FACTORS DETERMINING THE DISTRIBUTION OF POPULATIONS OF CHAETOGNATHS IN THE GULF OF MAINE [1]

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In aquatic environments, and particularly in large bodies of water, the movement of the water itself may profoundly affect both the distribution and numbers of the population. Pelagic organisms are carried with the water in its drift through each given region. Numerical abundance may thus depend on conditions in external regions from which the water comes. The moving water affects the climate of the region into which it flows, for it carries with it its inherent temperature, salinity, etc. At the same time these properties of the water may be profoundly altered in its course, through interaction with the atmosphere and with other bodies of water. The maintenance of a population in a given region under these conditions depends upon a balance of dynamic factors; the drift of the water and its interaction with its environment, as well as upon the rate of reproduction and mortality of the population under the environmental conditions determined by these circumstances (Russell, 1936). The pelagic population is at the mercy of the hydrodynamic factors, since it must move with the water. It is only by taking advantage of fortuitous hydrographic conditions, such as the existence of permanent eddies and dead waters, that they may gain a truly endemic relation to a given region.

The use of plankton as indicators of water movements has attracted deserved attention of late (Russell, 1936*a*, 1939). The effect of the circulation of water on the distribution and maintenance of permanent populations of specific organisms has received less explicit attention, but is exemplified by the studies of Damas (1905), Sømme (1933, 1934) and Redfield (1939).

As Huntsman (1919) has shown, the chaetognaths are an unusually interesting group for studies in oceanic zoögeography. Of the half-dozen species found in the coastal waters between Cape Cod and the Grand Banks, three are of deep-water origin and are drawn into the deeper basins of the Gulf as an immigrant population which perishes without reproducing. Three other species are inhabitants of the upper layers of the sea, of which one breeds endemically on the continental

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shelf, while the other two are immigrants from the oceanic waters offshore. These six species must have essentially similar habits of life, yet each has a characteristically different distribution, depending upon the water body in which it maintains itself endemically, and upon the degree to which these waters are drawn into the various regions of the coast. The value of Sagittae as indicators of water movements in British waters has been demonstrated by Russell (1935, 1936*b*), Fraser (1937, 1939) and Pierce and Orton (1939).

The present paper is an examination of the populations of chaetognaths found in the Gulf of Maine during the year 1933–34, when the research vessel of the Woods Hole Oceanographic Institution, the "Atlantis," made a systematic survey of the region. While the results confirm in the main the observations of Bigelow (1926) in this region and

TABLE I

Statistics of collections of chaetognaths in the Gulf of Maine, 1933–1934.

Dates of Cruise	Number of Stations at Which Chaetognaths were Present						
	S. elegans	*S. serratodentata*	*S. maxima*	*S. lyra*	*S. enflata*	*E. hamata*	Total Stations
Sept. 2–14, 1933	30	12	6	2	1	14	35
Dec. 2–11, 1933	17	9	5	1	0	13	22
Jan. 3–13, 1934	11	7	2	2	0	9	12
Mar. 21–28, 1934	10	8	0	0	0	15	18
April 17–May 13	20	9	2	0	0	16	32
May 21–June 2	32	20	4	1	0	21	44
June 25–July 1	6	2	0	0	0	2	7
Sept. 17–24, 1934	20	16	4	3	1	15	25
Total	146	83	23	9	2	105	195
Per cent present	75	43	12	46	1	54	

Dates of Cruise	Numbers of Chaetognaths Taken at These Stations						
	S. elegans	*S. serratodentata*	*S. maxima*	*S. lyra*	*S. enflata*	*E. hamata*	Total
Sept. 2–14, 1933	2,961	104	9	4	2	107	
Dec. 2–11, 1933	3,608	45	17	1	0	300	
Jan. 3–13, 1934	194	8	3	3	0	87	
Mar. 21–28, 1934	105	13	0	0	0	95	
April 17–May 13	785	137	8	0	0	274	
May 21–June 2	1,698	104	21	2	0	289	
June 25–July 1	368	33	0	0	0	2	
Sept. 17–24, 1934	453	534	5	3	5	133	
Total	10,170	978	63	13	7	1,287	12,418
Per cent of total	82	7.9	0.51	0.10	0.06	9.5	—

Dates of Cruise	Mean Catch per Haul at Stations at Which the Species was Present						
	S. elegans	*S. serratodentata*	*S. maxima*	*S. lyra*	*S. enflata*	*E. hamata*	Total
Sept. 2–14, 1933	98.7	8.7	1.3	2.0	2.0	7.6	
Dec. 2–11, 1933	212.0	5.0	3.4	1.0		22.1	
Jan. 3–13, 1934	17.6	1.1	1.5	1.5		9.7	
Mar. 21–28, 1934	10.5	1.6	—	—		6.3	
April 17–May 13	39.1	15.2	4.0	—		17.0	
May 21–June 2	53.0	5.2	5.3	2.0		13.7	
June 25–July 1	61.5	16.5	—	—		1.0	
Sept. 17–24, 1934	22.7	33.4	1.25	1.0	5.0	8.9	
Mean catch per haul for entire period	69.8	11.8	2.74	1.44	3.5	11.3	

Dates of Cruise	Per Cent of Total Hauls in Each Period at Which Each Species was Present						
	S. elegans	*S. serratodentata*	*S. maxima*	*S. lyra*	*S. enflata*	*E. hamata*	Total
Sept. 2–14, 1933	86	34	17	5.7	2.9	40	
Dec. 2–11, 1933	77	41	23	4.5		59	
Jan. 3–13, 1934	92	58	17	17		75	
Mar. 21–28, 1934	56	45	0	0		83	
April 17–May 13	63	28	6.3	0		50	
May 21–June 2	73	45	9	2.3		48	
June 25–July 1	86	29	0	0		14	
Sept. 17–24, 1934	80	64	16	12	16	60	
Entire period	75	43	12	4.6	1	54	

of Huntsman (1919) in Canadian waters, it has seemed worthwhile to examine them together with those of Bigelow and Huntsman from the point of view outlined above.

Material and Data

General Statistics

The cruises were planned to include lines of stations extending from shoal water across the Gulf so as to sample all the principal parts of the Gulf and the enclosing banks. While exigencies of weather and the loss of nets interfered with the completeness of the program, the 195 hauls included in this study amount to a fairly satisfactory random sampling of the region, throughout the year.

The collections were made with a standard 1.5 meter Heligoland larva net (No. 0 silk, 38 meshes to the inch) drawn vertically from a point near the bottom to the surface. The opening of the net had an area of 1.7 square meters. Table I contains some statistical data on the collections.

Numerical Abundance.—The 12,418 specimens taken give a mean catch of 64 per haul or 37.5 per square meter of sea surface. Of these by far the most abundant was *S. elegans,* amounting to 82 per cent of the total. With *S. serratodentata* yielding 7.9 per cent, these two shallow-water forms accounted for 90 per cent of the total population. Of the three deep-water species *E. hamata* accounted for 9.5 per cent of the catch, with *S. maxima* and *S. lyra* making up 0.5 and 0.1 per cent respectively.

FIG. 1

FIG. 2

FIG. 1. Locations at which *Sagitta maxima* has been taken in the Gulf of Maine.

FIG. 2. Locations at which *Sagitta lyra* has been taken in Gulf of Maine. Figures in circles indicate the numbers taken per haul from "Atlantis" in 1933–34. Solid circles indicate Bigelow's captures.

The relative breadth of distribution of the species is indicated by the percentage of stations at which each was taken. The general order is the same as for the numerical abundance. The species differ, however, far less in distribution than in numerical abundance, e.g., *S. serratodentata* and *E. hamata* which accounted for only 8 and 9 per cent of the total numbers but occurred at more than 40 and 50 per cent of the stations.

Numerical abundance depends on both the extent of distribution and the density of population within that distribution. A general idea of the latter is given by the mean size of the catch at each station at which a given species is present. Again the order is essentially the same, *S. elegans* leading with a mean density of 70 per haul, *S. serratodentata* and *E. hamata* following with 12 and 11 per haul, while *S. maxima* and *S. lyra* occur sparsely when at all.

Seasonal Fluctuations

Sagitta elegans and *S. serratodentata* show a decline in total numbers taken, and in the mean density of the population at the stations where they were present during the colder part of the year. The figures are irregular as both forms occur occasionally in dense swarms, but it appears that these species are reduced to perhaps one-tenth their numbers during the winter. The cruises in December, January and March did not sample adequately the waters of Georges Bank where the larger catches of *S. elegans* were taken at other seasons and this may exaggerate the apparent effect of winter on this species, although it can scarcely do so in the case of *S. serratodentata,* which occurs chiefly over the deeper part of the basin which was adequately sampled.

Contrasted with these inhabitants of the upper levels, in which the seasonal change in temperature is great, the deep-water species *E. hamata* shows no systematic fluctuation either in total numbers, the percentage of stations at which it is present, or numbers taken per haul, during the year. Bigelow (1926) has pointed out that this is to be expected since the depths at which it lives are not subject to much change in temperature.[2]

THE DISTRIBUTION OF THE DEEP-WATER SPECIES

Sagitta maxima, S. lyra and *Eukrohnia hamata* are inhabitants of the deeper waters of the Gulf of Maine. Figures 1 and 2 record the location and numbers of the two former species taken in each haul while Fig. 3 shows the general pattern of distribution of the more abundant *E. hamata.* All our specimens of *S. maxima* were taken in water of over 170 meters depth and it occurred in greatest abundance in depths of over 200 meters. It seems safe to conclude with Huntsman and Bigelow that it occurs only in the deeper parts of the Gulf, chiefly below the 150-meter level. The distribution of the catches of *S. lyra* is essentially the same as that of *S. maxima.* The regional occurrence of *E. hamata* is similar to that of the deep-water sagittae, though it was taken more frequently in the shoaler regions along the margins of the Gulf, occasionally in water of as little as 100 meters depth. It appears to occur rather nearer the surface than do the deep-water sagittae.

The distribution of catches of the three species agree in showing the highest frequency of successful catches and the greatest numbers per haul in the Eastern Channel through which deep water has access to the Gulf. Inside the Gulf the populations are concentrated in the eastern

[2] Bigelow considered that *S. maxima* occurred in the Gulf more frequently in winter, *S. lyra* in summer. Our data do not confirm this. Their numerical abundance is rather closely correlated throughout the year and neither shows a clear seasonal variation.

basin, and diminish in abundance northward and westward as the Eastern Channel becomes remote.

Dynamic contours give the best available information concerning the probable circulation of the deeper water. Contours representing the circulation at 140 meters in May–June, 1934 are indicated in Fig. 5.[3] They represent a pattern which occurs with some variation in detail from month to month at this and greater depths. The center of abundance of the three deep-water chaetognaths lies in the rapidly moving inflow or in the eastern side of the eddy which has its vortex in the deep basin northwest of the Eastern Channel. Once the creatures pass beyond the vortex they become scattered and decrease in numbers.

The distribution of the deep-water chaetognaths suggests strongly that they are carried into the Gulf from offshore, along with the warm

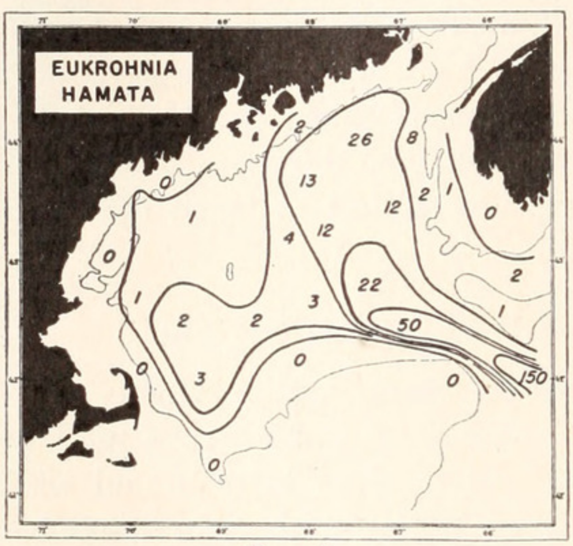

FIG. 3

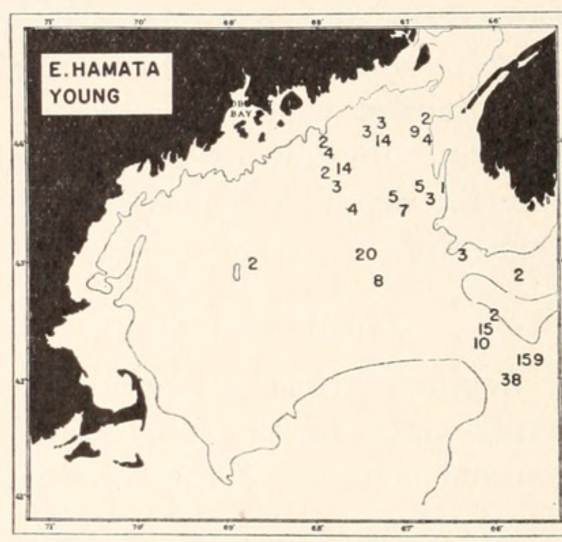

FIG. 4

FIG. 3. Relative abundance of *Eukrohnia hamata* in different parts of the Gulf of Maine. Numbers represent the average catch per haul in various regions.

FIG. 4. Locations at which young specimens of *Eukrohnia hamata* were taken in 1933–34. Numbers indicate the number of young taken per haul at each position.

saline water which Bigelow (1927) found to enter through the Eastern Channel. Since there is no evidence that they breed within the Gulf, they are to be considered as terminal immigrants from other regions in which they breed endemically. While some of those which are carried into the Gulf may complete the circuit of the eddy and be carried out again, the greater number are probably trapped within the dead waters of the inner Gulf, live as long as circumstances permit and die without leaving progeny.

The foregoing observations and conclusions are in entire agreement with those of Bigelow (1926). In certain details, however, our findings

[3] A hydrodynamic analysis of the circulation of the Gulf of Maine during the period of our survey is being prepared by Dr. E. E. Watson, to whom I am indebted for the use of this and subsequent figures.

differ from his. While he considered *E. hamata* to occur with regularity throughout the year, the sagittae were thought to fluctuate with the season, *S. maxima* being taken predominantly in the colder part of the year and *S. lyra* in the warmer. He proposed that *S. maxima,* an inhabitant of northern waters, is barred from the Gulf by the warmth of the water entering the Eastern Channel during the summer months. The statistics recorded in Table I fail to show a clear fluctuation in any of the deep-water species which may be correlated with the season. That *S. maxima* may enter the Gulf at a time when the water is warmest is evidenced by our taking 12 and 6 specimens in two hauls made in the Eastern Channel in May when the temperature of the deeper water was 8°–9° C. and 2 in a September haul from water varying in temperature from 6.5° to 8.76°.

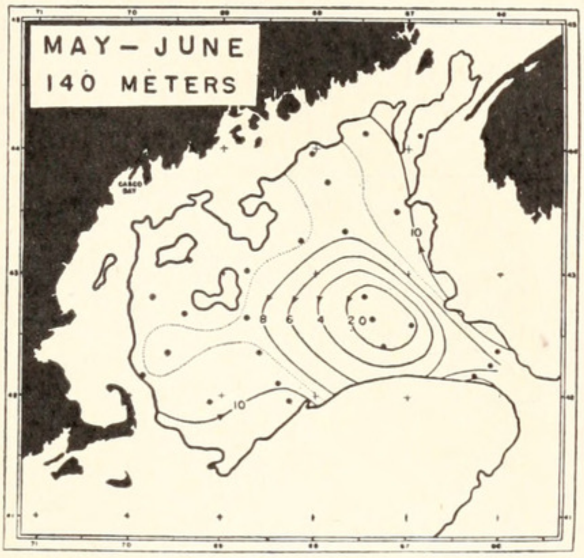

FIG. 5

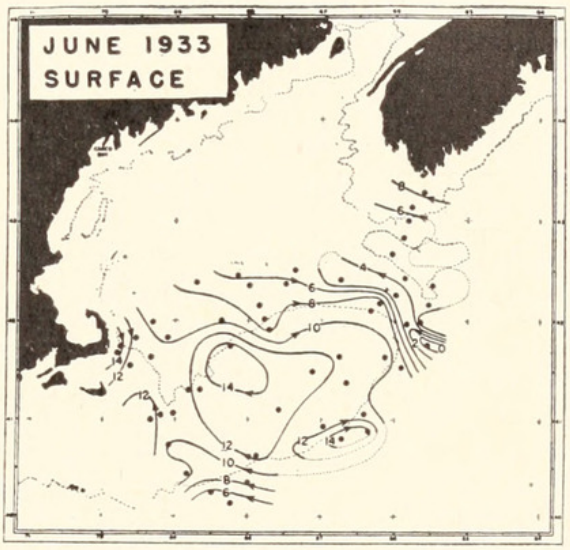

FIG. 6

FIG. 5. Dynamic contours indicating theoretical circulation in the basin of the Gulf of Maine at depth of 140 meters in May–June, 1934.

FIG. 6. Dynamic contours indicating theoretical circulation at surface of Georges Bank in June, 1933.

We believe he was misled, particularly in the case of *S. lyra,* of which he took only 6 examples, by the fact that his cruises did not sample the center of abundance of the populations as thoroughly as the more remote and colder periphery of the range.

Factors Limiting the Distribution within the Gulf

In attempting to evaluate the relative importance of the circulation of the water and of environmental factors in determining the abundance and distribution of the species, it is crucial to inquire whether the numerical relations are due to the degree to which the three species are " adapted " to the conditions in the Gulf, or whether they are to be explained by the relative numbers in which they enter from offshore.

In the former case the numerical ratios should shift as one compares waters increasingly remote from the point of entrance. In the latter they should remain unchanged.

To examine these possibilities, we have divided the catches in which any of the species occurred into three groups: (1) those taken in the deep water of the Eastern Channel (east of 66°30′ and south of 42° 40′N); (2) those lying immediately within the basin (a quadrangle lying between 42°10′ and 43°30′N and 66°30′ and 67°30′W), and (3)

TABLE II

Relative numbers of deep-water chaetognaths taken in different areas in Gulf of Maine.

Total Numbers	*E. hamata*	*S. maxima*	*S. lyra*
Eastern Channel	434	34	2
Southeastern quadrangle of basin	411	25	6
Remainder of basin	442	4	5
Total area	1287	63	13
Relative Numbers Taken			
Eastern Channel	100	7.8	0.5
Southeastern quadrangle of basin	100	6.1	1.5
Remainder of basin	100	0.9	1.1
Total area	100	5.0	1.0
Stations Present			
Eastern Channel	9	6	1
Southeastern quadrangle of basin	19	11	3
Remainder of basin	87	5	5
Total area	105	23	9
Relative Numbers of Stations Present			
Eastern Channel	100	67	11
Southeastern quadrangle of basin	100	58	5.7
Remainder of basin	100	5.7	5.7
Total area	100	22	8.6

the remainder of the Gulf. These three areas yielded *E. hamata* in about equal numbers. They differ in proximity to the external sources of the deep water of the Gulf.

The numbers of specimens and the relative numbers of each species taken in these areas are given in Table II. They show that a great disparity between the abundance of the three species already occurs in the water entering the Channel. In the main the relative abundance is established by conditions external to the Gulf, and cannot be attributed merely to the selective effect of conditions within.

There is, however, clear evidence that some selective mechanism is at work limiting the penetration of *S. maxima* into the remoter region. The ratio in which *S. maxima* is taken in proportion to the catch of *E. hamata* is eight times as great in the Eastern Channel as in the remoter region. The distribution of *S. lyra* appears to resemble that of *E. hamata* more closely than that of *S. maxima*.

TABLE III

Catches of Sagitta maxima and Sagitta lyra classified according to highest temperature of the water column (below 100 meters) from which they were taken.

Temperature, ° C.	*S. maxima*							
	5–5.5	5.5–6.0	6.0–6.5	6.5–7.0	7.0–7.5	7.5–8.0	8.0–8.5	8.5–9.0
Number per haul	1 •	1	2	3	2	6	12	6
		1			2	2	6	2
					1	1	6	
					1		3	
					1		2	
							1	
Total	1	2	2	3	7	9	30	8
Per cent of total	1.59	3.18	3.18	4.76	12.7	14.3	47.7	12.7
Integrated per cent	1.59	4.77	7.95	12.71	25.4	39.7	87.4	100
Mean catch per haul	1	1	2	1.5	1.3	3	5	4
Temperature, ° C.	*S. lyra*							
	5–5.5	5.5–6.0	6.0–6.5	6.5–7.0	7.0–7.5	7.5–8.0	8.0–8.5	8.5–9.0
Number per haul					1	1	3	
					1		2	
					1		2	
					1		1	
Total	0	0	0	0	4	1	8	
Per cent of total	0	0	0	0	30.8	7.7	61.6	
Integrated per cent	0	0	0	0	30.8	38.5	100	
Mean catch per haul	0	0	0	0	1	1	2	

In the discussion of the geographical distribution of the chaetognaths,—as of marine plankton in general,—temperature and salinity are commonly considered as factors limiting the distribution of the species. The water in which the chaetognaths of the depths appear to be carried as they penetrate the Gulf undergoes admixture with subsurface layers. As a result it becomes colder and less saline. While not wishing to suggest that these factors are not in a broad way influential in determining the survival of the species, we do wish to question whether they, or similar environmental conditions, are essential in accounting for the differences in their distribution within the Gulf of Maine. While our data suggest that *E. hamata* invades colder water more frequently than *S. maxima* and *S. lyra,* there is no evidence that these latter cannot survive in water at least as cold as any in which we have taken the former species. Bigelow (1926, p. 325) records captures of *S. maxima* off the continental slope in waters of 3° to 6° C. and considers this species to be a distinctly cold-water form. *S. lyra* was taken by him in water of 6° C.—below which only 8 per cent of the total catch of *E. hamata* was taken. Though it may be considered a creature of relatively warm water, we have shown that it penetrates into the colder parts of the Gulf, relatively as frequently as does *E. hamata.*[4]

We believe the disparity in distribution of the deep-water chaetognaths in the Gulf can be explained more readily in another manner. We have presented in Tables III and IV data showing the incidence of

TABLE IV

Catches of Eukrohnia hamata classified according to highest temperature of the water column (below 100 meters) from which they have been taken. Total catch = 1287.

Temperature, ° C.	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11
Total hauls	7	13	15	32	40	28	11	4	1
Total caught	7	11	33	61	213	407	310	244	1
Per cent of total	0.54	0.86	2.56	4.74	16.5	31.5	24.0	18.9	—
Integrated per cent	0.54	1.40	3.96	8.70	25.2	56.7	80.7	99.0	100
Mean catch per haul	1.0	0.85	2.2	1.9	5.3	14.5	28.2	60	1

the species in water of different maximal temperatures. The catches have been classified according to the temperature of the water in which they were taken. We have chosen the highest temperature recorded below 100 meters, since there is no way of knowing the level at which an animal caught in a vertical haul is taken, and since this temperature will represent the least departure from the condition under which the water entered the Gulf. The temperature profiles shown in Fig. 7 give

[4] Salinity cannot readily be separated from temperature as a possible limiting factor within the deep water of the Gulf because variations in temperature and salinity alike are due to mixtures in varying proportion of the deep, warm, and saline water with the superficial, cold, and dilute water. As a result, the temperature-salinity diagram for waters in all parts of the Gulf below the level of homogeneous winter mixing is almost a straight line and is nearly the same in each region.

It is, moreover, extremely difficult in view of what is known experimentally concerning the osmotic regulation of marine invertebrates, to believe that changes of one or two parts per mille would vitally affect animals native in 34 or 35 ‰ salinity.

some idea of the possible range of temperature in various regions of the Gulf.

Tables III and IV show the result of this classification. Though not corrected for the relative number of hauls taken in each kind of water, this correction may be neglected in comparing the different species since the data for each are derived from the same collection of catches. For each species the numbers fall off sharply as the temperature declines. In the case of *S. maxima* and *S. lyra* the great change occurs at about 7° C. *E. hamata* appears to succeed better in penetrating the colder parts of the Gulf, the numbers caught falling markedly only below 6° C.

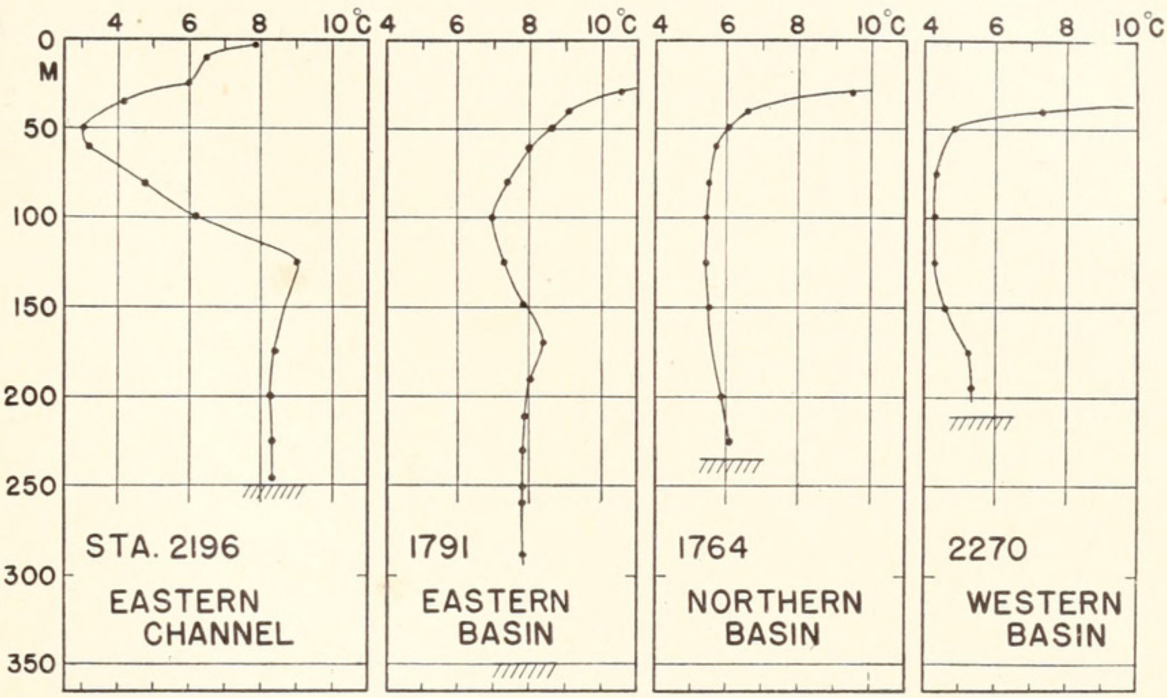

FIG. 7. Distribution of temperature with depth at a number of stations at which *Sagitta maxima* was taken.

In Fig. 8 we have plotted the integrated data showing the fraction of the total catch of each species which has penetrated to regions of decreasing temperature. The curves in Fig. 8 might be interpreted as representing the relative tolerance of individuals of the three species for the physical characteristics of the water. When the dynamic nature of the situation is considered, we believe they may be more plausibly interpreted as depending on the time of survival to be expected by the numbers which enter the Gulf, and irrespective of any change in the physical characters of the environment to be encountered therein except insofar as the conditions in the Gulf are unsuitable for its reproduction. Since the changes in the physical characteristics of the deep water depend on mixing processes, and since these must proceed relatively uniformly in all parts, the change in temperature and salinity is a function of the time during which the water has been exposed to these processes. Temperature and salinity are thus a function of the age of the deep water in the Gulf. The abscissa of Fig. 8 may be replaced by a time scale reading from right to left and measuring in a general way the time since the water with its included population entered the Gulf.

With these considerations in mind, the curves in Fig. 8 may be interpreted as probability integrals representing the expectancy of life of the groups of chaetognaths which appear in the Eastern Channel. *E. hamata* has an expectancy of longer life than the others. Hence it has time to be carried into the remoter parts of the Gulf in large numbers

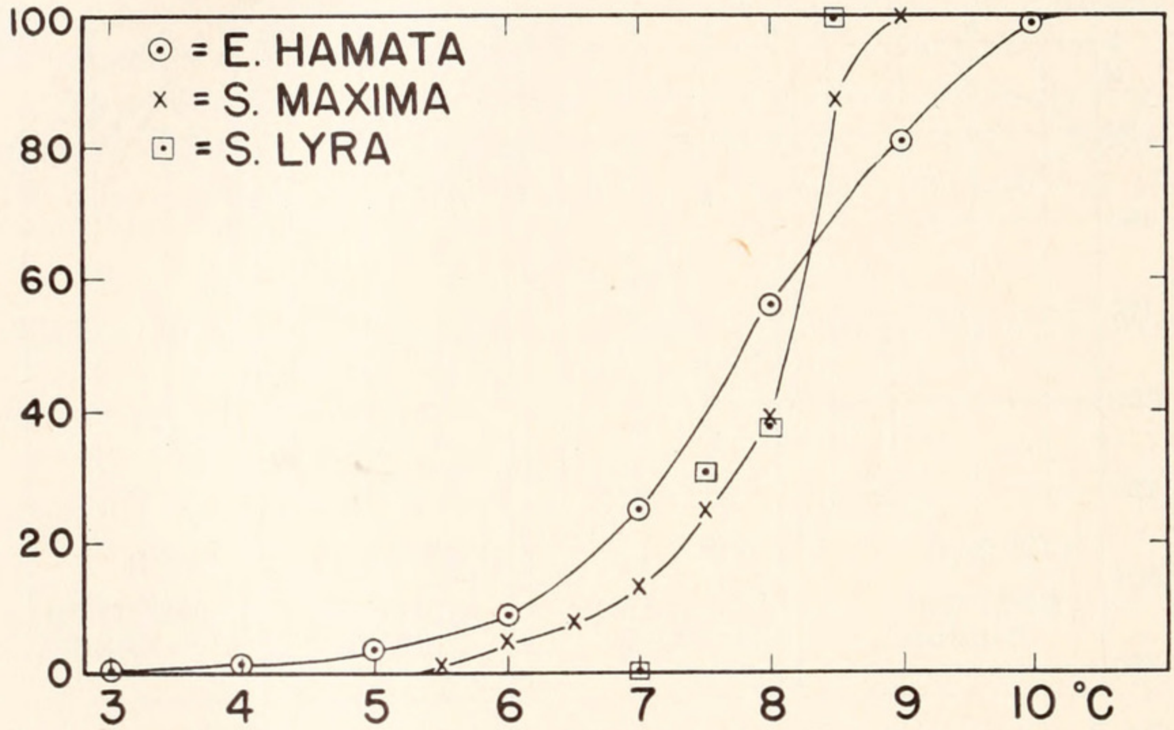

FIG. 8. Percentage of the total catch of *Eukrohnia hamata, Sagitta maxima* and *S. lyra* taken at stations at which the water below 100 meters was colder than the temperature shown on the abscissa. Based on integrated percentages shown in Tables II and III.

before it dies. Why its expectancy is longer may depend merely on its inherent longevity. It may, however, depend on its relative age at the time when it enters the Gulf. For the latter alternative there is some evidence, for we have found that young individuals of this species appear in the eastern side of the basin during the winter months (Fig. 4). This interpretation renders any special considerations of the relative fitness of the environment for the three species unnecessary, though it does not exclude them as contributory causes.

The distribution within the Gulf appears to depend essentially upon the current system and upon the age of the population which enters the region. This in turn must depend upon the relative remoteness from the Eastern Channel of the centers of reproduction for each species—a remoteness to be measured in terms of the length and velocity of the transport system which bears the population to its destination.

The Sources of the Deep-water Population

Turning to the external sources of the population which enter the Gulf, the question is: Do the different species have a common source in the slope water which enters the Eastern Channel, or do they come from different sources to be mingled during their passage into the Gulf? The first alternative demands the same relative abundance of the species in the slope water as within the immediate entrance of the Gulf. Huntsman records catches of chaetognaths from 20 stations along the coast of the maritime provinces in water of over 1,000 meters depth made with vertical hauls from depths between 200 or 375 meters and the surface. In these hauls he counted 408 *E. hamata,* 235 *S. maxima,* and 49 *S. lyra.* The numerical ratios are 100: 59: 12. The relative abundance of *S. maxima* and *S. lyra* are almost the same as their occurrence in the Gulf of Maine. *E. hamata* was, however, very much scarcer relatively in these collections than in those made in the Gulf of Maine and was absent from a number of stations at which the others occurred. If Huntsman's catches may be considered characteristic of the slope water to the eastward of the Eastern Channel, then this body—at least in its upper layers—cannot be considered the sole source of the *E. hamata* population of the Gulf of Maine.

Bigelow considered *S. maxima* to come to the Gulf of Maine with the slope water from the northeast. He suggests that *E. hamata* is confined to waters so deep, except in high latitudes, that it never reaches the Gulf of Maine from the oceanic basin abreast of it, a consideration which seems to limit its origin also to the slope water. The absence of *S. lyra* from Huntsman's inshore and eastern stations, together with its more limited distribution in the north Atlantic, seem to preclude its origin from the boreal sources of the slope water. Since Huntsman's and Bigelow's studies were published, Rossby (1936) has shown that there are important forces at work transporting deep oceanic water into the region of the slope water, as the result of which this body owes its origin to oceanic as well as to boreal sources. Redfield (1936) has discussed the ecological consequences of these facts. The diverse origin of the waters which enter the Gulf of Maine and their inhabitants are thus more clearly understood. Hydrographic observations emphasize the complexity of the water bodies occurring close to the mouth of the

Eastern Channel. These facts seem to favor a diversity in the origin of the chaetognaths which penetrate the Eastern Channel.[5]

The Distribution of the Chaetognaths of the Upper Levels

Sagitta enflata, S. serratodentata, and *S. elegans,* all of which are more commonly taken in tows from the upper 100 meters, present much greater contrasts in numbers, distribution, and seasonal fluctuations than do the deep-water chaetognaths. Their occurrence and abundance can be attributed to the circulation of water and its relation to the areas suitable for their reproduction in great detail. On the one hand, *S. elegans* is capable of reproducing in the shallow waters which encircle the Gulf and occurs in numbers and at times which can be attributed to the nature and stability of local hydrographic conditions. On the other hand, *S. serratodentata* is an inhabitant of the warm ocean offshore and is carried into the Gulf as a periodic immigrant at times dependent on a cyclic change in the major circulation of the region, while *S. enflata* represents a rare straggler from (hydrographically) more remote regions which can reach the margins of the Gulf only at such times as the temperature of the water permits its survival for a sufficient period.

Sagitta enflata

S. enflata is a tropical form ranging to 40°N in the surface water of the Gulf Stream. Huntsman found it only at the outermost stations along the continental margin and in considerable numbers only at his more western stations in the offing of the Eastern Channel. He captured one specimen in July over the coastal shelf north of Sabro Bank. It has been taken occasionally over the continental slope south of Cape Cod, Bigelow and Sears (1939) recording a large catch of juveniles close to Martha's Vineyard in 1935. South of Delaware it is not infrequent 30 miles in from the continental slope and south of the Chesapeake it occurs frequently close in to land. The invasion of the coastal waters south of Cape Cod occurs at all seasons but most often in the autumn. We captured *S. enflata* on two occasions only. On September 3, 1933

[5] Bigelow found *E. hamata* to vary markedly in abundance from season to season, a fact which might arise from variations in the inflow and its origin from year to year. His capture of *S. maxima* chiefly in winter and *S. lyra* in summer, as well as our failure to find these species dissociated in time may have their origin in similar fluctuations. Bigelow concluded, from hydrographical evidence, that the inflow through the Eastern Channel is variable. Our data have been searched for correlations between the distribution of the species and that of the hydrographic factors in the region of the Eastern Channel, but we have failed to find any good evidence of a dissociation in the time at which the different species enter or in their presence in separate bodies of water within the neighborhood of the Eastern Channel.

one specimen occurred in a haul made in the South Channel in association with large numbers of salpae. On September 23, 1934 five specimens occurred in a haul taken well within the Eastern Channel.

S. enflata is thus one of the many tropical forms which in small numbers find their way in over the margin of the continental shelf in the latter part of each summer. Our records are the first for the margins of the Gulf itself. In the present connection the species is of interest as the extreme example in a series of forms relating frequency of occurrence to the remoteness of the area of reproduction, and to seasonal fluctuations.

S. serratodentata Krohn

This inhabitant of the upper layers of the warmer parts of all oceans extends farther north than most such, being able to survive, though not to breed, in relatively cold water and consequently it extends farther inshore than do most forms of like origin. Huntsman found *S. serratodentata* at practically all stations off the continental slope as far east as the Newfoundland Banks. It extended into the Laurentian Channel over the deep trough but did not penetrate into the Gulf of St. Lawrence. It occurred over the western half of the Nova Scotian Banks well in toward shore and in numbers increasing westward. Bigelow records its occurrence off the continental shelf to the south of Georges Bank and states that from New York southward it is the prevailing chaetognath right in to the shore in warm summers, though outnumbered by *S. elegans* in cooler seasons, at least over the inner part of the shelf as far south as Delaware Bay. North of Chesapeake Bay, and especially east of New York, it is much less frequent close to the land. Bigelow and Sears (1939) find no seasonal fluctuation in its abundance, either inshore or offshore in the coastal belt west of Cape Cod. They consider it to be maintained by local reproduction within that area.

In the Gulf of Maine Bigelow (1926) found it to penetrate the eastern part of the basin regularly and to extend westward along the New England coast in diminishing numbers as far as Massachusetts Bay. He took it only occasionally in small numbers on Georges Bank. It was absent from the southwestern quarter of the basin at all times and disappeared almost completely from the entire Gulf in the late autumn. Its occurrence was highly seasonal, the invasion of the Gulf beginning in late spring and culminating in September. There is no evidence that it reproduces successfully in the Gulf.

Our collections confirm abundantly Bigelow's general conclusions. The center of abundance is in the eastern half of the Gulf, agreeing well with that of the deep-water chaetognaths, though extending into the shoaler water over Brown's Bank and the Northern Channel. Access to the Gulf is available over this route from the concentrations Huntsman observed on the western Nova Scotia Banks and from the slope water over the Eastern Channel. The inner and western part of the Gulf is penetrated in smaller numbers and in general along the northern side of

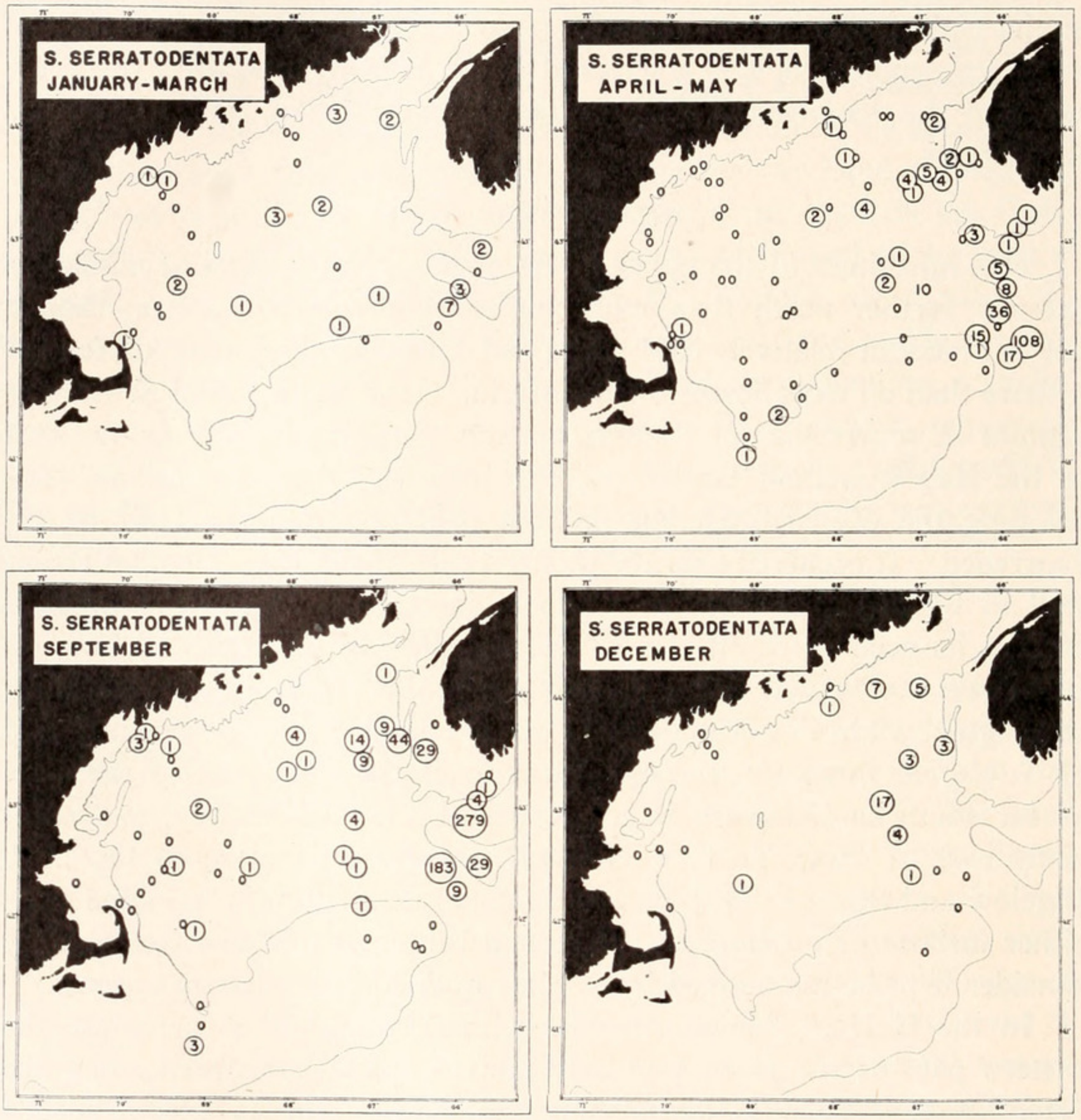

FIG. 9. Locations at which *Sagitta serratodentata* has been taken in the Gulf of Maine at different times of year. Figures in circles represent numbers taken per haul. Small circles represent positions of hauls in which none were taken.

the Gulf. Only in isolated cases were small numbers taken within the 100-meter contour or from the deep basin south and west of Cashes Ledge.

The seasonal picture during 1933–34 is given by Fig. 9, showing the combined catch in cruises grouped according to the time of year. Between January and March the population was at its low ebb, the distribu-

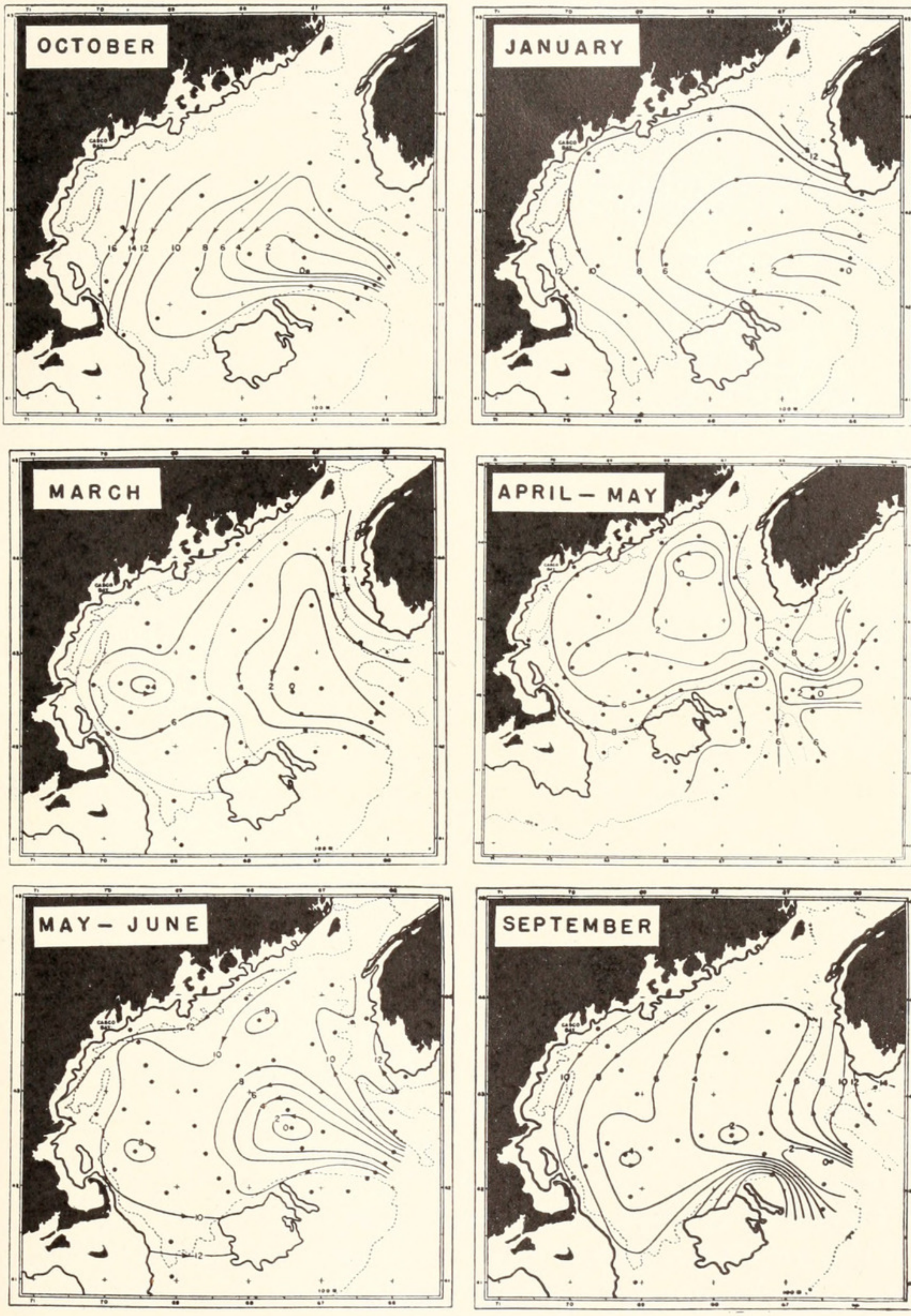

FIG. 10. Dynamic contours showing the theoretical circulation in the Gulf of Maine at a depth of 40 meters from October, 1933 to September, 1934.

tion was almost uniform throughout the Gulf. Such concentration as existed occurred in the northeastern quarter. By April and May the species had disappeared from the western side of the Gulf almost completely, but a new invasion was apparent from the southeast. By September the numbers had increased in this area of concentration and smaller numbers had extended westward as far as Portland while scattered individuals had again reached the remoter parts of the Gulf. By December the inflow of water carrying *S. serratodentata* appeared to have ceased and the remnants of the earlier invasion remain in small numbers still concentrated in the eastern region.

The course taken by *S. serratodentata* in its invasion of the Gulf is that expected of superficial water, entering from the outer Scotian Banks, in its circuit of the Gulf. It follows closely the drift of the population of *Limacina retroversa* which entered the Gulf in December, 1933 and circumnavigated the entire basin (Redfield, 1939). Unlike *Limacina,* this sagitta population did not survive to reach the western basin in significant numbers, and it was rarely found in the southwestern quarter, where lies the most ancient water in the Gulf. It also differed from *Limacina* in invading the Gulf continuously from late April through September.

Bigelow pointed out that neither temperature nor salinity explains the disappearance of *S. serratodentata* in the fall. The water is considerably warmer in November than it is at the time when invasion commences in the spring. Salinity is not very different then from that in late summer. He suggests that increases in numbers in the summer mirror the accumulation of a population which finds conditions favorable there. With the cessation of the invasion in autumn, the visitors of the summer die off from natural causes, leaving no progeny and so the species disappears until new immigrants enter in the spring. This explanation is clearly in accord with the picture we have obtained of the deep-water chaetognaths, save for the periodic character of the invasion.

Bigelow (1926) proposed that the periodic invasion of *S. serratodentata* may be connected with the seasonal reproductive cycle. The lack of any seasonal fluctuations in the numbers taken on the coastal belt west of Cape Cod, subsequently remarked by Bigelow and Sears (1939), leads us to suspect that the periodicity in the Gulf of Maine is due to a periodic change in the circulation of water, rather than to the seasonal character of the reproductive cycle.

The center of reproduction of *S. serratodentata* must lie in the warmer waters east of the continental slope, from which they penetrate the slope water and ultimately reach the Gulf in the indraft over the Eastern Channel. The dynamic contour charts (Fig. 10), showing the theoretical pattern of circulation in the superficial layers, show that in April–May, 1934 an extensive area of dead water appears to occupy the banks south of Nova Scotia, and that the only apparent movement into the Gulf is from the continental margin off the Eastern Channel. In late May and through October this offshore indraft strengthened, thus supplying the required medium for the invasion of *S. serratodentata* into the Gulf. During the winter months the circulation of sub-surface water into the Gulf alters the contours indicating a much more intense flow across the Scotian Banks. Bigelow (1927) has shown that this change occurs with regularity and results in a regular invasion of water of low temperature and salinity. Such a flow will supply the Gulf with water derived from the inner and more eastern regions of the Scotian Banks where, according to Huntsman (1919), *S. serratodentata* is absent even in summer. During the winter months the invasion of this species into the Gulf will be checked and the population will decline until the inflow of this barren water across the Banks is checked, as it was in April–May, and the offshore indrift becomes predominant.

Sagitta elegans

Sagitta elegans Verrill is the most interesting member of the group because it is the only one maintaining a center of reproduction within the area. It is the characteristic sagitta of the north Atlantic coast, being of general occurrence in the shoaler water. Huntsman found it generally distributed in Canadian waters as far east as the Grand Banks, with particular abundance over the deeper parts of the coastal banks. Offshore it occurs only sparsely beyond the 100-meter contour. Georges Bank is the most southern important center of reproduction, though it ranges south as far as Chesapeake Bay in some seasons (Bigelow and Sears, 1939). In the Gulf of Maine Bigelow found *S. elegans* to occur most plentifully on Georges Bank, in the North Channel and on the adjoining banks south of Cape Sable, in Massachusetts Bay and in smaller numbers along the coast of Maine and New Hampshire within the 100-meter contour. Over the deep basin it is at all times much scarcer. This species becomes very scarce in most parts of the Gulf in early spring. Particularly, in Massachusetts Bay, where dense populations occur in the late summer, it almost entirely disappears in late winter.

Our collections confirm in detail the general features of the distribution of *S. elegans* in the Gulf of Maine described by Bigelow. By combining our data with his records for vertical hauls, and by grouping the two sets of observations by periods in which the findings are essentially concordant, we are able to give in Fig. 11 a more detailed picture of the seasonal distribution than appeared from his analysis.

Georges Bank was the principal area of abundance of *S. elegans,* both in extent and density of population. Catches of hundreds or thou-

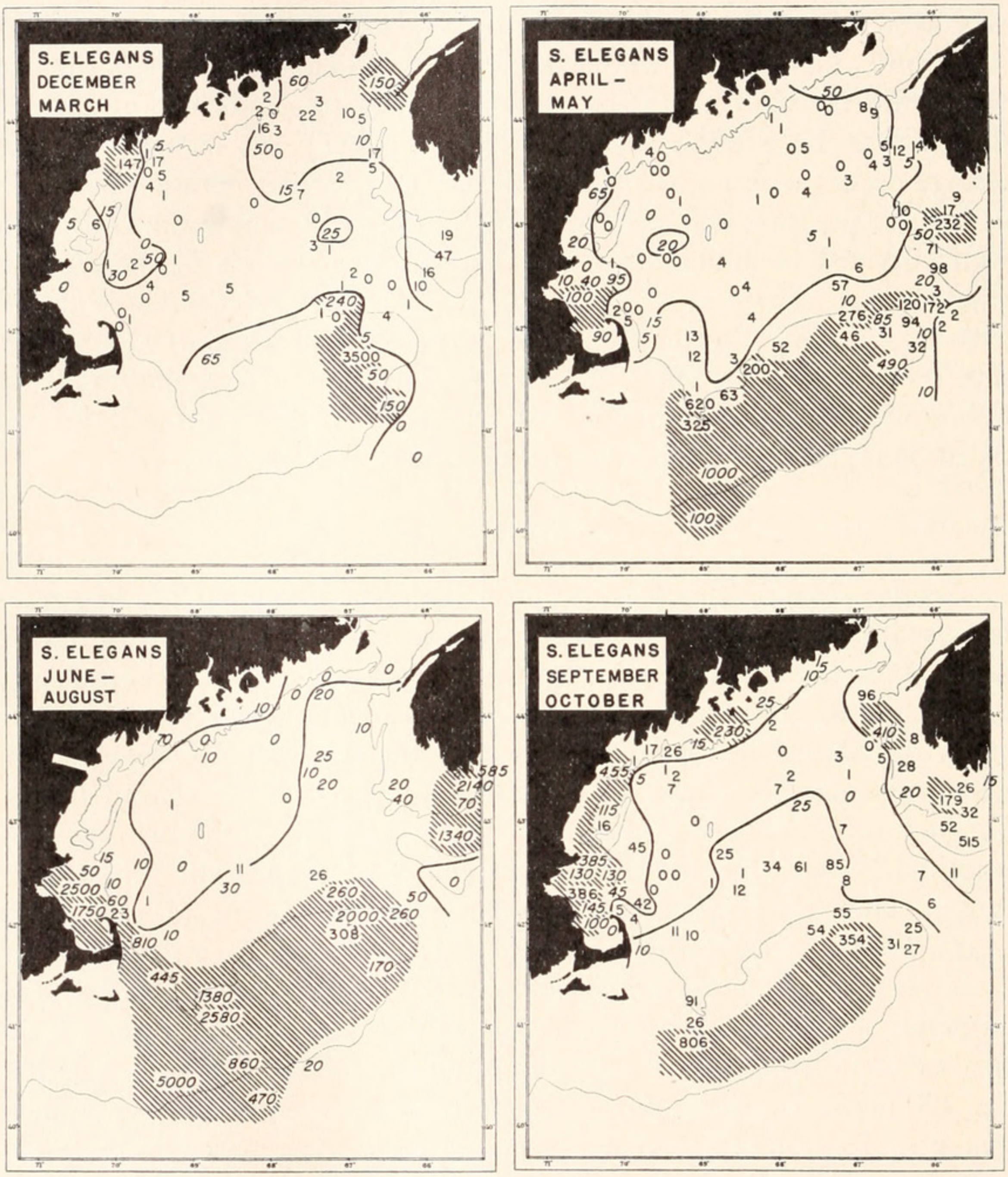

FIG. 11. Locations at which *Sagitta elegans* has been taken in the Gulf of Maine at different times of year. Upright figures represent numbers taken per haul by "Atlantis" in 1933–34. Italic figures represent numbers taken by Bigelow in vertical hauls. Contours enclose areas in which not more than ten specimens per haul were taken.

sands were taken there at all times of year. The area was not adequately explored during the winter months but on the eastern end, at least, the catches were as abundant then as at any other time. One catch of 3,500 was made in December. The greatest abundance was observed in July.

The Scotian banks south of Cape Sable and the waters over the North Channel was the second area of abundance. In midsummer, catches were obtained there equalling those on Georges Bank. The numbers were less permanent, however, declining in late summer and becoming scanty during the winter period. Recovery was not indicated before May. This area appears to be an extension of the center of abundance which Huntsman (1919) observed on the western Nova Scotia banks in July.

Massachusetts Bay and the coastal waters extending eastward to the Bay of Fundy form an area of intermediate abundance, marked by great seasonal fluctuation. In winter *S. elegans* was rare in these waters with only scattered catches yielding important numbers. In May the population became augmented in Massachusetts and Cape Cod Bays. In midsummer populations rivalling those on the offshore banks developed here and increased numbers were found all along the coast to the eastward by early autumn. These numbers did not maintain themselves, however, with the coming of winter.

The waters over the deep basin of the Gulf and over the Eastern Channel were always scantily populated. There was not much fluctuation in numbers with season in the northern and western parts of the basin. In the southeastern half, particularly in the region north of Georges Bank, there was a distinct increase in the numbers taken, beginning in July and developing clearly in September.

We propose the following considerations in explanation of the observed distribution of *S. elegans* in these different regions. Georges Bank is the seat of a great anticyclonic eddy (Huntsman, 1924; Bigelow, 1927). The dynamic contours in Fig. 6 indicate the magnitude of this eddy. Because of its size and attendant permanence, the population of sagitta remains on the Bank in sufficient numbers to maintain a dense breeding stock. Fluctuations in numbers are only such as are to be expected in an animal reproducing periodically. The decline in numbers at the close of the reproductive season is to be attributed to the natural death of the parental generation and the loss of small numbers to adjoining bodies of water. This situation represents the most favorable condition for maintaining an endemic population. Since, as Russell (1932) has shown, *S. elegans* produces several broods per year, since these are not exactly synchronized, and there is only a short period of reproductive inactivity in the early winter, fluctuations in numbers are too small to be discerned readily.[6]

The water south of Cape Sable is not recognized as forming a definite eddy, but it is spoken of as a " dead area " subject to strong tidal influence, but for considerable periods relatively free of residual drift. The dynamic contours presented in Fig. 10 show that this condition persisted from April through September in 1934. The freedom from strong currents enables the progeny of this population to accumulate in great numbers during the breeding season. At the end of the period of multiplication the population becomes rapidly scattered, as evidenced by the increased numbers over the coastal banks and deeper waters in the northeastern quarter of the Gulf in the fall and winter.

The alteration of the coastal currents during the winter, discussed in connection with *S. serratodentata,* contributes to the disintegration of this center of abundance. Adjoining extensive breeding areas to the eastward, however, this region remains populated throughout the year. Although the physical and biological conditions south of Cape Sable may be as favorable as on Georges Bank, and the areas to the eastward assure a constant supply of fresh immigrants, the hydrographic set-up does not have sufficient stability to maintain a rich population during the winter.

The coastal waters off the northern shores of the Gulf are the seat of a strong flow to the westward. A non-tidal drift of 7 miles per day is recorded at Portland lightship. Though conditions may not be unsuitable for reproduction in this area, the yield is swept on to the west and south. As a result, only in the relatively immobile waters of Massachusetts Bay is there an opportunity for large numbers to be produced by breeding early in the summer, while the stock grows more slowly in the region to the eastward. With the termination of multiplication the population of the entire coastal zone is rapidly reduced as the waters are swept on, and the population is incorporated into that of Georges Bank and the deeper basin to the north of it.

It is hard to believe that the deeper waters of the Gulf are scantily

[6] *S. elegans* appears to breed in the Gulf of Maine in the late spring and summer. Individuals less than 10 mm. in length may be taken from May to September in Massachusetts Bay and on Georges Bank. Huntsman and Reid (1921) consider the spawning season in the Bay of Fundy to extend from April to September, though the eggs do not develop properly until late summer and the authors doubt if conditions for reproduction are sufficiently favorable in that locality to enable the species to perpetuate itself except by immigration. In the Woods Hole region Fish (1925) found ripe eggs as early as March and April. Russell (1932) has detected four or possibly five successive broods of *S. elegans* in the English Channel, the first appearing as ripe adults in January, the last in October.

populated either because food is lacking or because its physical conditions are unfavorable. Plankton in general is rich in the deep basin, and though perhaps not as plentiful as on the banks, it would surely support more than one-thousandth as many sagitta. The differences in temperature and salinity in the surface waters are trivial. We suggest that the water over the basin is free from *S. elegans* for the same reason that it is populated with *S. serratodentata*. The reciprocal character of the distribution of the two forms is evident both from our own and Huntsman's observations. The superficial water lying over the deep basin of the Gulf is renewed from external sources, in which *S. serratodentata* occurs, but *S. elegans* is lacking. The flow of this water is sufficiently rapid at all times so that *S. elegans* becomes incorporated into it only in small numbers, particularly in the region of inflow and along the northern half of the Gulf. By the time the southern side of the Gulf is reached in the course of the flow about the great eddy which fills the Gulf, *S. serratodentata* has died off, but *S. elegans* has had time to penetrate in larger numbers into the waters overlying the deep basins. This penetration can occur, however, only at those times when a rich population has grown up in the coastal waters, that is, after midsummer, and when this supply is exhausted in early winter the offshore waters become depopulated, both from the death of their inhabitants and their transport out to sea.

Discussion

We have attempted to analyze the distribution and abundance of chaetognaths in the Gulf of Maine on the basis of certain biological characteristics of the species and the movement of the water in which they live. We believe the character of their distribution within the area studied can be accounted for in the main in these terms without recourse to considerations of the suitability of the physical characteristics of the water for survival of the adults or of nutritive conditions.

The biological characteristics taken as given are the depth of water which the species frequents and the character of the water in which it succeeds in breeding. The former is doubtless controlled by choice, tropisms, or avoidance reactions on the part of the individual. Such reactions are left out of account as necessary factors in determining horizontal distribution, it being sufficient to consider that this is determined by the flow and mixing of the water masses in which the animals live. Active swimmers such as the chaetognaths might be capable of definite migrations such as many fish perform. There is no evidence that such directed movements influence the distribution of these forms, though Meek (1928) has claimed that cross-current migrations do influence the character of the sagitta population along the Northumbrian coast. In the absence of directed migrations, their swimming may be expected merely to accentuate the scattering of the population in horizontal directions at rates greater than the concurrent mixing processes in the water itself.

The situations in which a species can breed are, of course, controlled in some way by the physical characteristics of the water, particularly its temperature. Many species are able to survive as adults in regions in which reproduction is not possible. Five of the six chaetognaths considered fall into this category in the Gulf of Maine. Success in breeding is itself a relative matter and in " marginal " regions insufficient eggs may develop to maintain the local stock. *S. elegans* in the Bay of Fundy appears to be a case in point. There Huntsman and Reid (1921) find that the conditions are unfavorable for the development of larvae and conclude that the very considerable fluctuations in their numbers are caused by the adults being carried into the Bay in varying quantities. We may classify each species as it occurs in a given locality in an order of fecundity which decreases in its favorable effect on the maintenance of the population thus: (1) successful breeder; (2) unsuccessful breeder; (3) non-breeding immigrant.

These categories are merely relative. Success in breeding will affect the abundance of the population both in proportion to the number of eggs spawned and the fraction of these which survive.

Fluctuations in the stock present at any time will depend in part on the purely biological facts relating to the breeding habits. Animals having an annual period of reproduction will show a marked fluctuation with maximal numbers immediately following the period of breeding. The fluctuations will be most marked if the adult does not long survive its first breeding, less pronounced if the adult survives through several breeding seasons. Species which maintain their abundance by the production of many eggs with small expectancy of survival will fluctuate more than those less fecund species with low mortality. The degree to which the reproduction of different species is synchronized with the season will also modify the seasonal incidence. The life histories of the sagittae are not sufficiently well known to permit of classification in these regards. Fluctuations appear to be relatively small in *S. elegans* on Georges Bank, the most stable region of its occurrence. The deep-water species are free from marked fluctuation as is *S. serratodentata* according to Bigelow and Sears (1939) in its reproductive area south of Cape Cod. The marked fluctuations in the latter and the periodic occurrence of *S. enflata* appear to depend on environmental causes, rather than on the biology of the reproductive cycle.

A final biological factor determining both abundance and distribution is longevity. Within a region of production the relation of mortality to reproductive rate is obvious and has been mentioned above in considering fluctuations of biological origin. In the case of immigrant plankton, which are carried beyond the areas of successful breeding, the longevity of the individuals will determine the distance which may be travelled and the relative numbers to be found in regions increasingly remote from the centers of production. The deep-water chaetognaths afford examples of this sort as do *S. serratodentata* and *S. lyra*.

In nature these biological factors are at play in a scene determined by the given hydrography of various regions. The permanence of a maximal population demands that the breeding stock shall not be scattered by the flow of water, or that such losses shall be balanced by recruitment from other rich areas. The most favorable conditions for endemic existence will be found in large areas where suitable conditions are found and in which the water remains more or less permanently. Such an area is provided by the great eddy which appears to exist on Georges Bank and here *S. elegans* maintains a dense and stable population in spite of the fact that there is little opportunity of recruitment from other regions. Russell (1936*b*) considers the source of the water which occasionally carries *S. elegans* into the English Channel to be an area of cyclonic circulation lying south of Ireland.

When opportunities for recruitment by immigration from adjoining areas are good, rich populations may be developed in regions which do not develop permanent eddies in spite of a relatively rapid dissipation, as in the case of the banks south of Cape Sable. In such areas the seasonal fluctuations become greater and increasingly so in small areas such as Massachusetts Bay in which little time is required to wash away the dense populations, as soon as the period of multiplication is passed. In such regions the population is pseudo-endemic inasmuch as it is dependent on immigration to a high degree.

Bodies of water originating in regions where a species cannot maintain a production center may acquire a population by immigration from such centers in the course of its drift. The scanty populations of *S. elegans* which are found in the waters over the central basin of the Gulf of Maine appear to be of this type. Such populations become richer the longer the water is in proximity to the source area of production. Whether the species can reproduce in the area or not, it cannot achieve significant numbers because the water moves on too rapidly to permit an accumulation. Such populations may show seasonal fluctuations reflecting the reproduction periods of the areas from which they are derived, as in the southern half of the basin.

The origin of water bodies having distinctive physical characteristics results primarily from the mixing of other characteristic waters. The formation of slope water through the admixture of tropical, boreal and coastal waters is a case in point. In its synthesis the inhabitants of the contributing regions become incorporated into it and are carried with it to regions remote from their centers of reproduction. Such immigrants, if unable to reproduce themselves, can travel only so far as their life span will permit. They may be regarded as terminal immigrants in contrast to the forms such as *S. elegans* in Massachusetts Bay which form pseudo-endemic populations in regions continuously swept out by the passing waters. *E. hamata, S. maxima* and *S. lyra* are examples of this category.

Immigrants, both terminal and pseudoendemic, may show fluctuations both as the result of the reproductive cycle and for hydrographic causes. While the fluctuation of the pseudo-endemic population of *S. elegans* in Massachusetts Bay is probably due to seasonal reproduction in an area of relatively constant dissipation by currents, a changing current pattern may contribute largely to the fluctuation of the population of this species off Cape Sable. *Limacina retroversa* fluctuates greatly in numbers in the Gulf because it enters intermittently presumably because of fluctuations in the sources of the water entering the Gulf. Though it may be classed as an unsuccessful breeder in the Gulf, the important reason for its failure to develop a truly endemic population is the rapid flow of water across the surface of the basin which carries it away following its intermittent periods of invasion. *Limacina retroversa* is thus an unsuccessful pseudo-endemic form fluctuating for hydrographic reasons.

S. serratodentata, essentially a terminal immigrant in the Gulf of Maine, fluctuates in its occurrence for reasons which appear to be largely hydrographic. Being unable to survive long after the cessation of the inflow which introduces it into the Gulf, its fluctuations so far as this area is concerned are more marked than any others. *S. enflata,* occurring as a rare straggler along the borders of the Gulf, is the extreme case of terminal immigration. Its occurrence in late summer, along with many other tropical forms, suggests a definite movement of tropical water onto our shores at that time. The water in which these forms occur does not differ from normal coastal water in salinity. Their presence is due to the admixture of exceedingly small amounts of tropical water into that of the coastal banks. Their seasonal occurrence is to be related to the annual temperature cycle of the coastal waters. Unable to survive the chilling of winter, these rare stragglers are unable to travel far from their production areas beyond the slope water until the latter part of summer.

Among the chaetognaths, only one—*S. elegans*—has established a truly endemic existence in the Gulf of Maine, and this on the coastal and offshore banks. It alone achieves important numbers for this reason, and it alone is sufficiently numerous so that nutritive conditions may limit its numbers. The other species are immigrants from other regions and occur in numbers depending on the remoteness of their areas of production and no doubt on their abundance in such regions.

We may inquire why the basin of the Gulf has acquired no successful endemic population of chaetognaths. So far as the surface waters are concerned, the answer seems to be that these circulate so rapidly that time is not permitted for the accumulation of even a considerable pseudo-endemic population. The evidence is found in the history of *Limacina retroversa* and of *S. elegans* in the southern half of the basin. In the deeper water this difficulty can scarcely obtain. These waters derived from the slope water undergo rapid modification within the Gulf by admixture with surface water and acquire lower temperatures and salinities than those characterizing the slope water at comparable depths, and lower salinities than slope water of the same temperature. The process of creating a characteristic water mass, such as the slope water is, is continuing actively in the basin of the Gulf. Perhaps for this reason no chaetognath has yet appeared capable of reproducing successfully in this unique and limited region. However this may be, it is clear that the basin of the Gulf does support a rich endemic population of Crustacea. How this is possible should be the subject of future study.

Summary

1. Data are presented concerning the distribution and numerical abundance of five species of chaetognaths taken in the Gulf of Maine during the year 1933–34 and the hydrographic features controlling their abundance is discussed.

2. It is concluded that *Eukrohnia hamata, Sagitta maxima* and *S. lyra,* which are carried into the Gulf by deep currents and do not breed there, occur in numbers which depend not only on their relative abundance in various offshore waters which mingle in the Gulf, but on their longevity after entering the Gulf.

3. *Sagitta serratodentata* is a terminal immigrant from the superficial waters of the Atlantic which fluctuates in its abundance as the result of periodic changes in the circulation of water entering the Gulf from the east.

4. *Sagitta elegans* is the only chaetognath truly endemic to the region. The permanence of its occurrence appears to depend on the presence of

a relatively stable eddy on Georges Bank. Its occurrence in other regions varies with the season to a degree which may be explained by local conditions of circulation.

5. *Sagitta enflata* is recorded for the first time from the margins of the Gulf of Maine.

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