The Diversity of Phytoplanktonic Populations in Oceanic, Coastal, and Estuarine Regions[1]

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ABSTRACT

In the deep ocean north of Bermuda, during spring and summer, conditions for growth are poor, but physical conditions, such as high salinity and great depth, are favorable to the marine phytoplankton. The dominant species in a sample constitute a modest proportion of the cells counted, and a considerable diversity of species is observed.

When very good growth conditions, resulting in extreme dominance, are coupled with an adverse physical environment, there is a reduction in diversity. These conditions are found in several New England estuaries, where the lower salinity would appear to be unfavorable to the marine phytoplankton and where extreme shoalness may strand the larger, more rapidly settling types of diatoms.

Populations from the open ocean and coastal water off New York in fall and winter typify an intermediate situation. Moderately good growth is associated with pronounced dominance, and diversity is low in very small samples of the populations. When a large number of cells is counted, however, there exists the considerable diversity that might be expected where the salinity and depth are favorable.

Introduction. Fisher (*in* Fisher *et al.*, 1943) has presented a theory of the distribution of species in nature, and from this he derived an index by which the diversity of a population may be evaluated. Hulburt *et al.* (1960) found that the distribution of species in phytoplanktonic samples from Bermuda conformed to this theory only when growth conditions were poor. With enhanced growth and a disproportionate abundance of one species there was a divergence between the diversity predicted and that observed. In the present paper an attempt is made to show that both conformity and divergence may be utilized in furthering an understanding of the diversity of populations in various stages of growth.

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Because such an understanding is dependent on Fisher's theory and its index of diversity, the method of enumeration of these planktonic populations is a critical concern. From a broader point of view our understanding must depend on a consideration of the character of the regions where the populations live and of the type of species predominant in those habitats.

Methods. The samples from the coastal and open ocean were preserved in formaldehyde and were concentrated by settling. Some of those from the estuaries were similarly treated; others were examined in the living condition either directly or after being concentrated by centrifugation. The counting chamber is rectangular, 5 × 2 cm and 1/3 mm deep. During the examination of a single sample, counts of the species composition were recorded from each traverse of the counting chamber, a traverse being 2 cm in length and the width of the microscope's field. When the number of cells to be counted was large, the species in each microscope field were enumerated. On one occasion the species composition of a population was studied from a series of samples taken from a single station over a 24-hour period.

The Regions Investigated. A section crossing the northern part of the Sargasso Sea, the Gulf Stream, and the slope water between Bermuda and the continental shelf off New York (Fig. 1) was occupied in February, May, August, and December of 1959 and in March and August of 1960; on each cruise, 5–9 samples were taken at a depth of 10 m. Seven bimonthly cruises to the continental shelf off Long Island, New York, were made in 1956–1957, and 16–18 samples were taken on each cruise, also from a 10-m depth. Inside the southern shore line of Long Island, in Great South Bay and in Moriches Bay, stations were occupied in the summers of 1956, 1957, and 1958. At Senix Creek, a tributary arm of Moriches Bay, the water at a point two-thirds of the length of the Creek from the Bay was studied in June 1957 and 1958 and in September 1958. Near Woods Hole, Massachusetts, two embayments—Salt Pond and Uncatena Island Pond—were visited throughout the year in 1950.

South of the continental shelf the water is very deep (> 2000 m). Over the shelf in the area covered by the quadrangle of stations, the depth is between 40 and 100 m. Great South Bay, Moriches Bay, and Senix Creek are very shallow, not over 3 m; Salt Pond is of a similar depth; and Uncatena Island Pond is even shallower, nowhere exceeding 1 m.

The open ocean to the south of the continental shelf had salinities between 33.5 ‰ and 35.5 ‰ at a 10-m depth. On the shelf, salinities (at 10 m) were only slightly lower, 31.50–34.5 ‰. In Great South Bay and Moriches Bay the range was 20–30 ‰, and in Senix Creek the salinity varied with the tide from 10 ‰ to 17 ‰ in 1957, and from 14 ‰ to 26 ‰ in June 1958. The lowest values, 5–10 ‰, were in Salt Pond. Uncatena Island Pond, however, had high values, 32–33 ‰.

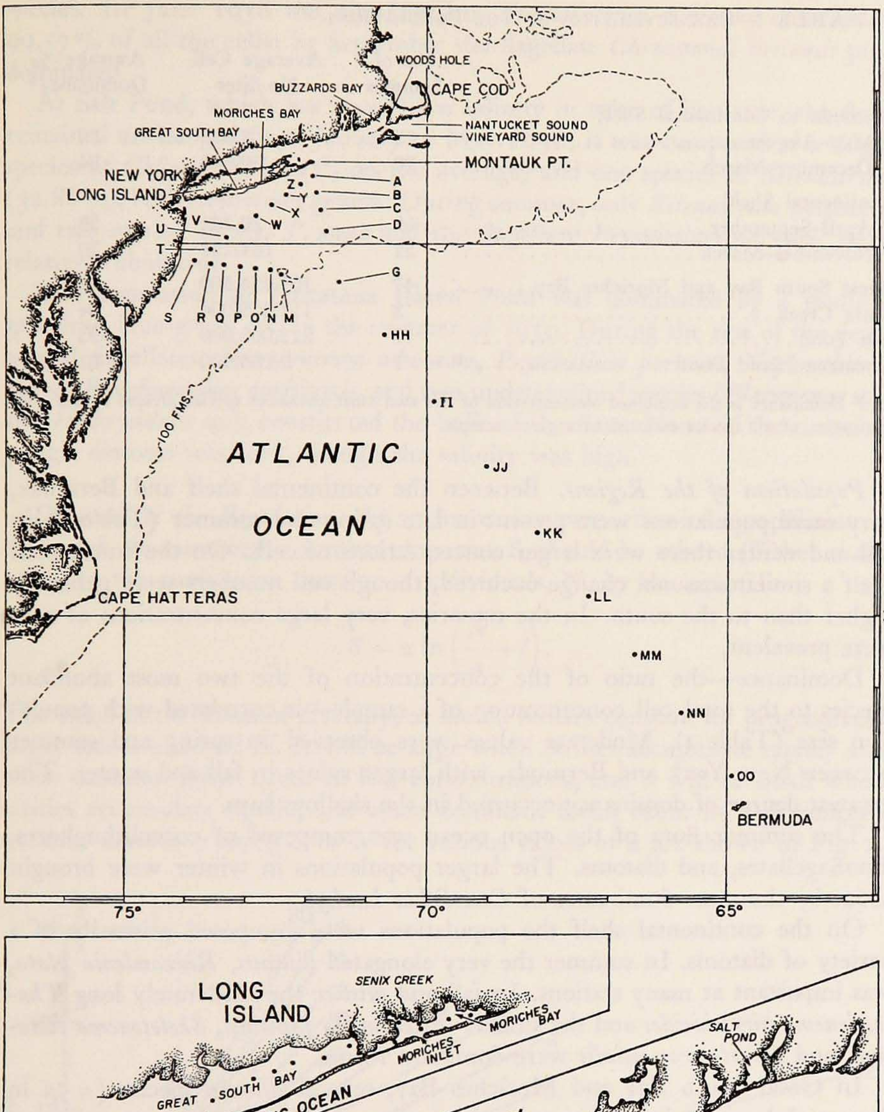

Figure 1. Stations where samples were taken.

TABLE I. CHARACTERISTICS OF THE POPULATIONS.

	No. of Samples	Average Cell No./liter	Average % Dominance*
Bermuda to Continental Shelf			
May–August	22	3,095	56
December–March	20	50,663	84
Continental Shelf			
April–September	69	20,731	58
November–March	52	164,233	70
Great South Bay and Moriches Bay	47	107,434,900	87
Senix Creek	3	114,259,000	94
Salt Pond	13	223,000,000	95
Uncatena Island Pond	7	9,206,000	81

* Dominance is the combined concentration of the two most abundant species divided by the concentration of all species counted in a given sample.

Populations of the Regions. Between the continental shelf and Bermuda, very small populations were present in late spring and summer (Table 1); in fall and winter there were larger concentrations of cells. On the continental shelf a similar seasonal change occurred, though cell numbers were generally higher than to the south. In the estuaries, very large concentrations of cells were prevalent.

Dominance—the ratio of the concentration of the two most abundant species to the total cell concentration of a sample—is correlated with population size (Table 1). Moderate values were observed in spring and summer between New York and Bermuda, with larger values in fall and winter. The greatest degree of dominance occurred in the shallow bays.

The summer flora of the open ocean was composed of coccolithophores, dinoflagellates, and diatoms. The larger populations in winter were brought about by the gross dominance of *Coccolithus huxleyi.*

On the continental shelf the populations were composed primarily of a variety of diatoms. In summer the very elongated diatom, *Rhizosolenia alata*, was important at many stations. In fall and winter the moderately long *Thalassionema nitzschioides* and the smaller *Asterionella japonica*, *Skeletonema costatum*, and *Chaetoceros socialis* were dominant forms.

In Great South Bay and Moriches Bay, several minute species ($<5\mu$ in diameter) dominated the flora—the chlorophycean *Nannochloris atomus* at some stations in 1956 and 1957, the flagellate *Calycomonas gracilis* and the diatom *Thalassiosira nana* at a number of stations in 1957, and a diatom similar to *T. nana* at many stations in 1958. The last form, abundant in Moriches Bay in June, spread to Great South Bay by September, and it became so grossly dominant as to preclude the appearance of much variety in the flora.

At Senix Creek in June 1957, *Thalassiosira nana* and an equally minute diatom, *Chaetoceros simplex*, shared dominance to the virtual exclusion of other species. In June 1958 the dinoflagellate *Prorocentrum minimum* constituted 99.57 % of all the cells; by September the flagellate *Chroomonas vectensis* predominated.

At Salt Pond, which has a very low salinity in spite of its name, the flora remained unchanged from January to May 1950; it was composed of a single species of *Chlorella* (66.72 % on the average) and one species of *Selenastrum* (32.86 %), both freshwater genera. During summer, only *Selenastrum* persisted, and two marine forms, *T. nana* and the flagellate *Prymnesium parvum*, were relatively abundant.

The population of Uncatena Island Pond was dominated by a minute, spherical, blue-green cell in the summer of 1950. During the rest of the year, several flagellates, *Prorocentrum minimum*, *Prymnesium parvum*, *Nephrochloris salina*, *Bipedinomonas pyriformis*, and two undetermined species (*Platymonas* sp., and *Isochrysidalis* sp.), constituted the bulk of the flora. None of the common pelagic diatoms was seen, though the salinity was high.

Diversity of the Population. As an increasing proportion of a population is examined, the cumulative number of species, S, should be related (Fisher *et al.*, 1943) to the cumulative number of individuals, N, by the equation

$$S = \alpha \ln \left(\frac{N}{\alpha} + l \right). \qquad (1)$$

The value of the index of diversity, α, should remain constant for progressively larger values of S and N. It will be large when rarities accumulate rapidly and when common forms occur in low concentrations, and it will be small when rarities accumulate slowly, and when dominant forms occur in high concentrations. Curves relating S to N for various values of α are shown in Fig. 2.

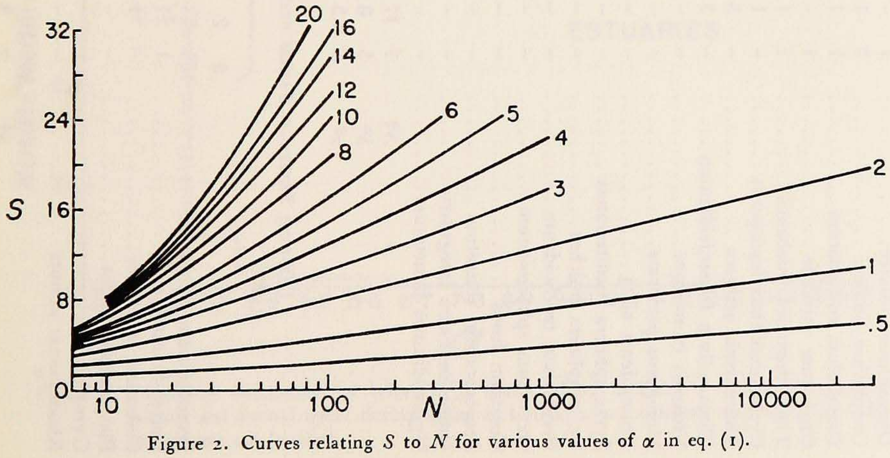

Figure 2. Curves relating S to N for various values of α in eq. (1).

TABLE II. SINGLE SAMPLE TAKEN AT ST. HH AT 10 M IN THE OPEN OCEAN, AUGUST 1959. VALUES ARE NUMBERS OF CELLS PER 3.33 CC OF OCEAN WATER.

	Traverse of Counting Chamber																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Discosphaera tubifer	1	–	–	–	1	1	2	–	1	–	1	–	–	–	–	2	–	–	1	1
Coccolithus huxleyi	3	1	2	1	5	3	3	3	2	1	–	5	2	2	–	3	4	1	6	1
Katodinium rotundatum	1	1	–	1	1	–	–	1	3	1	–	2	–	–	1	–	–	–	1	–
Oxytoxum variabile	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–
Trichodesmium thiebautii*	1	1	–	2	1	3	1	1	2	1	3	2	1	–	1	3	1	1	4	–
Cyclococcolithus leptoporus	–	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–
Rhizosolenia setigera	–	3	3	2	–	–	1	–	–	2	1	1	1	–	–	–	1	–	–	1
Climacodium frauenfeldianum	–	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia closterium	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mesoporus perforata	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata	–	–	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Syracosphaera mediterranea	–	–	–	–	–	1	–	–	1	1	1	2	1	1	–	–	–	–	–	–
Syracosphaera pulchra	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Peridinium trochoideum	–	–	–	–	–	1	–	–	–	–	1	1	–	–	1	–	–	–	–	–
Oxytoxum sphaeroideum	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Ceratium fusus	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Prorocentrum rostratum	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Umbellosphaera irregularis	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Gymnodinium punctatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
N†	7	17	26	32	42	53	61	67	77	85	93	107	113	116	119	128	135	138	151	154
S†	5	8	9	9	11	14	14	14	14	16	16	17	18	18	18	18	18	18	19	19
α	8	6.5	5.3	4.5	5.0	6.5	5.8	5.5	5.2	5.9	5.7	5.8	6.2	6.0	5.9	5.8	5.6	5.6	5.8	5.7

0.004 CC SAMPLES TAKEN FROM SENIX CREEK BETWEEN 7:00 PM JUNE 19 AND 7:00 PM JUNE 20, 1958

	Samples																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Prorocentrum minimum	165	33	79	74	127	110	19	68	169	117	20	33	174	288	166	271	41	132	42
Eutreptia marina	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cocconeis scutellum	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Platymonas suecica	–	–	–	4	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Gyrodinium glaebum	–	–	–	–	1	–	–	1	–	6	1	–	–	–	–	2	2	2	–
Rhodomonas minuta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
N†	166	201	281	359	487	597	616	685	854	977	998	1032	1206	1494	1660	1933	1976	2110	2154
S†	2	3	3	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6
α	0.4	0.7	0.6	0.8	0.8	0.8	0.8	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.6	0.6	0.6	0.6	0.6

* Values for this species refer to number of filaments. † Accumulated number of cells (*N*) and species (*S*).

Enumerations of the planktonic species in a sample from the ocean between the continental shelf and Bermuda in August (st. HH), and from a single location at Senix Creek over a 24-hour period are tabulated in Table II. The values of α read from Fig. 2 show little, if any, systematic change as species and individuals are accumulated. The lower diversity of the estuarine sample depends on a much smaller number of rare species and a much greater degree of dominance.

An oceanic sample taken in winter and one from the shelf taken in the fall are intermediate in character (Table III). Very small fractions of these samples, as represented by one or two traverses of the counting chamber, have low diversities, but when larger amounts are counted, the values of α are systematically higher. The preponderance of a single form is responsible for the appearance of so few rarities when a small number of cells is counted, as is clear from the sample from st. JJ in the open ocean. With high counts, however, there is a modest number of cells other than the dominant type, and this number may then include a considerable variety of forms. This is true both in

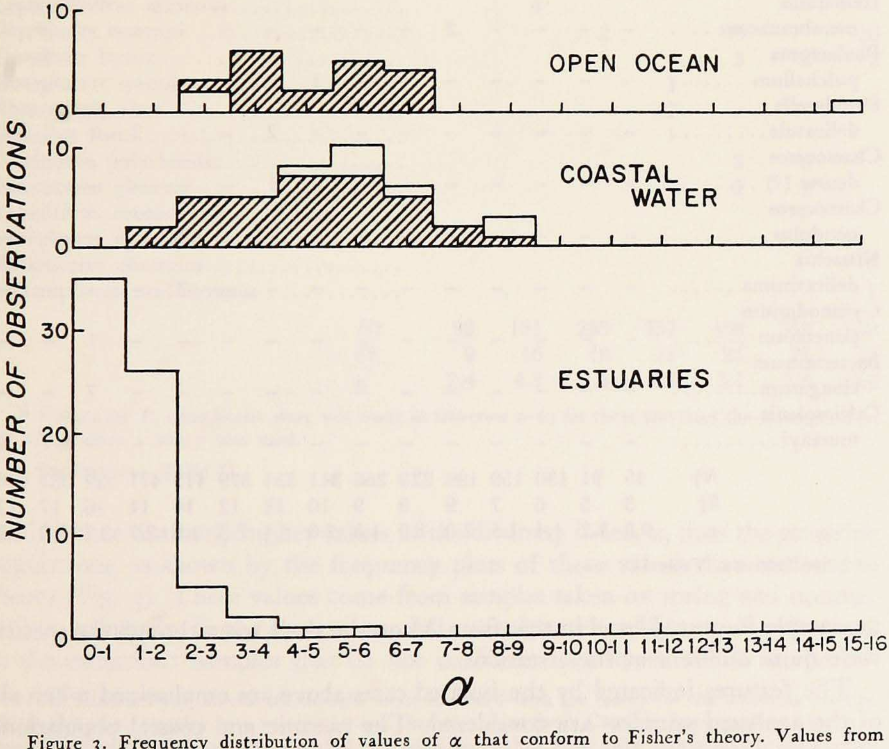

Figure 3. Frequency distribution of values of α that conform to Fisher's theory. Values from oceanic and coastal water during spring and summer are hatched; values for the other seasons are not hatched.

TABLE III. Single Sample from Oceanic St. JJ at 10 m in March 1960. Values are Number of Cells/3.33 cc.

	Traverse of Counting Chamber														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Coccolithus huxleyi	43	44	38	28	36	29	37	43	38	25	31	54	42	57	35
Umbilicosphaera mirabilis	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–
Nitzschia closterium	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Thoracosphaera heimii	–	1	–	–	–	–	1	1	1	–	–	–	–	1	1
Syracosphaera mediterranea	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–
Rhizosolenia calcar-avis	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Oxytoxum variable	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Cyclococcolithus leptoporus	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Hemiaulus membranaceus	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
Phalacroma pulchellum	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Shröderella delicatula	–	–	–	–	–	–	–	–	2	–	–	2	–	–	–
Chaetoceros densus (?)	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Chaetoceros pendulus	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Nitzschia delicatissima	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
Gymnodinium punctatum	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Bacteriastrum elongatum	–	–	–	–	–	–	–	–	–	–	–	–	7	–	–
Calciosolenia murrayi	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
N†	45	91	130	159	199	228	266	311	354	379	413	471	522	581	618
S†	3	5	6	7	9	9	9	10	12	12	14	14	16	17	17
α	0.8	1.2	1.4	1.5	2.0	1.9	1.8	2.0	2.4	2.3	2.8	2.7	3.2	3.3	3.2

† See footnote, Table II.

the sample from st. JJ and in that from M on the shelf, even though the species were quite different at these stations.

The features indicated by the isolated cases above are emphasized when all of the analyzed samples[2] are considered. The oceanic and coastal populations

[2] Only those samples with three or more traverses of the counting chamber were analyzed for the oceanic and coastal regions.

TABLE III (Continued). SINGLE SAMPLE FROM COASTAL ST. M AT 10 m IN NOVEMBER 1956. VALUES ARE NUMBER OF CELLS/3.33 CC.

	Traverse of Counting Chamber						
	1	2	3	4	5	6	7
Thalassionema nitzschioides	76	–*	–*	–*	–*	–*	58
Nitzschia closterium	4	2	1	2		3	
Prorocentrum micans	1						
Coscinodiscus excentricus	1			2		2	
Thalassiosira nordenskiöldii	3	4	9	12	4	5	1
Nitzschia delicatissima	2		1	2			
Asterionella bleakleyi	8	2	2	2	2	4	
Coscinodiscus marginatus	2			1		1	
Streptotheca tamensis	1						
Gyrosigma sp.		1	1		1		
Chaetoceros afinis		1					
Oxytoxum variable		1					
Rhizosolenia imbricata v. shrubsolei		1					
Dictyocha fibula		1					
Thalassiosira decipiens		2			1		
Leptocylindrus minimus		1					
Coscinosira oestrupi			2		14		10
Corethron hystix			1		3	2	2
Distephanus speculum				1			
Rhizosolenia alata				2			
Ceratium fusus				1			
Coscinosira polychorda					8	6	
Chaetoceros glandazi					2	1	
Katodinium rotundatum						1	
Distephanus speculum						1	
Skeletonema costatum							6
Syracosphaera mediterranea							1
N†	98	181	265	357	459	552	639
S†	9	16	18	21	23	25	27
α	2.4	4.3	4.4	4.9	5.1	5.3	5.8

* Counts for *T. nitzschioides* were not made in traverses 2–6; for these traverses the average value, 67, of traverses 1 and 7 was used.

† See footnote, Table II.

tend to have distinctly higher values of the diversity index, α, than the estuarine populations, as shown by the frequency plots of those values that conform to theory (Fig. 3). These values come from samples taken on spring and summer cruises, primarily, in the open ocean and coastal water, and from all collections in the estuaries.[3] Samples that do not conform have lower values at the be-

3 The estuarine populations are thought to be in accord with the theory for the following reasons. Thirty-five of 70 samples have values of α less than one, as at Senix Creek in June 1958, and in 10 of these 35, enough water had been searched to contain more than 2000 cells, approximately the number counted at Senix Creek. Furthermore, six samples from Salt Pond, taken during winter when there was no change in the flora, show no increase in α when species and individuals are accumulated.

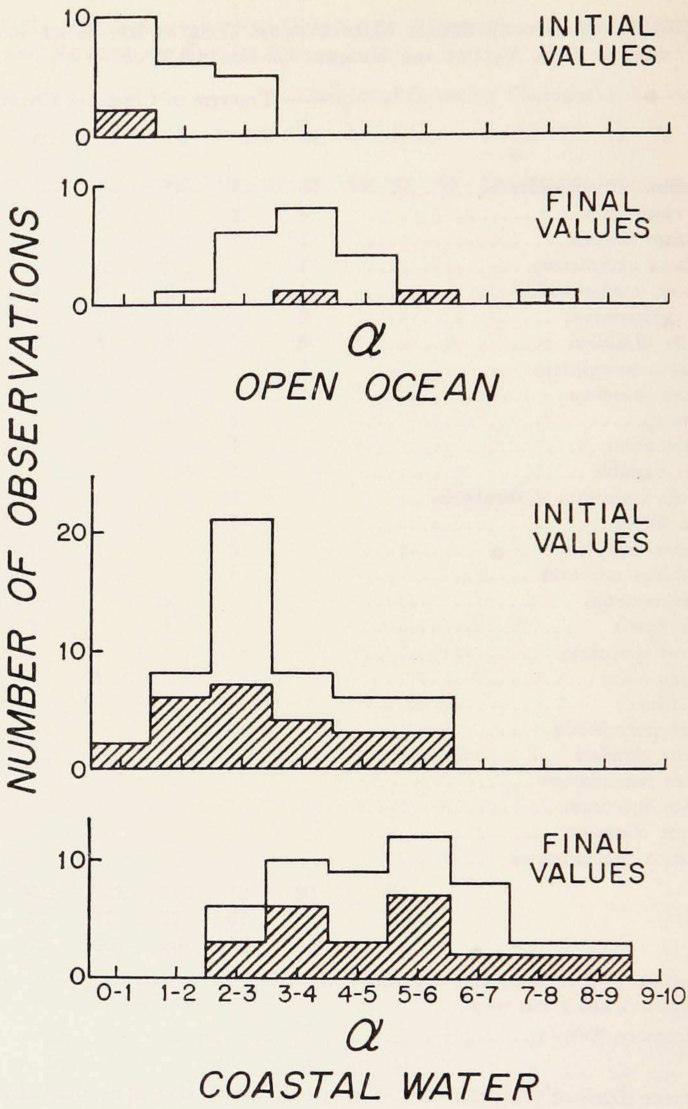

Figure 4. Frequency distribution of values of α that do not conform to Fisher's theory. Spring and summer values are hatched; fall and winter values are not hatched.

ginning of the count, after one traverse of the counting chamber, and have higher values at the end, after several or many traverses (Fig. 4). These samples are more frequent in the fall and winter than in spring and summer in the open ocean, and they are about equally frequent throughout the year in the continental shelf water.

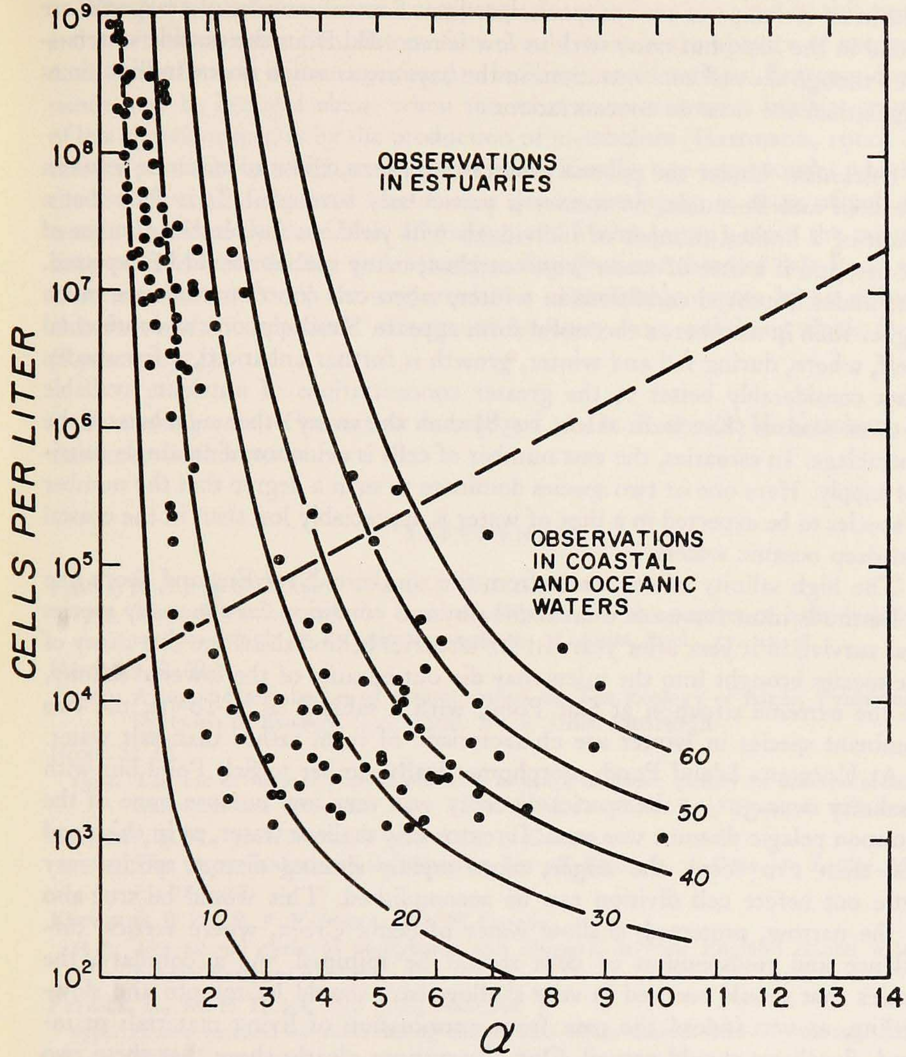

Figure 5. The relation of population size to diversity. Curved lines indicate 10, 20, 30, etc. species per liter derived for various values of cell number and α from eq. (2).

Relation of Diversity to Population Size. Values of α that conform to theory are inversely related to population size, as shown in Fig. 5. Hypothetical lines have been drawn to show how α would change for uniform growth of a population of 10, 20, 30, etc. species per liter. The observations from the coastal and oceanic waters lie predominantly within the envelope characterizing 20–60 species per liter, whereas those from the Bay waters lie almost completely within an envelope of 10–30 species per liter. Several samples of 10 species are found in the bays, but none with so few is recorded from the outside waters—even though the cell concentrations in the bays are as much as one million times larger than the oceanic concentrations.

Discussion. Under the poorest growth conditions, those of summer between the shelf and Bermuda, no species is particularly successful. It is then that a count of a limited number of individuals will yield a considerable number of species, and if a liter of water were searched, many species would be expected. But under improved conditions in winter, when cell concentrations are much higher than in summer, a successful form appears. Similarly, on the continental shelf, where, during fall and winter, growth is further enhanced, a few species react considerably better to the greater concentrations of nutrients available at those seasons (Ketchum *et al.*, 1958) than the many other members of the assemblage. In estuaries, the vast number of cells is evidence of an ample nutrient supply. Here one or two species dominate to such a degree that the number of species to be expected in a liter of water is appreciably less than in the coastal and deep oceanic waters.

The high salinity of the water from the southern New England shore line to Bermuda must represent a favorable physical condition for the many species that survive in it year after year. In the estuaries behind the shore line many of the species brought into the inlets may die out because of the lowered salinity. In the extreme situation at Salt Pond, with a salinity of 5–10‰, the two dominant species in winter are characteristic of fresh rather than salt water.

At Uncatena Island Pond, morphometrically similar to Salt Pond but with a salinity over 30‰, the species diversity was very low because none of the common pelagic diatoms was seen. In extremely shallow water, as in this pond (less than 1 m deep), the larger, more rapidly sinking diatom species may settle out before cell division can be accomplished. This would be true also in the narrow, protected, shallow water of Senix Creek, where vertical turbulence and resuspension of cells should be minimal. As a corollary, the species that should succeed in very shallow bays should be minute and slow-settling, as was indeed the case from examination of living material; or instead, flagellates should prevail. Our observations clearly show that these two types dominate.

Populations under moderately good growth conditions and under no limitation with regard to salinity and depth should have characteristics of both estuarine and deep-water summer plankton. It is quite reasonable, therefore, that on many occasions very small samples from the shelf water and deep ocean in winter should have low diversities, since availability of nutrients produces a preponderance of one or two forms; and larger samples (higher counts) should have higher diversities, because the salinity and depth conditions are favorable to an array of many planktonic forms.

Whether or not there is true competition in the bays observed in this study, and whether or not a rich diatom flora would exist in the absence of excessive dominance by one or two species, are baffling considerations. Extreme dominance may be brought about when the most numerous form inhibits growth of less abundant species by the production of metabolites (Hartmann, 1960) . . . this is a point about which we may speculate. Finally, one may wonder whether the low diversities reported here have a genesis analogous to those of polluted waters described by Patrick *et al.* (1954) and Hohn (1959), since the populations of Great South Bay and Moriches Bay (but not those of Salt Pond and Uncatena Island Pond) are supported to a considerable degree by an effluent rich in several compounds of organic nitrogen from adjoining duck farms (Ryther, 1954).

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REFERENCES

FISHER, R. A., A. S. CORBET, AND C. B. WILLIAMS
1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol., *12:* 42–58.

HARTMAN, R. T.
1960. Algae and metabolites of natural waters *in* The Ecology of Algae, Pymatuning Symposia in Ecology, Spec. Publ. No. 2, Univ. Pittsburgh.

HOHN, M. H.
1959. The use of diatom populations as a measure of water quality in selected areas of Galveston and Chocolate Bay, Texas. Publ. Inst. Mar. Sci., Texas, *6*: 206–212.

HULBURT, E. M., J. H. RYTHER, AND R. R. L. GUILLARD
1960. The phytoplankton of the Sargasso Sea off Bermuda. J. Cons. int. Explor. Mer, *25*: 115–128.

KETCHUM, B. H., R. F. VACCARO, AND N. Corwin
1958. The annual cycle of phosphorus and nitrogen in New England coastal waters. J. Mar. Res., *17*: 282–301.

PATRICK, R., M. H. HOHN, AND J. H. WALLACE
1954. A new method for determining the pattern of the diatom flora. Notul. nat. Acad. Philad., *259*: 1–12.

RYTHER, J. H.
1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. Biol. Bull., Woods Hole, *106*: 198–209.