and 1927 when several samples were secured by dip net early in summer.[11] Their lengths (table 21) agree closely with the terminal position of the growth curves described by the chosen homologies, and are far below a growth curve predicated on the alternatives. Hence it may be concluded that the chosen series consist of truly

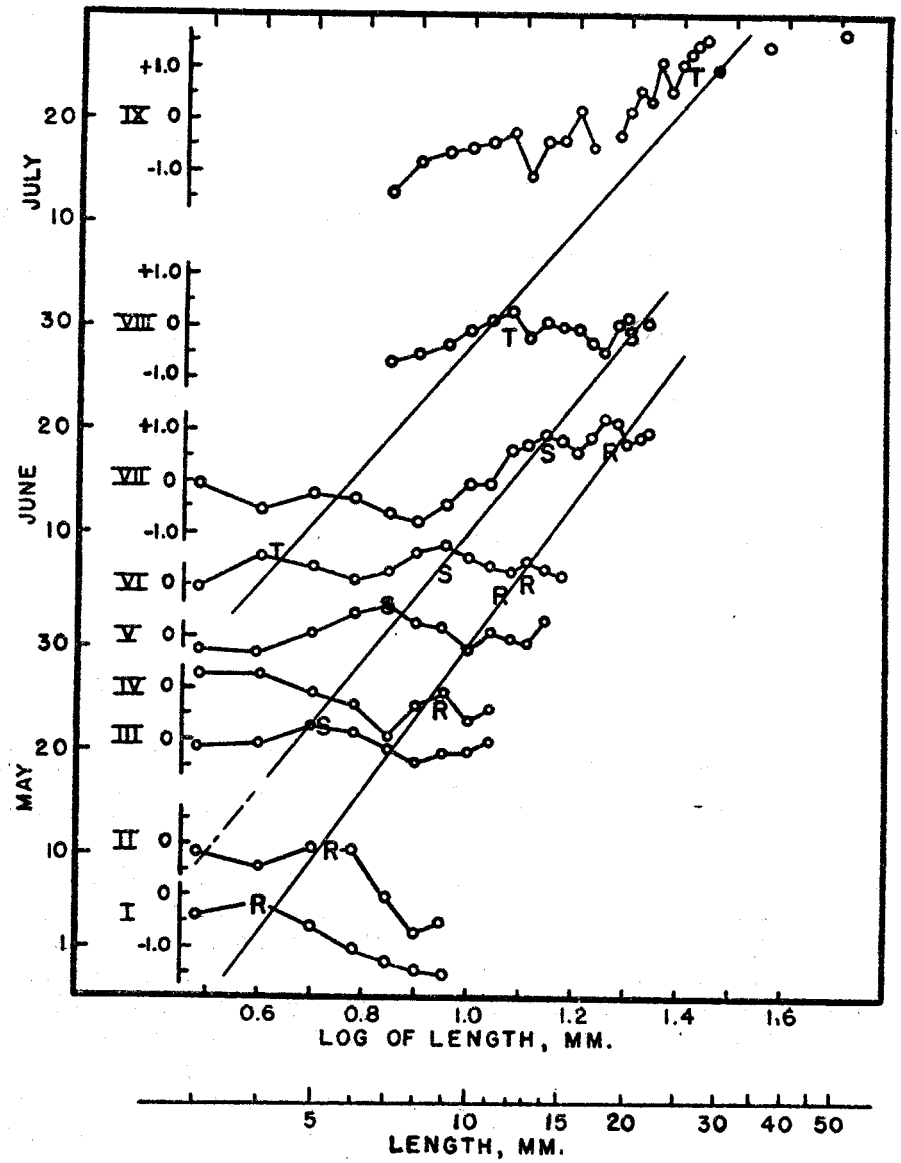


FIGURE 7.—Growth of mackerel larvae and post-larvae as indicated by the progress of modes in the deviations of numbers of specimens in each size-class taken on individual cruises from the average number taken on all cruises. The letters R, S, and T mark the positions of homologous modes referred to the scale of dates; and the straight lines are fitted to the homologous series. The vertical interior scale is the scale of deviations in logarithms. Roman numerals are cruise numbers.

homologous modes, and that the straight lines fitted to the respective series correctly describe the larval and post-larval growth in 1932.

[11] Schools of very small mackerel wander into pound-nets from which they can be removed by dip net if the pound-nets are visited before hauling. Once hauling commences they are frightened and usually escape through the meshes. In addition to samples so collected, one was taken from a school which wandered into the boat basin at the U. S. Fisheries Biological Station, Woods Hole.

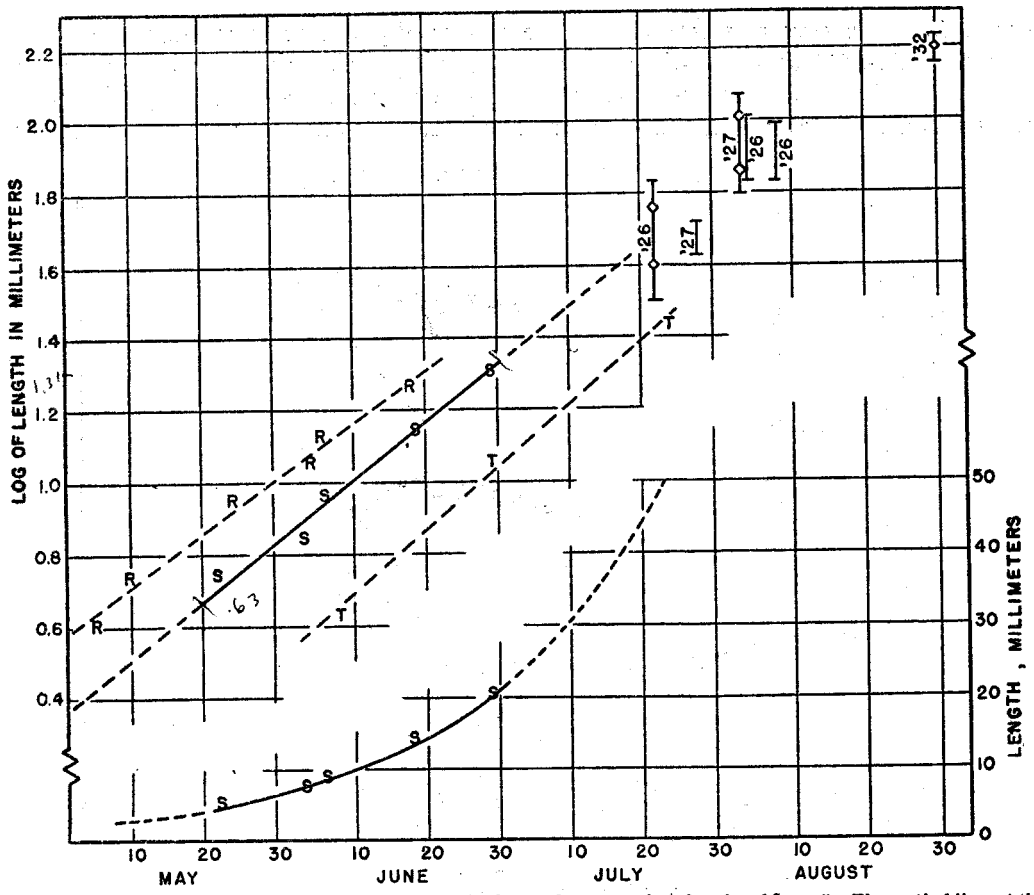


FIGURE 8.—Growth of mackerel larvae and post-larvae derived from the progression of modes of figure 7. The vertical lines at the upper right represent the range of sizes and position of modes (diamonds) of young mackerel collected by dip net from pound nets in the vicinity of Woods Hole, Mass., in the years designated. The straight lines in the upper part of the graph are on the logarithmic scale. The curved line in the lower part represents the actual growth of the S series being plotted on an arithmetic scale.

Inasmuch as the S series had its origin in the area and near the time of maximum spawning and formed the most distinct mode in the deviation curves, it may be taken as most nearly typical of the growth of larvae in the season of 1932. In the lower part of figure 8, the growth of this series has been plotted on an arithmetic scale from which it is readily seen that mackerel hatching in early May attain a length of 4 mm. by about May 20, 7 mm. by June 1, 12 mm. by June 15, and 22 mm. by July 1. This rate projected to the 22nd of July reaches 48 mm. (nearly 2 inches), which closely agrees with the largest larva of the final cruise and also with the length of individuals in the dip net sample of July 22, 1926, which ranged from 35 to 65 mm. (1.4 to 2.5 inches).

From the above relationship of sizes and ages, and from Worley's (loc. cit.) data on rates of incubation, it is possible to compute the duration and average age of each of the egg stages and of each size-class of larvae. Apart from its value *per se*, this is of use in further computations of mortality rate.

This was calculated as follows: the weighted mean temperature in which the stage A eggs were found during the cruises of 1932 was 10.9° C. At this temperature the incubation period occupies 7.23 days (Worley 1933, fig. 5). Stage A, representing the development from fertilization to complete epiboly constitutes 35 percent of the

incubation period, stage B, from complete epiboly to embryo ¾ around the yolk mass constitutes 32 percent, and stage C from embryo ¾ around the yolk mass to hatching constitutes 33 percent (Worley 1933, fig. 5). The average time occupied by these three egg stages was therefore 2.53, 2.31, and 2.39 days, respectively, and the average age of each stage was derived by simple arithmetic.

The duration of each larval length-class was computed from the formula:

$$\text{duration (in days)} = \frac{\log l_2 - \log l_1}{0.01591}$$

where l_1 is the lower boundary of the length class interval in mm., l_2 the upper boundary of the length class interval in mm. The constant 0.01591 is the increase per day of the logarithm of lengths computed from the straight line fitted to the points of the S series (fig. 8).

The average age of each length-class was computed by the formula:

$$\text{age (in days)} = \frac{\log l_2 - \log l_1}{0.01591} + 7.23$$

where l_1 is the length of newly hatched larvae (2.8 mm.) and l_2 the midvalue of the length class interval. The constant 7.23 is the average age of newly hatched larvae.

The boundaries of class intervals were as follows: for 3-mm. larvae, 2.9 to 3.5 mm.; for 4- to 25-mm. larvae, the designated length ±0.5 mm.; for 30- to 50-mm. larvae, the designated length ± 5.0 mm. The mid values of class intervals were: for 3-mm. larvae, 3.2 mm.; for all others, the designated lengths.

Accuracy of determination.—The resulting values for duration of egg stages and of larval-length classes are given in table 7 to hundredths of days, thus expressing a smooth curve that gives the most probable relationship for the body of data from which they are derived. Purely from the standpoint of instrumental and sampling accuracy, they have no such high degree of precision. The durations may be accurate to the nearest tenth of a day for the egg stages, and of lesser accuracy for the larval-length classes. The duration of the 3-mm. class, derived by extrapolation, is especially in doubt, and may be in error by as much as a day. The other classes probably are within several tenths of a day of true values.

From the standpoint of variability in growth itself, the values are even more approximate. While growth obviously follows a curve of percental increase, there must be fluctuations about this curve due to local variations in environment affecting accessibility of food and rates of metabolism. Furthermore, the particular curve of growth given pertains only to the S group, which developed under a particular set of environmental conditions. From figure 8 it appears that the earlier hatching R group, developing, on the whole, in cooler water, grew more slowly than the S group, while the later hatching T group grew faster in the generally warmer water in which it developed. Thus the R group took 56 days, the S group 50 days, and the T group 47 days in growing from a length of 4 to a length of 25 mm., a divergence from the S group of 12 percent in one instance, and 6 percent in the other. This is by no means the extreme variation to be anticipated, for it is conceivable that temperature or other influences might vary more widely than happened in these three instances, and correspondingly greater differences of growth would follow. On the other hand, the S group developed from eggs spawned somewhat early in a season that was slightly warmer than average (Bigelow, 1933, p. 46) and thus in temperatures that would likely be reproduced in the middle portion of less unusual seasons, and therefore

the rates computed from the S group must be near the usual rate, probably within 10 percent.

Discussion of growth.—Having determined the rate of growth of the mackerel through its early life, it would be interesting to have comparisons of the early growth of other fishes, particularly to see if logarithmic growth is the general rule. Unfortunately, there is a paucity of data on this subject, most of the material on growth of fishes being confined to the portion of life following the larval or post-larval stages. From various sources, however, it has been possible to assemble material on the early growth of three other species: the herring (*Clupea harengus*) in the Clyde Sea area, the haddock (*Melanogrammus aeglifinus*) in the waters off the northeast coast of the United States, and the northern pike (*Esox lucius*) of North American fresh waters.

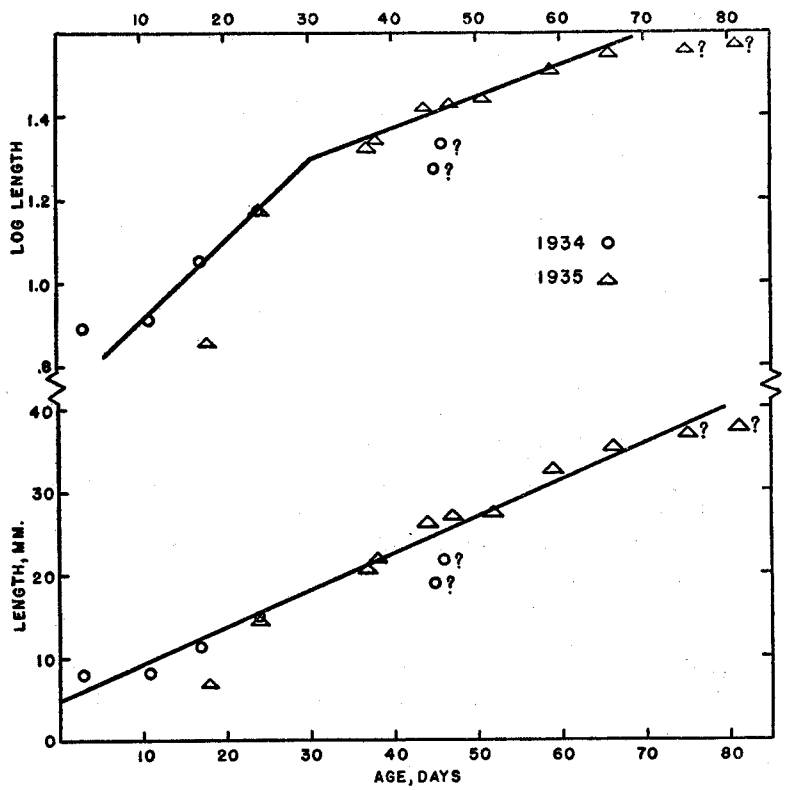


FIGURE 9.—Growth of pre-metamorphosis herring on the Clyde Sea area, after Marshall, Nicholls, and Orr, plotted logarithmically (upper part) and arithmetically (lower part).

Since the data on these need to be formalized for comparison with the mackerel, each will be presented in turn.

For pre-metamorphosis herring caught by tow net and sprat trawl in the Clyde Sea area in 1934 and 1935, Marshall, Nicholls, and Orr (1937, pp. 248–51) determined the median lengths at successive intervals of time. Plotting the median values against age, they concluded that "The points do not lie on a straight line but it is obvious that, apart from four points, a straight line expresses the relationship best." Their curve is reproduced in the lower part of figure 9, and the four exceptional points thought by them not to have represented the main shoals are indicated by question marks. When the same data are plotted logarithmically, as in the upper part of figure

9, it is seen that logarithmic curves with a change in slope at 30 days of age, or length of 19.5 mm., fit the points as well or better than does the straight line in the lower part of figure 9.

The observations on haddock (Walford, 1938, p. 68–69) were taken in a manner similar to those on mackerel. In fact, the material consisted mainly of haddock larvae caught on our mackerel cruises. Walford summarized these by months, giving frequency distributions for each of the four months: April, May, June, and July. From these polymodal frequency distributions, he selected modes that he considered to be homologous, recognizing three such series. Taking his middle series as perhaps the most typical, the modal values, as nearly as can be read from his figure 50, were

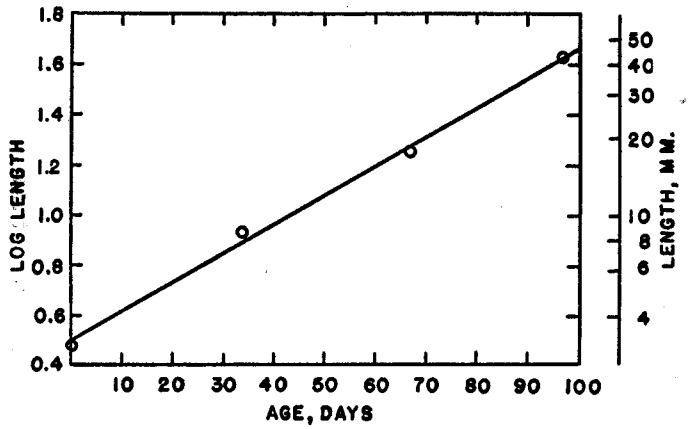


FIGURE 10.—Growth of haddock during early life. Data from Walford, 1938.

3, 3.5, 18, and 43 mm. on the mid-dates, April 11, May 15, June 17, and July 17, respectively. According to Walford, the 3 mm. mode of the first cruise consisted of recently hatched individuals. Assuming this size to be zero days old, the logarithms of the modal sizes were plotted against age in figure 10, whence it is apparent that the growth of the haddock was logarithmic as in the mackerel.[12]

Data on the northern pike (Embody, 1910) consisted of the average length in samples of two or more specimens drawn from a population reared in the laboratory at water temperatures of 65° to 72° F. Since the data are not readily accessible, they are repeated below:[13]

Age in days after hatching:	*Total length in millimeters*	Age in days after hatching:	*Total length in millimeters*
0	7	5	13
2	9. 25	7	[1] 14
3	10. 5	9	15. 25
4	11. 5	11	16

[1] Sac absorbed.

[12] Another of the series of modes selected by Walford also becomes logarithmic with slight re-interpretation of his fig. 49. The new interpretation involves the assumption that the group in question was under-represented in the April sample, an assumption that is reasonable in view of the fact that his samples for this month were from a more easterly area than that subsequently sampled. (This is true also of the central mode, above discussed, but the group forming this mode could have drifted into the area subsequently sampled, whereas the time sequences were such that the group here under consideration in all probability could not have so drifted). It further involves taking the mode for May at 12 instead of 17 mm. and for June at 30 instead of 33 mm. These selections are of prominences on the curve, which are equal to those selected by Walford, and by reason of parallelism with the middle group, seem more reasonable than the points given in Walford's figures 49 and 50. Walford's third series obviously consists of a younger group not present enough months to repay study.

[13] I am grateful to the late Professor Embody for communicating these data to me by letter.

Plotted on a logarithmic scale, these values describe the curve given in figure 11. It is interesting to note that the change in slope approximately coincides with yolk sac absorption.

For ready comparison the growth curves of mackerel and of these other species are assembled in figure 12. In all of them, length was used as an index of size. Mass or volume would be a more nearly true index. However, if there is no change in form, length would serve well to test for logarithmic growth since a certain power of length would be proportional to the mass or volume, and in logarithmic plots the only difference between the two would be a difference in vertical scale. Since the mackerel and haddock undergo little change in form during early life history, a simple logarithmic curve well fits their growth as indicated by length. The herring larva, on the other hand, is slender and almost eel-like when young, growing stouter as development proceeds. This being true, length overestimates size early and under-

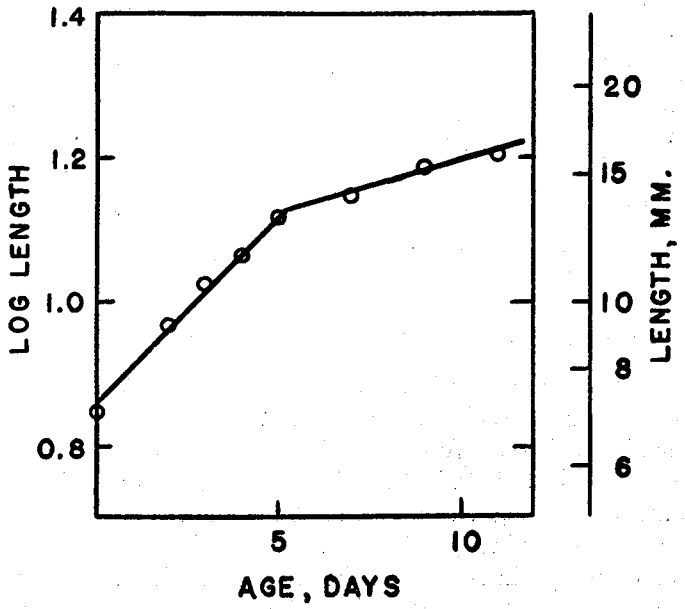


FIGURE 11.—Growth of northern pike during early life. Data from Embody, 1910.

estimates it later. This may be the reason for the nearly linear arrangement of points when lengths are plotted directly against age. Further, the change in slope when the logarithms of lengths are plotted against age suggests that the change in form is greatest at about 30 days of age when the herring is about 18 mm. long. The growth of the northern pike, too, shows a change in slope. In this instance it approximately coincides with yolk sac absoption, hence this might as easily be a real change in growth rate due to difference in food availability or assimilation rather than an apparent change due to altered form. Evidence from the information available on these several species supports the view that growth in the early life of other fishes, as well as the mackerel, is logarithmic in character and at a uniform percental rate throughout this stage of life except when there is a change in mode of living (e. g., yolk sac absorption) and that the use of length as an index of size may complicate interpretation of growth rates when there is considerable change in form.

DRIFT AND MIGRATION

The current system in the waters overlying the continental shelf between Cape Cod and Cape Hatteras has yet to be studied. Evidences collected during this investigation from releases of drift-bottles and computations of dynamic gradients, the latter subject to large errors of interpolation, were not sufficiently conclusive to deserve publication. They indicated slight tendency for movement in a southwesterly direction parallel to the coast, probably not strong enough to transport eggs and larvae of the mackerel important distances.

On the other hand, evidence from the distribution of mackerel eggs and larvae themselves leads to definite conclusions. From the growth curve of larvae, figure 8, or from the position of homologous modes in the deviation curves, figure 7, it is possible

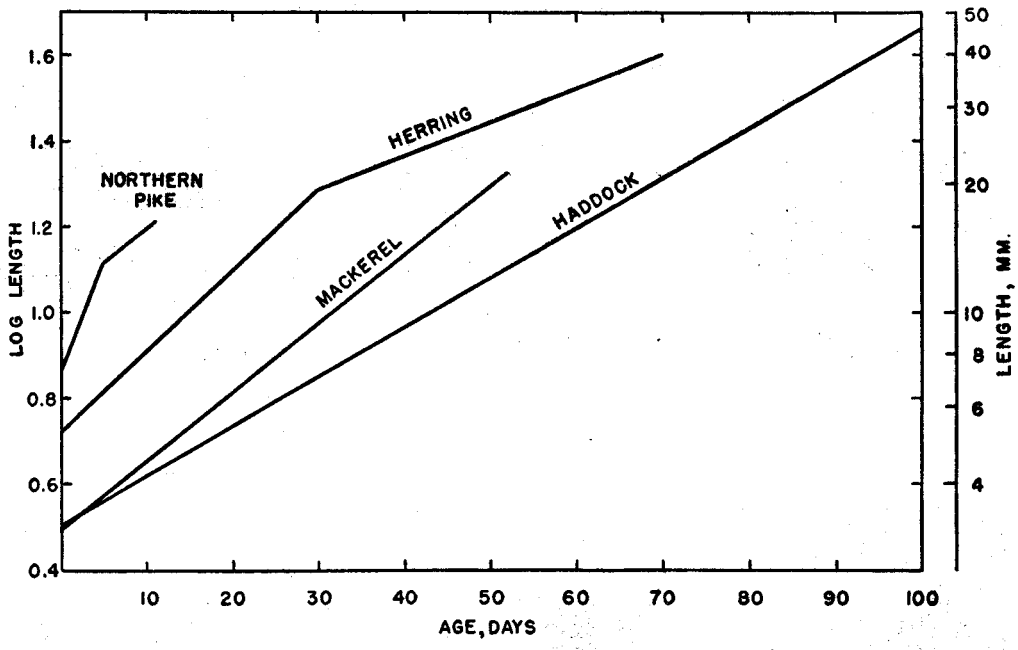
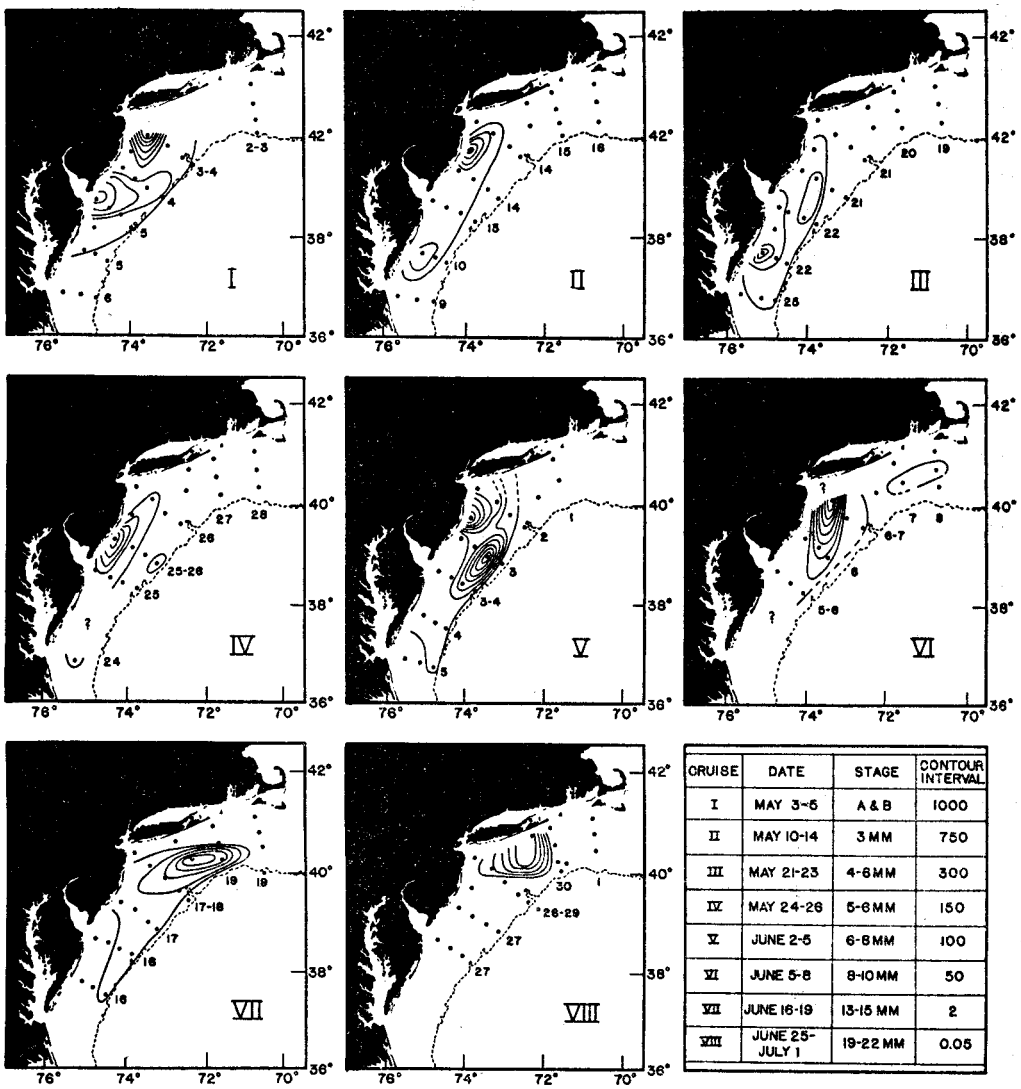


FIGURE 12.—Growth of northern pike, herring, mackerel, and haddock.

to ascertain the lengths attained by certain groups of larvae at each successive cruise. By plotting the geographical distribution of larvae of these particular lengths in successive cruises, as in figure 13 based on the S series, their movements may be followed.

In general, this series represents a population spawned over the continental shelf off the New Jersey coast. Larvae hatched from these eggs remained in this area until they reached a length of 8 mm. about a month later. Thereafter, there was a northeasterly shift which brought the population to the region just south of Long Island at the end of their second month when they were about 20 mm. long. Movement toward the northeast probably persisted still longer, for the only individuals large enough to have been members of this series were taken at stations along the east coast of Massachusetts (Chatham II and Cape Anne II in table 20) during the cruise of July 14 to 28. Although there is local spawning in Massachusetts Bay, it is unlikely that it was responsible for these large individuals, because spawning usually is later in Massachusetts Bay, and the locally produced larvae could not have grown to as large a size as the 37- and 51-mm. post-larvae taken on July 22.

Examining in greater detail the distribution in the successive cruises, two concentrations were evident within the area over which the larvae of this series were distributed. One may be called the northern center; the other, the southern center. The northern center was off the northern part of New Jersey (New York II) [14] in the



CRUISE	DATE	STAGE	CONTOUR INTERVAL
I	MAY 3-5	A & B	1000
II	MAY 10-14	3 MM	750
III	MAY 21-23	4-6 MM	300
IV	MAY 24-26	5-6 MM	150
V	JUNE 2-5	6-8 MM	100
VI	JUNE 5-8	8-10 MM	50
VII	JUNE 16-19	13-15 MM	2
VIII	JUNE 25-JULY 1	19-22 MM	0.05

FIGURE 13.—Location on successive cruises during 1932 of the population of mackerel comprising the S group, as indicated by the relative concentration of larvae of appropriate sizes. The Arabic numerals at the ends of rows of stations give the day of month on which each row was occupied.

early egg stages. In the successive cruises it may be traced to the north central coast of New Jersey (Barnegat I), to the southern part of New Jersey (Cape May II, III, Atlantic City II), back to the south central portion of the New Jersey coast (Atlantic City I), to the north central portion (Barnegat I), to the northern portion (New York II), to the offing of Long Island (Shinnecock II and Montauk III), to the Long Island coast (Shinnecock I and II), and finally to the offing of eastern Massachusetts (Chatham II and Cape Anne II).

[14] For location of this and below-mentioned stations see fig. 14.

The southern center shifted southward from off Delaware Bay (Cape May II) half way to the Chesapeake Capes (Winterquarter I) where it remained during the following cruise and possibly the next one also, though these stations were not visited on the fourth cruise. During the fifth cruise it was found farther north and seaward in the offing of the southern New Jersey coast (Atlantic City III and Cape May IV). Next it appeared to join the northern center and was apparent as a tongue extending from this center to the offing of the middle of the New Jersey coast (Atlantic City II). Thereafter its location apparently coincided with the northern center.

During the time that the two centers were separate they moved in essentially identical directions (fig. 15). Both moved southward from May 3 to May 22 and then northward until June 7, apparently under a common impulse. If the resultants of wind direction and force during the cruises be plotted,[15] as in figure 15, it is seen that the strong winds blew in essentially the same direction as the larvae moved, southerly until May 22 and then northerly until June 7. Obviously the wind, by drifting the surface water, was responsible for the transport of the larvae. After June 7, however, the movements of larvae did not correspond so closely with the movements of the wind (fig. 16) and must have been to some extent independent of them. Thus the movements of the population of mackerel larvae may be divided into two phases, an early passive phase and a later active phase. The break between the two came, as might be expected, when the larvae, at a length of 8–10 mm., developed fins (p. 171) and graduated from the larval state to the post-larval stage. The movements in the two stages will be considered in detail separately.

During the passive phase, although the movements of the two centers of larvae are essentially similar and both correspond to that of the wind, there are minor differences worthy of note. The southern center was found at the same place on cruises II and III in spite of considerable sustained wind from the northeast and corresponding movement of the northern center in the interim between the cruises. Later there was the great shift of the southern center between cruises III and V without correspondingly great wind movement and without correspondingly great drift of the northern center. To some extent these discrepancies may be due to failure precisely to locate centers of distribution with the stations as far apart as of necessity they were.[16]

But it is more likely that the peculiarity in the relation of the drifts of the northern and southern centers has a physical rather than statistical basis. The outstanding peculiarity was that the northern center traced a course in a southerly direction almost equal in distance to its return in a northerly direction (up to cruise VI) whereas the southern center moved southerly a much shorter distance and then returned northerly a much greater distance. Considering now the topographical features, it is noticeable that at the northern and middle portions of the area the continental shelf is broad and the water relatively deep, while at its southern end the shelf narrows sharply and the water is much shoaler. A water mass impelled by the wind could move in a southerly direction freely until it reached the narrow, shoal southerly end where it must either: (1) stream very rapidly through the "bottle neck" at the southern extremity; (2) turn out to sea; or (3) pile up temporarily.

[15] Records of the Winterquarter Lightship, 8 a. m. and 4 p. m., including only those winds of force 3 (Beaufort Scale) or higher, were plotted in vector diagrams to determine the resultants.

[16] The true position of the northern center at the time of cruise III (fig. 13) was particularly uncertain. On the chart of movement (fig. 15) it seemed logical to plot it at the center of gravity between the three northern stations with largest catches, that is, Atlantic City II, Cape May I, and Cape May III, but its true position most likely was between stations, there or elsewhere, and hence missed. This accounts also for the almost complete obliteration of mode S on this cruise, to which attention was earlier called in discussing progress of modes as indicating growth.

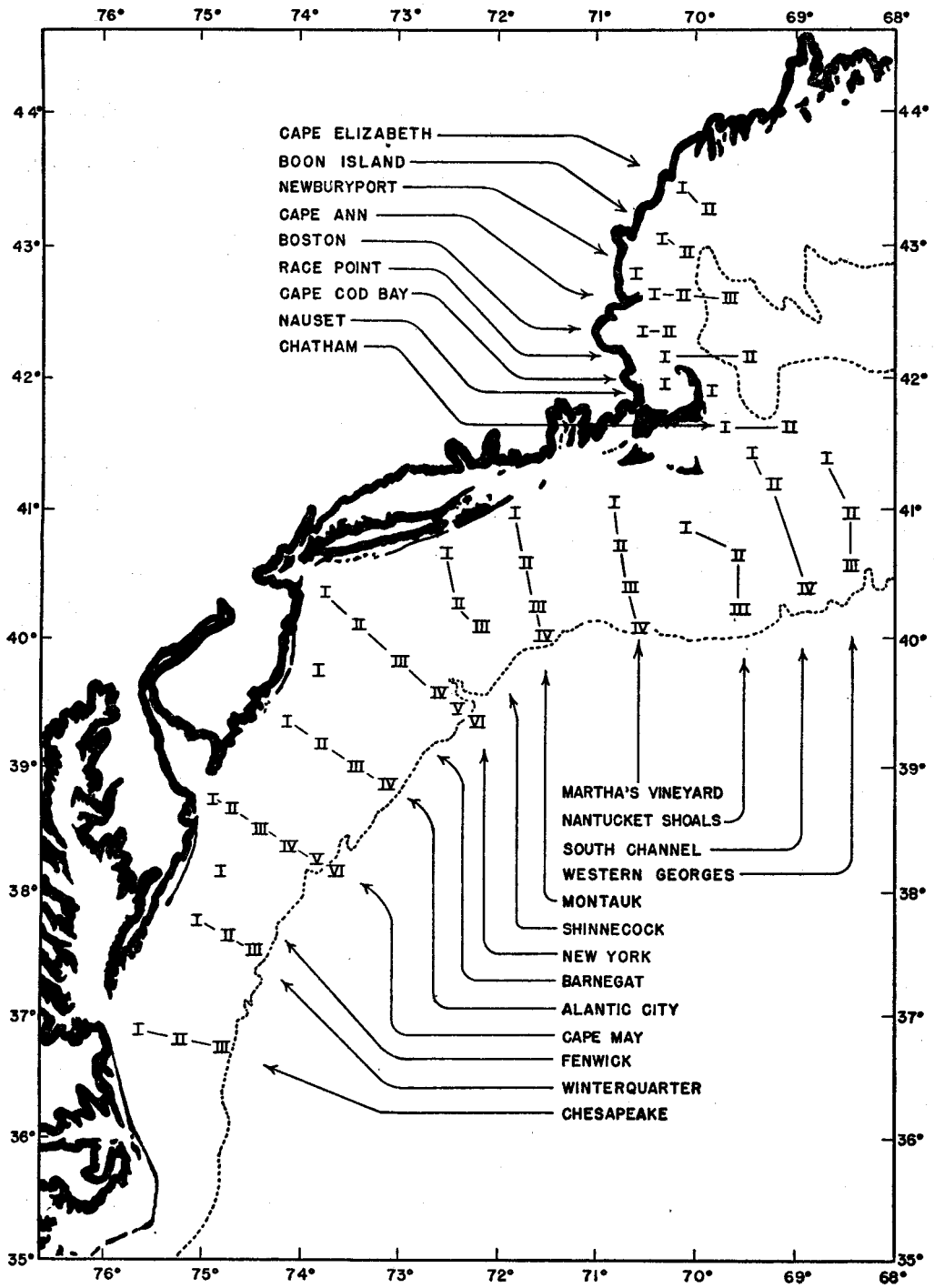


FIGURE 14.—Location of stations occupied during the 9 cruises of 1932.

That it did not do (1) or (2) is proved by the relative scarcity of larvae of appropriate sizes at stations of the Chesapeake section and the outer station of the Winterquarter section; though the few caught at Chesapeake II, III, and Winterquarter III indicate a slight tendency for southward and outward streaming. That (3) was the major result is shown by the "snubbing" of the southern center in its southward travel and by the increase in numbers of larvae in the southern center relative to the number

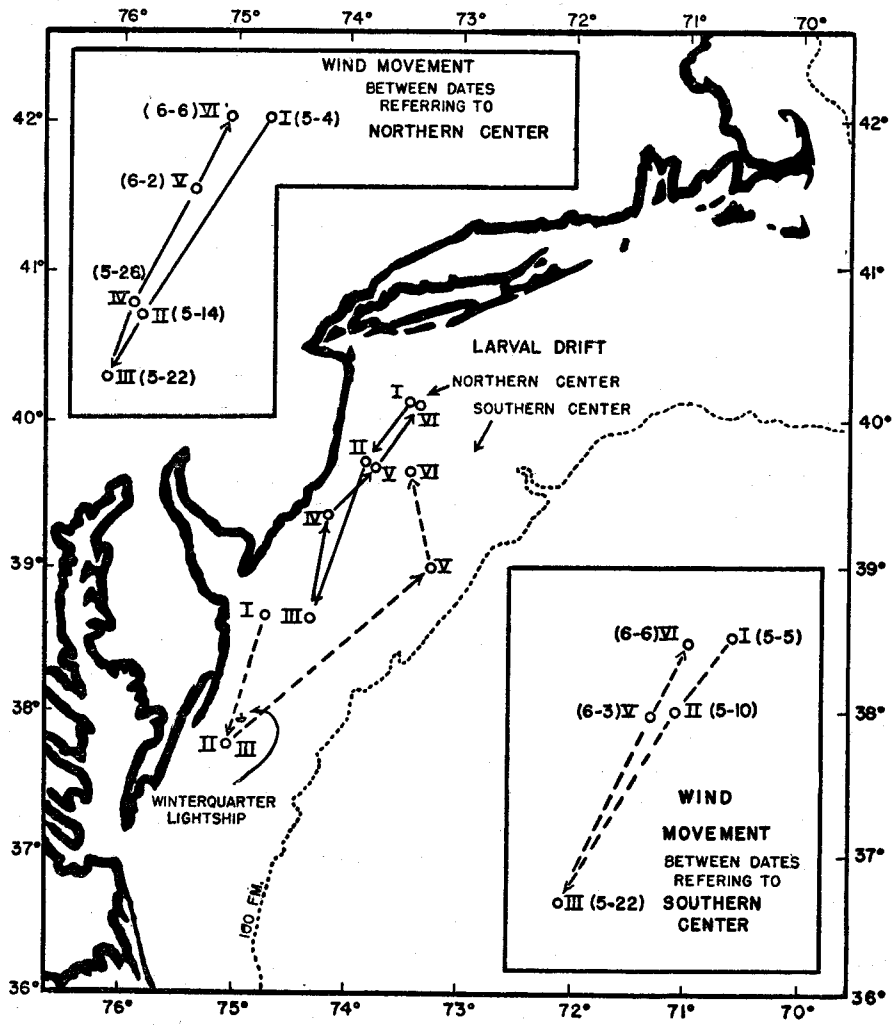


FIGURE 15.—Drift of the 2 centers of distribution of the S group compared with wind movements, as recorded at Winterquarter Lightship.

in the northern center,[17] as if indeed the water and its burden of larvae did pile up in the vicinity of Winterquarter I. This piling up very likely was in the nature of a thickening of the surface stratum of light water offset by a depression of the lower layers of heavier water rather than an outright raising of the water level. Of course, the depressing of the subsurface stratum would set up a subsurface flow to restore equilibrium. This flow would not transport the main body of larvae, since they were

[17] It is not supposed that the entire increase in relative number at the southern center was due to the mechanism being discussed. Part of it could have been due to random fluctuations of sampling.

confined to the upper stratum (p. 172); it could and probably did carry a few that happened to be near the interface as indicated by the light spread of larvae southward and outward to Chesapeake II and III and Winterquarter III.

While this accounts for the halting of southerly drift of the southern center and its increase in relative numbers, there is still to be considered the apparently too rapid drift of this center northward when the wind direction was reversed. Let it be supposed that the aforesaid piling-up of surface waters took place more rapidly than could be counterbalanced by subsurface flow. Then the sea surface would actually have risen and remained at a higher level as long as the wind continued to transport surface water to the area faster than the subsurface water could flow away. Then when the wind reversed its direction, the energy so stored would be released and act in the same direction as the wind. The two forces together would produce a faster drift than could result from the wind force alone, and thus account for the high rate of movement of the southern center between May 22 and June 3.

Whether the interactions of the wind forces and water movements here postulated were theoretically probable from dynamic considerations must be left to the physical oceanographer. He can find here an example of biologically marked water probably of considerable aid in the deciphering of the pattern of circulation in shallow water, where difficulties of dynamic analysis are heightened by topographical features, and where a better understanding would be of greatest practical use in dealing with fishery problems.

Whatever the outcome of any future examination of the dynamics of this situation, the outstanding resemblance of the main features of wind movement to larval drift, together with the fact that deviations from the parallelism between the two have a plausible though not proved explanation, leaves no doubt that the larvae (and the water with which they were surrounded) were drifted from place to place by the wind's action on the water, and that this alone accounted for their movements until they reached the end of the larval stage at a length of about 8 to 10 mm. and entered upon the post-larval stage.

Subsequently the movement of larval concentrations corresponded less perfectly with that of the wind (fig. 16). Between cruises VI and VII, when there was a gentle easterly wind movement, the post-larvae also moved eastward, but proportionately father than might have been anticipated from the moderate wind movement. Between cruises VII and VIII, when there was a northeasterly wind movement, they moved northwesterly. After cruise VIII it is difficult to be sure of the homology of the group under consideration, but the only post-larvae (lengths 37 and 51 mm.) of cruise IX identifiable as belonging to this group were caught at Chatham II and Cape Ann II, off eastern Massachusetts. The indicated movement was in the same general direction as the prevalent strong winds, but again sufficiently divergent to indicate some independence. Since the drift of water under impulse from the wind accounts for only a portion of their movement and since such evidence as is available on residual surface flow in this region [18] indicates water movement westerly, hence in a direction contrary to the movement of the post-larvae, the evidence does not favor the transport of the post-larvae as purely passive organisms, and it must be concluded that they moved to an important extent by their own efforts.

This is in complete harmony with their developmental history. As larvae, without swimming organs other than the rather flaccid finfold, they drifted with the

[18] Drift-bottles set out by Wm. C. Herrington (unpublished data) in connection with his haddock investigations in the spring of 1931 and 1932 drifted westward past Nantucket shoals, fetching up on beaches of southern New England and Long Island.

current; as post-larvae, with capable fins, they were able to swim and exercised this faculty. The change in locomotive ability coincided with change in method of transport.

Thus far, attention has been focused on the main centers of larval concentration. It will have been noted in figure 13 that there were indications of a smaller body of larvae not included in the groups whose centers were followed. This body probably became separated from the southern center about May 23, when the center was at its extreme southerly position, and, as previously pointed out (p. 187), there was a spread to Chesapeake II and III and Winterquarter III, probably consisting of only

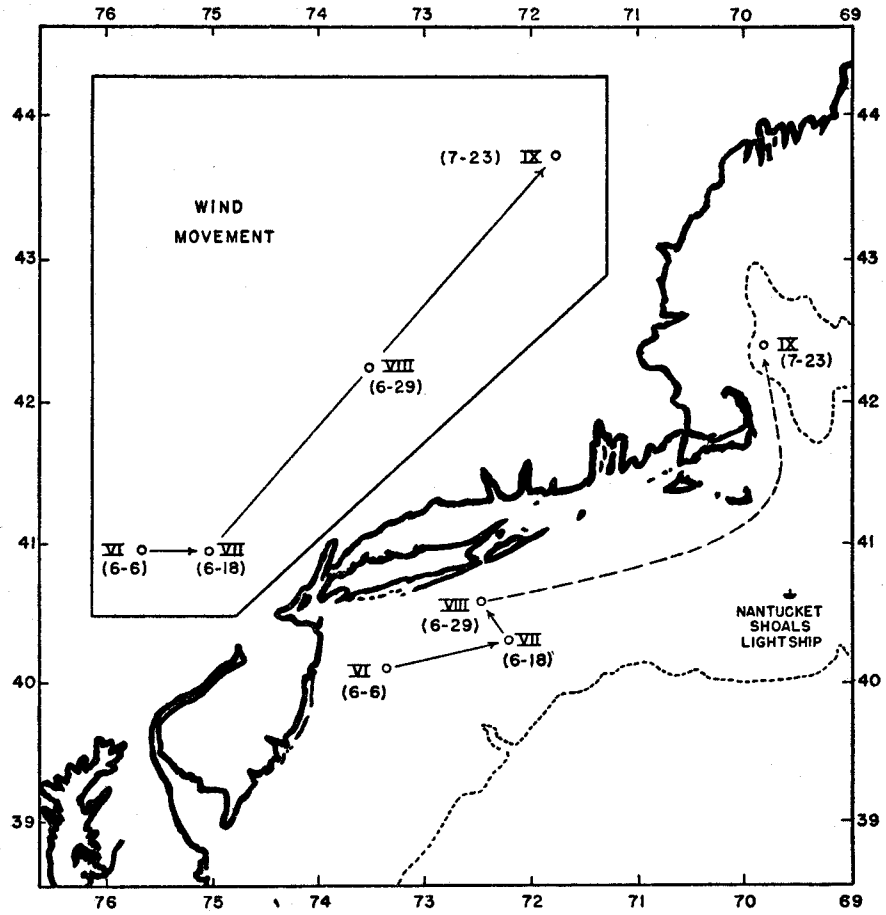


FIGURE 16.—Drift of post-larvae of the S group compared with wind movement, as recorded at Nantucket Shoals Lightship.

those larvae that were at the interface between the accumulating surface water and the outward streaming subsurface layer (p. 187). Having been caught in this outward and perhaps somewhat northerly flow, their northward drift could start sooner and would take place farther offshore than the drift of the southern center itself. With this in mind, it is easy to account for the catches at Atlantic City IV on cruise IV and at Montauk II and No Man's Land II on cruise VI. That they did not appear on other cruises is not surprising, for their numbers were few (1, 1, and 2 were caught at the respective stations above mentioned) and as the result of chance fluctuations in random sampling they could easily fail to appear in our hauls.

The average rate of movement of the S group larvae during the period from May 4 to June 6, while they were dependent for transport on wind-impelled drift, was 6 nautical miles per day. As nearly as may be estimated from data recorded on the Beaufort Scale, the net wind movement in the direction of the resultant (neglecting forces under Beaufort 3), was about 60 nautical miles per day. The movement of the center of post-larval abundance between June 6 and July 1, accomplished in part by swimming, averaged 3½ nautical miles per day. If the movement of post-larvae between June 27 and July 24 may be taken as from off Shinnecock to off Chatham, the average rate during this period was 6 nautical miles per day.

The movements of the R and T groups of larvae can be traced in the same manner as were those of the S group. The R group, beginning with cruise I, as 3 to 5 mm. larvae, moved southward from the Winterquarter section to the Chesapeake section. Like the S group, they remained at this southern extremity of the range through cruise III and also probably through cruise IV, though during the latter cruise there were not sufficient stations occupied in this area to prove this. On cruise V, however, they were found to have moved northward to Cape May, and on cruise VII were discovered off Shinnecock. At the beginning of this northerly movement, they were already 8 to 10 mm. long, and thus capable of swimming. With favoring winds during all but the last portion of this northerly trip, their movement was rapid, averaging 11 nautical miles per day.

The T group could not be so readily followed, but in general its movements were with the wind in the larval stage and indifferent to the wind in post-larval stages. Between cruises III and VI, when the winds were from the southwest, it shifted in an easterly direction from the Shinnecock section to the Martha's Vineyard section. The correspondence between wind direction and this movement was not as perfect as that of the S group, formerly described. From cruise III to cruise IV, there appeared to be a spread in both easterly and westerly directions, and between IV and V, there was a contraction toward the center of the group off Montauk Point. These changes in distribution may be indicative of spurts of spawning rather than movements of the egg population, for they occurred during periods of egg development, and the stages chosen may not have been exactly the continuation of the original stage A eggs of cruise III. It probably suffices to note that when first seen as stage A, they were off Shinnecock, and by attainment of lengths of 4 to 5 mm. at cruise VI, they were off Martha's Vineyard. Then between cruises VI and VII, with only a slight wind movement from the west, the zone of densest larval population remained at Martha's Vineyard, though fair numbers were as far west as Shinnecock. Between cruises VII and VIII, while the winds were from the southwest, the members of this group spread over the waters abreast of Long Island, extending from the New York to the Shinnecock section. During this interval they had grown into the post-larval stage, 10 to 12 mm., when swimming activity made their movements fairly independent of the wind.

It may be concluded therefore, that the movement of eggs and larvae (up to 10 mm. in length) in the southern spawning area between Cape Cod and Cape Hatteras was governed by the drift of surface waters, and this, in turn, by the direction of the stronger winds during the 40 days while the mackerel were passing through these phases of development and growth. These drifts may be as fast as 6 nautical miles per day and may convey the mackerel several hundred miles. After reaching the post-larval stage (10 mm. and upward) the movements are less dependent on drift, and probably are considerably aided by the tiny fishes' own swimming efforts. The

average rate of movement is sometimes about 3½ nautical miles per day and may at times, on the part of the largest individuals, attain eleven nautical miles per day. In 1932, the combined drift and swimming movements brought the larvae to the shores of Long Island and southern New England.

MORTALITY

Outstanding in the early life history of marine fishes is the high mortality in early stages. At sea, this is evident from the low numbers of larvae compared to the high number of eggs taken in plankton tows. In marine fish hatcheries, it has been evident from the high loss of larvae in all attempts to keep them beyond absorption of the yolk sac. It is probable that the fish cultural experience led to the generally accepted theory that the time of yolk sac absorption is the most critical period, and that it is so because the fish at that time must find proper food or die as soon as all the yolk is gone. Moreover, Hjort (see p. 207) believed that annual variation in the times and places of plankton increase during spawning might be such that an abundance of the right kind of food might coincide with this critical stage in one year and not in another. The coincidence of the two would produce a successful year class; the non-coincidence, a failure.

However elaborate the theory, it has yet to be proved at sea that the yolk sac stage is critical or that the annual variation of mortality in this stage is responsible for the variation in year-class strength. Thus, a determination of mortality of the young stages of mackerel in 1932 is not only of interest in itself, but has an important bearing on the general theory of fluctuations in fish populations. Inasmuch as the year class of 1932 has subsequently failed to appear in the commercial stock in important numbers (Sette, 1938), the present examination of mackerel mortality in the season of 1932 deals with the record of a failing year class and should bring to light the stages that were critical in its failure.

Determination of mortality.—There is at hand a simple way of determining the mortality rate of that year if it may be assumed that all the various egg and larval stages were sampled in proportion to their abundance in all parts of the spawning grounds, and during the entire period of planktonic existence. Then a frequency distribution of the summed numbers at each stage through the season would express their average relative numbers and constitute a survival curve. Although the sampling in 1932 approached a stage of perfection warranting treatment based on this general plan, there were nevertheless imperfections requiring secondary modifications, as will be explained.

The actual drawing of hauls appears to have been qualitatively and quantitatively adequate. At each station, all levels at which eggs or larvae might be expected to occur were sampled uniformly, and the subsequent adjustment for volume of water strained per meter of depth provided totals at each station which may be taken as the summation of individuals below 17.07 square meters of sea surface, irrespective of their level in the water. Comparison of 1-meter and 2-meter net hauls indicated that there was relatively little selective escapement from the nets (p. 215). Also, the towing stations formed a pattern reasonably well covering all parts of the important spawning grounds off the United States coast.

On the other hand, in some respects the samples did not adequately cover the entire season. At the time of the first cruise, spawning had already begun and larvae were taken for which there were no corresponding eggs. Similarly, force of circumstances prevented cruises from being taken as frequently in July as earlier in

the season, and also prevented their continuation into August. Thus, there was less opportunity for taking large larvae corresponding to the eggs and small larvae of the earlier cruises. However, the cruises did thoroughly cover the major portion of the season of maximal spawning and subsequent larval development; so there need be only a treatment which excludes from comparison the large larvae early in the season and the eggs and young larvae late in the season which were not proportionately represented in the other stages of their planktonic existence.

This was done by taking the average numbers of eggs and larvae per cruise for the several cruises that spanned the period of maximal numbers of each stage of egg and larva.[19] The selection of cruises for these averages was as follows: for egg stages A to C, cruises I to IV; 3-mm. larvae, cruises II to V; 4- to 7-mm. larvae, cruises III to VI; 8- to 9-mm. larvae, cruises IV to VII; 10- to 12-mm. larvae, cruises V to VIII; 13- to 15-mm. larvae, cruises VI to IX; 16- to 22-mm. larvae, cruises VII to IX; and 23- to 50-mm. larvae, cruise IX.

TABLE 7.—*Survival of young stages of mackerel in 1932*

Categories [1]	Duration of category [2]	Average age of category [2]	Frequencies		Survival per million newly spawned eggs			
			Average per cruise [3]	Average per cruise adjusted for duration of category [4]	Logarithmic values		Arithmetic values	
					Empirical [5]	Computed [6]	Empirical	Computed [6]
Egg stages:	*Days*	*Days*	*Number*	*Number*	*Log*	*Log*	*Number*	*Number*
A	2.53	1.3	16,900	6,680	5.866	5.915	735,000	822,000
B	2.32	3.7	12,600	5,430	5.776	4.759	597,000	574,000
C	2.38	6.0	12,500	5,250	5.761	5.609	576,000	406,000
Fish lengths (millimeters):								
3.2	5.14	9.9	9,310	1,810	5.299	5.354	200,000	226,000
4	6.86	16.0	4,270	622	4.835	4.957	68,400	90,600
5	5.48	22.1	1,760	321	4.547	4.559	35,200	36,200
6	4.56	27.1	717	157	4.237	4.233	17,300	17,100
7	3.91	31.3	403	103	4.054	3.959	11,300	9,100
8	3.41	34.9	192	56.3	3.791	3.724	6,180	5,300
9	3.04	38.1	73.5	24.2	3.425	3.516	2,660	3,280
10	2.73	41.0	18.4	6.74	2.870	2.950	741	891
11	2.48	43.6	7.70	3.10	2.532	2.483	340	304
12	2.28	46.0	4.95	2.17	2.377	2.372	238	236
13	2.10	48.2	2.98	1.42	2.193	2.271	156	187
14	1.95	50.2	3.38	1.73	2.279	2.179	190	158
15	1.82	52.1	1.72	.945	2.016	2.092	104	124
16	1.71	53.8	1.10	.643	1.849	2.013	71	103
17	1.60	55.5	1.10	.688	1.879	1.935	76	86
18	1.52	57.1	1.70	1.118	2.090	1.861	123	72
19	1.43	58.5	1.10	.769	1.927	1.797	85	63
20	1.37	59.9	.533	.389	1.631	1.733	43	54
21	1.27	61.3	.500	.388	1.630	1.668	43	47
22	1.24	62.5	.467	.377	1.617	1.613	41	41
23	1.19	63.8	1.300	1.092	2.078	1.553	120	36
24	1.14	64.9	.300	.263	1.461	1.502	29	32
25	1.09	66.0	.800	.734	1.907	1.452	81	28
30	8.65	71.0	3.900	.451	1.695	1.222	50	17
40	6.86	78.9	.300	.0437	.681	.858	5	7
50	5.72	85.0	.100	.0175	.284	.577	2	4

[1] The categories of egg stages are defined on p. 178, the categories of larval lengths are the midpoints of the class interval.
[2] See text p. 179.
[3] See text p. 192.
[4] Items in the third column divided by the items in the first column.
[5] Logarithms of the items in the fourth column plus the constant 2.041.
[6] These are the values represented by the heavy lines of fig. 17.

This selection provides a series that approximately follows the eggs of cruises I to IV through their subsequent stages. Since by far the largest numbers of eggs were

[19] Before the averages were drawn an adjustment was made in the numbers of larvae from cruise IV on which a group of stations, Fenwick I, Winterquarter I, II, and III, and Chesapeake I and III had been omitted. These stations were located in the area where only 2 days previously there had been found most of the 5- to 11-mm. larvae and the omission of these stations caused a marked, deficiency of these sizes in the totals of cruise IV (note in table 5, column 4, the abrupt drop in numbers from the 3- to the 5-mm. class). Since these particular stations were occupied at the very end of cruise III, growth and mortality in the few intervening days before cruise IV would have only slightly altered the catches at these stations by the time of the latter cruise. Therefore, to restore the deficiency, the catches of cruise III at these stations were added to the cruise IV totals, giving new values of 5381, 1998, 682, 150, 67, 31, 5, and 3 for the 4- to 11-mm. classes in the 4th column of table 5.

taken on the first 4 cruises, the treatment includes the population resulting from the major portion, perhaps 70 percent, of the season's spawning. It of course ignores the fate of the fewer eggs spawned prior to or later than the first four cruises, but the neglected portion is probably so small that it is unlikely that the survival of the whole season's brood of young differs from that of the treated portion. It could do so only if the mortality of the neglected portion differed widely from the included portion. There appears to be no reason for believing that there was any such wide difference. On the contrary, examination of the relative numbers of the various stages and sizes caught on those cruises which included a part of the history of the neglected portions suggests that these had a survival rate similar to that of the included portion.

Having the average relative numbers of each category of egg and larva from this selected series (table 7, column headed "Average per cruise") there remained the necessity of adjusting the numbers to compensate for the differences in the duration of

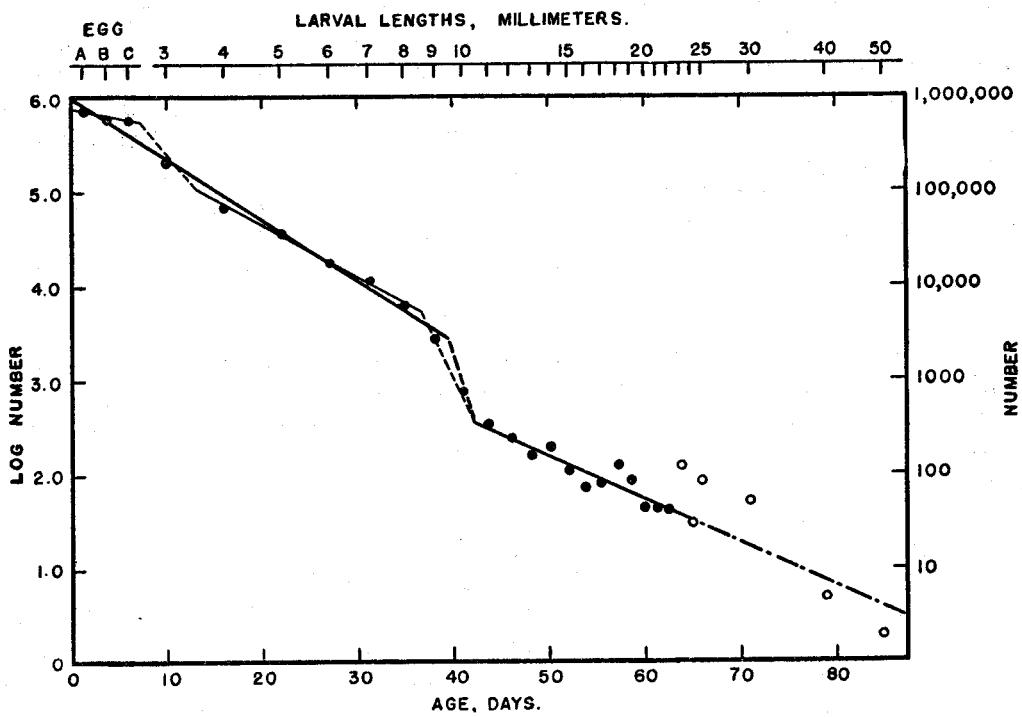


FIGURE 17.—Survival of young stages of mackerel in 1932. Solid dots represent the means of three or four cruises each. Open circles represent the less reliable values based on only one cruise. The heavy lines represent a simple interpretation of survival rates, and the fine lines, a more complex alternative interpretation. Solid lines are fitted to the solid dots by the method of least squares. Lines of dashes connect their ends, and the line of dots and dashes is an extrapolation.

time represented by each egg stage and each larval-length class. The stages or classes representing a long period of development would be passed slowly and the catches of such a category would represent a larger accumulation of individuals than a category representing a shorter period of development. Since the accumulation would be directly proportional to the duration of the category, the true relative values were obtained by dividing the numbers of individuals in each category by the number of days required to pass through that category, according to the schedule, given in the column headed "Duration of category" of table 7. This, in effect, reduces the data to represent what the relative numbers would have been had it been possible to subdivide the material into categories that occupied uniform time intervals—in this

instance, one day. The resulting values are given in the fourth column, and the logarithms of these (column 5) of table 7 are plotted in figure 17.

Reliability of the survival curve.—The determination of the survival curve was based on plankton hauls generally considered to be only approximately quantitative, it utilized only selected portions of the original material, and it involved extensive computations. The reliability of the result therefore depends not only on quantitative adequacy of the original material, but also on whether the subsequent procedure introduced any biasing influences. The following discussion will draw attention to the facts which appear to have an obvious bearing on reliability. Unless some pertinent features have escaped notice, the conclusion is inevitable that this survival curve has surprisingly high reliability for all stages up to the length of 22 mm., or, for the first 60 days of life.

Considering first the collection of material, attention may be confined to those influences that might possibly cause large larvae to be caught in relatively greater or lesser proportion than small larvae, for it is only by such "size selection" that the slope of the survival curve, and hence the conclusions as to mortality rates, could be affected. On this score there are two possibilities: the nets' catching ability might differ for different sizes of larvae; or the distribution of the larvae might vary in such a way as to cause a less complete sampling of one size than of another.

In the appendix (p. 215) there is given evidence which appears to be indicative, if not conclusive proof, that the nets caught practically all the larvae in the paths of their travel, at least up to the 22 mm. size; hence net selection was probably not a biasing influence in this size range.

Since the nets were fished from surface to below the thermocline, and since the larvae probably do not descend below that point (p. 173), and since straining was substantially uniform for all levels fished, there is little likelihood that differential vertical distribution was a biasing factor. There remains, then, the possibility that larvae of different sizes had different horizontal distributions, and that these distributions differed in a manner which would have affected the relative adequacy of the sampling of the various sizes.

For small larvae up to 10 or 12 mm. in length, the drift was determined (pp. 183 to 191) with sufficient precision to establish the fact that the population of these sizes did not drift out of the area sampled. The majority of large larvae 22 to 53 mm. long, however, taken off eastern Massachusetts on the final (ninth) cruise, were outside the area covered on earlier cruises. Could, then, a portion of the population of medium sizes (12 to 22 mm.) have left the waters south and west of Nantucket Shoals, that is, the area of survey, prior to the ninth cruise, and thus have been undersampled? If so, they should have been found in the intervening area during the eighth cruise, which, fortunately, included that area. This cruise took place shortly after the main portion of the larval population was in the 12- to 22-mm. size range. It included stations around Nantucket Shoals and on the portion of Georges Bank just east of the Shoals; [20] hence, in the area through which larvae would have been drifting or swimming if they had, by this time, begun their movement north and east past the Shoals. Since no larvae of these sizes were taken there, it seems unlikely that these sizes were undersampled as a consequence of emigration from the area south and west of the Shoals. In other words, the intermediate, as well as small sizes of larvae, were sampled in approximately their true proportions.

[20] These stations of cruise VIII have not been included in any of the tables because the hauls there lacked pertinent material.

For the larvae over 22 mm. long there is no evidence to determine whether or not they were caught by the nets in their true proportions. On general grounds, one would expect that they could elude the nets, though the taking of a specimen as long as 51 mm. shows that the gear could catch at least some large-sized larvae. Offsetting the probability of undersampling the larger sizes, there is the opposite probability of oversampling them, because the stations were somewhat more closely spaced (see fig. 14) in the area north and east of Nantucket Shoals, where they were found, than south and west of the Shoals, where the smaller sizes were most abundant. Whether or not the loss of large larvae by eluding the nets and the gain by possible oversampling as the result of closer station spacing offset each other perfectly is indeterminable from the available data. Hence, the mortality determination is of uncertain reliability for sizes over 22 mm. For those smaller than 22 mm., the determination is reliable as far as collecting methods are concerned.

Having found little reason to suspect size-connected biases in collecting, excepting possibly for sizes over 22 mm. long, two questions remain: were the hauls themselves sufficiently quantitative to give reliable indices of abundance for each station; and were the stations spaced properly to give a reliable summation of abundance for the entire area? To answer the first question separately would require a study of the variation in series of duplicate hauls, and is precluded for lack of material, but both questions may be answered simultaneously by a study of the relative numbers caught at the various stations in relation to the probable nature of distribution of numbers of individuals in the sea.

Inspection of charts of egg or larval distribution (fig. 13) suggests that the pattern of concentration has a form closely related to a normal frequency surface. Near the middle of the area in which eggs or larvae occur are one or several stations with very high concentrations corresponding to the mode; surrounding these are more stations with decidedly lower concentrations corresponding to the slopes; and at the periphery are many stations with very low concentrations corresponding to the "tails" of the normal frequency surface. Let us assume, for the moment, that the concentrations of eggs really do form a normal frequency surface. Then the number of a particular stage caught during a particular cruise is a reliable index of the abundance of that stage at that time, provided that: the stations where the catches were made were so located as to give proper relative representation of the various parts of this normal frequency surface, such as the mode, slopes, and tails; and that the catches also were sufficiently reliable to provide the true relative numbers to be found at the various parts of this surface. Therefore, a test as to the conformity of catches to the normal frequency surface would at once indicate whether the above assumption is correct; whether the catch stations were arranged so as to sample adequately the various parts of the distribution; and whether the hauls themselves were quantitatively reliable.

To translate the normal frequency distribution into a convenient form for making the tests, table 8 has been prepared.[21] It was derived from the curve of the normal frequency distribution where, for unit standard deviation and unit N

$$y=0.3989e^{-\frac{x^2}{2}}$$

[21] Buchanon-Wollaston (1935, p. 85) has given a table purporting to give the same statistics, but it appears to represent the results of sampling only along a line passing through the mode of a normal frequency surface, not the results of sampling over the entire surface. For the latter, account must be taken of the fact that in such a surface, so sampled, the areas of classes of equal range in ordinate height increase as the square of the distance from the mode.

by calculating for values of y (catch magnitudes) the corresponding values of x^2 (relative number of catches) over a range of y from 10,000 to 5 and at intervals of 500 for the first 19 classes, of 25 for the next 19 classes, and of 5 for the next 4 classes. For convenience the x^2 series was converted to values giving a cumulative total of approximately 1,000 (actually 999.96). This table can be used for any range of catch sizes in which the maximum is not more than 2,000 times as large as the minimum, by first multiplying the empirical values by 10,000 times the reciprocal of the maximum catch. Linear interpolation is fairly accurate in the table ranges of 10,000 to 5,000 and of 500 to 250; but the work is facilitated and is more accurate for all parts of the range when the tabular values are graphed.

TABLE 8.—*Relative number of catches of given magnitudes to be expected from a population of organisms distributed in the form of a normal frequency surface*

Magnitude of catch	Number of catches, cumulative	Number of catches, by classes	Magnitude of catch	Number of catches, cumulative	Number of catches, by classes
10,000		6.71	425	415.44	7.96
9,500	6.71	7.11	400	423.40	8.49
9,000	13.82	7.50	375	431.89	9.08
8,500	21.32	7.96	350	440.97	9.74
8,000	29.28	8.49	325	450.71	10.53
7,500	37.77	9.08	300	461.24	11.45
7,000	46.85	9.74	275	472.69	12.57
6,500	56.59	10.53	250	485.26	13.88
6,000	67.12	11.45	225	499.14	15.53
5,500	78.57	12.57	200	514.67	17.57
5,000	91.14	13.88	175	532.24	20.26
4,500	105.02	15.53	150	552.50	24.02
4,000	120.55	17.57	125	576.52	29.34
3,500	138.12	20.26	100	605.86	37.83
3,000	158.38	24.02	75	643.69	53.36
2,500	182.40	29.34	50	697.05	91.19
2,000	211.74	37.83	25	788.24	29.34
1,500	249.57	53.36	20	817.58	37.83
1,000	302.93	91.19	15	855.41	53.36
500	394.12	6.71	10	908.77	91.19
475	400.83	7.11	5	999.96	
450	407.94	7.50			

In table 9 there are given, as an example, the computations involved in determining the class limits for dividing the catch magnitudes into 5 categories, using the data for stage A eggs from cruise I. Since the sampling of the plankton usually was of a portion that permitted detection of eggs down to 20 per station, 20 was taken as the minimum, giving a range of 5806 to 20 for catch magnitudes (first and last items in column 4 of the example). Multiplying these by $\frac{10,000}{5,806}$ gives 10,000 to 34 as the corresponding tabular range (first and last items of column 3 of the example). Entering table 8 with catch magnitude 34, by interpolation, it is found equivalent to a cumulative catch number of 755, and this figure is entered as the last item in column

TABLE 9.—*Example of the computation of limits for 5 classes within each of which an equal number of catches would be expected if the distribution of stage A eggs during cruise I conformed to a normal frequency surface; and the actual and theoretical number of catches for these class limits*

1	2	3	4	5	6
Equal fifths, cumulative	Tabular number of catches expected, cumulative	Tabular class limits for catch magnitudes	Actual class limits for catch magnitudes	Actual number of catches	Theoretical number of catches
0.0		10,000	5,806		
				2	1.8
0.2	151	3,190	1,853		
				1	1.8
0.4	302	1,010	586		
				4	1.8
0.6	453	321	186		
				2	1.8
0.8	604	102	59		
				0	1.8
1.0	755	34	20		
Total				9	9.0

2 of the example. It indicates that 755/1000 of the frequency surface is to be taken into account. Then 755 is multiplied by the items in column 1 of the example, giving the series of items in column 2. Successive differences in this series would represent equal fifths of the frequency surface out to 755, but it is, of course, not necessary to compute these differences. The corresponding catch magnitudes are secured by entering table 8 in the column of "Number of catches, cumulative," and reading, by graphical interpolation, from the column of "Magnitude of catch." This gives the series of column 3 in the example. These represent the class limits within each of which one-fifth of the catches would fall if the maximum and minimum had been 10,000 and 34, respectively, and the distribution of catch magnitudes conformed perfectly to the distribution expected from a normal frequency surface. Since they were, instead, 5,806 and 20, respectively, the factor 5,806/10,000 is used to convert them from the tabular to the actual basis, giving the values in column 4 in the example. Between each pair of successive figures there should be found, theoretically, an equal number of catches of stage A eggs from cruise I. In the first column of table 19, cruise I, the adjusted totals of individuals of stage A are given, and a count of those lying between each pair of specified class limits gives the numbers in column 5 of the example. Since the total number of catches was 9, neglecting those below 20, the theoretical number for each class is 9/5, or 1.8, as given in column 6 of the example.

When the same computations are performed for the stage A eggs of cruises II, III, and IV, and the actual number of catches are added together, by classes, there results the series of values given under the appropriate heading in the first line of table 10. There are now enough items in each class to apply the χ^2 test; and the probability P, that random variation would exceed the actual variation, is found to be 0.85. This value would appear to be rather high; but when the work is done for the remaining stages up to 22 mm. with due regard to the necessity of having fewer classes for the later stages in order to keep the numbers per class high enough to use the χ^2 test, it is found that the values of P are distributed almost exactly as would be expected, for there are 7 of them below and 8 above 0.5, and the mean is 0.53. Hence it must be concluded that the catch magnitudes of stages up to 22 mm. larvae are related to each other quite as would be expected had these stages been distributed in the sea in conformity with the normal frequency surface.

TABLE 10.—*Summary of test to determine whether the magnitudes of catches of eggs and larvae conformed to the distribution expected from sampling a normal frequency surface*

Stage	Cruises included	Lower limit of catch magnitude	Actual number of catches by classes					Expected number of catches in each class	χ^2	P
Eggs:										
A	I-IV	20	8	8	10	6	6	7.6	1.4	0.85
B	I-IV	20	8	13	9	9	9	9.6	1.6	.80
C	I-IV	20	13	9	6	9	12	9.8	2.1	.70
Larvae (millimeters):										
3	II-V	20	7	8	13	6	7	8.2	3.7	.44
4	III-VI	20	9	7	9	4	5	6.8	3.0	.55
5	III-VI	10	6	6	8	9	4	6.6	2.4	.67
6	III-VI	5	10	4	8	3	4	5.8	6.3	.18
7	III-VI	1	7	8	6	9	5	7.0	1.4	.85
8	IV-VII	1	6	5	4	4	10	5.8	4.3	.36
9	IV-VII	1	(1)	4	4	3	9	5.0	4.4	.22
10	V-VIII	1-[2] 0.10	(3)	(3)	8	6	7	7.0	.3	.82
11	V-VIII	1- [2].10	(3)	(3)	7	2	10	6.3	5.2	.07
12	V-VIII	1- [2].10	(3)	(3)	7	5	2	4.7	2.7	.27
13-15	VI-IX	1- [2].10	(3)	(3)	6	5	7	6.0	.3	.82
16-22	VII-IX	1- [2].10	(4)	(4)	(4)	7	4	5.5	.8	.35

[1] The catches were divided into four classes, leaving this class vacant.
[2] Lower limit for cruises VIII and IX where 2-meter nets were used.
[3] The catches were divided into 3 classes, leaving this class vacant.
[4] The catches were divided into 2 classes, leaving this class vacant.

This result may seem one in which the empirical data are closer to theoretical expectation than they should be, for it will be recalled that the frequency surfaces, as exemplified by the charts of figure 13, were not normal, but were skewed in one direction or another, and were elongated rather than circular in form. The skewing might not necessarily be detectable in the test, for the loss on one side may be approximately offset by the gain on the other, but the elongation should have its effect, as is readily apparent if one imagines such elongation carried to its logical extreme. Then the distribution would be in a band so that constant values would be found when sampling longitudinally to the band, and values distributed in accordance with the normal frequency curve, rather than the normal frequency surface, when sampling across the band. At this extreme the catch magnitudes should be related to each other as if drawn from the normal frequency curve instead of the normal frequency surface. With intermediate elongation, such as indicated by the isometric lines of figure 13, it is uncertain whether the distribution of catch magnitudes might be intermediate between the type expected from the frequency curve and that from the frequency surface, and hence fit neither; or whether it might still closely conform to the type expected from the frequency surface as would easily be true if, in the elongated surface, the form of the normal frequency curve were retained in the section along its major axis.

In any event, it is probably significant that the elongation of isometric shapes of figure 13 is generally parallel to the coast, and also that the station grid is rectangular rather than square, so that the mean spacing between stations in a direction longitudinal to the coast is greater than that in a direction perpendicular to the coast, the ratio of the latter to the former averaging 0.44. Furthermore, by measurement it may be found that the mean ratio of the minor to the major axis in the isometric shapes of figure 13 is 0.47. Thus the sampling pattern was warped about the same amount and in about the same direction as the egg and larval distribution patterns. One compensates almost exactly for the other, and it is therefore less surprising that the empirical data should fit the theoretical distribution, even though the latter did not specifically take into account the elongation of the egg and larval distributions.

Since it is impossible that hauls of indifferent quantitative accuracy, or that sampling at a pattern of stations that did not adequately explore the area could,

by chance, produce a series of catch magnitudes conforming so well to hypothesis, it has been proved not only that the hauls were quantitative, but also that the sampling provided adequate representation of all parts of the distribution of each of the various stages of eggs and larvae up to 22 mm. long. Nothing is yet proved as to the extent of random variability, either of the quantities caught per haul or per cruise. This would control the scatter of points in figure 17 and will receive consideration in the final paragraphs of this section.

The foregoing has dealt with the collection of material. Turning now to the mathematical treatment, the initial step was to total the catches of a given stage for each cruise and then average these totals for certain groups of cruises. This use of total per cruise is equivalent to a direct arithmetic integration of the frequency surface and could introduce no errors if the same stations were occupied on each cruise, and if all stations represented equal unit areas. These requirements were approximately met because the same station plan (fig. 14) was used for each cruise, and the stations were distributed uniformly enough to represent approximately equal unit areas. The principal change from cruise to cruise was the omission of some stations. As earlier mentioned, stations north and east of Nantucket Shoals were omitted from the first seven cruises, and it already has been pointed out that this probably had no effect on the computation because these northeasterly stations could have contributed nothing to the totals of the group of mackerel that is followed in the survival curve. Besides this the stations at Martha's Vineyard IV, Montauk IV, New York V and VI, and Cape May I were usually omitted. Since they proved always to be at the periphery of the egg and larval concentrations, their exclusion or inclusion could make little difference. However, on four of the first seven cruises, there were additional omissions which could possibly have had important effects.

On cruise I the station at New York I and all of those on the Montauk and Shinnecock sections were omitted. Judging from the catches at adjacent stations, and also from the distribution of appropriate stages on the following cruise, three of these omitted stations might have added low to medium catches to the totals for stage A and B eggs, but this could not have increased their totals for that cruise by more than 5 percent, and could have modified the average per cruise of the four cruises used for these stages by less than 2 percent, so the effect of this omission is inappreciable.

On cruise IV all stations on the Winterquarter section, and those at Chesapeake I and III were omitted. This omission would have a serious effect on the total for that cruise, for these stations could have been expected to yield nearly maximal numbers of 4- to 8-mm. larvae, but the effect of this omission was rectified by substituting the cruise III values for these stations in calculating the average per cruise. (See footnote p. 192.) This substitution could have introduced error only to the extent of 2 days' growth and mortality—an effect that would not be perceptible after inclusion of the data for the three other cruises in the group average.

On cruise V the stations on the Martha's Vineyard section, at Montauk III, and at Shinnecock I and II were omitted. This probably reduced the totals of 3-mm. larvae appreciably, and 4-mm. larvae slightly. If the effect on the 3-mm. larvae is estimated by examining the result of substituting numbers interpolated from the previous and subsequent sampling at these stations, the total for this size of larvae is increased from 5,215 to 12,549 for cruise V and the average per cruise for cruises II to V is increased from 9,310 to 11,144. Substituting the latter in table 7 and carrying the work through to the logarithm of the empirical number surviving per million, it is

found that the value increases from 5.299 to 5.378, indicating that the point for 3-mm. in figure 17 should probably be raised by an amount nearly equal to the diameter of the dot representing it. Similar examination of catches of 4-mm. larvae indicates that the total for cruise V might be raised from 8,236 to 9,945, a change that becomes imperceptible when worked through to the values on the graph of survival.

On cruise VIII the stations at Fenwick, Winterquarter, and Chesapeake were omitted. At the very most these could have contributed nothing to any of the averages involving this cruise, excepting possibly a very few individuals in the 7-, 8-, and 9-mm. classes. These would not cause a perceptible change in the survival curve.

By the time of cruise IX, only one larva was found along the New York section, and it was so probable that none at all remained south of that locality that the omisson of all stations from there southward could not have had any effect on the survival curve.

Hence it may be concluded that the use of cruise totals introduced no errors other than a slight lowering of the 3-mm. point on the survival curve.

Turning now to the possibility that errors were introduced by the selection of certain cruises, it will be recalled that the successive points on the survival curve consist of averages of the catches in groups of cruises, using successively later cruises for the successively older larvae so as to follow the main population through the season from egg stages to late post-larvae. Owing, however, to exigencies of boat operation, the cruises toward the end of the season were separated by wider intervals of time, so that the average numbers of older larvae were calculated from samples more widely spaced in time. This would tend to include relatively more submaximal values for the older larvae than were included for the eggs and younger larvae. Although the effect of this cannot be directly measured, it is possible to deduce the extreme amount of distortion to be expected from the inclusion of submaximal values.

This can be done by restoring submaximal values to the computation of the average number of young larvae. For instance, for 5-mm. larvae, the average of the catches for cruises III to VII, which were the ones used in the mortality determination, was 1,760. Inclusion of cruises I, II, and VII would restore submaximal values and produce an average of 1,220. Substituting the latter figure in column 3 of table 7 and carrying the computation over to column 5 gives a figure of 4.387 instead of 4.547 for the 5-mm. class. This would lower the point for 5 mm. in figure 17 by about 1½ times the diameter of the dot representing that point in the graph. This is a very small alteration brought about by a relatively large increase in submaximal values. Therefore the inclusion of what was probably a relatively small number of submaximal values for the older larvae by the method used in averaging cruises to obtain the mortality curve could have lowered the points representing the older larvae very little indeed, and therefore have altered the curve by only the slightest amount.

Next may be examined the distortion that could be connected with the growth-rate data employed in computing the mortality curve. Evidences of the reliability of the growth-rate determination were given in the section on that subject, and it was concluded that the general course of the growth curves must be essentially correct. It remains to be considered here whether there might nonetheless actually have been irregularities in growth, and because they were not reflected in the growth statistics used in computing mortality rates, they could have produced the observed peculiarities in the survival curve.

The outstanding peculiarity in the survival curve is, of course, the abrupt change of level and slope at the age of 40 days, or length of 10 mm. To investigate the possibility that this might have been due to the mathematical effect of a fluctuation in growth rate, rather than a fluctuation in mortality rate, let it be assumed that the mortality rate through and beyond this period was constant, and compute the changes in growth rate required to fit this hypothesis. The resulting new values for growth rate, in terms of days required to grow one mm. in length, are as follows:

Millimeters:	*Days*	Millimeters—Continued.	*Days*
9	3.04	13	.15
10	.80	14	.18
11	.38	15	.09
12	.24		

Thus, this hypothesis would require growth at an ever-accelerating rate from 10 mm. on, such that less than a day would be occupied in growing from a length of 10 to a length of 15 mm., and by that time growth would be at the rate of 10 mm. per day. Clearly this hypothesis is untenable, for such high growth rates are not only absurd *per se*, but also inconsistent with the distributions of lengths of larvae taken on successive cruises; and it may be concluded that the outstanding peculiarity in the mortality curve cannot have resulted from a fluctuation in growth rate. This demonstration, having proved that it requires striking changes in growth rate to produce material effects on the survival curve, indicates also that errors of the order of magnitude which likely exist in the determination of growth would not materially affect the determination of mortality rates.

Thus far attention has been centered on the possible elements of selective error or bias connected either with collection of the material or the subsequent mathematical treatment. There remains the question of the effect of random variability. This could not alter the level or the trend of the survival curve, for random variability would produce empirical values that tend to deviate equally above and below the true values, so that the sole effect would be on the scatter of points, or, in other words, the relative reliability of fit by any lines expressing their trends. This is readily investigated by conventional statistical methods.

Because the points in the curve obviously lie along straight lines over considerable segments, such lines have been fitted, by the method of least squares, to various combinations of segments. Since our interest lies principally in the mortality rates expressed by the slopes of the lines, attention may be focussed on the b value, or regression coefficient, in the equation: [22]

$$y=a+bx$$

which describes these lines. The standard deviation s of the regression coefficient b may be estimated by the formula

$$s=\frac{S(y-Y)^2}{n^1-2}$$

To investigate the reliability of the slopes of the lines for various segments of the diagram, one may calculate

$$t=\frac{b-\beta\sqrt{S(x-\bar{x})^2}}{s}$$

and find, from published tables, the probability, P, that any other slope β might result from sampling the same universe. Being interested in knowing the limits of

[22] The symbols given in this and following equations are those used by Fisher (1932).

accuracy of the slopes, values of t may be selected for P=0.05, and by substituting these in the equation,

$$b-\beta=\frac{st}{\sqrt{S(x-\bar{x})^2}}$$

values of $b-\beta$ may be calculated which, when added to b, or subtracted from it, will give the limits of a range of slope values. The chances will then be 19 out of 20 that the true slope lies within this range.

From these calculated ranges (table 11), it is clear that there was so little random variability of the points about the lines of best fit, that mortality values are accurate to within one or 2 percent per day for all segments other than A to C.

There still remains the question: which of these combinations of straight lines gives the most probably true series of survival rates? This may be investigated by the formula for the significance of the difference of two slopes, again going through the t test, using the formula

$$t=\frac{b_1-b_2}{\sqrt{s^2\left[\frac{1}{S(x_1-\bar{x}_1)^2}+\frac{1}{S(x_2-\bar{x}_2)^2}\right]}}$$

where

$$s^2=\frac{S(y_1-Y_1)^2+S(y_2-Y_2)^2}{n'-4}$$

From the results given in table 11, where the subscripts of b represent the initial and terminal points of the segments, it is apparent: (1) That b_{A-C} differs from b_{4-8} just enough to indicate that the survival rate probably is significantly higher in the larval stages than in the egg, and therefore the two lines A–C and 4–8 better describe this segment than the one line A–9. However, the latter does not differ significantly enough from each of the former to preclude the possibility that it fairly well represents the general course of survival from the early egg stage to the 9-mm. larva. (2) That b_{11-22} is certainly significantly different from b_{A-9}, though not from b_{4-8}. The interpretation of these findings will be discussed in the following section.

TABLE 11.—*Estimates of accuracy of slopes of lines in figure 17*

Segment	b	s	$b-\beta$	Equivalent mortality rates in percent per day		
				Indicated (b)	Lower limit $b-(b-\beta)$	Upper limit $b+(b-\beta)$
A–C	−0.02246	0.0307	0.1170	5.0	−21.0	27.5
4–8	−.05465	.0337	.00716	11.8	10.4	13.3
A–9	−.06521	.0905	.00515	13.9	13.0	15.0
11–22	−.07467	.1165	.0128	10.1	7.4	12.7

TABLE 12.—*Significance of the differences of the slopes of the lines fitted to various segments of the survival curve*

Slopes compared	Difference	s	S. E. b_1-b_2	t	P
b_{A-C} and b_{4-8}	0.03219	0.03294	0.0102	3.169	0.05–0.02
b_{A-9} and b_{11-22}	.01901	.10562	.0058	3.276	<.01
b_{A-C} and b_{A-9}	.04275	.08574	.0259	1.651	.2–.1
b_{4-8} and b_{A-9}	.01056	.07898	.0056	1.875	.1–.05
b_{4-8} and b_{11-22}	.00845	.01030	.0086	.988	.4–.3

Mortality rates.—When the logarithms of the fully adjusted survival numbers are plotted, as in figure 17, the series describes nearly straight lines over certain portions of its extent, indicating that in each of these straight-line segments, mortality must have proceeded at a uniform percental rate. The major feature to be noted is the break at about 35 days when the larvae are 10 mm. long. At this point there is a change of level and of slope which may be considered as dividing the curve into three portions: (1) egg, yolk-sac, and larval stages, (2) transition between larval and post-larval stages, and (3) post-larval stage. Each will be discussed separately.

The first portion representing stages up to 10 mm. in length is subject to alternative interpretations due to the nearly, but not wholly, linear arrangement of points. The simplest interpretation is that the mortality rate was uniform and that the deviations from linearity were due to defective sampling. If so, the single heavy straight line drawn from A to 9 mm. in figure 17 expresses the mortality. Accordingly, this mortality was at a constant rate, and amounted to 14 percent per day. On the other hand, it has been shown in the previous section that there is little ground for suspecting serious defects in sampling, and also that the slope of the line A to C differs significantly from that of the line 4 to 8 mm. This being true, the mortality rate would be better described by the three fine lines of figure 17, the one extending from A- to C-stage eggs; another from 4- to 8-mm. larvae; and still another joining their ends across the 3-mm. (yolk-sac) stage. According to this interpretation, the initial rate, i. e., the rate during the egg stage, was 5 percent per day. The next rate, i. e., during the yolk-sac stage, was 23 percent per day, and the third rate, i. e., during the larval stage, was 12 percent per day.[23] However, according to both interpretations, mortality has reduced the population to about one-tenth of its original numbers by the time the larvae reach 4 mm. long, and when they attain 9 mm. in length at 35 days of age, to one-thirtieth of the original number.

If any one period is to be singled out as the most critical, it must be the ensuing period during the transition from larval to post-larval stages, when in passing from 9 to 11 mm., the numbers are reduced by 90 percent in the short space of about 3 days. The rate of mortality may be variously computed, depending on the choice of straight lines in figure 17. The lowest is 30 percent, and the highest, 44 percent per day. Either of these rates is distinctly higher than the highest alternative estimate (23 percent per day) in the yolk-sac stage. The high mortality during this short period, coupled with the losses previous to this stage, reduced the survivors to only one three-hundredth of their original numbers; thus the population was already severely decimated on entering the post-larval stage.

During the post-larval stage, the rate of mortality apparently was more moderate than in earlier stages. The data on which the rates are based appear fairly reliable up to the 22-mm. stage, or 62 days of age, and the fitted line for the segment 11 to 22 mm. in figure 17 represents a mortality of slightly over 10 percent per day. Beyond 22 mm. the catches of larvae were few and were confined to only one cruise, so that the reliability of their relative numbers is in doubt; but the evidence, such as it is, points towards the continuation of the same rate of mortality to the size of 50 mm., or age of 85 days.

Restating the history of mortality, it appears that there was a general basic rate of 10 to 14 percent mortality per day throughout the period studied. The most important deviation from this general rate was during the 9- to 11-mm. stage, when the population suffered about 30 to 45 percent mortality per day. Other deviations

[23] Also, according to this interpretation, the data in the last column of table 7 should be taken as representing the number of survivors per 840,000 newly spawned eggs instead of per million, as given in the column heading.

of somewhat doubtful significance occurred during the egg stages, when a lower rate of 5 percent per day was indicated, and during the yolk-sac stage, when a higher rate of about 23 percent may have intervened. The net survival to the 22-mm. stage, or 62-day age, was 40 per million newly spawned eggs, and, assuming a continuation of the 11 to 22-mm. rate of mortality to the 50-mm. stage, or 85-day age, it was 4 per million newly spawned eggs.

Discussion.—Since it is probable that the success or failure of year classes is determined during early life, and since it is known that the year class of 1932 was a failure, it is natural to assume that the mortality curve just given represents the record of that failure. That this is true appears from the following considerations. From fecundity data (p. 156) it is estimated that a female spawns about 500,000 eggs per year, and from the size composition of the adult stock (unpublished notes) it may be estimated that each female spawns over an average period of about four years, producing a total of 2,000,000 eggs. Therefore, to keep the population constant, from 2,000,000 eggs, one female on the average should reach average spawning age; i.e., a survival of one fish per million. But in 1932 only four fish per million were left at the early age of three months. At this age, the rate of mortality was about 10 percent per day. Were this rate to continue only 35 days longer, the survivors would number only 0.1 per million; i.e., only 0.1 the number required to reach average spawning age. Of course, it should not be assumed that the 10 percent mortality would continue indefinitely. But even should it be as low as 2 percent per day, the year class would be reduced to the 0.1 per million level before the end of the first year of life; and even then they are at least 2 years removed from average spawning age. To reach that age with survival of one per million, mortality could not average more than 0.12 percent per day during the time intervening between 50 mm. and average spawning age. It is unreasonable to suppose that the mortality, last observed at 10 percent per day, could immediately drop to such a low rate and remain there. Hence it is likely that a year class, to be successful, must have a survival well above four per million at the 50-mm. size, and that the 1932 class was a failure because of the high mortality during stages preceding the 50-mm. length.

The causes of this failure may be sought in the record of mortality during the various stages. The outstanding feature in this record is that no single period could be considered crucial in the survival of the year class with which we are concerned. Mortality in all phases of development contributed substantially to the decimation of the population. This fact is most readily appreciated when the contribution to total mortality by the periods of relatively high rate is compared with the contributions by the periods of low rate. The mortalities in the yolk-sac stage and in the transition between larval and post-larval stages (taking the highest alternatives in each case) together represent the passage through 1.9 logarithmic phases. All the other stages together represent 3.6 logarithmic phases. Hence, one may say that about one-third of the mortality was suffered during the so-called "critical" stages, and the other two-thirds during what might be called "non-critical" stages.

The question naturally arises, which of these was in 1932 the determining factor in the failure of the year class? To answer the question calls for comparable data on mortality during the early life history of a successful year class. Lacking this, one can only speculate. If in 1932 the so-called critical stages were to have been eliminated, the survival to the 50-mm. point would have been 250 per million eggs spawned. If the so-called noncritical stages were to have been eliminated, it would have been 12,500 per million eggs spawned. Of course, it is difficult to conceive of complete

elimination of mortality from any of these stages, but if a year class is to be successful there is obviously greatest opportunity for improved survival in the noncritical stages, for they contributed most heavily to the failure of the year class. For this reason, one must look with at least as much suspicion on the mortality during non-critical stages as on the mortality during critical stages when in search for casual agencies that may have been operative during 1932.

In looking for such agencies, there are two features of the 1932 season that appeared to be unusual and of the sort likely to have affected survival. One of these was the relative paucity of zooplankton in the area of survey during the spring and early summer (i.e., May and June). The zooplankton catches averaged only 280 cc. per haul, as compared with 556 cc. in 1931 and 547 cc. in 1930 (Bigelow and Sears, 1939, p. 200). Both of the last named seasons produced good year classes, and there is, therefore, an indication of correlation between zooplankton abundance and the survival of a mackerel year class. If failure to survive in good numbers in 1932 was in fact due to dearth of food, and the dearth was continuous throughout the season

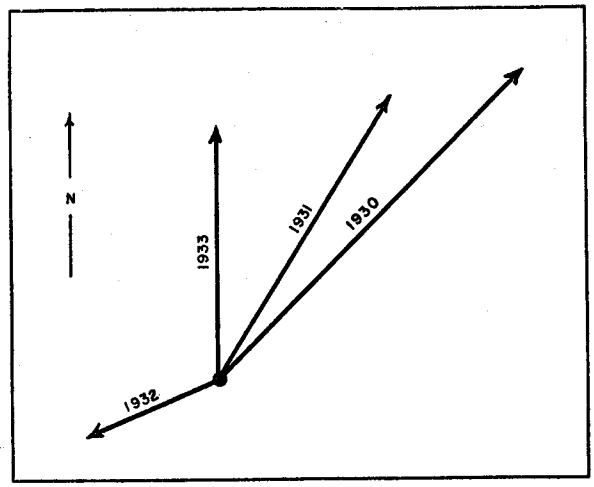


FIGURE 18.—Resultants of wind movement, as recorded at Winterquarter Lightship during May of each year 1930–1933.

of larval development, as the data indicate, it could easily affect the mortality through virtually all stages, for the smaller fish larvae probably feed on the young stages, and larger larvae on the adult stages of zooplankton forms.

The other distinctive feature was the prevalence of northeasterly winds during the period of larval development in 1932. Figure 18, in which are plotted the resultants of wind movement of force 3 Beaufort scale or higher, during May of each year, 1930–33, demonstrates how 1932 differed from the other years in having an excess of northeasterly over southwesterly winds. That this may well be related to the production of successful year classes is indicated by the fact that 3 years, 1930, 1931, and 1933, all with an excess of winds from the southwest, gave rise to successful year classes, while 1932, the only one with an excess from the northeast, failed to produce a successful year class [24] (Sette, 1938, p. 19).

Since the discovery of this relation between successful mackerel year classes and wind movement, similar phenomena have been reported for other fishes. Carruthers

[24] The wind directions in 1928 and 1929 were not consistent with this rule of correspondence of southwesterlies and successful year classes, but there were other unusual features of the year classes from these seasons and therefore consideration of them will be left to a subsequent paper of this series.

and Hodgson (1937) reported correspondence of relative success of six herring year classes and the strength of winds from certain quarters as inferred from pressure gradients; and Carruthers (1938) amplified these findings, presenting the relation for 11-year classes in the East Anglian herring fishery. He concluded: "It is reasonable to argue along these lines:—as from year to year, increased 'from-Channel' air flow means increased 'from-Channel' water flow, and this in turn means:—(1) That the passively drifting spawning products will be drifted farther afield—apparently a good survival augury for the herring * * *." In the same paper, Carruthers demonstrated the parallelism between changes in both certain pressure gradients and east wind component, on the one hand, and relative strength in a series of 15 haddock year classes on the other hand. These illustrations support the theory that local winds affect year-class survival. Though they demonstrate the importance of transport, the remainder of the survival (or mortality) mechanism, particularly its biological aspects, has yet to be elucidated.

For the mackerel of the American Atlantic seaboard, however, it is possible to advance a reasonable explanation for the connection between wind direction and survival. The center of spawning, it will be remembered, is southwest of Fire Island. The juvenile nursery grounds, judging from relative quantities of young mackerel usually found along various parts of the Atlantic seaboard, is along the coast of southern New England from Cape Ann to about the eastern end of Long Island. Therefore the prevalent southwest winds during May of 1930, 1931, and 1933 conveyed the larvae toward the nursery grounds. Conversely, the prevalently northeasterly winds of May 1932, on the average, were of hindrance rather than help to the larvae in reaching their nursery ground.

If this be true, there is the further probability that the significantly higher mortality in 1932 at the transition phase when fins were developing was a consequence of the pattern of drift in that year. The formation of fins and their subsequent use undoubtedly enlarged the expenditure of energy and hence increased the food requirement at the transition phase. At this time, on the average, the larvae were still distant from their nursery ground and if feeding was poorer where they were than on the nursery ground, the observed heightened mortality at this phase would thus be explained. Shortly after, by directional swimming, and with some assistance from favorable winds, some of the larvae did reach the presumedly more favorable location and thereafter were subject to a distinctly lower mortality rate.

Thus, there are evident two influences that contributed to the failure of the 1932 class. One was the general paucity of plankton, which probably increased mortality throughout the entire early life history; the other was the apparently unusual direction of their drift, which probably heightened mortality mainly during the transition from larval to post-larval stages. Though either one of these influences might conceivably have been the sole cause of the failure of the 1932 class, the shape of the survival curve suggests that both contributed substantially. Indeed, the two might be related to each other as well as to the mortality of the mackerel. To be sure, these are speculative conclusions. However, they furnish hypotheses that should be useful in planning further observations, especially in seasons of successful survival.

Significance of observed mortality in 1932.—Although one season's observations on one species of fish form a slender basis for generalizations, the fact that it is perhaps the only determination of mortality of a marine species under natural conditions gives special significance to the results, for it affords opportunity, for the first time, of comparing actual observations with theory.