The Distribution of Phytoplankton, and its Relationship to Hydrography, between Southern New England and Venezuela[1]

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ABSTRACT

Data obtained on numerous cruises, from southern New England to the Caribbean Sea, between September 1956 and August 1963 form the basis for this study on the relationship of flora to hydrography. Seaward from the southern New England coast, with salinity increasing, the quantity of phytoplankton in near-surface water (0–25 m) decreases while the proportion of oceanic species increases. In the Sargasso Sea, in summer, the stratification and flora are similar from north to south, but in winter, when there is a difference in stratification of the upper 200 m in the northern and southern portions, there is a parallel difference in the abundance of many species. Along the coast of Venezuela, the variation in phytoplankton correlates with the variation in upwelling. At stations near land (southern New England, Caribbean Is., and S. America), where the thermocline is more marked, the vertical distribution of plankton is more variable than in the open ocean, where lesser temperature differences occur in the upper 100 m.

Cruises and Methods. In the following paper, typical features of phytoplanktonic distribution between the coasts of southern New England and Venezuela are described. These features are related, insofar as is possible, to hydrographic features. The relationship of phytoplankton to hydrography in this area has been studied previously, but from data taken on single cruises only (Hulburt 1962, Hulburt and Rodman 1963, Hulburt 1964). In this paper, the description of features of the planktonic flora, and of hydrography, is based on data from many cruises.

Fig. 1 shows the cruises and stations involved in this study. Twenty-one crossings of the continental shelf waters off southern New England between September 1956 and August 1963 were made at Sts. A-G. Ten of these

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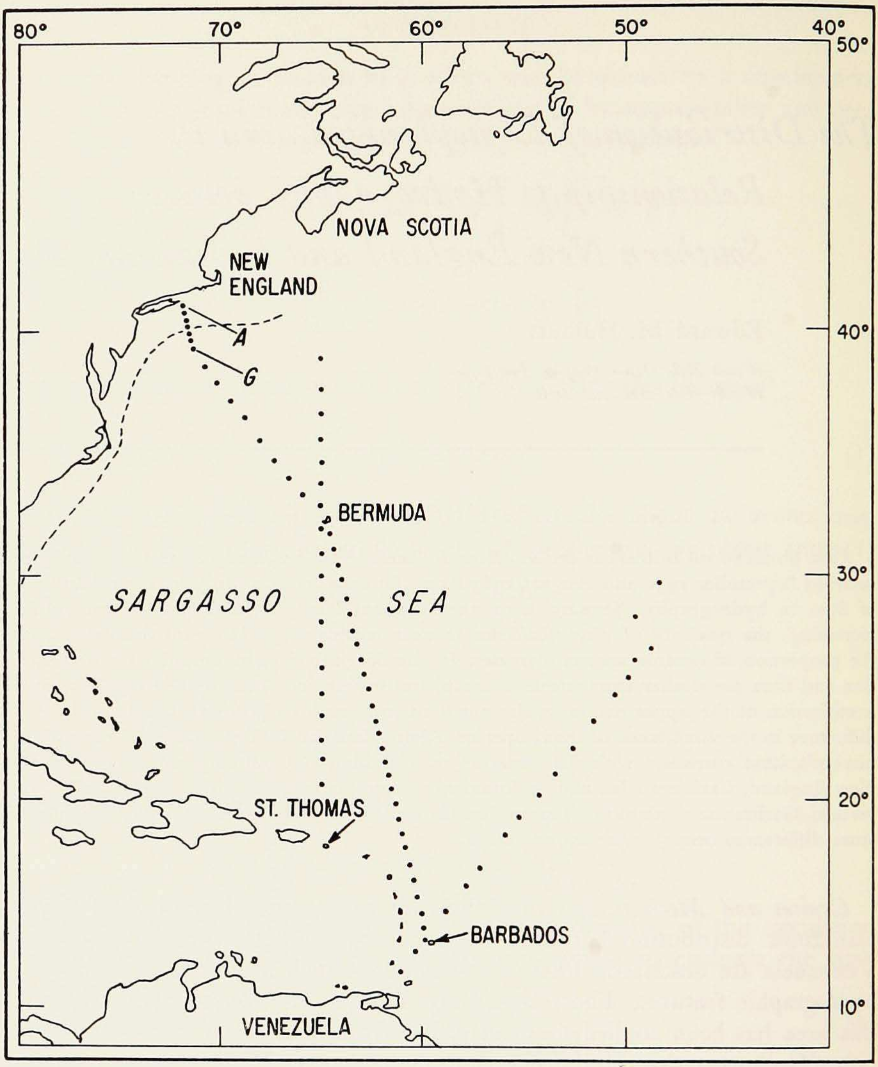

Figure 1. The western North Atlantic, showing positions of the stations occupied. Stations within the Caribbean Sea not shown.

cruises, during the years 1958–1963, extended from St. A, near the southern New England coast, to Bermuda. Another cruise, in April 1962, obtained data from Nova Scotia south to St. Thomas, and in January 1963 the southern part of this section, from Bermuda to St. Thomas, was repeated. In August 1963 a section from Bermuda to Barbados was occupied. In February 1961 a run from 30°N, 48°W ended just southwest of Barbados. Stations within

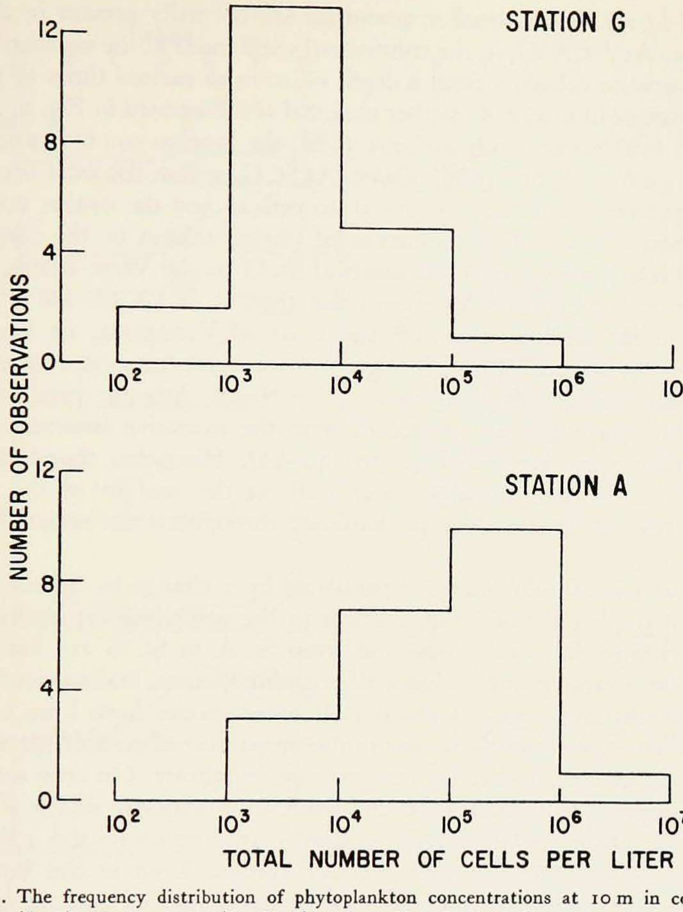

Figure 2. The frequency distribution of phytoplankton concentrations at 10 m in coastal water (St. A) and slope water (St. G) off southern New England, September 1956–August 1963.

the Caribbean Sea were occupied on only one cruise, in April and May 1962; these are shown in Fig. 5.

Most of the phytoplankton counts were made on 200-cc water samples preserved in formalin (3 parts to 100 parts of water), though a few were done aboard ship on live samples. In the preserved samples, settling of the plankton occurred, the supernatant water was sucked off, and the remaining sample was concentrated by centrifuge. The untreated samples were concentrated by centrifuge only. Cells were counted and identified in a chamber shallow enough for use with either low- or high-power objective.

Regional Differences in the Quantity of Phytoplankton, Species Composition, and Hydrography. At the northern and southern margins of the western North Atlantic, large but variable quantities of phytoplankton occur in the surface water (0–25 m). Much smaller quantities are normally present in the open-ocean area. At Sts. A-G, in the continental shelf water at the northern margin, 21 samples were collected from a depth of 10 m at various times of year, and the wide ranges in total cell number observed are illustrated in Fig. 2. At St. A, where the total water depth is about 35 m, the average count is 230 cells/cc, with a range from 6.5 to 1886 cells/cc. At St. G, where the total water depth is about 2200 m, the average count is 20 cells/cc and the counts range from 0.14 to 209 cells/cc. The abundance of phytoplankton in the Sargasso Sea (discussed later), extending from south of St. G to the West Indies, averages 3.45 cells/cc for 110 samples—even less than at St. G. Of the 43 samples collected in the shallow water off the coast of Venezuela, 10 have counts exceeding 100 cells/cc. Thus, the counts used here, taken at various seasons of the year on a path that crosses the North Atlantic gyre of circulation (Iselin 1940: 33), are in accord with the extensive observations in the South Atlantic by Hentschel (1936: 36–42). Hentschel found that large quantities of plankton usually occur only at the margin of the southern gyre and that small quantities predominate throughout the remainder of the gyre's area.

This variation in abundance is paralleled by a change in the species composition of the population. The changes in the percentage of oceanic species and the changes in salinity observed from St. A to St. G are illustrated in Fig. 3. The oceanic group includes all coccolithophores, and species belonging to the dinophycean genus *Oxytoxum*; all other species have been considered coastal. There is a seaward increase in the proportion of oceanic species, corresponding, in general, to the seaward increase in salinity. On only a few occasions, however, do the oceanic species make up a majority of the population, even at the offshore stations; for example, only seven of the 125 samples counted contained 75 °/₀ or more oceanic species. Even in the Sargasso Sea (see below), many species not included in my group of oceanic species are commonly found.

Southward, across the Sargasso Sea, there is a parallel between total abundance, species composition, and hydrography, though this parallel is of a different sort from that over the continental shelf. In Table I are shown the number of samples taken, the amount of water examined from them, the total number of cells enumerated, and the count of the more abundant species between 38°N and 34°30′N, 34°N and 30°N, 29°N and 25°N, and 24°N and 20°N. Data are grouped for cruises from December to April and from May to August. In winter there is a greater number of cells in the northern than in the southern Sargasso Sea, while in summer there is very little difference across this large section of ocean. This is the result of a seasonal change in the abundance of many of the species. In winter, 17 species are more abundant in the northern Sargasso Sea, seven are ubiquitous, and six are more abundant in the south. In late spring and summer, these differences in abun-

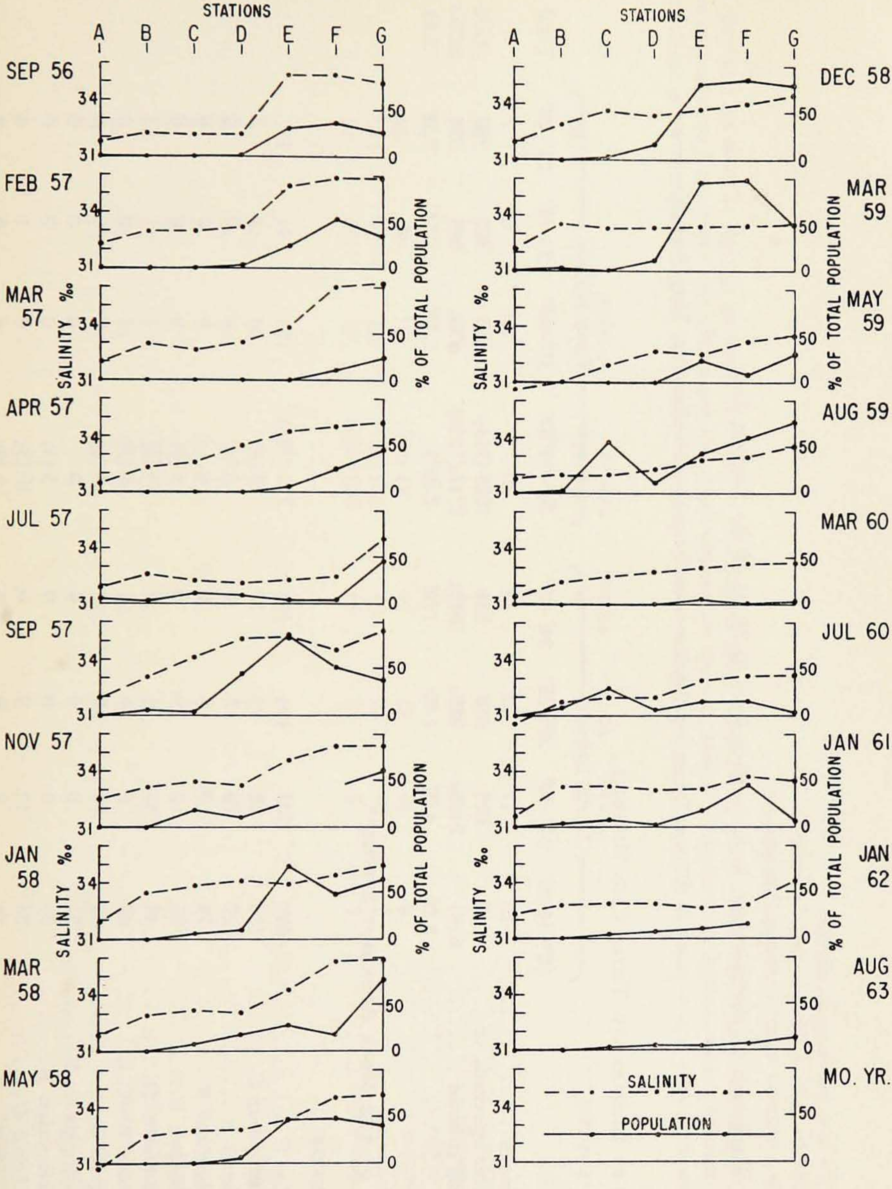

Figure 3. The relation of oceanic species, as per cent of the total cell number, to distance from shore off southern New England at 10 m. A similar relationship for salinity is shown.

Table I. The distribution of phytoplankton in the surface layer (0–25 m) of the Sargasso Sea.

	Winter, December–April				Summer, May–August				
Distribution of Samples and Total Cell Numbers	North latitude				North latitude				
	38°–34°30′	34°–30°	29°–25°	24°–20°	38°–34°30′	34°–30°	29°–25°	24°–20°	Total
Number of samples	23	17	13	14	20	10	6	7	
Amount of water searched, cc.	818	621	510	554	1028 (514)	557	300	350	4738
Number of cells counted	6781	2495	920	1017	2712 (1356)	996	549	883	16353
Cells/cc	8.29	4.02	1.80	1.83	2.64	1.79	1.83	2.52	3.45
Distribution of the More Abundant Species**									
Northern Species									
Coccolithus huxleyi C	4692	1701	194	194	725 (363)	123	41	115	
Cyclococcolithus leptoporus C	224	82	28	37	17 (8)	14	4	8	
Skeletonema costatum B	127	28	0	0	0	0	0	0	
Rhizosolenia stolterfothii B	73	9	0	0	0	0	0	0	
Nitzschia delicatissima B	56	16	0	0	5 (3)	0	0	0	
Gymnodinium punctatum D	44	35	11	7	4 (2)	1	1	3	
Nitzschia closterium B	42	6	1	1	6 (3)	1	0	0	
Cerataulina bergonii B	40	5	0	0	4 (2)	0	0	0	
Thalassionema nitzschioides B	37	0	0	0	0	0	0	0	
Bacteriastrum delicatulum B	33	9	0	0	5 (3)	0	0	0	
Thoracosphaera heimii C	33	14	9	0	10 (5)	0	1	0	
Anoplosolenia granii C	18	6	0	0	5 (3)	2	0	0	
Michaelsarsia elegans C	14	1	0	0	0	0	0	0	
Nitzschia seriata B	11	8	0	0	5 (3)	0	0	0	

Rhizosolenia delicatula B	0	22	0	0	0	0	0	0
Rhizosolenia alata B	9	0	0	0	22 (11)	1	0	0
Hemiaulus membranaceus B	3	4	0	0	11 (6)	4	0	0
UBIQUITOUS SPECIES								
Oxytoxum variabile D	25	23	32	28	76 (38)	12	12	6
Syracosphaera mediterranea C	20	10	4	18	63 (32)	70	10	10
Katodinium rotundatum D	21	24	18	50	57 (29)	21	23	29
Coccolithus pelagicus C	12	4	5	8	2 (1)	0	0	1
Oxytoxum sp. D	2	6	16	15	43 (27)	3	8	3
Hemiaulus hauckii B	1	7	12	2	6 (3)	10	40	19
Cyclococcolithus fragilis C	1	1	1	-	8 (4)	10	24	11
SOUTHERN SPECIES								
Umbellosphaera irregularis C	1	3	12	30	206 (103)	38	20	73
Discosphaera tubifer C	4	38	83	92	178 (89)	182	64	115
Syracosphaera pulchra C	0	14	47	34	87 (44)	60	62	40
Rhabdosphaera stylifer C	0	5	6	17	4 (2)	2	2	3
Calyptrosphaera oblonga C		0*	11*	12*	11*	14*	28	18
Stigmophora rostrata B	0	1	1	5	24 (12)	0	0	10
SUMMER SPECIES								
Trichodesmium thiebautii	1	0	0	0	91 (46)	1	0	140
		*203 cc	*310 cc	*304 cc	*175 cc	*400 cc		

** Values are number of cells counted in the number of cubic centimeters given above, except that bracketed values are 0.5 cell counts (making summer counts roughly comparable on a basis of cubic centimeters searched), and except that values for *Trichodesmium* are number of filaments, and except where noted by asterisks. Only species with at least one count of 10 cells or more are included.

C, represents a member of the Coccolithophoridaceae.
B, represents a member of the Bacillariophyceae.
D, represents a member of Dinophyceae.

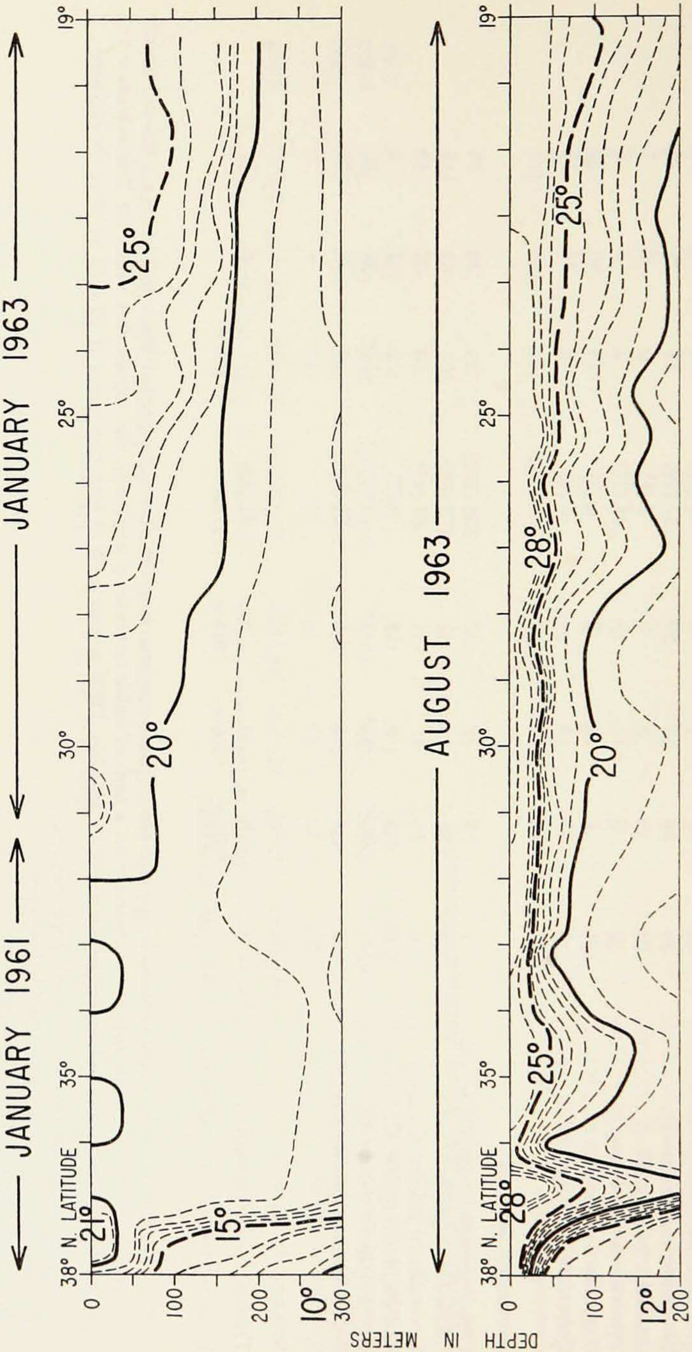

Figure 4. The temperature distribution from the Gulf Stream southward to the West Indies in winter and summer.

dance largely disappear; most of the northern forms of winter are rare and the remaining species are ubiquitous.

Many of the northern forms of winter do not fall in my category of truly oceanic species; most of these are diatoms and the most notable example is *Skeletonema costatum*—often very numerous near shore but on rare occasions observed in moderate numbers far from shore (Hulburt 1963b). But in summer the more abundant species are the oceanic coccolithophores and *Oxytoxum*; to this group should be added the blue-green alga, *Trichodesmium thiebautii*, seen in only 4 of 125 samples between Sts. A and G, and the diatoms *Stigmophora rostrata* and *Hemiaulus hauckii*, observed once and twice, respectively, across the continental shelf. The only abundant species of summer not included in the oceanic category is *Katodinium rotundatum* (synonymous with *Massartia rotundata*); this species, though well adapted to the Sargasso Sea, may become grossly abundant in estuaries (Hulburt 1956).

In Fig. 4 are presented two profiles of temperature obtained at the same time that plankton were collected. In January the water is homogeneous to 200 m in the north but is stratified in the southern Sargasso Sea; in August, stratification, though more intense than in January, extends throughout the section. These profiles typify, for winter and summer, the near-surface aspects of the seasonal hydrographic cycle—a cycle that is well described elsewhere (Iselin 1940: 21, Ryther and Menzel 1960, Menzel and Ryther 1960 and 1961, Worthington 1959) and that parallels the seasonal change in the flora.

In Fig. 5 are shown total cell counts for the Caribbean Sea and its eastern approaches. Most of the area has planktonic concentrations ranging from 1 to 10 cells/cc. However, along the Venezuelan coast, concentrations may exceed 100 cells/cc; greater concentrations along this coast than in the rest of the Caribbean Basin have previously been reported by Takano (1960). Cell numbers are greater along the eastern section of the coast, which was traversed in mid-April, than along the western section of the coast, occupied in early May. The southern end of the section from the Virgin Islands to Venezuela has greater amounts in mid-April than in May. The differences in total cell concentration are matched by changes in species composition, the productive eastern stations of April averaging 90 % coastal forms (Hulburt 1963 a) and the western stations of May averaging 67 % coccolithophores and *Oxytoxum*.

The hydrography, nutrient concentrations, and wind conditions for the Virgin Islands–Venezuela section for mid-April and early May are shown in Fig. 6. At both times, cooler, more saline, denser water rises toward the surface at the southern end of the section in accord with the current that flows westward in this part of the Caribbean Sea. Appreciable amounts of phosphorus, 0.4 μg-at/L, and of nitrogen, 5 μg-at/L, are found at 200 m in the northern part of the section but at 50 m in the southern part. This upwelling is slightly more marked in mid-April than in early May; in mid-April the wind is strong from the east, and parallel to the coast; in early May the wind is light, more

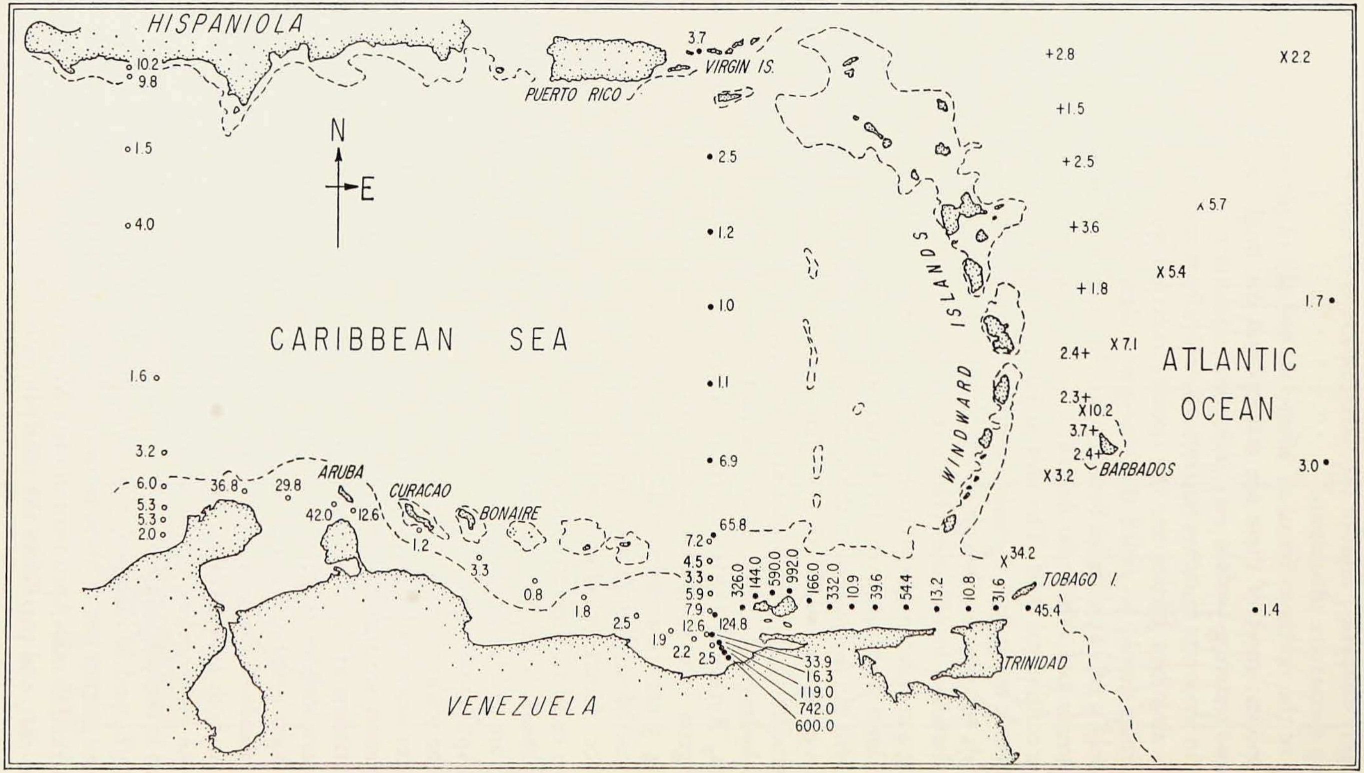

Figure 5. The total phytoplanktonic concentration, as cells per milliliter, in the Caribbean Sea and its eastern approaches. Solid points indicate stations occupied in April 1962, and circles, stations occupied in May 1962. Crosses are for August 1963 and X's for February 1961. Samples are from 0 or 10 or 25 m.

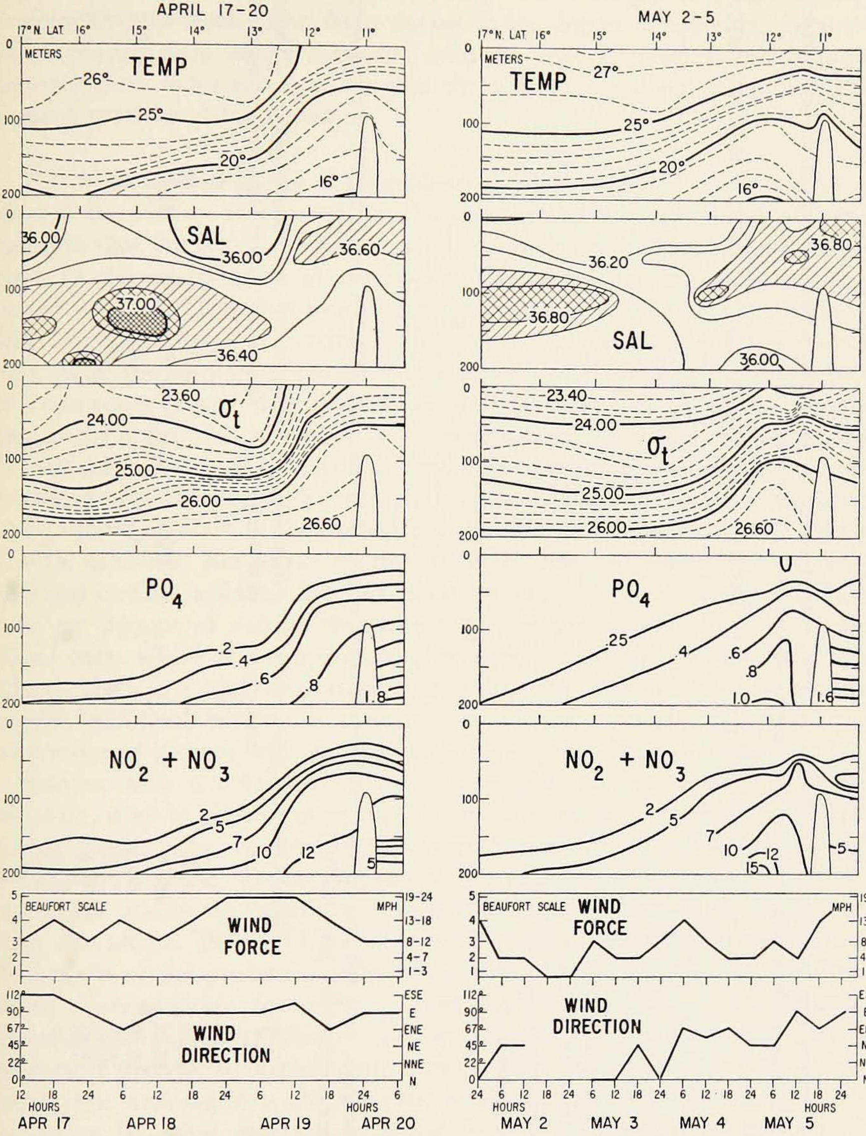

Figure 6. The distribution of properties and the strength and direction of wind from St. Thomas southward to Venezuela. Salinity in ‰; NO_2, NO_3, and PO_4, in μg-at/L of N or P.

Table II. The numbers of stations with a 1–2 fold, 2–4 fold, etc. change in cell concentration between 0 and 100 m, or between surface and bottom. Only stations with three or more depths of sampling are included.

	1–2	2–4	4–8	8–16	16–32	32–64	64–128	128–256	256–612	612–1224	1224–2448
Sargasso Sea, 38°N to 20°N......	14	10	4	2							
Continental shelf and slope water, Caribbean Sea and approaches...	5	12	7	3	6	2	1		1		1
In water with <2°C temperature difference between 0 and 100 m	16	14	4		2						
In water with a 2°–15°C temperature difference between 0 and 100 m	3	8	7	5	4	2	1		1		1

Table III. Temperature, total cell concentration, and concentration of abundant species at 39°26.5′N and 71°28.6′W, off the continental shelf of New England on July 12, 1957.

Depth (m)	Temp. (°C)	Total Cells no./cc	*Cyclococcolithus leptoporus*	*Nitzschia delicatissima*	*Leptocylindrus danicus*	Undetermined coccolithophore	*Ophiaster hydroideus*
0............	22.24	11.2	5.8	.7	0	0	0
10............	22.26	12.9	5.9	.7	0	0	0
25............	16.82	622.8	1.5	488.0	105.0	25.8	0
50............	15.80	18.5	.5	6.7	0	.8	5.4
75............	15.24	.6	.03	0	0	0	0
100............	14.81	.5	.3	0	0	0	0

northerly, and thus more onshore. In May the water at 50 m at the southern end of the section is separated from the surface by a somewhat greater density gradient than in April. The slight change in the degree of upwelling between mid-April and early May is correlated with the large difference in the plankton between these dates and thus between the populations along the eastern and western portions of the coastline.

The Vertical Distribution of Phytoplankton. An evaluation of the degree of vertical fluctuation in the total cell count in the western North Atlantic indicates that the regional differences in cell totals result from regional differences in the stratification of the water. The degree of vertical fluctuation, shown in Table II, ranges from about two-fold to a value greater than 1000-fold. Thus the greatest cell count in the water column at a given station may be only twice the minimum count at that station, or the maximum count may be 1000 times greater than the minimum at the same station. In the Sargasso Sea, in the upper 100 m, 14 out of 30 stations have a two-fold change, or less, in total cell number. Since this is an amount of variation hardly distinguishable from counting and sampling error, the plankton at half of the stations appears to be nearly uniform in its vertical distribution. No station has more than a 16-fold variation. But in the continental shelf and slope water off New England and in the Caribbean Sea and its eastern approaches, 40% of the stations have an amount of vertical fluctuation greater than 16-fold. Table II also shows that, where the temperature difference is less than 2° C in the upper 100 m, there is a high proportion of stations with slight variation in vertical counts, and that, where the temperature difference is more than 2° C, the proportion of stations with marked variation (> 16-fold) is considerable.

Stations with a difference of more than 2° C and more than a 16-fold variation, nine in all, are close to, or over, the continental shelves of neighboring coasts; there are three such stations off southern New England, five off Venezuela, and one close to Hispaniola. These nine stations have a maximum abundance within the upper 50 m, in which the upper portion of the thermocline also occurs. Table III gives the temperature, total cell density, and concentrations of the predominant species at one of these stations. In the upper 10 m, *Cyclococcolithus leptoporus* is most abundant, but at 25 m, *Nitzschia delicatissima* and *Leptocylindrus danicus* are grossly abundant and thereby produce a maximum in the total count at that depth. A change in species dominance with depth is characteristic at these nine stations. Such a vertical succession has been observed to occur even when there is no temperature gradient (Ryther and Hulburt 1960), but the degree of vertical fluctuation in the total count was much less (< 16-fold).

Below the euphotic zone (100 m at most of the stations), the plankton is less abundant—usually much less abundant—than above. Out of 35 stations, only one had a maximum cell count below 100 m.

Discussion. Hydrography serves to indicate transition from one water mass to another, as between St. A in the coastal water and St. G in the slope water (Iselin 1936: 11), and to indicate the mixing between these water masses and thus between their planktonic floras. The hydrographic structure may affect the phytoplankton directly. In the northern Sargasso Sea, the deepening of the homogeneous water with the coming of winter permits many species to become more abundant there than they are to the south, though a few are adversely affected. When summer comes again and the homogeneous layer becomes thinner, this differential effect disappears and the species assemblage in the northern Sargasso Sea is similar to that toward the south. Another direct effect is that of the nutrient-rich, cooler water upwelling toward the surface to support an abundant population, as along the Venezuelan coast. Whether the slight changes in hydrography that we have described are enough to account for the population differences observed is a point of considerable uncertainty, even though upwelling and planktonic changes appear to have occurred at the same time. The most direct effect of hydrography on phytoplankton should be in its control of the vertical distribution of the plankton. There is a tendency toward an accentuation of phytoplanktonic abundance in the upper part of the euphotic zone when a thermocline is present.

In spite of the association between planktonic distribution and hydrography, at least one feature of the phytoplankton remains unexplained. It has been pointed out that species of the Coccolithophoridaceae and the dinoflagellate genus *Oxytoxum*, the blue-green alga *Trichodesmium thiebautii*, and the diatoms *Hemiaulus hauckii* and *Stigmophora rostrata* usually make up the bulk of the species assemblage in the open ocean, where growth conditions are characteristically poor and the total number of cells is low. However, in winter in the northern Sargasso Sea, when growth conditions are somewhat improved, many of these species are matched or exceeded in abundance by coastal species, mainly diatoms. Conversely, when growth conditions are poor along the coast of Venezuela, as in the western part in May, the oceanic forms dominate. What defines the low growth potential of these oceanic species and why a low growth potential should be of advantage under poor conditions are matters of speculation and interest.

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