BIOLOGY OF THE ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) OF NORTH AMERICA

PART II: MIGRATIONS AND HABITS

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The commercial catch of mackerel, *Scomber scombrus* Linnaeus 1758, along the Atlantic coast of North America has fluctuated widely (Sette and Needler 1934) owing to similarly wide changes either in abundance or in availability of the fish to fishermen. Since such fluctuations vitally affect both the fishery and the trade in its products, and also because they confuse the conservation problem, the United States Bureau of Fisheries (now a part of the Fish and Wildlife Service) in 1925 undertook an investigation of the causes of these fluctuations. The work involved not only studies of the fluctuations, but also of the many phases of life history and habits which had to be understood to interpret the observations of the changes in catch.

This report is one of several resulting from the mackerel investigations. In it there have been collected the facts that pertain to habits and migrations, particularly those that are pertinent to the understanding of changes in abundance or availability. The first number of this series of reports (Sette 1939) was on the early life history with special reference to mortality; others will be on age and rate of growth and on fluctuations in abundance.

In considering the subjects included in this paper it is necessary to draw on results which are to be reported later. This is particularly true with respect to the ages of certain size categories of mackerel. To a limited extent the data have appeared in preliminary reports (Sette 1931, 1932, 1933, and 1934) but for the most part the technical details are to be included in reports now in preparation and as yet unpublished.

ACCOUNT OF INVESTIGATIONS

The major conclusions of this report rest on the size composition of the mackerel population as determined from measurements of individual fish in thousands of samples drawn from the commercial catch at the principal ports of landing. The collection of data began in 1925 after part of that fishing season had elapsed. Much of the work in that year was preliminary in nature and not strictly comparable with subsequent observations. During the ensuing 10 years, 1926 to 1935, the program was carried out consistently so that data are comparable and the present report is confined to this period, except for the inclusion of certain data from tagging initiated in 1925.

The interviewing of fishermen for catch-date and locality and the sampling was done by Magnus I. Gregorsen in 1925, R. A. Nesbit in 1926, E. W. Bailey in 1927 and 1928, and by F. E. Firth in subsequent years. In many of the seasons R. A. Goffin contributed many samples from minor ports, principally Woods Hole, Mass., and also assisted in tagging experiments at that place.

Tagging of mackerel was recommended by the North American Council on Fishery Investigations and initiated under the supervision of Wm. C. Schroeder early in the 1925 mackerel fishing season, and after I undertook an investigation of the mackerel in all its phases during midseason of that year the tagging program was transferred to me. After completing the 1925 tagging season and upon comparing the size composition of the tagged fish with that of the samples taken from catches landed by mackerel vessels at Boston, it was obvious that the population from which the fish were drawn for tagging differed strikingly from the population upon which the vessel fishery was based.

This was not particularly surprising inasmuch as the tagging utilized fish from alongshore traps and pound nets whereas the vessel catch came mostly from offshore schools. Since the vessel catch was by far the major element in the mackerel fishery as a whole (Sette and Needler 1934: 14) and presumably consisted of fish that were representative of the main population whereas the trap and pound-net catch presumably represented an inshore fringe of the main population, it was considered unlikely that tagging returns would be representative of the migrations of the population as a whole, or even of a very important segment of the whole population.

It also became apparent by the end of the first season's tagging that the tags were injuring the fish, with unknown effects on their survival and their migratory pattern.

For these reasons the emphasis on tagging was shifted from large-scale releases to small-scale experimental work directed toward improvement of tags and exploring the possibilities of tagging fish from the offshore population. The details of these experiments, in which I was ably assisted by R. A. Goffin in getting and caring for the fish in captivity and by R. A. Nesbit in developing ideas for devising and testing various tags, are given in appendix B.

The Biological Board of Canada kindly furnished records of mackerel tagged in Canadian waters and recaptured off the United States coast.

In the meantime the major activity of the investigation, aimed at discovering the causes for fluctuations in the mackerel catch, including the interviewing of fishermen, the measuring of samples of their catch and the collecting of catch records suitable for abundance indices proceeded regularly. By 1935, partial analysis of these data appeared to afford insight into many phases of mackerel biology and it was decided to report upon the material accumulated up to the end of the 1935 season.

In studying this wealth of material I have had the able assistance of Mildred S. Moses in preparing tabulations and performing computations, the helpful counsel of Henry B. Bigelow, and the use of facilities at the Harvard Biological Laboratories.

In 1937 the study of this subject was interrupted by other duties and could not be resumed until 1947, with facilities at the Stanford University's School of Biology and with the counsel of Willis H. Rich, at whose suggestion and encouragement the investigation was originally started in 1925.

SYNOPSIS OF RESULTS

The mackerel is found in the western Atlantic from North Carolina to the Straits of Belle Isle and is sufficiently abundant for commercial fishing from the Chesapeake Capes on the south to the Magdalen Islands and the Gaspé Peninsula on the north. During the season of fishing it is most abundant in the open waters of the inner third or half of the continental shelf.

The mackerel appears in April near the southerly end of its range and by July is found from southern New England to the Gaspé coast. In September it begins to disappear from the most northerly regions and in December it vanishes from all places. During the summer season the smaller and younger sizes are usually found closer to the shore line than the adults.

When mackerel disappear in the fall they go southward and offshore to the zone of warm water which flanks the outer edge of the continental shelf and during wintertime occupy this relatively narrow strip of water running more or less parallel to shore, but some 20 to 100 miles distant from it, from Cape Hatteras northward surely to the southern edge of Georges Bank and possibly as far as Sable Island. While there they probably occupy middepths and so are seldom seen or caught. In this location their food supply probably is uncertain and may depend on local swarms of plankton whose occurrence is irregular.

The pronounced schooling habit of the mackerel is dependent on a special tropism involving vision, and hence schools may disband and reform according to diurnal variations in light. Luminescence probably is important in keeping schools together at night in the spring and fall. Schooling tends to be according to sizes, perhaps owing to a connection between size and swimming ability. This in turn is probably dependent on the ratio of volume to surface which of course increases with size of body.

During spring, summer, and fall, the mackerel stay in the warm surface layer of the ocean because they are prevented from descending below the thermocline by the comparatively low temperature of the underlying waters. Variation in availability to fishermen, depending as it does on sighting schools at the surface, is therefore probably dependent on the varying depth of the thermocline. Fishing is best moderately close to shore where in summer the thermocline lies only 15 to 20 meters (8 to 11 fathoms) deep, and, as a rule, poorer farther offshore where the thermocline may be as deep as 40 to 50 meters (22 to 27 fathoms).

Mackerel feed principally on plankton but the possibility that the larger individuals may in late summer subsist mainly on young fishes should be examined. Feeding is so much better in the summertime than in winter that the fat content of mackerel increases from a minimum in April to a maximum in August.

Two subdivisions are detectable in the western Atlantic mackerel population: A southern and a northern contingent which perform different spring migrations, occupy different areas in the summertime, and withdraw in the fall by different routes. The southern contingent comes from its offshore winter habitat toward the Virginia, Maryland, and New Jersey coasts in April, thence migrates northeastward to occupy the western part of the Gulf of Maine in summer. The northern contingent migrates toward the southern New England coast in May and thence goes northeastward to occupy the Gulf of St. Lawrence in summer. During the spring migration both contingents are joined by additional members of their kind which move from offshore directly toward the coast joining the main bodies as they pass along on their northeastward journey. For a short while in May both contingents are together in the area off southern New England, otherwise their courses are fairly independent. In the fall migration, both contingents approximately retrace their spring courses in returning to the winter habitat; but the northern contingent travels through more westerly waters in fall than in the spring, passing through the western part of the Gulf of Maine, and then disappearing off Cape Cod. The southern contingent, on the other hand, disappears, sometimes north of and sometimes west of Nantucket Shoals. The disappearance of both contingents north of the areas of their spring appearance may be due to their descent to deeper levels as the thermocline is lowered or obliterated by autumnal chilling.

DISTRIBUTION

RANGE

The mackerel is found on both sides of the Atlantic in the Northern Hemisphere, extending from the Mediterranean Sea to Norway in the eastern Atlantic and from North Carolina to Newfoundland in the western Atlantic. Since those of the eastern Atlantic are racially distinct from those on the western side (Garstang 1898), we need not consider them here.

The southernmost record on this side of the Atlantic is of two individuals taken in a pound net near Beaufort, N. C. The northern limit is the Strait of Belle Isle.[1] Reports of mackerel along the south and west coasts of Newfoundland are not uncommon, but occurrence seems not to be consistent enough to support a regular fishery for mackerel in Newfoundland. The region habitually occupied (in the fishing season) is from the Chesapeake Capes on the south to the Magdalen Islands and the Gaspé Peninsula in the Gulf of St. Lawrence on the north; in other words, between the thirty-seventh and forty-ninth parallels of north latitude.

Although the mackerel is distinctly an open-sea species, it is rarely found beyond the waters overlying the continental shelf; and while mackerel have been found at one time or another in the waters overlying the entire shelf, the greatest concentrations during the fishing season appear to be within its inner third or half. Often mackerel are found very close to the shore line, occasionally even inside of harbors and inner estuaries. Usually it is only the small sizes that are found in the semi-enclosed waters, the adults generally keeping to the open water, though they too enter some of the more or less open bays in the spring.

It is difficult, if not impossible, to determine whether the species is more abundant in the southern half of its range (that is, off the coast of the United States) than it is in the northern half of its range (that is, off the coast of Canada). Of the total annual catch along the North American coast in recent years, more than two-thirds have been taken off the coast of the United States and less than one-third off the coast of Canada; but this does not necessarily reflect the relative abundance, because the principal methods of fishing and also the intensity of fishing differ widely in the two countries. In the United States there is a fishery by pound nets and traps along shore, a minor offshore fishery using drift gill nets, and also a much more important offshore fishery using purse seines. In Canada fishing is confined almost entirely to pound nets, traps, and gill nets operated almost exclusively in inshore waters. It is likely that the international boundary, extended seaward, would divide the mackerel population into parts that are more nearly equal than total catch statistics indicate.

[1] Hearsay evidence cited by Goode, Collins, Earle, and Clark (1884: 3–4) of occurrence farther north along Labrador has yet to be confirmed by authentic records of capture.

SEASONAL CHANGES IN DISTRIBUTION

Along the Atlantic seaboard of North America the mackerel is a seasonal visitor, appearing in the spring, remaining during summer and autumn and then disappearing. Judging from the location of catches, mackerel appear first early in April about 30 to 40 miles offshore abreast of the coast line between Chesapeake and Delaware Capes. Soon they approach closer to the coast and during April and May they are found successively farther up coast until they reach southern New England. At this time or shortly afterward they also appear along the Nova Scotian coast. During the ensuing 2 to 4 weeks they disappear from the waters south of Cape Cod and spread throughout the western portions of the Gulf of Maine and the Maritime Provinces of Canada up to the Gaspé Peninsula, where they remain until sometime in September. During that month they begin to disappear from the most northerly region and withdrawal proceeds from north to south during October and November until finally in December they disappear from all coastal waters. These changes in distribution are charted, by months, in figure 2.

While the above description holds true for mackerel generally, there are differences that should be

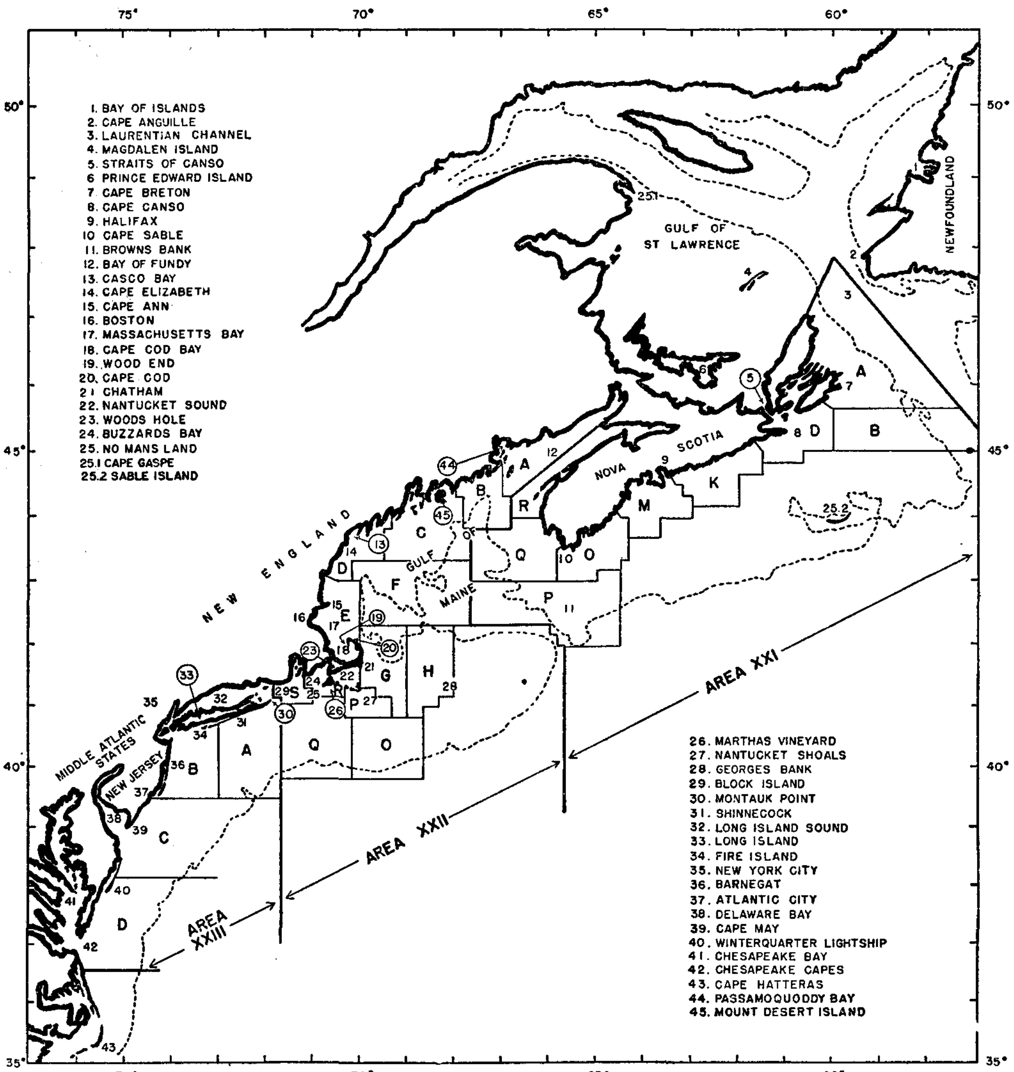

FIGURE 1.—Geographic features, landmarks, and delineation of statistical areas mentioned in this report. The statistical areas are those adopted by the North American Council on Fishery Investigations except for the lettered subareas of area XXVIII which were adopted for the purpose of this report, only, and have no official status. The broken line marks the 100-fathom contour.

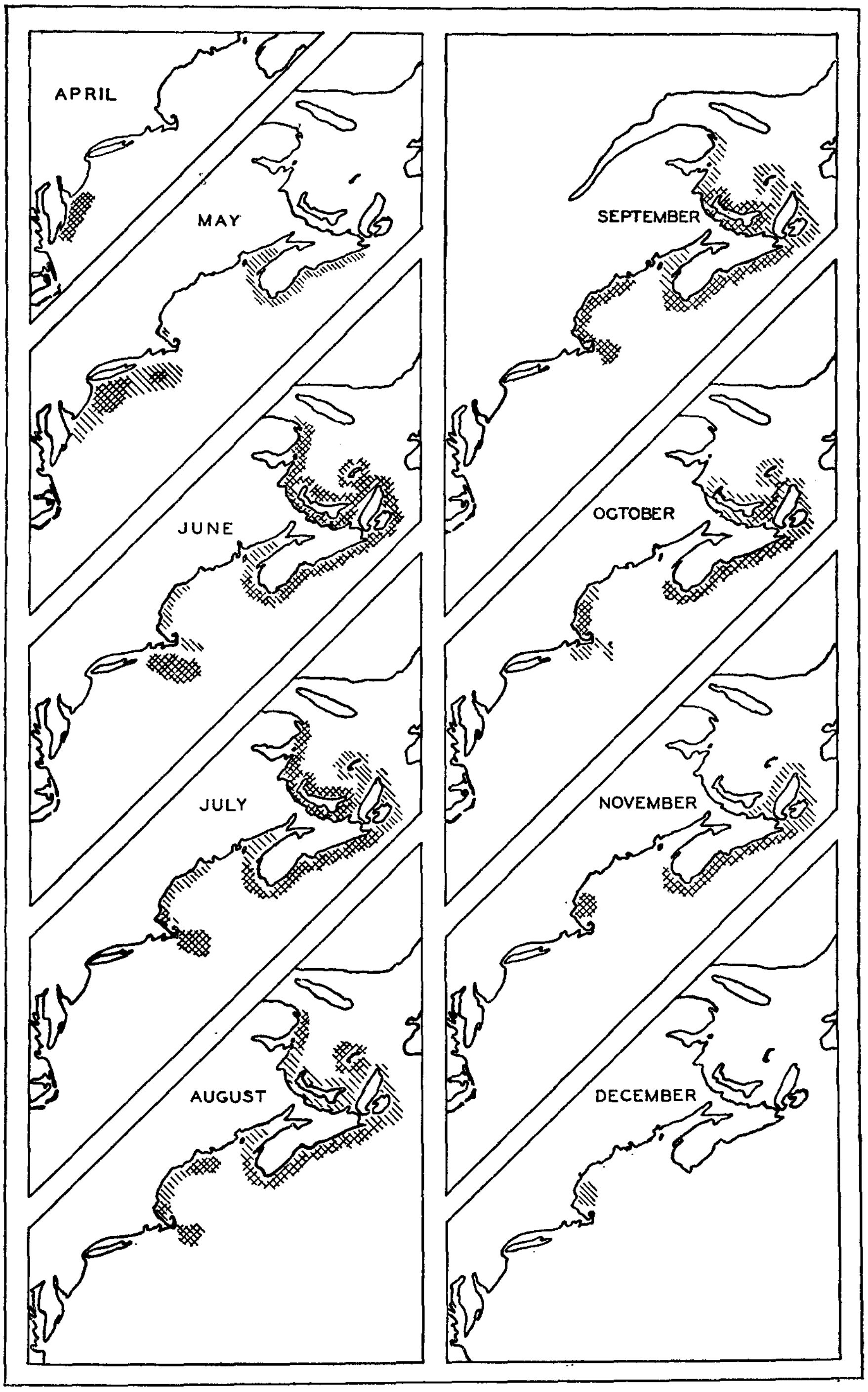

FIGURE 2.—Approximate seasonal distribution of the mackerel as indicated by location of the commercial fishery in the various months of the fishing season.

noted in the distribution of various size categories: (1) Juveniles, (2) yearlings, and (3) adults.

The juvenile sizes are fish from the current spawning season, hence less than a year old, and range from 2 inches up to about 8½ inches in length. Early in summer they are too small to be retained by the meshes of commercial nets, but toward late summer and fall, though not sought after, they are caught incidentally. To fishermen they are known as "tacks" and "spikes." Drift-gill-netters never take them in quantities, though we have an occasional sample of fish whose teeth caught in the twine of gill nets. Purse seiners usually avoid them because they plug the meshes of the seine, sometimes causing loss of gear. Some of the largest sizes of juveniles are, however, caught by purse seiners late in fall. Pound nets, traps, and weirs are the form of gear taking them most consistently. The schools of juveniles are deflected by the coarse-meshed leader of these forms of gear and turn offshore into the fine-meshed pound, where the smaller ones may be taken by dip net before they slip out through the meshes while the pound is hauled; the larger ones, of course, are retained through the hauling process and regularly form a part of the commercial catch. It is the catch by this form of gear that provides most of the information on distribution of juveniles. Due to the selective nature of fishermen's catches of those small sizes, the conclusions must be inferential.

Their distribution early in summer is probably determined largely by the location of the grounds on which they were spawned and on their subsequent drift from these grounds (Sette 1939: 83–191). In United States waters, they are found most consistently along the shore from Long Island to Cape Ann. The maximum concentrations appear along the southern shore of Massachusetts, though some have been occasionally taken along the coast of New Jersey and the coast of Maine. Doubtless, such as survive on the spawning grounds of the Gulf of St. Lawrence would be found along the shores of that Gulf, presumably mostly along its easterly portions, but published records of this are lacking.

Although the available records of occurrence are almost entirely from along the very shore line, this may be because there is no form of gear employed offshore which will catch the juveniles. Late fall catches of these sizes by purse seiners sometimes have been at a moderate distance from shore (up to 20 miles) and it is probable that large bodies of these small mackerel exist offshore as well as inshore.

In the inshore locations, the juvenile mackerel seem to stay all summer, into late fall and even early winter, catches of them having been made as late as December. From their distribution, there is little indication of any extensive migrations before their disappearance.

Yearling mackerel range from about 20 centimeters (8 inches) in the spring to about 35 centimeters (14 inches) in late fall. They are called "blinks" and "tinkers" by fishermen and in the trade. The term "blinks" is usually applied to the smaller ones, "tinkers" to the larger ones of this category.

During summer and fall, their distribution parallels that of the adults (p. 254) but their appearance in the spring is usually later than that of the adults. Occasionally schools are taken during the spring run of adults in both pound nets and purse seines (drift gill nets almost never take them at any season); but it is not until July and August that they are taken regularly in large numbers. From that time onward they are taken all along the coast from southern Massachusetts to Maine. Although samples of yearlings have been secured from Passamoquoddy Bay and from the vicinity of Halifax (Pennant, Nova Scotia), Dr. Cox found no "small" mackerel at the Magdalen Islands in 1925 (North American Council on Fishery Investigations, 1932, p. 27) and samples taken during this investigation from the catches of United States mackerel purse seiners fishing off the Nova Scotian coast have never contained yearling mackerel. It is likely that yearlings are much less abundant, as a rule, off Canada than off the United States. Like the juveniles and the adults, the yearlings disappear from coastal waters in late autumn and early winter.

The adult mackerel are known simply as mackerel by the fishermen, sometimes with the qualifying adjectives "medium" or "large." They are fish of 35 centimeters (14 inches) and upward and include all aged 2 years and older. They are the most desirable sizes and usually form the bulk of the catch. Their distribution corresponds with the general description at the beginning of this section.

WINTER HABITAT

LOCATION

Whence the mackerel come in the spring and whither they go in the autumn have been subjects of conjecture for many years. Bigelow and Welsh (1925: 197) surmised that they winter "on the upper part of the continental slope at a depth rather greater than the otter trawlers reach—say at 100 to 200 fathoms—but so close at hand that odd fish stray or remain on the banks." The present available data support this view as to the general winter location. It suggests, however, somewhat different conclusions as to the depths inhabited in the wintertime.

That the late autumn chilling of the water drives the mackerel from their customary summer haunts appears so obvious that most investigators have accepted this assumption as fact. It is true that the months during which the mackerel are absent are the coldest months of the year but there is no experimental evidence as to the minimum temperature that can be withstood by the species. As far as observational evidence is concerned, mackerel have been found in abundance in temperatures as low as 8° C. (fig. 14). They are often present in water of 7° C. in sufficient numbers to make commercial fishing profitable. Below this temperature they have been taken only as stragglers in American waters where there is record of one occurrence in water as cold as 4.5° C.[2] Thus it appears that the American mackerel prefers temperatures above 8° C., that it frequently tolerates temperatures down to 7° C., and that its toleration may extend to temperatures as low as 4.5° C.

This being true, the winter temperature in the northern portion of its range, that is in the Gulf of St. Lawrence and along the inner portions of the continental shelf of Nova Scotia where ice often forms in the wintertime, is certainly too low for this species. The inner parts of the Gulf of Maine with winter temperatures from 2° to 3° C. must also be too cold for mackerel. South of Cape Cod in cool winters when temperatures of 2° to 4° C. usually prevail over the inner half of the continental shelf, the mackerel should be normally absent; but there are instances such as the winter of 1932 (Bigelow 1933: 8–27) when water as warm as 7° C. persisted throughout the winter almost to the shore line and north nearly to New York. Obviously, temperature alone cannot explain the absence of mackerel from these waters during such exceptionally warm winters, and thus we may not assume their disappearance in the fall to be a simple direct response to temperature.

Yet it is reasonable to look for their winter habitat where temperatures approach those prevailing in their summer habitat. Waters with such temperatures flank the North American coast from 30 to 100 miles offshore, their inner border lying near the edge of the continental shelf where depths increase rapidly beyond the 100-fathom contour (fig. 3). It is not necessary to look farther than this, for mackerel have never been found south of Beaufort, N. C., or far enough beyond the continental shelf to indicate that they wander far out into truly oceanic waters.

The constancy in location and warmness of this flanking zone of water as a regular winter home for the mackerel is of particular significance. Although the temperatures of each profile in figure 3 pertain to only 1 year, it is highly probable that the warm zone has the same position year after year. This is certainly true along the continental edge between Cape Cod and Cape Hatteras. This region has been examined hydrographically in five different winters with very little variation except in the unusually warm winter of 1932. In that year nearly the entire continental shelf south of the middle of New Jersey was covered with water 7° C. or higher, but even then the temperatures at the edge of the shelf were very little different than in cold winters. Hydrographical surveys of the southern edge of Georges Bank in the winter have been less frequent, but examination of early spring conditions in 1929, 1930, and 1931 reveal no striking variations.[3] It may be assumed, therefore, that the mackerel can always find temperatures surely suited to its existence at one depth or another by moving offshore to about the continental edge along the southern part of Georges Bank or to the outer third of the continental shelf between Cape Cod and Cape Hatteras, and possibly suited to its existence along the edge of the Nova Scotian Banks. It remains to be seen what direct evidence there may be of the actual presence of mackerel in this warmer zone.

The occasional capture of mackerel incidental to the fishery for other species in the winter has been reported often in the literature. Goode, Collins,

[2] In European waters, large quantities have been taken by trawlers in northern parts of the North Sea, notably Great Fisher Bank, in the wintertime when 6° and 7° C. water prevails on those grounds, and in the English Channel where they are also trawled in the wintertime, the temperatures according to Bullen (1908: 284–285) are between 8° and 9° C. However, the European mackerel differs structurally from the American mackerel, sufficiently to be regarded as racially distinct, so it may be physiologically different as well. Hence, it is wise not to lay much stress on the evidence provided by the European representatives of the species.

[3] Unfortunately, there are no data on an extremely cold winter when it is possible that the warm zone may shift to a more offshore position. The disappearance of the tilefish in 1881 (Bigelow and Welsh 1925: 354) has been thought to have been caused by such a shift and if this supposition is correct, it must mean that the warm zone shifts far enough offshore so that it does not come into contact with the sea bottom at the continental edge. However, just as the tilefish disappearance may be taken as evidence of possible offshore shifting of the warm zone in severe winters, it also constitutes evidence that such shifts are extremely rare, for as far as is known this has happened only once during the past century. Even then it apparently had no effect upon the mackerel which may have been wintering on or near the tilefish grounds, for mackerel reappeared in normal numbers during the summer following the tilefish disappearance.

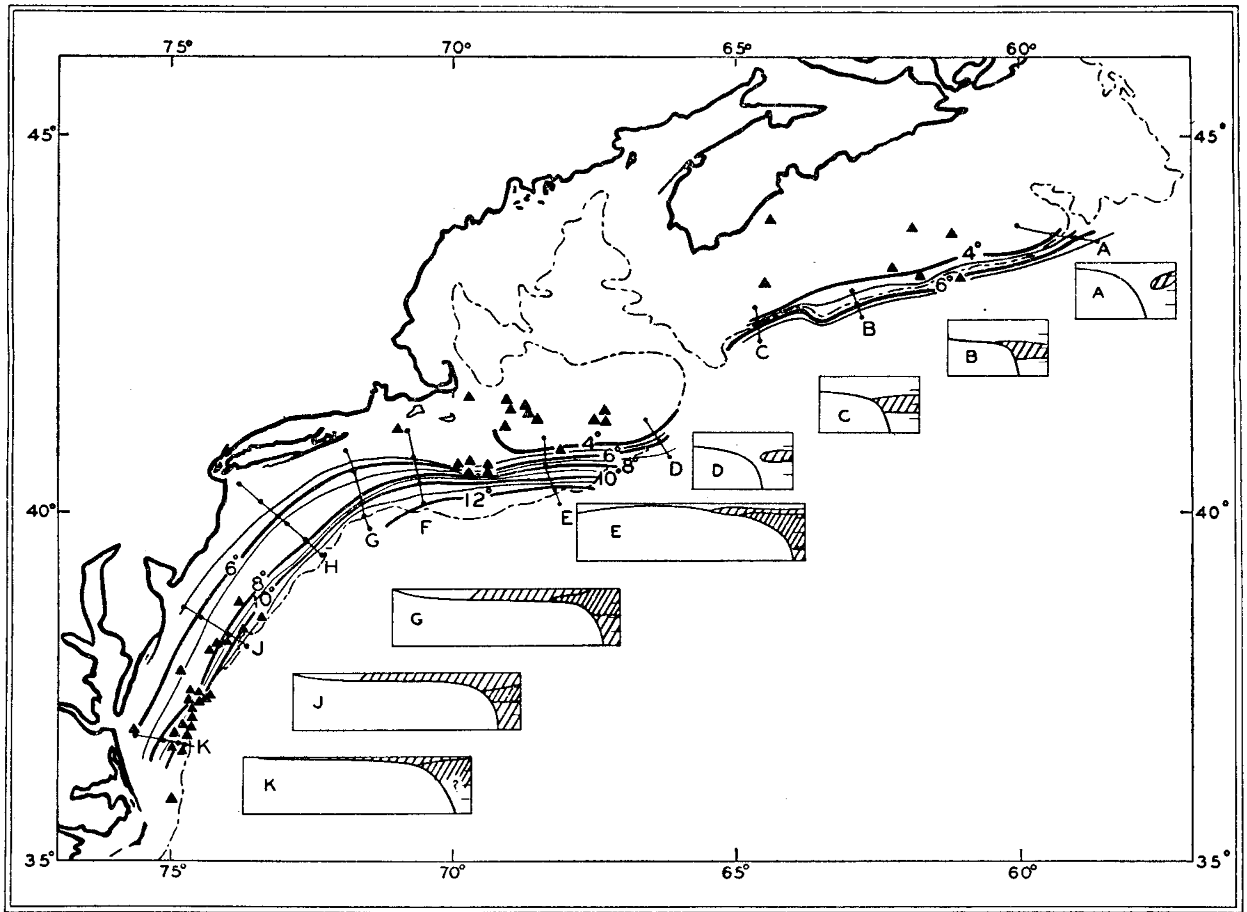

FIGURE 3.—Winter captures of mackerel (triangles) and winter temperatures. The isotherms mark the greatest inshore extension of water of designated temperature; insets A to D represent a width of 80 miles, E to K a width of 35 miles, and all represent depths of 400 meters (218 fathoms). Light shading designates temperature above 6° C. and heavy shading temperatures above 10° C. Sources of temperature data are: Section A, C. G. S. *Acadia* Stations V, 6–8–9–10, May 30, 1915 (Bjerkan 1919: 384). Sections B and C, *Atlantis* Stations 2510–11–12–15–16–17, March 6 and 15, 1936 (Bull. Hydrographique Cons. Perm. Internat. pour de l'Explor. de la Mer). Sections D and E, *Albatross II* Stations C20044–45–46–47–66–67–68–69, March 11–12 and 22–23, 1920 (U. S. Bureau of Fisheries Rept. 1921: 154, 160). Section F to K, *Albatross II* Stations 20618–19–20–21–22–23–24–25–26–28–29–30–31–32–34–35–36–37–40–41–42–43, Feb. 5–10, 1930 (Bigelow 1933: 113).

Earle, and Clark (1884: 98) list 7 or 8 taken in a gill net on Georges Bank on a January 3 or 4, a number taken by a schooner on Georges Bank, in March 1856, tinkers taken from the stomachs of cod, sometimes 5 or 6 from one fish, and used for bait on Georges Bank in February 1878; 30 caught on a trawl line set on Middle Bank in January 1868 or 1869, and "two fine fat fresh mackerel were found among the kelp at Green Cove on Friday, December 28, 1878," reported by the Yarmouth (Nova Scotia) Herald. Bigelow and Welsh (1925: 196) give additional instances of mackerel taken from cod stomachs on Georges and La Have Banks and off the coast of New Jersey in winter, also occasional catches by otter trawlers in the South Channel and on Georges Bank in February and March. Such records can now be augmented materially by instances that have accumulated during the course of the present investigations. These are listed in table 1, and their positions appear in figure 3.

TABLE 1.—*Winter records of mackerel*

Locality	Date	Depth (fathoms)	Quantity	Size	Remarks
In the offing of Nova Scotia:					
Western Bank, 50 to 100 miles west of Sable Island.	Jan. 9–16, 1931			12–15 centimeters	Lot of pollock containing a number of small mackerel.
Do	do		2	Large	
Do	do		Few	Small	
La Have Bank	Dec. 12, 1931		100 pounds		
Lat. 43°10′ N., long. 61°40′ W	Feb. 3, 1932	4–5	95 pounds	26.8–28.7 centimeters	
Lat. 43°50′ N., long. 61°50′ W; Lat. 43° 45′ N., long. 61°10′ W	Feb. 15, 1932	32–60	100 pounds	Tinker	
Lat. 43°05′ N., long. 64°25′ W	do	50–60	75–100 pounds	Small	
Lat. 43°20′–30′ N., long. 62°5′–15′ W	do	50–70	60 pounds		
Lat. 43°55′ N., long. 64°25′ W	Feb. 1, 1934	70	5	15–20 centimeters	Found alive in stomachs of hake and pollock.
Emerald Bank	Jan. 8, 1935	30–42	1	1½ pounds	
North of Emerald Bank	Feb. 14, 1935	53–55	Many	13–15 centimeters	
Lat. 43°15′ N., long. 61°00′ W	Mar. 13, 1935	50–60	35	About 2½ pounds	
Browns Bank	Mar. 28, 1935	60	1	41 centimeters	
In the offing of New England:					
Georges Bank	Jan. 18, 1929		36	Small	
Lat. 41°11′ N., long. 69°00′ W	Feb. 9, 1929	50	1	48.5 centimeters	Debris and mucus in stomach.
Do	do	50	3	Tinker	In stomach of a pollock.
60 miles southeast Highland Light	Mar. 12, 1929	70	1	44 centimeters	Stomach empty.
Do	do	70	6	Tinker	
7 miles south of South Shoal Lightship	Dec. 23, 1929		100 pounds	1½ pounds	
Southeast part of Georges Bank	Jan. 21, 1930	42	1	32.5 centimeters	Very thin.
90 miles southeast Highland Light	do	38	1	31 centimeters	Very thin; stomach empty.
80 miles southeast Highland Light	Mar. 31, 1930	36	1	30 centimeters	Very slender; much sand on gills, gill rakers, and mouth.
Southeast part of Georges	Jan. 10, 1931	27	1	21 centimeters	
Southeast ½ east Highland Light	Jan. 16, 1931	28–30	12	17.5–21 centimeters	
78 miles southeast ½ south Highland Light	Jan. 21, 1931	60	1	44.2 centimeters	Weighed 2 pounds in round condition.
Lat. 40°50′ N., long. 68°00′ W	Jan. 22, 1931		19	12–20 centimeters	In pollock; cod and haddock also eating them.
Southwest Georges	Mar. 25, 1931		40	Tinker	
Do	do		1	19 centimeters	In stomach of a haddock.
Georges Bank	Dec. 21, 1931		65 pounds		
Do	Jan. 1, 1932		1	Large	
Off South Shoal Lightship	Jan. 7–14, 1932		200 or 300	Mixed	Fishing boats report catching a number of mackerel of mixed sizes. 1 steamer got as many as 200 or 300.
Lat. 40°40′ N., long. 69°50′ W	Jan. 5–13, 1932		1		
Lat. 40°40′ N., long. 69°20′ W	do		174	17–40 centimeters	Temperature 4.5° C.
Lat. 40°30′–40′ N., long. 69°20′ W	do		66		
Lat. 40°40′ N., long. 69°20′ W	do		12		11 were in stomach of 1 pollock; 1 in stomach of another.
Lat. 41°35′ N., long. 69°40′ W	Feb. 15, 1932	60–75	35 pounds	Small	
Lat. 41°20′–30′ N., long. 68°30′–50′ W	do	70	12	Large	
Lat. 41°10′–30′ N., long. 69°00′–10′ W	do	45–60	About 6	Tinker	
		90	do	Large	
Georges Bank	do		About 50		
Do	Feb. 19, 1932			Large and tinker	A number of vessels caught mackerel both large and tinkers. A large school of large mackerel was sighted.
South Channel	Mar. 23, 1932		120 pounds		
Lat. 41°10′–20′ N., long. 67°10′–20° W	Dec. 3, 1932	26	1	31.6 centimeters	Temperature 10.5° C.
Lat. 41°10′–20′ N., long. 67°20′–30° W	do	27–31	18	17.1–20.3 centimeters	
Lat. 41°20′–30′ N., long. 67°10′–20′ W	Dec. 6, 1932	27	2	30.7 and 34.4 centimeters.	
Lat. 41°10′–20′ N., long. 67°10′–20′ W	Dec. 7, 1932	27	1	19.2 centimeters	
Nantucket Shoals	Dec. 12, 1932		290 pounds		
Do	Dec. 23, 1932		300 pounds		
20 miles southwest of No Man's Land	Dec. 5, 1934	29	50 pounds	All sizes	
Southeast part of Georges Bank	Jan. 9, 1935	35–45	4	Medium	
Lat. 40°41′ N., long. 69°40′ W	Dec. 3, 1935	27	51	14–24 centimeters	Temperature 7.3° C.
In the offing of the Middle Atlantic States:					
Lat. 38°13′ N., long. 73°49′ W	Mar. 2, 1931	52	9		In hake stomachs; 4 in 1, 3 in 1, and 2 in 1.
Do	do	52	1	Small	In hake stomach.
180 miles south of Cape May, 30 miles east of Bodie Island.	Mar. 10, 1931	30	1	25	
70 miles south ¼ west Winterquarter Lightship.	Mar. 17, 1931	57	1	10 centimeters	"Spike."
52 miles east by south Cape Charles	Feb. 2–3, 1932	43–59	6	Small	3 to pound.
45–50 miles east by south Chesapeake Lightship.	Feb. 13, 1932	42–46	3	Small	2 in hake stomachs.
65 miles east-northeast Chesapeake Lightship	Feb. 17, 1932	38–60	Several	Small	
45 miles east by south Chesapeake Lightship	Feb. 25, 1932	38–40	1	Small	
20 miles southeast Winterquarter Lightship	Apr. 7, 1932	35–40	18	25.5–42.5 centimeters	Thin and in poor flesh.
Lat. 36°50′–60′ N., long. 74°30′–40′ W	Jan. 4, 1933		1	44.5 centimeters	Very large and fat.
60 miles east by north ½ north, Chesapeake Lightship.	Jan. 12, 1933	45	1	30–35 centimeters	Large, in good condition, showed fatness.
40 miles east ½ south Chesapeake Lightship	Feb. 3, 1933	45	1	31.5 centimeters	Very thin. Crustacea and worms in stomach.
62 miles east-southeast Cape May	———, 1933	40	About 50	50 centimeters	Very large and fat. Stomachs crammed full of shrimplike crustacea 1 inch long.
50 miles east by south Chesapeake Lightship	Feb. 19, 1933	32	1	33 centimeters	Stomach partially filled with fragments of copepods, Euthemisto, and unidentified fragments.

TABLE 1.—*Winter records of mackerel*—Continued

Locality	Date	Depth (fathoms)	Quantity	Size	Remarks
In the offing of the Middle Atlantic States—Con.					
100 miles northeast by east Chesapeake Lightship.	Feb. 18, 1934	60	1	2 pounds	Thin.
58 miles east by north—east by north ½ north Chesapeake Lightship.	Mar. 3, 1934	51–60	3	37–45 centimeters	
45 miles east ½ north Chesapeake Lightship	Mar. 4, 1934	58	1	46 centimeters	
106 miles northeast by east Chesapeake Lightship.	Mar. 12, 1934	43–50	10 pounds		
70 miles east by north ½ north Chesapeake Lightship.	Mar. 23, 1934	60–65			Very thin.
63 miles east by north ½ north Chesapeake Lightship.	Mar. 28, 1934	55–63	7	29–39 centimeters	
65 miles east-southeast Five Fathom Lightship.	Feb. 8, 1935	58	20 pounds		
East-southeast Cape Henry	Feb. 14, 1935	90	2 tinkers, 1 large		
55 miles east by north Chesapeake Lightship	Mar. 2, 1935	55	11 pounds	29–44 centimeters	
100 miles southeast Cape May	Mar. 28, 1935		35 pounds	1–2 pounds	

The significance of these records must be weighed in relation to the distribution of fishing in the wintertime, for the lack of records from any particular area would be meaningless unless fishing took place in that area. Thus, the lack of winter catches along the southern edge of Georges Bank is due to the failure of fishermen to trawl there.[4] Similarly, the dearth of any winter records between the western portion of Georges Bank and the offing of Delaware Bay has no significance because no fishing takes place near the edge of the shelf in this sector during the wintertime. From about the offing of Delaware Bay to Cape Hatteras, on the contrary, numerous otter trawlers fish intensively during the entire winter along the continental edge and accordingly there are a number of instances in which mackerel were caught on these grounds. Thus, where fishing takes place in the warm zone in the wintertime, mackerel appear in the catch, and only portions of the warm zone that are not fished in the wintertime fail to contribute winter mackerel records.

There are, however, two features of this series of winter records that are contrary to the theory that the warm zone constitutes the winter habitat of mackerel. These are, first, the numerous specimens of mackerel taken on Georges Bank and along the coast of Nova Scotia considerably inshore of the warm zone and in water that presumably was much colder than is considered suitable for mackerel, and secondly, that even in the sector between the offing of Delaware Bay and Cape Hatteras where mackerel have been taken by otter trawlers, the numbers encountered are so very few that they cannot be taken as representing the main body of the mackerel population.

Since it is hardly likely that there are warm pools or lateral extensions of warm water along the bottom on Georges Bank (hydrographers have never encountered them), the records of mackerel well up on the bank must be accepted as evidence of their presence in rather cold water; indeed one of the catches was made in water that tested 4.5° C. at the time. Either our notions of the temperatures tolerated by mackerel are erroneous, or for brief periods of time small groups may stray away from the main population. That these records of stray mackerel exist is more likely owing to the thoroughness with which the waters there are dredged by the trawlers rather than to the occurrence of quantities of mackerel.

Winter catches of mackerel in the sector in the offing of the Middle Atlantic coast between Delaware Bay and Cape Hatteras nearly all fall within the warm zone at the continental edge as might be expected. Although their location agrees well with the theory set forth above, the number of records and the quantities of fish taken are far too low for a region supposed to harbor the main bodies of mackerel in the wintertime and where winter trawling is intensively practiced. This can hardly be attributed to deficiencies of the otter trawl as a means of catching mackerel for mackerel are regularly taken by trawl in the wintertime along the slope of the North Sea plateau toward the Norwegian Channel and in the English Channel. Hence it must be concluded that the American mackerel are not concentrated near bottom in the wintertime.

It is also apparent that mackerel are not at the surface in the wintertime as has often been remarked upon in the literature. Exceptional reports of the

[4] During the period 1931–33 the location of fishing during each trawler trip was ascertained in connection with the Bureau of Fisheries investigation of the haddock fishery. Among the thousands of fishing locations which were recorded only one fell within the area bounded by the 6° C. isotherm and the edge of the bank.

sighting of such schools as have appeared in the literature may be discounted (Bigelow and Welsh 1925: 196) on the basis that the reports are not authenticated by specimens from such schools, the inference being that some other scombroid or even clupeoid species was concerned. Furthermore, mackerel fishermen often have striven to extend the fishing season by searching for fish earlier in the spring and later in the fall than the regular season. During the 10 years of this investigation when the activities of the mackerel fleet were under close observation, seiners have scouted in early spring farther to the south and farther offshore than the area in which the first catches are customarily made. In the fall also, they have often persisted in looking for mackerel some weeks after the final catches were made, and although such searches extended farther offshore and farther southward than the ordinary range of the fishery, they have been in vain.[5] Then too, the trawlers that frequent the warm zone in the offing of the Chesapeake Capes each winter would surely recognize mackerel schools if they saw any, for these same fishermen, as a rule, engage in mackerel fishing in the summertime and would not only be quick to report any schools sighted in the wintertime but also would very likely outfit for seining and try to catch them, for the winter prices would make the fishery quite lucrative if considerable quantities could be caught. Hence it must be concluded that mackerel in disappearing in the fall, sink below the surface [6] and if they reappear at the surface subsequently, it is only for short periods of time and at infrequent intervals.

In summary, it may be concluded that the winter home of the mackerel is in the warm zone along the continental edge from Cape Hatteras to the middle of the southern edge of Georges Bank, for here the water is surely warm enough and enough stragglers have been taken to indicate that the main population is nearby. It may possibly extend even as far to the northeast as the offing of Sable Island, for 6° C. water extends that far and stragglers have often been taken on the Nova Scotian banks in the wintertime. Although present in this zone of warm water, they do not regularly appear at the surface nor do they stay close to the bottom. In all probability they are in middepths, perhaps above rather than below about 100 fathoms. Whether their schooling habits are preserved in the wintertime or whether the individuals are widely scattered, must remain a mystery probably until means of fishing the middepths have been devised.

PROBABLE CONDITIONS OF EXISTENCE IN THE WINTERTIME

Whether or not food is of any consequence to the mackerel in wintertime is called into question by early theories of hibernation of the mackerel which include such fanciful suppositions as inspired the statement of a French Admiral whom Ehrenbaum (1914: 10) quotes as declaring that "his men had seen thousands of mackerel in the bays of the Greenland coast in the spring, the fish having buried their heads in the mud, and hibernating in that position, as a result of which they became blind, and were thus very easily caught." Needless to say, such evidence of the mackerel's food requirements in the wintertime need not be taken seriously, since mackerel are now known not to inhabit Greenland waters; but Ehrenbaum, whose extensive study of this species entitles his views to great respect was not convinced that the European mackerel may not be in at least semihibernation during the wintertime, for he stated (1914: 13):

> There is thus no longer any doubt that the mackerel at certain seasons of the year seek the bottom, and the lower water layers, and although they do not appear to spend the whole of this period in passive hibernation, but rather to be, at times, eager for food, it is nevertheless highly probable that they hibernate for a part of their stay at the bottom, viz, from November to January, when, according to the observations of Irish investigators, as also my own, the taking of food is as a rule suspended. During this time, the stomachs of mackerel taken with the trawl are found to be entirely empty, and not until February and March do we find a slowly increasing percentage of fish containing food.

Bigelow and Welsh (1925: 197), commenting on Ehrenbaum's view of mackerel hibernation, say:

> It is not likely, however, that the American mackerel do so, though they may be semitorpid or at least very sluggish during the cold season, the presence of mackerel in the stomachs of other fish as well as the fact that they sometimes have food in their own stomachs in midwinter, proving that they move about more or less even then, though they certainly feed very little, for not only

[5] In December of 1932, for instance, schools of mackerel were reported from the easterly portions of Georges Bank and at least one seiner cruised to these grounds but failed to find the mackerel. Again in December 1933, the schooner *Old Glory*, Capt. Frank Foote, sailed to the southerly offshore grounds for mackerel and although a school was sighted 25 miles southeast of Fire Island Lightship, deficiency of the gear prevented a catch, and when the vessel reoutfitted and returned some days later, no mackerel schools were to be found.

[6] A bit of experimental evidence on this point is afforded by the action of mackerel held in a large outdoor pool at Woods Hole in 1932. These frequently were schooling at the surface during summer months but toward the end of September when the water cooled they stayed well below the surface and even when food was thrown on the water, appeared reluctant to rise to the surface as formerly was their habit. Unfortunately, the occurrence of a heavy rain flooding the harbor and making the water markedly turbid at this time leads to uncertainty as to whether turbidity, decrease in salinity, or lower temperatures caused the change in habit.

are most of the European fish trawled at that season empty, but European and American mackerel alike are thin when they reappear in the spring.

I agree with Bigelow and Welsh that there must be some feeding activity in the wintertime. If, as is supposed, mackerel at this season are at mid-depths, some activity would be required and some energy consumed in maintaining this position. That some of the needed energy is acquired currently by feeding is indicated by the food in the stomachs reported by Bigelow and Welsh, and observed by F. E. Firth during the present investigations. That they fare less well in winter than in summer and are forced to draw on stored energy, is proved by the low average fat content in early spring (p. 268). It also appears that not all portions of the population are equally successful (or unsuccessful) in obtaining food in the wintertime, for of the winter-caught specimens that came to the hands of F. E. Firth during the course of the present investigation, some were fat and some were lean. This suggests that food is not distributed uniformly, or that the concentrations of mackerel and of mackerel food do not always coincide.

What little is known about plankton (the principal food of mackerel) is consistent with the view that food is generally scarce in this area in the winter and that it may be spotty. In the Gulf of Maine, Bigelow (1928: 190–191) found *Calanus finmarchicus* (the dominant plankton species of the region and the most important food organism for mackerel) so scarce in February and March (1920) as to yield hauls of only 3,900 per square meter on the average. Whereas in May and June (1915) the average for all stations was 86,000 per square meter. Thus, in the Gulf of Maine, the winter populations of *Calanus finmarchicus* appeared to be less than one-twentieth as large as the summer population. On the continental shelf between Cape Cod and Chesapeake Bay, this copepod is also very scarce in the wintertime. Bigelow and Sears (1939: 306) found tow-net catches to be only one-eighteenth as large in February as in April 1930, and only one-twentieth-ninth, one-ninth, and one-tenth as large in February as in May of 1930, 1931, and 1932, respectively.

Not only is there a general scarcity of plankton in the wintertime, but the waters at the outer edge of the continental shelf where the mackerel are supposed to winter, have as little plankton as the waters farther inshore, and south of Cape Cod, even less. However, among all the plankton tows taken along the edge, both by Bigelow and by ourselves, there was one at the southern edge of Georges Bank that yielded 103,000 *Calanus* per square meter (Bigelow 1926: 190–191) which is an abundance comparable to spring or early summer in the Gulf of Maine. Bigelow regarded this as a local swarm. Towings along the continental shelf in the wintertime have neither been closely enough spaced to indicate how many such swarms exist at a given time nor have they been made at enough different times during winter to prove or disprove their existence as a characteristic winter phenomenon. Their occasional occurrence, suggested by the catch at the southern edge of Georges Bank, would not only enhance the suitability to mackerel of continental edge waters in the wintertime but would also account for the fatness of some winter-caught mackerel despite the leanness of most.

SCHOOLING HABITS

MECHANISM OF SCHOOLING

One of the most characteristic habits of the mackerel is its tendency to associate in dense schools. On the basis of observations and experiments principally on *Pneumatophorus grex*, a related species of similar schooling habit, Parr (1927) evolved the theory that the school is maintained by simple reactions which "may be regarded as automatically controlled by a special kind of tropism giving responses of approach and adjustment of direction to the stimulus of a perceived prospective companion." That perception is by visual means appears adequately proved by Parr's observations and experiments and has particular significance in connection with the formation and stability of schools.

As Parr pointed out, if the aggregation into schools depends on vision, it should take place during the daytime and the schools should be broken down during every sufficiently dark night. If this is true, the nightly reshuffling of individuals should tend to keep the population homogeneously mixed. At certain seasons, however, the break-down of schools obviously does not take place at night, for purse seiners locate and catch schooled mackerel at night both in the springtime and in autumn. At these seasons the schools are located by the luminescence which is associated with them. This occurrence of schools at night need not be contrary to Parr's theory, for obviously the luminescence may be as effective as daylight in permitting the visual perception necessary for schooling. However, there should be a tendency toward greater permanence of schools in spring and autumn, which might be reflected in greater divergence between schools in respect to certain characters such as size-composition. This has not been so obvious for me to have noted it, but admittedly the data have not been collected or analyzed in a way which would be adequate to demonstrate this point.[7]

ADVANTAGES OF THE SCHOOLING HABIT

In addition to his inquiry as to the method in which the schools are maintained, Parr (1927: 31) discussed the usefulness to the species of the schooling habit, pointing out that if individuals of a much preyed-upon species like sprat or herring traveled around separately, "scarcely a single one of them would escape the enemies sufficiently long to be able to propagate, while the occurrence of a great number of specimens united in schools among scattered enemies may give a certain percentage a chance to survive and continue the existence of the species." This, however, overlooks the fact that the enemies of schooling fish often are banded together and thus tend to overcome this advantage of their prey.

In view of this, it appears to me more reasonable to suppose that the advantage of schooling, if any, would lie in the increased ability to capture prey rather than to elude predators. This is suggested by observation on the feeding activity of mackerel held in confinement in an outdoor pool open to tidal circulation (p. 352). When food was offered to these mackerel in the form of ground squid or fish, i. e., in relatively large particles compared with plankton, the mackerel darted toward certain particles and secured them individually. When feeding thus the schooling habit was broken down and although the individuals congregated in the vicinity of food their actions were not coordinated. On the other hand, when not so—feeding, the mackerel collected in a definite school coursing around the pool in a fair degree of unison though even at such times their actions were less concerted than when feeding on plankton. Such feeding took place very close to the surface, usually in calm weather and often in the early morning or late evening. At least it was most easily observed at such times.

When feeding on plankton the mackerel assembled in a much more compact school than at other times. The school swam in a path describing a small circle or ellipse perhaps 8 or 10 feet in diameter and lying in an inclined plane, the upper limb of the ellipse touching the surface, the lower limb about 2 or 3 feet deep. On the descending segment the individuals swam vigorously, perhaps at twice the speed customary in coursing movements, obviously getting up speed. As they returned up the ascending segment of the ellipse, they opened their mouths to the fullest extent and extended their operculums widely, obviously to pass the maximum of water past the gill rakers. In this condition the school formed a group of miniature tow-nets spaced hardly more than their own diameter apart. If it be supposed that copepods (the principal element in their diet) are capable of darting 1 or several centimeters at a time through the water, as observation indicates they do, they might elude one such miniature tow-net; but with a group of miniature tow-nets as closely spaced as these, the success of a copepod in eluding one of them would frequently only put it in the path of another. Thus mackerel, acting in concert probably would average more copepods each than if they acted individually.

This theory supposes that the copepods and other planktonic food organisms are capable of detecting a mackerel at a small distance, and it needs support from critical experiments or observations indicating the sensory ability of a copepod in such a situation. If they do not possess this faculty the individual mackerel would be at no disadvantage as compared with a school in catching copepods.

Despite the lack of proof that schooling is an advantage in plankton feeding, there is strong indication that schooling is related to this method of feeding in the fact that schooling is so prevalent among species whose principal food is plankton. Furthermore, those schooling fishes (bluefish, tuna, bonito) which do not subsist primarily on plankton, feed instead mainly upon schooling fish, crustacea or cephalopods (menhaden, herring, sardines, euphausids, squid). Here the relation of predator to prey is essentially similar, i. e., a menhaden eluding one bluefish would be in the path of another, if the bluefish were in schools.

[7] To do this would require that each sample be sufficiently large to describe the size (or age) composition of a school. With limited resources it seemed better to take small samples from each of many catches (schools) rather than larger samples from fewer catches (schools). However, even these small samples might yield information if studied by statistical methods developed for quality control (Shewhart 1931).

SCHOOLING ACCORDING TO SIZE

A further feature of schooling, significant to the study of age composition, is the tendency of individuals of the same size to school together. Fish of the year, as far as we know, always school separately from the rest. Yearlings usually do, but, judging from samples, may sometimes join schools of adults, especially when the latter are predominately in their third year. The adults—third-year fish and upwards—seem not to separate themselves according to age or size in any sharply defined manner. Nevertheless there is often enough difference in the size distribution among samples from different catches to suggest some tendency of mackerel in a given size range to band together in schools distinct from those of another but overlapping range.

A physical explanation of the tendency for mackerel of different sizes to form separate schools is suggested by the activities of fish whose swimming was timed as they circled around the live car in which they were enclosed. Among several dozen mackerel thus observed together, there were two yearlings, while the remainder were of juvenile size. The juvenile mackerel schooled together traveling in circuits around the enclosure at the rate of 10 feet per second and keeping in the middle or upper levels. The two yearling mackerel traveled in company with each other around the enclosure at the rate of 19 feet per second, i. e., distinctly faster than the small ones, always keeping below the small ones, sometimes circling in the same direction, sometimes in the opposite.

There is a simple explanation for this difference in speed if the work performed by the mackerel is proportional to its weight and if it serves mainly to overcome friction between water and the surface of the fish.[8] Then large fish should move faster through the water because the weight of musculature increases as a cube of length and the area of the surface only as the square. So, with less surface friction to overcome per gram of muscle in large fish than in small the "cruising" speed of the former should exceed the latter for a given output of energy per unit weight of muscle.

[8] The work done in displacing water as the mackerel moves should increase in proportion with the weight, if stream-lining is equally efficient in all sizes. But since musculature is also proportional to the weight, the expenditure of the same amount of energy per unit weight at a given speed should accomplish the displacement of water for small as well as large fishes. Therefore, the work of displacing water should not differentially affect the speed of small as compare with large fishes.

Moreover, there probably are lower and upper limits on swimming speed imposed by the inherent capacity of the mackerel's physiological processes and these are reinforced or perhaps even narrowed by special features of the physiological and physical systems involved in the mackerel's swimming.

For instance, a lower limit on swimming speed is imposed by the mackerel's respiratory requirements. F. G. Hall (1930) found that the mackerel depends on swimming to produce sufficient flow of water past its gills for its respiration. This no doubt accounts for the generally observed facts (1) that mackerel are always swimming and never at rest and (2) that when the scope of swimming movements is restricted by putting them into small aquaria they soon die. Thus there must be a certain limit below which the swimming may not fall without disequilibrium between respiration and metabolic requirements. Although the existence of such a lower limit was established by Hall's experimental demonstration that respiration of the mackerel depended on swimming, he neither located this limit nor determined whether or not it varied as a function of size.

An upper limit would be imposed by the amount of energy the mackerel may expend in swimming without causing disequilibrium in its metabolic system. If resistance to passage of a mackerel through the water depends not only on its surface-volume ratio but also is a function of speed such that the resistance increases more than proportionally with speed, then the upper limit would tend to be sharpened. An inordinate amount of energy would be required to swim even moderately faster than that point at which the energy expended on swimming is currently replenished and exhaustion would quickly ensue.

Obviously the swimming rate is dependent on a number of physical and physiological interactions and my single set of observations on the swimming rates of the two sizes of mackerel is hardly sufficient to prove that the rate is dependent primarily on size. Indeed the considerable range in sizes of individual fish found in a single school argues against it.

With speed directly dependent on size one might expect the sorting, by sizes, to be fairly precise, for each size of fish would have a particular speed differing from that of other sizes, and only fish of one size could stay together. Actually, rather diverse sizes are found in the same school. This can occur if the smaller fish put forth relatively more exertion than the larger ones. This probably takes place within a moderate size range. The size composition in a school perhaps is in a state of dynamic equilibrium where the tropistic tendency for aggregation causing uniform speed is opposed to the physical tendency toward different swimming speeds. Within certain size ranges the former tends to keep the individuals together, while the latter tends to separate them. This would produce the effect observed: that mackerel school together according to size but that schools contain individuals of enough diversity in sizes to provide extensive overlapping in the size range.

VERTICAL DISTRIBUTION

The American mackerel is generally regarded as a surface fish because practically all of the catch is taken at or near the sea surface. But at times some of them are on bottom for they are occasionally taken by trawlers in autumn and winter, and it cannot be assumed *a priori* that they may not also inhabit intermediate depths. It has already been indicated (p. 261) that in winter most of the mackerel probably inhabit mid-depths. What their lowermost limit is in summer must be determined by indirect means, for gear that is effective in mid-depths has yet to be developed.

Bigelow and Welsh (1925: 195) were of the opinion that "there is no reason to suppose that they ever descend more than a few fathoms during their [summer] stay, the supply of small crustaceans on which they feed being invariably richer above than below 50 fathoms depth in the Gulf of Maine." The vertical gradient of temperature in the summertime, in my opinion, affords additional reason to suppose that they stay in the upper levels and that the temperature influence would tend to keep them even nearer the surface than 50 fathoms, which, after all, is a considerable depth from the standpoint of fishermen using surface gear such as the purse seine.

Temperatures in the western part of the Gulf of Maine during July 1932 (fig. 4) prove the existence of a very pronounced thermocline in the region where mackerel were being caught at the time. At a typical station (A) the temperature was 16° C. (60° F.) at the surface and at 10 meters, but fell to 8° C. (46° F.) at 20 meters, and to 6° C. (42° F.) at 30 meters. Although other stations varied from this in detail, all had temperatures above 13° C. (55° F.) at the surface and all had temperatures below 7° C. (45° F.) at the 30-meter level. At most of them the temperature gradient crossed the 7° C. line near the 20-meter level.

While mackerel have been found in temperatures as low as 4° or 5° C., it is not likely that they would voluntarily enter or stay in water of temperatures lower than 7° or 8° C., for they are rarely found in surface waters as cold as this and only in the wintertime have they been found at any level in lower temperatures. Hence it is likely that the thermocline in the summertime forms a barrier or floor, constituting a lower limit of depth-range.

This floor may move up and down during the season; and its depth varies from place to place. It is formed by the warming of surface layers in the spring and summer and destroyed by their chilling in autumn. During the season when it is in existence, stormy periods lower it and calm warm periods raise it. It tends to be higher in inshore areas and lower in offshore areas; but vertical turbulence, which may attend currents or be induced by storms, modifies this rule. Judging from such few of the temperatures given by Bigelow (1926: 978–997) as are pertinent,[9] the 20-meter level shown in figure 4 is fairly typical for the western part of the Gulf of Maine in early summer. Later in the season and farther offshore the thermocline tends to be deeper, perhaps with 40 or 50 meters as the lower limit. The probability that the mackerel are located at levels too deep to show at the surface in offshore waters where the thermocline lies deeper may explain the dearth of catches (p. 297) from over the central deeps of the Gulf of Maine. However, it is also possible that they seldom occur at any depth in that area.

In summary, it appears that the vertical range of the mackerel is limited by temperature. During the height of the fishing season and throughout the major portion of the fishing area, they must be kept within 15 to 20 meters (8 to 11 fathoms) of the surface. At certain times and places they are free to descend to greater depths, but probably not much below 40 or 50 meters (22 to 27 fathoms) and usually not that deep.

From the standpoint of studying fluctuations in abundance and age composition, the additional question arises: Does their vertical distribution render all of the mackerel accessible to fishermen at all times during the summer, or only part of them

[9] Unfortunately, most of the serial temperatures did not include observations between the surface and 40–50 meters, hence, do not fix the position of the thermocline except to indicate that it was above rather than below 50 meters

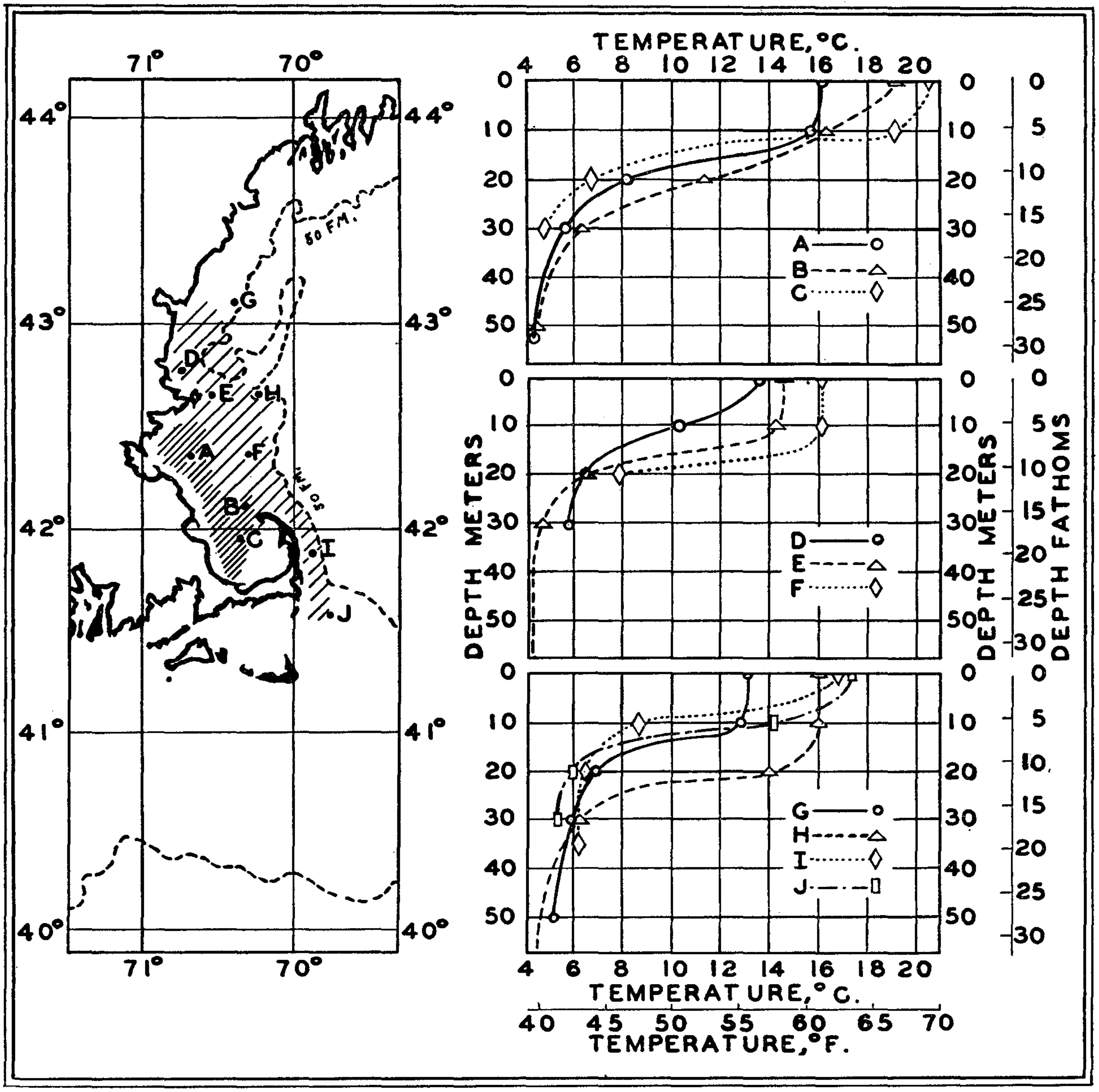

FIGURE 4.—Temperature gradients (vertical) in mackerel fishing waters. At the left are shown the areas where many catches were made (heavy shading), the areas where few were made (lighter shading), and the places where the temperatures were taken (lettered dots). On the right are the temperature gradient curves for each of the lettered positions. The catch data refer to the period, July 16–31, 1932, and the temperatures were taken July 22 and 23, 1932.

part of the time? Purse seines of ordinary size reach down to 20 fathoms, but their effectiveness depends not only on how deep they reach but also on how deep the schools can be seen and thus located before the seine is set.

In the daytime the schools are betrayed by a rippling of the water if they are at the surface, or by dark, shadowy, and sometimes reddish patches in the water if they are somewhat below the surface. How deep they may be detected depends on the height of the observer above the water, the quality of illumination, the roughness of the sea surface, the turbidity of the water, the keenness of vision and the alertness of the observer. Thus the depth at which they can be located is highly variable and not readily ascertained. It is reasonable to believe that it seldom exceeds 10 fathoms and is usually less than that in the daytime.

On moonless nights, when the schools are visible as a luminescent patch in the water, it is probable that they can be seen at greater depths, because there is no interference from surface reflection. One instance illustrating the depth to which such luminescence is visible was reported by F. E. Firth in a letter written April 16, 1935, as follows: "Several, about 7, vessels went out Friday noon and returned Saturday P. M. without success." Captain Firth stated, "Saw a school firing deep in the water, made a set, pursed seine, got nothing, and the fish were still visible under the seine." He said, "the fish must have been down 25 fathoms, for his seine reaches down 22 fathoms. Water firing exceptionally well." This was, undoubtedly, an instance of remarkably good visibility. There is considerable variation in how well "the water fires"—to use fishermen's parlance—hence it cannot be expected that schools would always be seen at such great depths. It seems reasonable, however, to suppose that they can usually be seen down to a depth of 10 fathoms during night fishing.

Taking these considerations together, it is probable that the fishery is effective throughout the vertical range of the species only when favorable visibility coincides with a shoal thermocline. At other times, which must be frequent, a substantial portion of the mackerel population is inaccessible to the fishery on account of poor visibility, or because the fish are too deep, or combinations of these two impediments to the sighting of schools.

Although it is not possible to express the effect of vertical distribution quantitatively, it is obvious that the variations in the success of fishing may be modified considerably by the shifting up and down of the thermocline. When it is close to the surface, say within 10 fathoms, fishing should be good because nearly all of the population should be within vertical range of the fishing method. Unfortunately, serial temperature records are inadequate for determining the correlation between position of the thermocline and success of the fishery, but perhaps it is significant that fishing is less uniformly successful in spring and fall (when the thermocline is less well-defined) than in summer, and that even when fishermen sight mackerel in offshore waters where the thermocline is deeper it is only rarely that good catches are made there regularly over extended periods of time. The bathythermograph, developed after the close of this investigation, offers a new instrument for examining vertical temperature gradients speedily and in detail. Its application to this problem might demonstrate relationships that would be of high practical value in actual fishing operations as well as serviceable in biological research on population abundance and related subjects.

According to direct observations on mackerel in captivity during the present investigation and judging from fishermen's reports, the larger mackerel tend to swim deeper than the smaller ones. This is particularly true in mid and late summer. At such times fishermen often report that the schools of large individuals are deep and "hard to stop," meaning difficult to encompass with the seine. Accordingly, there may be a tendency toward catching a larger proportion of small mackerel than of large ones whenever and wherever the thermocline is relatively deep. This probably is the explanation of the "disappearance" of the large mackerel in the late summer of many seasons (p. 268). For these reasons it is probable that the fishermen's catch in the aggregate undersamples the larger mackerel and oversamples the smaller ones within the range of commercially desirable sizes.

This is one aspect of mackerel behavior among many others which may be grouped together under the heading of "availability." By this is meant all of the various elements in the behavior of the fish and of the fishermen which cause the catch to be out of proportion to the stock of fish. With pelagic fishes such as the mackerel, where the vertical as well as the horizontal extent of distribution affects the quantity caught, there is opportunity for availability to have a much more pronounced effect on the quantity caught than with nonpelagic fishes; and there is evidence that effects of availability extend also to the size categories caught.

It has become standard procedure in studying marine fish populations to use the commercial catch per unit of fishing effort as an estimate of abundance and the size composition or age composition of the commercial catch as an approximation of the size or age composition of the stock. This has worked well, notably with demersal fishes. With pelagic fishes the element of availability is so strong that it is safer to assume that the catch per unit of effort only indicates apparent abundance—not abundance itself, also that the distribution of sizes or ages in the catch registers something other than the size or age distribution of the general stock in the sea. When these more limited assumptions are adopted, most of the established techniques for studying the dynamics of recruitment, natural mortality, and catch mortality of fish populations are no longer applicable. If they are applied, nonetheless, they are likely to lead to anomalous results.

In view of this, it appears likely that progress in understanding the dynamics of the mackerel population will be impeded until more is learned about the reactions of the mackerel to its environment and the quantitative effects these have on commercial catches as samples of the abundance and size composition of the mackerel stock. The discussions of this and the preceding sections are intended to point out some of the features which appear significant and some of the lines of study which might prove fruitful of results.

FOOD

According to Bigelow and Welsh (1925: 201), the American mackerel feeds chiefly on plankton, of which copepods form the dominant part, and among the copepods *Calanus finmarchicus* is by far the most important. In Europe the same is true in spring and early summer but in late summer and autumn the mackerel there turns its attention more to small fishes of various species.

Present observations, admittedly limited in extent, agree with those of Bigelow and Welsh. It is suggested, however, that the difference between the feeding habits of the mackerel in American waters and those in European waters in late summer may be more apparent than real, for we have found that the larger ones usually are not caught in quantity in late summer in American waters, and it may be that their search for larger food animals like euphausids and young fish leads them away from surface inshore waters at this time. Examination of stomach contents of such large mackerel as are occasionally caught offshore and in deeper water in late summer should be instructive on this point.

Whatever mackerel eat they are more successful in obtaining food after they have reached coastal waters in the spring than during their winter stay along the edge of the continental shelf. In April when mackerel first appear on the fishing grounds their fat content is very low and it increases markedly during ensuing months, according to analysis of the oil content of the flesh by Stansby and Lemon (1941: 10–11). Their values, supplemented by additional information communicated to me by Dr. Stansby, are summarized in table 2 While the data leave no doubt as to substantial fattening during the spring and early summer months, with the oil in the flesh increasing from about 4 percent in April to nearly 20 percent in August, the course of events during the remainder of the season is not clear. The values seem to fluctuate from sample to sample through a range from 6 to 19 percent. This, together with the wide variation between individuals within samples indicated by the minimum and maximum values, suggests that there is considerable difference in the success of individuals and groups of individuals either in feeding sufficiently or upon sufficiently nutritious food to provide an excess, over metabolic requirements, for fat storage. With some of the high oil content values attained as early as August, it also appears that feeding, on the whole, is usually better prior to August than after. However, the wide variation precludes any conclusion as to whether there is an average gain or loss of fat through the late summer and autumn months.

TABLE 2.—*Oil content of mackerel*

Date fish were caught	Number of fish analyzed	Oil content, percentage		
		Maximum	Minimum	Average
Apr. 18, 1935	13	------	------	3.9
Apr. 22, 1935	8	7.6	2.7	4.8
May 3, 1935	4	------	------	8.0
May 21, 1935	4	------	------	9.0
June 1, 1935	6	------	------	9.8
June 5, 1934	------	------	------	[1] 6.8
July 23, 1934	13	17.3	6.1	10.6
Aug. 13, 1934	7	25.6	10.6	17.5
Aug. 15, 1934	7	21.6	16.0	19.2
Sept. 11, 1934	20	11.4	2.0	6.5
Oct. 1, 1934	25	16.2	3.0	10.1
Oct. 20, 1934	------	------	------	[1] 15.7
Nov. 17, 1933	12	15.2	2.2	8.2
Nov. 17, 1934	------	------	------	[1] 19.5

[1] This value was derived from Stansby and Lemon's (1941) table 4, by taking the simple average of the percentage of oil content in the 31½- to 36½-inch, 36½- to 38-inch, and 39- to 42-inch size categories. The number of fish in the sample was not given.

MIGRATION OF ADULT MACKEREL

That mackerel migrate seasonally is generally accepted, but concerning the direction and extent of their travels there are two schools of thought—one that they migrate great distances from north to south when they leave the coast in the fall and back again in the spring; the other, that they sink and move directly out to deeper water in the fall and merely rise and move inshore in the spring. The controversy between the schools was lively in the latter part of the nineteenth century in connection with the dispute between the United States and

Canadian Governments concerning the right of United States fishermen to participate in the mackerel fisheries in Canadian waters (Goode, Geo. B., et al., 1884: 95). With both sides basing their argument on fragmentary data largely from testimony of unscientific observers, the question was in the realm of conjecture and remained there at least until 1908 (Kendall 1910: 293). Latterly, with more facts at hand, with respect to European as well as American mackerel, there was a decided leaning toward the school favoring the on-and-off-shore as against the north-and-south migration (Bigelow and Welsh 1925: 191).

With the more extensive, systematic, and detailed information available from the present studies, it now appears that neither school was wholly wrong or wholly right, for a critical comparison of all evidence points definitely toward the existence of a complex combination of the two (or three, if we include the vertical) sorts of movement. The general course of the migrations is diagrammatically charted in figures 5 and 6. Proof of the essential correctness of the routes shown requires consideration of their winter habitat, the existence of two migrating populations, a northern and a southern contingent, and various other relations which will be taken up in detail. But for the convenience of those who may not be interested in proofs and details, a summary of the migration will be given here.

SUMMARY DESCRIPTION OF MIGRATION

Although both the northern and the southern contingents are supposed to spend the winter in the zone of warm water, some thirty to one hundred miles out to sea along the continental edge from Virginia to Nova Scotia, it is probable that the members of the southern contingent tend to be at the southerly end of this zone, and those of the northerly contingent at the northerly end.

The southern contingent first appears in the surface waters overlying the continental shelf somewhere between Cape Hatteras and the offing of Delaware Bay, and usually in the early days of April. Though at first some thirty to fifty miles offshore, they soon come closer inshore occupying the inner third or half of the continental shelf which is about fifty miles broad at Delaware Bay. From here they move northward and eastward at a rate not faster than the progressive northerly warming of the surface water and reach the offing of southern New England during the month of May. During the northerly journey they are joined by additional schools moving in from the edge of the continental shelf in wavelike incursions. Although the southern contingent always tarries a month or more in the vicinity of southern New England, toward the end of June or early in July its members make their way around Nantucket Shoals and reach the Gulf of Maine where they make their summer sojourn.

The northern contingent makes its appearance during the latter half of May forming a wave advancing toward the coast along a broad front, perhaps from Hudsonian Channel eastward. The western end of this wave strikes the southern coast of New England, the middle portion, southern Nova Scotia and the eastern, the more easterly portions of Nova Scotia. Once inshore, the members of this contingent migrate along shore. Those that strike the coast of southern New England mix temporarily with the southern contingent among which they are detectable by their different (usually larger) sizes. But after staying only a week or two they separate from the southern contingent and toward the end of May some filter into Massachusetts Bay, but the major portion are next to be found on the Nova Scotian coast reaching there during the early days of June about the same time as those that approached that coast directly. During June, the run is heavy along the entire length of the Nova Scotian coast, Cape Breton, and eastern portions of the Gulf of St. Lawrence. During this June run there are perhaps additional minor waves of mackerel coming shoreward from the outer edge of the Nova Scotian shelf if any have wintered in the more chilly waters of this region (p. 261). Most of the northern contingent probably summers in the Gulf of St. Lawrence though part may remain along the coasts of Maine, Nova Scotia, and Capte Breton Island.

In withdrawing from the coastal areas in the fall, the movements of the two contingents, for the most part, are simply the reverse of their approach in the spring. The southern contingent in retiring from the Gulf of Maine goes southeastward past Cape Cod and in some years then trends westerly off No Man's Land and Block Island. This usually take place in September or October. About the same time, though sometimes earlier and sometimes later, the northern contingent begins retiring from Canadian waters. In doing so, a large portion, if not all, passes through the Gulf of Maine providing the basis for the late fall fishery off Cape Anne in October, November, and December. They, too, leave the Gulf of Maine by going toward the offing of Cape Cod, but have never been observed southerly or westerly of that area. During the fall migration, as during the spring migration, there is a brief period when the two contingents are mixed. The fall withdrawal differs from the spring approach mainly by the mixing of the two contingents north rather than south of Nantucket Shoals; the disappearance of each contingent while still well north of the points at which they first appeared in the spring; and the occupation by the northern contingent of the western portion of the Gulf of Maine to a greater extent and for a longer period in the fall than in the spring.

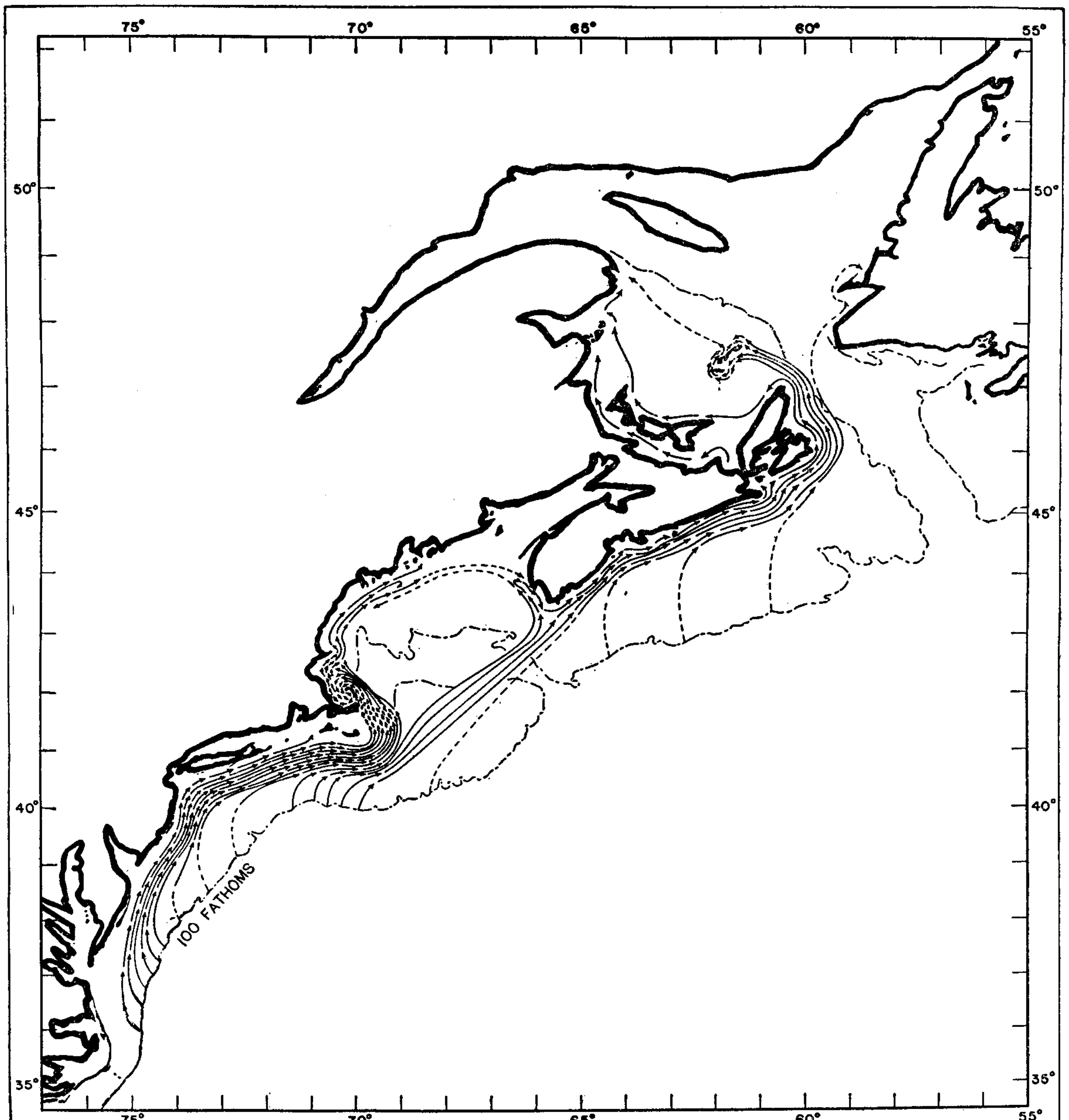

Figure 5.—Diagrammatic representation of the spring migration. The number of arrowshafts is roughly proportional to the relative number of mackerel believed to traverse the several localities. The number of arrowheads is roughly proportional to the relative amount of commercial catch taken in the several areas. Lines of dashes indicate weak evidence as to the origin or route of migration.