted in figure 50 for April is the mode of that curve.

If all the larvae taken south of Cape Cod in May be plotted together in a frequency curve (fig. 49), two modes appear and hence two possible points for May in figure 50.

The polymodalism in the frequency curve for June makes it difficult to be certain which mode represents larvae hatched in April. Therefore, three possible points are plotted for June in figure 51. Similarly, three points are plotted for July.

If the points thus plotted in figure 51 be connected so as to deviate least from smoothness, two possible growth curves may be drawn. That indicated by a solid line seems to express the average for all the points and has been used in this paper to estimate roughly the age of the larvae taken in the tow nets. Should the upper curve, drawn in dotted line, be the correct one, the argument is not changed by the difference in the indicated growth rate.

SUMMARY OF APPENDIX

1. The distribution of eggs and larvae was determined by sampling the population with plankton nets at points placed about every 30 miles on the bank. At these points the depth was divided into two or three equal strata, each of which was sampled by a net drawn approximately obliquely from bottom to top during a period of about 30 minutes.

2. Even though the sampling errors were of high absolute magnitude, the distributional pictures obtained in this study are consistent and probably representative of the actual distribution of the population at that time.

3. The number of eggs taken at each station was adjusted to give a "population index," viz, a representation of the total population under unit surface area.

4. The rate of embryonic development at different temperatures and an approximate growth curve for haddock larvae are described.

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