

# YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

## JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.  
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



# *Species Diversity in Net Phytoplankton of Raritan Bay<sup>1</sup>*

Bernard C. Patten

*Virginia Institute of Marine Science  
College of William and Mary  
Gloucester Point, Virginia*

---

## ABSTRACT

The annual diversity cycle in Raritan Bay net phytoplankton is described, using entropy-related diversity indices. A theory of diversity change during succession is developed. Mean diversity levels in the estuary increased downbay in association with diminishing pollution, and the spatial pattern was strikingly related to general patterns of water mass circulation.

*Introduction.* An ecological community may be defined simply as any aggregation of mixed taxa, and particular attention to its composition may raise the question: how are the individuals distributed amongst the species? This is the *diversity* problem. The present study is concerned with the annual cycle of species diversity in the net planktonic flora of Raritan Bay.

The numbers of species ( $m$ ) and the total individuals ( $N$ ) determine the range of diversity available to a community. The extremes are (i) all individuals belong to one species ( $m = 1$ ); (ii) every individual belongs to a different species ( $m = N$ ). Between these lies a number of possibilities, determined by the values of  $m$  and  $N$ .

A number of approaches to the diversity problem have been proposed, for example, by Gleason (1922), Fisher *et al.* (1943), Preston (1948), Goodall (1952), Williams (1952), and Koch (1957). Margalef (1956, 1957, 1958a, 1958b) has advocated using an entropy measure, and this is the approach taken here. The following derivation of such a diversity index is after Branson (1953) and Brillouin (1956).

A mixed species population in a biotope space consists of  $n_1, n_2, \dots, n_i, \dots, n_m$  individuals of  $m$  different types, the total number being

<sup>1</sup> From a dissertation presented to the Graduate Faculty of Rutgers University in candidacy for the degree of Doctor of Philosophy, 1959.

$$N = \sum_{i=1}^m n_i. \quad (1)$$

The probability of selecting in sampling a species of  $i$ -th type is

$$p_i = n_i/N, \quad (2)$$

where

$$\sum_{i=1}^m p_i = 1.$$

The permutations of  $N$  objects having  $n_1$  elements alike of one kind,  $n_2$  elements alike of a second kind, and so on for  $m$  kinds, are

$$NP_{n_1, n_2, \dots, n_m} = \frac{N!}{n_1! n_2! \dots n_m!} = \frac{N!}{\prod_{i=1}^m n_i!}. \quad (3)$$

If each permutation is equally probable, then the Boltzmann equation from statistical mechanics gives the entropy of the aggregation as

$$H = k \log P, \quad (4)$$

or, from (3),

$$H = k \left[ \log N! - \sum_{i=1}^m \log n_i! \right]. \quad (5)$$

Assuming a reasonably large sample, the logarithms of the  $\Gamma$  functions may be approximated by Stirling's formula:

$$\log \Gamma(z+1) = \log z! = z(\log z - 1). \quad (6)$$

Eq. (5) then becomes

$$\begin{aligned} H &= k \left[ N(\log N - 1) - \sum_{i=1}^m n_i (\log n_i - 1) \right] \\ &= k \left[ N \log N - N - \sum_{i=1}^m n_i \log n_i + \sum_{i=1}^m n_i \right] \\ &= -k \left[ \sum_{i=1}^m n_i \log n_i - N \log N \right] \\ &= -k \left[ \sum_{i=1}^m n_i \log \frac{n_i}{N} \right], \end{aligned} \quad (7)$$

and the mean entropy per individual is



$$\bar{H} = -k \left[ \sum_{i=1}^m \frac{n_i}{N} \log \frac{n_i}{N} \right], \quad (8)$$

or, from (2)

$$\bar{H} = -k \sum_{i=1}^m p_i \log p_i \quad (9)$$

(Shannon, 1948; Wiener, 1948). If base 2 logarithms are used, the entropy is expressed as binary digits (*bits*), one bit representing the information required to make a choice between two equally probable alternatives.

The variables  $H$  and  $\bar{H}$  possess a number of properties which make them reasonable measures of species diversity. If all the  $p_i$ 's except one are zero ( $m = 1$ ), the outcome of sampling is certain and  $H$  vanishes ( $H_{\min} = 0$ ). At the other extreme ( $m = N$ ), where uncertainty is greatest,  $H$  is maximal ( $H_{\max} = \log N!$ ). Least diversity when  $m > 1$  corresponds to the situation where all individuals except ( $m - 1$ ) belong to a single species, and the remainder are distributed one each to the other species:

$$H_{\min} = k \{ \log N! - \log [N - (m - 1)]! \}. \quad (10)$$

Any change toward equalization of the  $p_i$ 's increases  $H$ , resulting in maximum diversity whenever  $n_i \geq 1$  when the individuals are equally apportioned among the species, thereby minimizing the second term of

$$H_{\max} = k [\log N! - m \log (N/m)!]. \quad (11)$$

The position of  $H$  in the range between  $H_{\max}$  and  $H_{\min}$  is denoted by the *redundancy*, which we define here to be

$$R = \frac{H_{\max} - H}{H_{\max} - H_{\min}}. \quad (12)$$

The following table illustrates some of the properties of  $\bar{H}$  and  $R$  which make them satisfactory extensive and intensive (respectively) expressions for diversity.

Species	Communities										
	(N = 6)										
	A	B	C	D	E	F	G	H	I	J	K
$s_1$ . . . . .	1	2	2	3	2	3	4	3	4	5	6
$s_2$ . . . . .	1	1	2	1	2	2	1	3	2	1	—
$s_3$ . . . . .	1	1	1	1	2	1	1	—	—	—	—
$s_4$ . . . . .	1	1	1	1	—	—	—	—	—	—	—
$s_5$ . . . . .	1	1	—	—	—	—	—	—	—	—	—
$s_6$ . . . . .	1	—	—	—	—	—	—	—	—	—	—
$\bar{H}$ (bits) . . . .	2.58	2.25	1.93	1.79	1.61	1.47	1.25	1.00	0.92	0.65	0.00
$R$ . . . . .	0.00	0.13	0.25	0.30	0.38	0.43	0.52	0.61	0.64	0.75	1.00

Note how  $\bar{H}$  vanishes as the probability of selecting a particular species becomes a certainty, and increases the more uncertain the choice becomes.  $R$ , on the other hand, is maximal when no choice exists and disappears when there is most choice. The fact that one bit constitutes a binary choice between two equally probable alternatives is illustrated by community  $H$ .

Diversity indices permit large amounts of information about numbers and kinds of organisms to be succinctly, if implicitly, summarized. More than this, they allow direct study of communities *at* the community level. Detailed analysis at the species level of cumbersome lists which summarize the same information more explicitly is obviated. If details are required, however, they can be evinced readily by traditional methods. It is the purpose of this paper to illustrate how  $H$  and  $R$  may be employed as *bona fide* ecological variables to describe changes in community composition and to denote successional status precisely and unambiguously.

The study is based on net phytoplankton collections made in Raritan Bay from July 1957 through September 1958. Since the emphasis was to be more methodological than descriptive, the total phytoplankton were partitioned for convenience in a repeatable, if arbitrary, manner to obtain a study unit which was discrete, if also arbitrary. This unit, the *net phytoplankton*, is defined to include all recognizable forms which remained in a preserved sample.

*Methods.* Six sampling stations were established in Raritan Bay (Fig. 1). Hydrographic observations included temperature, salinity, turbidity and dis-

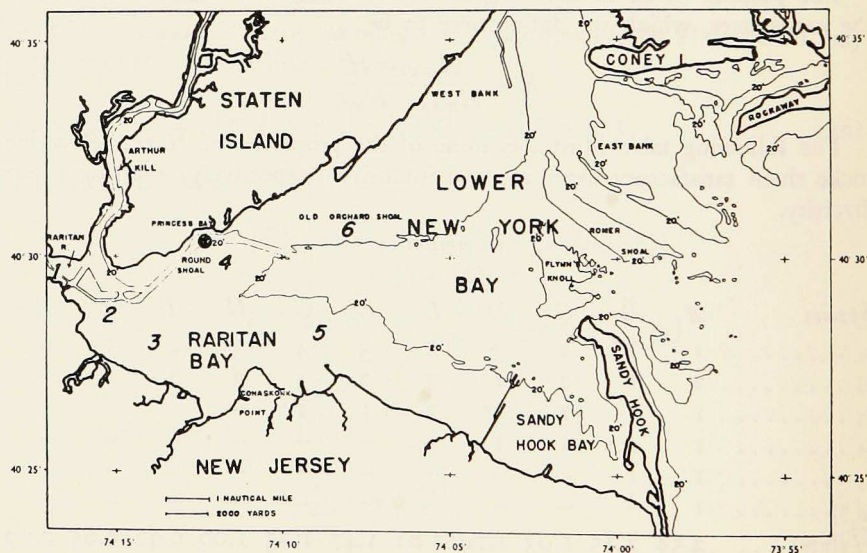


Figure 1.



solved oxygen. Nitrate and orthophosphate were determined. The net phytoplankton were sampled by oblique hauls of 90 seconds duration with a Clarke-Bumpus sampler to which a no. 20 net was attached. The samples were preserved in approximately 3% unneutralized formalin. Physical units (chains, colonies or individual cells) were counted in a Sedgwick-Rafter chamber and results tabulated as *units,  $n_i$* , of each species per liter. Diversity indices were computed from equations (5), (10), (11), and (12) with an IBM Type 650 Data Processing Machine at the Rutgers University Computation Center.

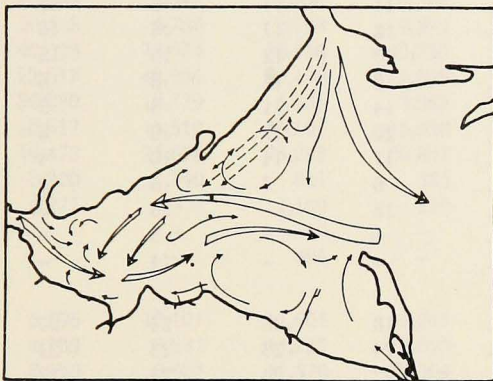


Figure 2.

*The General Circulation.* Water mass movements in the estuary have been discussed by Ayers *et al.* (1949), and hydrographic and nutrient details have been given by Jeffries (1959, 1961) and Patten (1959). The main source of fresh water is the Raritan River (highly polluted before the opening of a trunk sewer in 1959), exchange between the Hudson River and Raritan Bay being impeded by a sluggish eddy at Old Orchard Shoal. Sea water, diluted by discharge of the Hudson into Lower Bay, enters the Raritan between Sandy Hook and Romer Shoal. Moving westward along the Staten Island shore, it thrusts southwestwardly in the vicinity of Princess Bay to a point just west of Conasskonk Point. This tongue is presumed to accelerate the seaward movement of fresher water along the south shore while damming back low salinity water accumulated at the head of the Bay. These general relationships are diagrammed in Fig. 2.

*The Flora.* During this study 133 taxa were identified in the net phytoplankton. (A list with record of monthly occurrence is available from the author upon request.) In Table I, the numbers of taxa (*m*) recorded on each sampling date are given. Total units (*N*) per liter are listed in Table II. Table I indicates (i) generally fewer species downbay, presumably due to mixtures of

TABLE 1. RECORD OF THE NUMBER OF TAXA (*m*) RECORDED IN THE NET PHYTOPLANKTON AT STS. 1-6.

Date	Stations					
	1	2	3	4	5	6
1957						
Jul 5.....	-	3	7	-	-	-
11.....	14	13	9	6	8	6
18.....	11	12	7	8	-	-
26.....	5	-	9	6	9	9
Aug 1.....	15	-	9	-	10	13
8.....	11	11	18	15	17	18
15.....	18	17	15	16	-	-
21.....	10	12	13	16	16	9
29.....	18	11	8	16	11	11
Sep 14.....	14	11	5	5	7	6
24.....	20	17	10	6	9	13
Oct 8.....	17	14	10	4	11	13
29.....	8	7	5	4	4	15
Nov 11.....	18	-	10	8	9	9
26.....	-	-	5	-	5	-
Dec 17.....	-	-	14	-	15	-
1958						
Jan 20.....	18	25	24	21	22	25
Feb 6.....	24	23	23	21	20	19
Mar 1.....	27	24	24	13	18	18
11.....	21	21	17	17	16	18
25.....	23	22	18	11	19	18
Apr 10.....	26	20	20	16	20	20
24.....	25	20	12	-	14	11
May 10.....	15	16	8	14	12	10
30.....	23	22	16	9	12	14
Jun 23.....	18	14	13	14	17	15
Jul 7.....	10	8	10	11	13	15
24.....	10	11	9	12	12	10
Aug 11.....	9	10	8	8	7	-
21.....	6	9	7	10	11	16
Sep 11.....	22	19	20	12	-	-

brackish and salt water populations in the headwaters, (ii) maximum values of *m* during early spring, with a secondary pulse in late summer, and (iii) smallest species numbers in autumn following the summer bloom, and in early summer following the spring bloom (Table II).

The net flora may be grouped into four associations based on seasonal distribution patterns:

1) *Constants*, collected the year round. The three major species were *Coscinodiscus asteromphalus* Ehrenberg, *C. subtilis* Ehrenberg and *Lithodesmium undulatum* Ehrenberg, all of which have similar habitat preferences: temperate or south temperate, and neritic, although *C. subtilis* is a low-salinity form.



TABLE II. RECORD OF THE TOTAL NUMBER OF COUNTING UNITS (N) PER LITER OF ALL NET PHYTOPLANKTON TAXA AT STS. 1-6.

Date		Stations					
		1	2	3	4	5	6
1957							
Jul	5.....	-	3,771	4,494	-	-	-
	11.....	5,660	9,501	7,057	4,458	3,531	5,967
	18.....	27,730	23,104	19,646	6,690	-	-
	26.....	56,511	-	21,134	39,180	12,588	5,727
Aug	1.....	170,922	-	16,382	-	19,615	3,877
	8.....	13,108	2,362	7,636	6,328	73,846	7,563
	15.....	10,146	4,780	2,933	9,371	-	-
	21.....	40,028	73,674	76,118	43,738	118,163	12,571
	29.....	22,617	42,984	31,129	2,608	29,382	255,718
Sep	14.....	30,830	10,729	3,551	3,369	949	5,569
	24.....	18,817	15,510	40,107	15,920	10,592	15,120
Oct	8.....	16,473	25,875	25,292	20,847	16,611	5,250
	29.....	3,208	1,740	621	335	175	1,595
Nov	11.....	3,875	-	1,139	239	1,098	125
	26.....	-	-	240	-	757	-
Dec	17.....	-	-	495	-	788	-
1958							
Jan	20.....	5,986	12,101	11,604	16,245	7,649	17,998
Feb	6.....	7,289	8,631	17,225	13,055	22,101	10,387
Mar	1.....	2,950	6,427	11,570	27,064	10,152	16,243
	11.....	94,290	193,764	236,128	296,942	331,594	288,843
	25.....	46,041	61,161	105,141	326,162	303,609	360,260
Apr	10.....	86,115	125,129	84,056	141,710	133,855	134,032
	24.....	117,046	1,289,403	2,377,179	-	1,392,188	1,360,673
May	10.....	603	466	167	228	360	298
	30.....	3,050	1,530	1,586	6,347	6,046	6,018
Jun	23.....	15,903	2,718	15,240	6,303	18,490	3,454
Jul	7.....	33,408	41,912	30,174	114,887	100,903	93,395
	24.....	21,004	36,401	25,443	50,999	44,209	80,946
Aug	11.....	42,064	73,484	88,325	50,501	56,514	-
	21.....	1,548	4,999	7,995	7,200	2,785	23,499
Sep	11.....	11,815	21,118	3,851	5,649	-	-

2) *Vernal-serotinal species*, present bimodally in spring and late summer. The four most important species were *Skeletonema costatum* (Greville) Cleve, *Thalassiosira gravida* Cleve, *Chaetoceros decipiens* Cleve, and *Gyrosigma acuminatum* (Kützing) Cleve, which range in preferences from fresh water (*Gyrosigma*) to oceanic (*Chaetoceros*); most are species of the northern seas, except *Gyrosigma*, a temperate form.

3) *Serotinal species*, collected in late summer. The most abundant were *Nannochloris atomus* Butcher, *Prorocentrum micans* Ehrenberg, *Peridinium trochoideum* (Stein) Lemmermann, *P. breve* Paulsen, and *P. divaricatum* Meunier, which, with the exception of *Nannochloris*, are dinoflagellates.



These are neritic or estuarine forms with preference for low salinities, excepting *Prorocentrum*, which tolerates oceanic salinity.

4) *Hiemal species*, dominant in winter. The winter flora is diatomaceous, the most important species being *Nitzschia seriata* Cleve, *Leptocylindricus danicus* Cleve, *Rhizosolenia setigera* Brightwell, *R. imbricata* Cleve, *R. alata* Brightwell, *Asterionella japonica* Cleve, *Thalassionema nitzschioides* Grunow, *Guinardia flaccida* (Castracane) Peragallo, *Melosira sulcata* (Ehrenberg) Kützing, and *Actinoptychus undulatus* (Bailey) Ralfs, which are neritic or oceanic and typical of northern areas, excepting *Asterionella*, a south temperate form.

The obvious seasonal gaps in the foregoing classification were occupied by two nannoplanktonic associations: 1) *Aestival species* of early summer, dominated by the small dinoflagellate *Massartia rotundata* (Lohmann) Schiller; and 2) *Autumnal species*, also dominated by a dinoflagellate, the colorless *Oxyrrhis marina* Dujardin.

The two most significant species in the estuary were *Skeletonema costatum* and *Nannochloris atomus*. The former dominated the spring bloom, achieving a maximum of  $17.3 \times 10^6$  units/L on March 11 at st. 5. Conover (1956) has recorded  $35 \times 10^6$  cells/L for Long Island Sound. Since a *Skeletonema* unit, as used here, probably averages 6–10 cells or more, it seems that the Raritan maximum is at least 3–5 times greater than that of Long Island Sound. With respect to sheer numbers of cells, and possibly also with respect to contribution to total productivity of the estuary, the chlorophyte *Nannochloris* is probably the most important single phytoplankton. The highest concentration recorded was  $57.3 \times 10^7$  units/L (unfiltered, fresh sample) on August 11, 1958, more than half of Ryther's (1954) record of  $10^9$  "small forms" (*Nannochloris* and *Stichococcus*) in nearby Moriches Bay.

Summarizing the annual succession of communities, diatoms dominated the cold-water floras while phytoflagellates and *Nannochloris* were dominant during the warmer seasons. Hence, from termination of the spring diatom maximum until midautumn, the most important forms were nannoplanktonic flagellates and *Nannochloris*. From autumn until termination of the spring flowering, diatoms prevailed.

*Annual Diversity Cycle.* In describing the annual cycle of diversity, both *H* and *R* will be reported together in a decimal notation. In 1133.41, for instance, the digits to the left of the point (1133.) denote *H* in bits/L while those to the right (.41) represent the redundancy. Data from the six Raritan sampling stations are reported in this manner in Table III, which shows that, during the study period, *H* varied from 87 bits/L in November to 487,220 in April while *R* ranged from 0.99 in October to 0.17 in May. The annual cycle may be divided into four periods.

TABLE III. DIVERSITY AND REDUNDANCY OF NET PHYTOPLANKTON AT STS. 1-6. THE DIGITS TO THE LEFT OF THE DECIMAL POINT REPRESENT H IN bits/L; THOSE TO THE RIGHT DENOTE R.

Date	Stations					
	1	2	3	4	5	6
1957						
Jul 5.....	-	309.95	262.98	-	-	-
11.....	4,952.78	1,597.96	3,004.87	2,455.79	904.92	869.95
18.....	2,550.97	1,569.98	3,941.93	3,991.80	-	-
26.....	4,057.97	-	3,097.96	8,461.92	1,796.96	8,944.51
Aug 1.....	30,379.95	-	5,220.90	-	10,389.84	7,959.45
8.....	9,202.80	4,965.39	13,530.52	12,346.50	159,045.47	20,890.34
15.....	10,345.76	10,055.49	8,481.26	24,156.46	-	-
21.....	41,712.69	131,544.50	138,640.51	58,601.67	108,023.77	12,183.70
29.....	46,251.51	34,119.77	12,592.87	5,345.49	19,118.81	51,181.94
Sep 14.....	4,857.96	2,322.94	2,082.75	2,798.65	656.77	6,774.53
24.....	5,190.94	6,082.91	3,102.98	1,960.95	2,068.94	5,862.90
Oct 8.....	3,051.96	2,642.98	2,823.97	505.99	6,334.89	8,293.58
29.....	1,041.90	732.86	203.88	287.59	101.75	2,788.56
Nov 11.....	1,420.92	-	196.97	151.85	279.94	128.77
26.....	-	-	87.89	-	118.95	-
Dec 17.....	-	-	1,133.41	-	1,686.46	-
1958						
Jan 20.....	5,636.78	18,169.68	8,754.84	15,376.79	7,438.79	21,435.75
Feb 6.....	17,918.47	19,515.50	31,628.60	27,662.52	59,140.38	26,701.40
Mar 1.....	7,434.48	10,214.66	19,284.64	13,414.87	9,136.79	11,242.84
11.....	57,335.86	82,941.90	68,141.93	90,917.93	76,314.94	145,848.88
25.....	37,239.82	28,478.90	37,266.92	65,394.94	116,141.91	157,551.90
Apr 10.....	53,028.87	52,315.90	32,290.91	51,673.91	66,254.89	63,805.89
24.....	45,099.92	350,744.94	487,220.94	-	448,701.92	268,233.94
May 10.....	1,171.52	1,531.17	216.61	497.45	715.46	328.71
30.....	5,827.59	4,321.37	3,015.53	2,993.86	4,483.80	8,593.63
Jun 23.....	20,407.69	4,273.59	18,901.67	12,695.47	26,686.65	4,726.66
Jul 7.....	18,640.83	19,162.85	11,350.89	23,074.94	23,925.94	26,721.93
24.....	11,439.84	9,232.93	4,468.95	9,708.95	14,802.91	5,805.98
Aug 11.....	10,065.93	8,912.96	8,731.97	5,557.96	6,658.96	-
21.....	1,865.54	5,229.67	13,365.40	14,099.41	3,351.46	28,625.70
Sep 11.....	30,424.42	47,585.47	4,954.71	13,348.34	-	-

JULY 5-AUGUST 21, 1957 (SEROTINAL). On July 5, only sts. 2 and 3 were sampled, with low diversities and high redundancies prevailing: 309.95 and 262.98, respectively. *Nannochloris atomus* was the only significant species. Subsequently, by August 21, diversity at both stations had increased steadily to peaks of 131,544.50 at st. 2 and of 138,640.51 at st. 3, associated with increased importance of several other species (*Skeletonema costatum*, *Coscinodiscus asteromphalus*, and *Peridinium trochoideum*). At st. 1 a similar increase to 41,712.69 occurred (and, on August 29, 46,251.51). The increase at st. 4 was virtually exponential, from 2455.79 on July 11 to 58,601.67 on August 21. At st. 5 a steep increase from 904.92 to 108,023.77 occurred during this



period, reaching a maximum of 159,045.47 on August 8. At st. 6, alternate increases and decreases prevailed, with a net increase during the period from 869.95 to 51,181.94. Thus, highest diversity levels during this period were encountered along the south shore of the estuary at sts. 2, 3 and 5, the lowest at sts. 1, 4 and 6.

Unlike *H*, *R* did not show any uniform trends during this period, except at st. 1, where the values decreased on each successive sampling date. In spite of the uneven rates of change, the general pattern for *R* was similar at all stations: decreases to minima followed by increases (Table III). The curves in Table III are out of phase along the time axis, minimum values being obtained in early August downbay, in mid-August at the midbay stations, and in late August at st. 1. Thus, the tendency to realize higher proportions of the available diversity developed first in the lower reaches of the estuary, where oceanic influences were greatest, and then spread upbay. The lowest redundancy obtained at each of sts. 1-6 was, respectively, .51, .39, .26, .36, .47, .34.

AUGUST 21-NOVEMBER 26, 1957 (AUTUMNAL). This period was marked by a general diversity decrease throughout the Bay, although small isolated increases occurred at various times and places. St. 4 seems to represent the general trend; in the week between August 21 and 29, diversity here decreased from 58,601.67 to 5345.49, and the decline continued steadily to its low for the year, 151.85 on November 11. The lowest values of *H* (bits/L) recorded for sts. 1-6 were 1041, 732, 87, 151, 101, and 128, indicating that the stations upbay maintained a considerably higher diversity level than those downbay. These generally low diversities of the autumnal period were associated with dominance by one form, *Nannochloris*. Further downbay (especially at st. 6), several other species, e.g., *Coscinodiscus asteromphalus* and *Chaetoceros decipiens*, maintained some degree of importance.

The situation at st. 5 was slightly different from the others. In the three weeks between August 21 and September 14, diversity declined precipitously from 108,023.77 to 656.77 (well below the other stations), and in the next month it rose again tenfold to 6334.89 (October 8) before falling to its lowest value of 101.75 on October 29, where it remained, approximately, throughout November. The same pattern of abrupt decline to a low on September 14, followed by subsequent increase before the final decline, was also expressed, though less markedly, at south-shore sts. 2 and 3, and very slightly at st. 6. These patterns presumably reflected local environmental conditions in the estuary at the time. Less than a week before September 14, high northeasterly winds and heavy seas produced great turbidity throughout the Bay on September 9. Examination of samples collected on this date revealed much silt and many fragments of lysed cells and diatom frustules. Even *Nannochloris* was reduced to only 842 units/L at st. 5 compared to 30,367 at the relatively



protected st. 1. Even more sensitive to this environmental disturbance than  $H$  was  $H_{\max}$ . Although  $H$  remained fairly unaltered at sts. 2, 3, 4, and 6,  $H_{\max}$  was depressed throughout the Bay on September 14 and increased sharply in the weeks following.

The general trend of  $H_{\max}$  during the autumnal period was downward. The behavior of  $H_{\min}$  was more erratic, with a net decline at some stations and an increase at others. Counting units (Table II) remained quite high during September and early October, while number of species (Table I) was generally low. The net result of decreasing  $H_{\max}$  while leaving  $H_{\min}$  relatively unaffected was to diminish the range of available diversity to a very narrow spread in November. This would be expected, *a priori*, to depress the values of  $R$ . But Table III indicates very high redundancies. The lowest values recorded after decline of the summer bloom were, for sts. 1-6, .90, .86, .75, .59, .75, and .53, markedly higher upbay and along the south shore. The highest redundancies obtained were .96, .98, .98, .99, .94, and .90, higher at the head than downbay. Thus, in spite of the small spreads between the limits  $H_{\max}$  and  $H_{\min}$ , the realized diversity was so low during this period that it constituted a very small proportion of the total diversity available.

NOVEMBER 26, 1957-MAY 10, 1958 (HIEMAL). This extended period was characterized at all stations by a gradual rise in diversity accompanied by an increase in the spread between  $H_{\max}$  and  $H_{\min}$ . These trends were least pronounced at sts. 1 and 2, but greater and fairly similar for the remaining stations downbay. The long diversity ascent (Table III) culminated in maxima at all stations on April 24, except st. 4 which was not sampled then, and st. 1 which had a higher diversity (53,028.87) on April 10. The diversity levels recorded on April 24 were 45,099.92, 350,744.94, 487,220.94, ---, 448,701.92, and 268,233.94 at sts. 1-3, 5, 6. The corresponding number of species diminished downbay (25, 20, 12, ---, 14, 11), and the number of units per liter was greatest at st. 3 and least at st. 1 (117,046; 1,289,403; 2,377,179; ---; 1,392,188; 1,360,673). Redundancies were high throughout the Bay, as indicated.

The most important species during the spring flowering were *Skeletonema costatum*, *Leptocylindricus danicus*, *Thalassiosira gravida*, *Goniaulax* sp. Die-sing, *Rhizosolenia setigera*, *Tropidoneis lepidoptera* (Gregory) Cleve, and *Asterionella japonica*. Although each of these species had high cell counts, resulting in high total diversity, *Skeletonema* was abundant enough to produce high redundancy. This unusual condition has special significance which will be discussed later.

Although generally high redundancies prevailed throughout the spring and at the peak of the diatom bloom, the lower values obtained during the winter months through early March (Table III) indicate that no species dominated. In January, *Nitzschia seriata* became more important than the other members,

and in February the distribution of increased total numbers among many species produced higher diversities and lowered redundancies.

A slight interruption of the general upward diversity trend resulted on March 1 from several days of heavy rainfall that produced a heavy silt load and the highest turbidity levels encountered during the study. The resultant depression of diversity was followed by rapid recovery to former levels, which led eventually to the spring maximum.

Spring freshets with their entrained nutrients and growth factors presumably made the spring diatom flowering possible. The cause of the rapid diversity loss following the flowering peak is uncertain. Nutrient levels were very high on May 10, and high *N/P* ratios were recorded. This leaves as possible factors (i) growth factor, silicate, and/or trace metal impoverishment, (ii) build-up of toxic "exocrines", or (iii) zooplankton grazing (record concentrations of *Eurytemora* were present during this period). Regardless of the cause, on May 10 very low diversity levels prevailed throughout the estuary, which was in striking contrast to the annual maxima recorded on April 24. In the upper reaches, at st. 1 in particular, the rate of decline was not quite so cataclysmic, partly because communities here were less diverse during the spring maximum than those at other stations. St. 1 declined from 45,099.92 to 1171.52, whereas, st. 3, for example, decreased from 487,220.94 to 216.61.

The general pattern of redundancy change from November through April was from prevailing low values in winter (.47, .50, .60, .52, .38, .40 on February 6) to extremely high values during the spring bloom (.92, .94, .94, —, .92, .94 on April 24) reflecting *Skeletonema* dominance. Disappearance of the diatom pulse was followed on May 10 by low redundancies (.52, .17, .61, .45, .46, .71).

MAY 10—SEPTEMBER 11, 1958 (VERNAL-AESTIVAL-SEROTINAL). This period may be regarded as the counterpart in 1958 of the first period (July 5—August 21) in 1957, but it differed from that period in several respects. The low diversity levels of early May were followed by subsequent increases to moderate maxima in early July, and these levels were maintained through August and into September. The highest diversity recorded during the summer of 1958 was 47,585.47 on September 11, only one-third of the maximum levels of 1957 (159,045.47 on August 8, 1957). Redundancies increased during this period from lowest values following the spring flowering to highest in July and early August (Table III) associated with increased dominance by *Nannochloris*. Low values prevailed again in late August and early September, corresponding to similar troughs in the preceding year.

Summarizing, each of the four periods distinguished displays describable trends in net phytoplankton diversity at each station considered. Gross disturbances in the general trend and subsequent recovery were recorded



on two different occasions, these being associated with corresponding environmental changes.

*Diversity and Succession Theory.* Alterations in the structure of a phytoplankton community may occur through (i) differential reproduction and selective elimination of component species, and (ii) water mass transfer and consequent dispersal or concentration (Gran and Braarud, 1935). The resultant diversity changes, although more or less cyclic over many years, give in a single year the appearance of ecological succession (Margalef, 1958 a). Margalef construes a phytoplankton succession as a gradual, irreversible change in community composition from loosely organized systems of smaller organisms with rapid dynamics and high productivity/biomass ratios to stabler communities having larger organisms with a slower thermodynamic output as well as lower productivity/biomass relationships. Margalef (personal communication) also conceives that niche structure develops in succession and that each niche tends to become occupied by a single species in accordance with the principle of competitive exclusion (Volterra, 1926; Winsor, 1934; Gause, 1934, 1935; Hardin, 1960; Cole, 1960). Since niche theory is critical to a consideration of diversity trends in succession, Hutchinson's formal theory (1957) is briefly outlined below, slightly modified.

In Hutchinson's model, a *fundamental niche*,  $v_i$ , of a species,  $s_i$ , is a phase space whose dimensions correspond to the range of each significant environmental variable permitting  $s_i$  to survive under all conditions of variable interaction. Each point in this space corresponds to an environmental state at which  $s_i$  can exist. Now, considering the ordinary  $n$ -space of the physical biotope,  $\beta$ , it is clear from the definition of niche that  $v_i \simeq \beta$  (the niche space is isomorphic to the biotope space), so that any point in  $v_i$  can correspond to one or more points in  $\beta$ . If there are no such 1-1 correspondences, then  $v_i$  is not approximately equal to  $\beta$ , and  $\beta$  is regarded as *incomplete* with respect to  $s_i$ .  $\beta$  may also be *complete* or only *partially complete* with respect to  $s_i$ .

The niches of different species in a biotope may be *separate* ( $v_i$  is not  $\cap v_j$ ) or *intersecting* ( $v_i \cap v_j$ ). In the first case there is no basis for interspecific interactions; such phenomena occur only in the intersection subset ( $v_i \cap v_j$ ). In Hutchinson's view, competitive exclusion posits that for any small element of  $v_i \cap v_j$  there do not [at equilibrium] exist in  $\beta$  corresponding small parts, some inhabited by  $s_1$  and others by  $s_2$ . Hence, a biocoenose at equilibrium may be construed as an aggregation of mutually exclusive species occupying mutually exclusive niches in a perfectly partitioned biotope. This obviously never occurs, but it is a helpful ideal to have in mind. Several cases of interspecific relationships are distinguishable: (i)  $v_1 = v_2$ , but  $s_1 \neq s_2$  is so unlikely that it may be disregarded [One wonders, however, whether Hutchinson has not nominally provided an ecological definition of species such that  $v_i \equiv s_i$ ]; (ii)  $v_2 \subset v_1$ , in which competition may lead to survival of  $s_1$  throughout, or



survival of  $s_2$  in  $(v_1 \cap v_2)$  and of  $s_1$  in  $(v_1 \sim v_2)$ ; (iii)  $(v_1 \cap v_2) \subset v_1, v_2$ , leading to survival of  $s_1$  in  $v_1 \sim v_2$ , of  $s_2$  in  $v_2 \sim v_1$ , and of  $s_1$  or  $s_2$  (but not both) at any point in the  $\beta$ -space where  $v_1 \cap v_2$ . If the *realized niche*,  $v'_1$ , is defined as  $(v_1 \sim v_2) \cup [(v_1 \cap v_2) \supset s_1]$ , and  $v'_2$  as  $(v_2 \sim v_1) \cup [(v_1 \cap v_2) \supset s_2]$ , then the competitive exclusion principle implies that  $v'_1 \cap v'_2 = \varphi$ , where  $\varphi$  is the null set.

In a  $\beta$ -space containing an equilibrium community of  $m$  species  $s_1, s_2, \dots, s_m$ , each represented by  $n_1, n_2, \dots, n_m$  individuals, it is possible to identify for each  $s_i$  ( $i = 1, 2, \dots, m$ ) a number of elements in  $\beta$  corresponding to a whole or part of  $v'_i$ . Thus, if at any given instant, each such element,  $\Delta_i \beta$ , is occupied by one individual of  $s_i$ , then the total partition of  $\beta$  by  $s_i$  will be  $n_i \Delta_i \beta$ , the *specific biotope* of  $s_i$ . Since, at equilibrium, the biotope universe will be perfectly partitioned into nonoverlapping subsets by the  $m$  species present, it follows that

$$\beta = \sum_{i=1}^m n_i \Delta_i \beta. \quad (13)$$

From this we get

$$\sum_{i=1}^m n_i = \frac{\beta}{\sum_{i=1}^m \Delta_i \beta},$$

which may be substituted into (7) to obtain

$$\begin{aligned} H &= -k \left[ \sum_{i=1}^m \frac{\beta}{\Delta_i \beta} \log \frac{n_i}{N} \right] \\ &= -k \beta \left[ \sum_{i=1}^m \frac{1}{\Delta_i \beta} \log \frac{n_i}{N} \right], \end{aligned} \quad (14)$$

which displays (i) a direct relationship between community diversity and magnitude of the biotope space, and (ii) an inverse relationship between diversity and  $\sum_{i=1}^m \Delta_i \beta$ , the sum of the sizes of each element of  $\beta$  occupied by an individual of  $s_i$ . Hence, "larger" organisms (in the sense of occupying more of the biotope phase space) lead to a reduction of diversity independently of their numbers  $n_i$ , all else being equal.

This applies to communities at equilibrium. As mentioned above, true equilibrium could hardly ever be expected to prevail in nature. Nonequilibrium conditions fall into two basic classes: (i) early in succession when the community is inchoate and the biotope incompletely utilized:

$$\beta > \sum_{i=1}^m n_i \Delta_i \beta; \quad (15)$$

and (ii) later in the sere when biotope resources are competed for:

$$\beta < \sum_{i=1}^m n_i \Delta_i \beta. \quad (16)$$

In the first case equilibrium can be approached by (i) increase in number of species,  $m$ , (ii) increase in  $n_i$ , and (iii) increase in  $\sum_{i=1}^m \Delta_i \beta$ , which, if  $m$  is held constant, can only be accomplished by increase in some or all of the  $\Delta_i \beta$ . In general, all three of these changes are characteristic of ecological succession, which may be defined by the transformation

$$S: \begin{array}{l} \beta > \sum_{i=1}^m n_i \Delta_i \beta \\ \downarrow \\ \beta = \sum_{i=1}^m n_i \Delta_i \beta, \end{array} \quad (17)$$

with the implied diversity changes, which cannot be specified without actual data, since  $n_i$  and  $\Delta_i \beta$  affect  $H$  in opposite ways (eq. 14). Therefore, although diversity within a niche must decline in succession, the total diversity of the community is a function of niche development, and may therefore either decrease or increase at various stages. Hence it appears unrealistic to try to assert categorically that a climax community will have a higher or lower diversity than a particular seral stage since it would depend upon whether that stage were characterized by (15) or by (16). Hence, Margalef's (1958 b) statement that successions proceed from high to low diversity would seem to be theoretically untenable, although such may often be the case in actuality.

Based on the idea of diversity decline in succession, Margalef advocated  $H$  as a succession index. The present data indicate that redundancy rather than diversity reflects successional status better. Although no formal basis can yet be provided for using  $R$  to measure succession, we proceed on strictly empirical grounds on the assumption that in phytoplankton, where biotope monotony seriously restricts niche diversification, redundancy tends to increase and is maximal at climax. Diversity and redundancy relationships for st. 3 are graphed in Fig. 3, where suggested seres are indicated by the heavy, broken, vertical lines. During each period designated, the communities evolved from a condition of low to one of high redundancy. Three successions are indicated for August 1957 to August 1958. The other stations had similar patterns (Table III), excepting st. 6, which had considerably less redundant communities during autumn 1957.

In the first succession from August to November 1957 (Fig. 3), diversity declined steadily in accordance with Margalef's (1958 b) thesis. The terminal



phase may be regarded as a "climax" since it persisted for three months, indicating considerable stability and approach to the condition of (13). In the second series, from November 1957 through April 1958, both diversity and redundancy increased. The two variables were simultaneously maximal at the height of the spring flowering. Apparently this is a function of large  $N$  since, by (12),  $H$  and  $R$  would appear inversely related. When  $N$  is very large,  $H_{\max}$  must grow faster than  $H$ , producing redundancy increase coincident with diversity increase. Such a condition is construed to correspond to equation

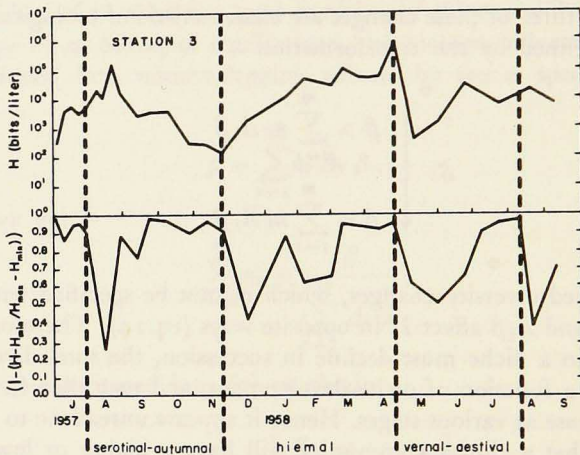


Figure 3.

(16) and must be marked by extreme exploitation of the biotope. The ultimate consequence, when some essential resource becomes impoverished, must be a precipitous return of the community to the condition in (15). This is expressed in nature as the catastrophic disappearance of the spring diatom bloom, to be followed subsequently by a new succession (17).

It seems clear from these results, viewed against the theoretical background developed, that diversity-redundancy relationships offer considerable promise for development of a formal theory of compositional changes during succession, and that the methods explored here could lead to rigorous criteria for denoting the successional status of any ecological community at any time. Further development will be necessary, however, before such an ideal can be realized.

*Conclusion.* Mean redundancy levels in the Raritan net phytoplankton during the term of study were .85, .81, .86, .83, .85, .85 for sts. 1-6, a remarkably consistent set of values. If high redundancy signifies late successional stages in plankton, then these figures indicate the Raritan net flora to be, on the average, in essentially long term steady state (climax). If this is true,



then by (14) the mean diversity at a given location logically reflects the quality of the biotope there, greater  $\beta$ -spaces being capable of sustaining higher diversity communities. The mean diversity (in bits  $\times 10^{-3}/L$ ) at each station, based only on dates for which data from all six stations were complete, was 17.7, 22.0, 21.2, 20.6, 35.2, 30.5; these relationships are displayed spatially in Fig. 4. The similarity between Fig. 4 and Fig. 2 depicting the general circulation of the Raritan is striking and constitutes an effective testimony to the basic efficacy of the method.

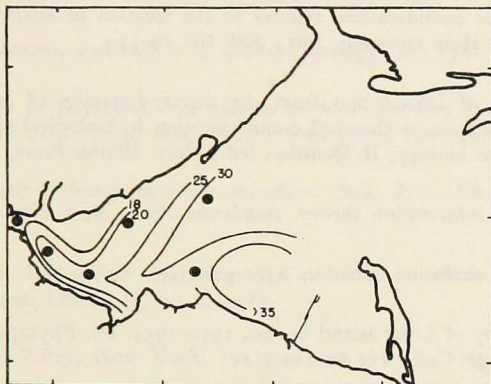


Figure 4.

As Fig. 4 indicates, higher mean diversity levels prevailed in the lower estuary, signifying higher biotope quality proceeding toward Lower Bay. Progressive diminution of diversity upbay indicates a more unsatisfactory biotope, undoubtedly a reflection of the gross pollution originating at the head of the estuary. Consequently, the Raritan is interpreted to be a generally poor quality ecosystem with respect to its capacity for developing a niche structure adequate to maintain high diversity steady states, at least relative to its lower segment. This interpretation is supported by additional data from a series of production experiments performed off Princess Bay during summer 1959 which indicated a mean daily energy loss in the water column of  $0.37 \text{ g cal/cm}^2$  (Patten, 1961). The extent to which the established diversity relationships will be altered by the lifting of pollution from the Raritan River should provide an interesting area for investigation against the background presented here.

*Acknowledgments.* This study was supported by NIH grant 5278, H. H. Haskin and E. T. Moul, Rutgers University, principal investigators. The field program was jointly carried out with H. P. Jeffries, who concurrently studied the zooplankton for his doctoral dissertation. David Trend graciously volunteered the use of a power boat without which sampling could

not have continued through cold weather. F. G. Fender of the Rutgers Computation Center wrote the program for the IBM 650 Computer. The diversity-succession model was developed to its current state at the author's present institution, and represents Contribution No. 111 from the Virginia Institute of Marine Science.

## REFERENCES

- AYERS, J. C., B. H. KETCHUM, and A. C. REDFIELD  
 1949. Hydrographic considerations relative to the location of sewer outfalls in Raritan Bay. Woods Hole Oceanog. Inst., Ref. No. 29-13.
- BRANSON, H. R.  
 1953. A definition of information from the thermodynamics of irreversible processes and its application to chemical communication in biological systems; *in* Information theory in biology, H. Quastler, (ed.) Univ. Illinois Press, Urbana, pp. 25-40.
- BRILLOUIN, L.  
 1956. Science and information theory. Academic Press, New York. 320 pp.
- COLE, L. C.  
 1960. Competitive exclusion. *Science*, 132: 348-349.
- CONOVER, S. A. M.  
 1956. Oceanography of Long Island Sound, 1952-1954. IV. Phytoplankton. Bull. Bingham Oceanogr. Coll., 15: 62-112.
- 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.
- GAUSE, G. F.  
 1934. The struggle for existence. Williams and Wilkins, Baltimore. 163 pp.  
 1935. Verifications experimentales de la theorie mathematique de la lutte pour la vie. *Actual. Sci. Industr.*, 277. 61 pp.
- GLEASON, H. A.  
 1922. On the relation between species and area. *Ecology*, 3: 156-162.
- GOODALL, D. W.  
 1952. Quantitative aspects of plant distribution. *Biol. Rev.*, 27: 194-245.
- GRAN, N. H., and T. BRAARUD  
 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *J. biol. Bd. Canada*, 1: 279-467.
- HARDIN, G.  
 1960. The competitive exclusion principle. *Science*, 131: 1292-1297.
- HUTCHINSON, G. E.  
 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol., 22: 415-427.
- JEFFRIES, H. P.  
 1959. The plankton biology of Raritan Bay. Ph. D. Thesis. Rutgers Univ., New Brunswick, N.J.  
 1961. Physical-chemical studies on Raritan Bay, a polluted estuary, *ms.*
- KOCH, L. F.  
 1957. Index of biotic dispersity. *Ecology*, 38: 145-148.



MARGALEF, D. R.

1956. Información y diversidad específica en las comunidades de organismos. *Invest. Pesquera*, 3: 99-106.
1957. La teoría de la información en ecología. *Mem. R. Acad. Cien. Artes*, 32: 373-449.
- 1958a. Temporal succession and spatial heterogeneity in phytoplankton; *in Perspectives in marine biology*. A. A. Buzzati-Traverso (ed.). Univ. California Press, Berkeley.
- 1958b. Information theory in ecology. *Gen. Systems*, 3: 36-71.

PATTEN, B. C.

1959. The diversity of species in net phytoplankton of the Raritan estuary. Ph. D. Thesis, Rutgers Univ., New Brunswick, N.J.
1961. Plankton energetics of Raritan Bay. *Limnol. Oceanogr.*, 6: 369-387.

PRESTON, F. W.

1948. The commonness, and rarity, of species. *Ecology*, 29: 254-283.

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.

SHANNON, C. E.

1948. A mathematical theory of communication. *Bell. Syst. Tech. J.*, 27: 379-423, 623-656.

VOLTERRA, V.

1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Acad. Lincei*, (6) 2: 181-187.

WIENER, N.

1948. *Cybernetics*. Wiley, New York. 194 pp.

WILLIAMS, C. B.

1952. Diversity as a measurable character of an animal or plant population. *Colloque intern. C.N.R.S. sur l'Ecol.*, Paris, 1950: 129-144.

WINSOR, C. P.

1934. Mathematical analysis of the growth of mixed populations. *Cold Spring Harbor Symp. Quant. Biol.*, 2: 181-187.