DIVERSITY OF SURFACE NANNOPLANKTON COMMUNITIES

SAMPLED ON CHESAPEAKE BAY CRUISES

OF R/V PATHFINDER AND R/V OBSERVER

JANUARY 1960 - JANUARY 1961

VIRGINIA INSTITUTE OF MARINE SCIENCE

VIRGINIA FISHERIES LABORATORY

SPECIAL SCIENTIFIC REPORT NO. 23

1961

DIVERSITY OF SURFACE NANNOPLANKTON COMMUNITIES SAMPLED ON CHESAPEAKE BAY CRUISES OF R/V PATHFINDER AND R/V OBSERVER

JANUARY 1960 - JANUARY 1961

Data on the diversity of surface nannoplankton communities sampled on 24 cruises in the lower Chesapeake Bay in connection with a 12-month survey conducted by the Planktology Research Section are reported. Five stations along the salinity gradient were occupied at approximately biweekly intervals. Station locations (Fig. 1) and mean low water depths were:

1) York River, opposite VFL (37°14', 76°30'); 30 ft.

2) York River, mouth (37°15', 76°21'); 30 ft.

3) Chesapeake Bay, York Spit Light (37°13', 76°16'); 12 ft.

4) Chesapeake Bay, off York Spit Channel (37°10', 79°09'); 25 ft.

5) Chesapeake Bay, north of Inner Middle Ground (37°08', 76°02'); 20 ft.

Data on hydrography, nutrients, chlorophyll, seston and cell counts are reported in Report No. 20 of this series, and species lists for the surface nannoplankton are the subject of Report No. 21.

Diversity indices are convenient for summarizing the compositional structure of mixed species aggregations of organisms--that is, how the N individuals present are distributed amongst the m species. The values of m and N determine the range of diversity available to a community. The extremes are (i) all individuals belong to one species (m=1, minimum diversity), and (ii) each individual belongs to a different species (m=N, maximum diversity). A number of diversity indices have been proposed (Gleason 1922, Fisher et al. 1943, Preston 1948, Goodall 1952, Williams 1952, Koch 1957). Margalef (1956, 1957, 1958) has advocated use of an entropy measure, and it is this approach which is used here. Derivation follows.

A mixed species population consists of $n_1, n_2, \ldots, n_m$ individuals of m types, the total number being

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

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

$$p_i = n_i/N \qquad (2)$$

where

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

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 is

$$_N P_{n_1, n_2, \ldots, n_m} = N! \Big/ \prod_{i=1}^{m} n_i! \qquad (3)$$

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

$$H = \log P \ , \qquad (4)$$

or (from 3)

$$H = \log N! - \sum_{i=1}^{m} \log n_i! \quad . \tag{5}$$

Assuming a reasonably large sample, the logarithms of the factorials may be approximated by Stirling's formula:

$$\log x! = x \log (x-1).$$

Equation (5) then becomes

$$H = N \log (N-1) - \sum_{i=1}^{m} n_i \log (n_i-1)$$

$$= N \log N - N - \sum_{i=1}^{m} n_i \log n_i + \sum_{i=1}^{m} n_i$$

$$= - \left[\sum_{i=1}^{m} n_i \log n_i - N \log N \right]$$

$$= - \sum_{i=1}^{m} n_i \log \frac{n_i}{N} \quad , \tag{6}$$

where H may be taken as a measure of the diversity of the aggregation. The mean diversity per individual is then

$$\bar{H} = - \sum_{i=1}^{m} \frac{n_i}{N} \log \frac{n_i}{N} \quad , \tag{7}$$

or (from 2)

$$\bar{H} = - \sum_{i=1}^{m} p_i \log p_i \quad . \tag{8}$$

If base 2 logarithms are used, diversity is expressed in binary digits (bits), the familiar units of information theory.

The variables H and $\bar{H}$ have a number of properties which make them a reasonable measure 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:

$$H_{min} = \log N! - \log [N-(m-1)]! \quad . \tag{9}$$

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

$$H_{max} = \log N! - m \log (N/m)! \tag{10}$$

Between these limits lies a large number of possibilities, depending upon the values of m and N. The unique composition of the community when sampled is expressed unambiguously by the H function, as the following example of mixed populations with fixed N and variable m illustrates.

	COMMUNITIES (N=6)										
Species	A	B	C	D	E	F	G	H	I	J	K
n_1	1	2	2	3	2	3	4	3	4	5	6
n_2	1	1	2	1	2	2	1	3	2	1	-
n_3	1	1	1	1	2	1	1	-	-	-	-
n_4	1	1	1	1	-	-	-	-	-	-	-
n_5	1	1	-	-	-	-	-	-	-	-	-
n_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 $\bar{H}$ (i) uniquely specifies the composition of each community, (ii) vanishes as the probability of selecting a particular species becomes a certainty, and (iii) increases the more uncertain the choice becomes. The fact that one bit constitutes a binary choice between two equally probable alternatives is illustrated by community H.

In studying community diversity, it is often helpful to have intensive as well as extensive criteria available. Two intensive variables have been suggested by Branson (1953), H/H_{max} and H/H_{min}. Although data for these variables are reported below, a more useful measure is the redundancy, R, defined as

$$R = 1 - \frac{H-H_{min}}{H_{max}-H_{min}}$$

$$= \frac{H_{max}-H}{H_{max}-H_{min}} \quad . \qquad (11)$$

Redundancy specifies the position of H between H_{max} and H_{min}. In the example above, community A has no redundancy, while K is completely redundant.

In the tables which follow, data are presented for values of m, N, H_{max}, H_{min}, H, $\bar{H}_{max}$, $\bar{H}_{min}$, $\bar{H}$, H/H_{max}, H/H_{min}, and R for the surface nannoplankton at the five sampling stations. The computations were performed on an IBM Type 1620 data-processing machine at the Narragansett Marine Laboratory; the program was written by Mr. Joel S. O'Connor under the direction of Dr. Saul B. Saila.

Distribution of this report does not constitute publication, and the data are subject to correction and/or revision.

Bernard C. Patten
16 June 1961

LITERATURE CITED

Branson, H. R. 1953. A definition of information from the thermodynamics of irreversible processes and its application to chemical communication in biological systems, pp. 25-40 in H. Quastler, [ed.], Information theory in biology. Univ. Illinois Press, Urbana.

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.

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.

Koch, L. F. 1957. Index of biotic dispersity. Ecology 38:145-148.

Margalef, D. R. 1956. Información y diversidad especifica en las communidades de organismos. Invest. Pesquera 3:99-106.

__________ 1957. La teoría de la información en ecología. Mem. R. Acad. Cien. Artes 32:373-449.

__________ 1958. Temporal succession and spatial heterogeneity in phytoplankton, pp. 323-349 in A. A. Buzzati-Traverso, [ed.], Perspectives in marine biology. Univ. California Press, Berkeley.

Preston, F. W. 1948. The commoness, and rarity, of species. Ecology 29:254-283.

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.

CRUISE DATES

Cruise No.	Dates
1	4 January 1960
2	26 January 1960
3	8 February 1960
4	23 February 1960
5	7 March 1960
6	21 March 1960
7	4 April 1960
8	19 April 1960
9	2 May 1960
10	23 May 1960
11	3 June 1960
12	17 June 1960
13	5 July 1960
14	18 July 1960
15	1 August 1960
16	11 August 1960
17	26 August 1960
18	19 September 1960
19	3 October 1960
20	21 October 1960
21	14 November 1960
22	28 November 1960
23	19 December 1960
24	11 January 1961

Figure 1. Diagram of the lower Chesapeake Bay, showing locations of stations 1-5.

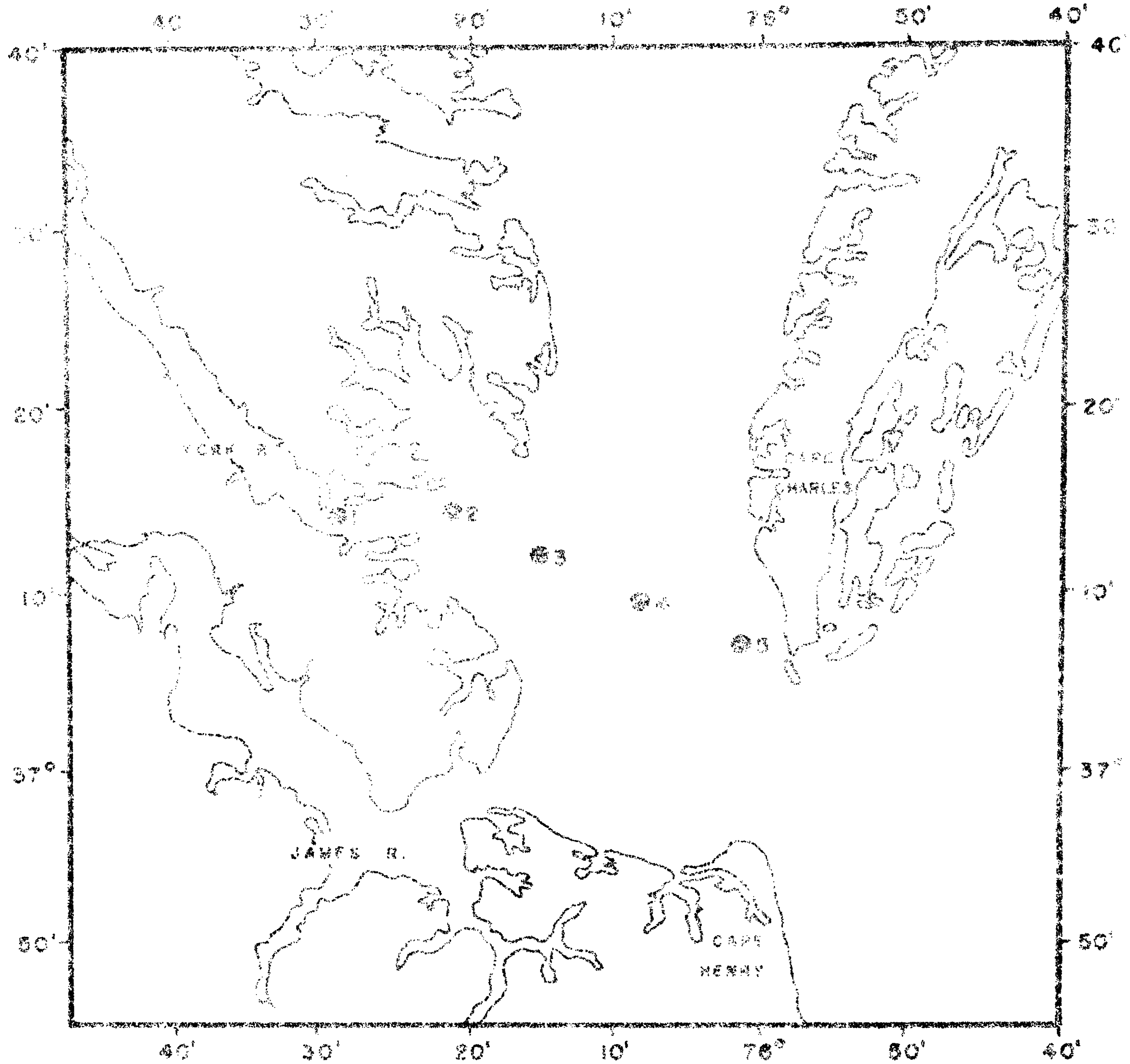
40'
30'
20'
10'
76°
50'
40'
50'
20'
10'
37°
50'
YORK R.
JAMES R.
CAPE CHARLES
CAPE HENRY
1
2
3
4
5

Table 1. Number of nannoplankton taxa (m) recorded at the surface, exclusive of ciliates.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	7	4	6	3	-
2	6	9	9	5	6
3	11	12	5	6	6
4	15	14	16	10	14
5	16	14	24	20	14
6	14	9	11	11	6
7	20	15	10	10	13
8	14	11	10	11	7
9	7	10	7	8	8
10	16	8	7	10	7
11	13	11	3	5	7
12	6	10	7	8	11
13	13	13	10	10	5
14	14	11	15	5	3
15	7	8	11	6	7
16	9	13	13	8	14
17	5	12	11	18	8
18	10	17	16	15	15
19	-	-	-	-	-
20	5	5	6	6	12
21	11	9	17	20	17
22	11	15	14	17	17
23	11	13	13	10	6
24	11	12	14	13	16
$\bar{x}$	11.0	11.1	11.1	10.2	9.5

Table 2. Cell counts (N) at the surface, in units (cells, chains or colonies) per ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	3154	4524	3284	3828	-
2	3001	2737	5026	2374	2026
3	2305	3507	6380	2001	4368
4	1812	3447	2769	2220	2283
5	1025	1427	2165	1387	823
6	2996	1530	1198	1209	1043
7	1512	2128	1141	1197	1287
8	2461	3741	3585	3246	1948
9	509	4519	5336	3267	1669
10	1656	2050	2168	3003	4518
11	3812	3750	986	1251	640
12	363	1809	2502	711	1394
13	2384	2454	1765	655	1043
14	3434	720	1837	244	412
15	1968	273	1210	910	565
16	723	677	828	572	680
17	161	808	1008	1026	446
18	926	2254	1213	1218	1907
19	-	-	-	-	-
20	375	488	231	300	399
21	802	982	2233	2277	1309
22	1345	1643	2760	5700	3503
23	787	1839	1231	1058	168
24	1293	946	1294	1627	1308
$\bar{x}$	1687	2098	2267	1795	1534

Table 3. H_{max}, bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	8854.4	9048.0	8489.0	6067.2	-
2	7757.4	8676.1	15932.0	5512.2	5237.1
3	7974.0	12572.4	14813.9	5172.5	11291.1
4	7079.3	13123.9	11076.0	7374.7	8692.2
5	4100.0	5433.1	9926.4	5994.5	3133.4
6	11406.8	4850.0	4144.4	4182.4	2696.1
7	6534.7	8313.8	3790.3	3976.3	4762.4
8	9369.9	12941.7	11909.1	11229.3	5468.7
9	1428.9	15011.7	14980.0	9801.0	5007.0
10	6624.0	6150.0	6086.3	9975.7	12683.6
11	14106.0	12972.8	1562.8	2904.7	1796.7
12	938.3	6009.3	7024.0	2133.0	4822.4
13	8821.8	9080.8	5863.2	2175.9	2421.8
14	13074.4	2490.8	7176.9	566.5	653.0
15	5524.9	819.0	4185.9	2352.3	1586.1
16	2291.8	2505.2	3064.0	1716.0	2589.0
17	373.8	2896.6	3487.1	4278.3	1338.0
18	3076.1	9213.1	4852.0	4758.6	7450.4
19	-	-	-	-	-
20	870.7	1133.1	597.1	775.5	1430.4
21	2774.5	3112.9	9127.3	9841.0	5350.5
22	4652.9	6419.0	10508.3	23298.5	14318.3
23	2722.6	6805.1	4555.2	3514.6	434.3
24	4473.0	3391.4	4926.7	6020.6	5232.0
$\bar{x}$	5862.2	7085.6	7307.7	5809.6	4927.0

Table 4. H_{min}, bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	69.7	36.4	58.4	23.8	-
2	57.7	91.3	98.4	44.8	54.9
3	111.7	129.5	50.6	54.8	60.5
4	151.4	152.7	171.5	100.0	145.0
5	149.9	136.1	254.7	198.1	125.8
6	150.1	84.6	102.2	102.3	50.1
7	200.5	154.7	91.4	92.0	123.9
8	146.4	118.7	106.3	116.6	65.6
9	53.9	109.3	74.3	81.7	74.9
10	160.3	77.0	66.5	104.0	72.8
11	142.7	118.7	19.9	41.4	55.9
12	42.5	97.4	67.7	66.3	104.4
13	134.6	135.1	97.0	84.1	40.1
14	152.7	94.8	151.7	31.7	17.4
15	65.6	56.5	102.3	49.1	54.8
16	75.9	112.7	116.2	64.1	122.1
17	29.3	106.1	99.7	169.8	61.5
18	88.6	178.1	153.5	143.4	152.5
19	-	-	-	-	-
20	34.2	35.7	39.2	41.1	94.8
21	96.4	79.5	177.9	211.8	165.5
22	103.9	149.5	148.6	199.6	188.3
23	96.1	130.1	123.1	90.4	36.9
24	103.3	108.6	134.3	128.0	155.2
$\bar{x}$	105.1	108.4	108.9	97.3	92.0

Table 5. Community diversity, H, in bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	4342.2	5057.3	2258.2	1494.6	-
2	2571.9	3977.1	10737.3	3281.3	3055.7
3	6278.1	7940.6	8317.8	4217.6	3567.6
4	4412.9	6318.3	5711.5	3604.9	2875.2
5	3303.4	4058.8	7269.5	4647.1	2038.6
6	9623.5	4235.8	3269.4	3443.0	2389.3
7	5462.0	5068.2	2612.6	3378.7	3510.1
8	6072.9	9917.1	7424.6	7331.8	3647.7
9	1060.5	11792.9	8624.3	7382.7	3984.6
10	4448.3	3308.8	4299.4	7056.4	9810.3
11	10485.2	10390.5	1143.3	2496.3	1487.9
12	770.9	4979.0	5417.9	1623.0	4078.7
13	6880.5	7144.1	3713.9	1793.4	1764.0
14	9116.5	1998.9	5905.7	429.0	395.6
15	2866.5	556.5	3300.7	2046.4	1450.4
16	1789.0	2038.3	2180.6	1504.9	1972.4
17	263.2	2111.0	2702.4	3724.3	1009.4
18	2553.8	7547.7	4396.8	4017.7	5728.6
19	-	-	-	-	-
20	199.7	1092.0	467.6	562.1	1164.6
21	1995.1	2799.1	8288.9	7398.1	4120.2
22	3641.5	4861.1	6271.3	15578.6	10534.5
23	2177.0	4852.8	3067.7	3036.5	305.2
24	2777.2	2486.4	3720.3	4826.2	3943.6
$\bar{x}$	4047.5	4979.7	4830.5	4125.0	3310.6

Table 6. $\bar{H}_{max}$, bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	2.807	2.000	2.585	1.585	-
2	2.585	3.170	3.170	2.322	2.585
3	3.459	3.585	2.322	2.585	2.585
4	3.907	3.807	4.000	3.322	3.807
5	4.000	3.807	4.585	4.322	3.807
6	3.807	3.170	3.459	3.459	2.585
7	4.322	3.907	3.322	3.322	3.700
8	3.807	3.459	3.322	3.459	2.807
9	2.807	3.322	2.807	3.000	3.000
10	4.000	3.000	2.807	3.322	2.807
11	3.700	3.459	1.585	2.322	2.807
12	2.585	3.322	2.807	3.000	3.459
13	3.700	3.700	3.322	3.322	2.322
14	3.807	3.459	3.907	2.322	1.585
15	2.807	3.000	3.459	2.585	2.807
16	3.170	3.700	3.700	3.000	3.807
17	2.322	3.585	3.459	4.170	3.000
18	3.322	4.087	4.000	3.907	3.907
19	-	-	-	-	-
20	2.322	2.322	2.585	2.585	3.585
21	3.459	3.170	4.087	4.322	4.087
22	3.459	3.907	3.807	4.087	4.087
23	3.459	3.700	3.700	3.322	2.585
24	3.459	3.585	3.807	3.700	4.000
$\bar{x}$	3.351	3.401	3.331	3.189	3.169

Table 7. $\bar{H}_{min}$, bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	.022	.008	.018	.006	-
2	.019	.033	.020	.019	.027
3	.048	.037	.008	.027	.014
4	.084	.044	.062	.045	.064
5	.146	.095	.118	.143	.153
6	.050	.055	.085	.085	.048
7	.133	.073	.080	.077	.096
8	.059	.032	.030	.036	.034
9	.106	.024	.014	.025	.045
10	.097	.038	.031	.035	.016
11	.037	.032	.020	.033	.087
12	.117	.054	.027	.093	.075
13	.056	.055	.055	.128	.038
14	.044	.132	.083	.130	.042
15	.033	.207	.085	.054	.097
16	.105	.166	.140	.112	.180
17	.182	.131	.099	.166	.138
18	.096	.079	.127	.118	.080
19	-	-	-	-	-
20	.091	.073	.170	.137	.238
21	.120	.081	.080	.093	.126
22	.077	.091	.054	.035	.054
23	.122	.071	.100	.085	.219
24	.080	.115	.104	.079	.119
$\bar{x}$	.084	.075	.070	.077	.090

Table 8. Diversity per organism, $\overline{H}$, in bits/ml.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	1.377	1.118	.688	.390	-
2	.857	1.453	2.136	1.382	1.508
3	2.724	2.264	1.304	2.108	.817
4	2.435	1.833	2.063	1.624	1.259
5	3.223	2.844	3.358	3.350	2.477
6	3.212	2.769	2.729	2.848	2.291
7	3.612	2.382	2.290	2.823	2.727
8	2.468	2.651	2.071	2.259	1.873
9	2.083	2.610	1.616	2.260	2.387
10	2.686	1.614	1.983	2.350	2.171
11	2.751	2.771	1.160	1.995	2.325
12	2.124	2.752	2.165	2.283	2.926
13	2.886	2.911	2.104	2.738	1.691
14	2.655	2.776	3.215	1.758	.960
15	1.457	2.038	2.728	2.249	2.567
16	2.474	3.011	2.634	2.631	2.901
17	1.635	2.613	2.681	3.630	2.263
18	2.758	3.349	3.625	3.299	3.004
19	-	-	-	-	-
20	.532	2.238	2.024	1.874	2.919
21	2.488	2.850	3.712	3.249	3.148
22	2.707	2.959	2.272	2.733	3.007
23	2.766	2.639	2.492	2.870	1.817
24	2.148	2.628	2.875	2.966	3.015
$\overline{x}$	2.350	2.481	2.345	2.420	2.275

Table 9. H/H_{max}.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	.490	.559	.266	.246	-
2	.332	.458	.674	.595	.583
3	.787	.632	.561	.815	.316
4	.623	.481	.516	.489	.331
5	.806	.747	.732	.775	.651
6	.844	.873	.789	.823	.886
7	.836	.610	.689	.850	.737
8	.648	.766	.623	.653	.667
9	.742	.786	.576	.753	.796
10	.672	.538	.706	.707	.773
11	.743	.801	.732	.859	.828
12	.822	.829	.771	.761	.846
13	.780	.787	.633	.824	.728
14	.697	.803	.823	.757	.606
15	.519	.679	.789	.870	.914
16	.781	.814	.712	.877	.762
17	.704	.729	.775	.871	.754
18	.830	.819	.906	.844	.769
19	-	-	-	-	-
20	.229	.964	.783	.725	.814
21	.719	.899	.908	.752	.770
22	.783	.757	.597	.669	.736
23	.800	.713	.673	.864	.703
24	.621	.733	.755	.802	.754
$\bar{x}$	.687	.729	.695	.747	.715

Table 10. H/H_{min}.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	62.27	138.83	38.67	62.79	-
2	44.54	43.55	109.17	73.17	55.65
3	56.22	61.31	164.52	76.93	59.01
4	29.14	41.37	33.31	36.04	19.83
5	22.04	29.81	28.55	23.46	16.21
6	64.12	50.07	31.99	33.64	47.68
7	27.24	32.76	28.60	36.73	28.34
8	41.48	83.57	69.88	62.87	55.64
9	19.68	107.93	116.10	90.36	53.19
10	27.75	42.98	64.67	67.88	134.68
11	73.46	87.53	57.49	60.67	26.62
12	18.15	51.14	80.00	24.49	39.07
13	51.12	52.88	38.27	21.32	44.00
14	59.72	21.08	38.92	13.54	22.78
15	43.67	9.85	32.25	41.65	26.46
16	23.56	18.09	18.77	23.49	16.15
17	9.00	19.89	27.11	21.93	16.41
18	28.81	42.37	28.64	28.02	37.57
19	-	-	-	-	-
20	5.84	30.59	11.94	13.68	12.28
21	20.70	35.22	46.59	34.93	24.89
22	35.06	32.52	42.22	78.05	55.93
23	22.65	37.31	24.92	33.60	8.28
24	26.88	22.88	27.70	37.72	25.41
$\bar{x}$	35.35	47.54	50.45	43.35	37.55

Table 11. Redundancy, R.

Cruise No.	Station 1	Station 2	Station 3	Station 4	Station 5
1	.514	.443	.739	.757	-
2	.673	.547	.328	.408	.421
3	.216	.372	.440	.187	.688
4	.385	.525	.492	.518	.681
5	.202	.259	.275	.232	.364
6	.158	.129	.216	.181	.116
7	.169	.398	.318	.154	.270
8	.357	.236	.380	.351	.337
9	.268	.216	.426	.249	.207
10	.337	.468	.297	.296	.228
11	.259	.201	.272	.143	.177
12	.187	.174	.231	.247	.158
13	.223	.216	.373	.183	.276
14	.306	.205	.181	.257	.405
15	.487	.344	.217	.133	.089
16	.227	.195	.300	.128	.250
17	.321	.282	.232	.135	.257
18	.175	.184	.097	.161	.236
19	-	-	-	-	-
20	.802	.037	.232	.291	.199
21	.291	.103	.094	.254	.237
22	.222	.248	.409	.334	.268
23	.208	.292	.336	.140	.325
24	.388	.276	.252	.203	.254
$\bar{x}$	.321	.276	.310	.258	.293