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THE ENVIRONMENTAL AND CLIMATIC DISTRIBUTION OF DINOFLAGELLATE CYSTS IN MODERN MARINE SEDIMENTS FROM REGIONS IN THE NORTH AND SOUTH ATLANTIC OCEANS AND ADJACENT SEAS[1]

DAVID WALL, BARRIE DALE[2], G.P. LOHMANN and WOOLLCOTT K. SMITH

Woods Hole Oceanographic Institution, Woods Hole, Mass., 02543 (U.S.A.)

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Abstract

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Quantitative treatments of 168 dinoflagellate cyst assemblages from modern marine sediments were used to decipher the salient environmental and climatic features of the distribution of common living cyst-based taxa. Surface sediment samples were studied by routine palynological methods from estuarine, continental shelf, slope and rise zones, and abyssal plains between latitudes 62° N and 27° S within fourteen geographic regions of the North and South Atlantic Oceans, the Caribbean and Mediterranean Seas and from one region in the southeastern Pacific Ocean near Peru, to meet this general objective. The results were expressed as percentages of species present and statistically analyzed by multivariate *Q*-mode factor analysis, cluster analysis and by calculation of a diversity index, using pre-existing computerized routines.

Inshore to offshore and latitudinal (climatic) variations in distribution were identified and they involved individual taxa, associations of species, species diversity and specimen densities (cysts per gram of sediment). They were related empirically to changing surface water environments above and this suggested that biologic—ecologic phenomena, which involve species—water type relationships for different taxa, combined with hydrodynamic (current) systems, are the most important factors that control cyst distribution in the bottom thanatocoenosis. However, geologic factors such as recycling of older specimens and outcroppings of relict Pleistocene—Early Holocene sediments exert their influence too.

An ecologic classification for extant cyst-based species is proposed in the format of classical "plankton elements". This format is dictated by the existence of dual trends (environmental and climatic) in cyst distribution. It is suggested that genesis of ecologic species-groups of this nature during evolution can be interpreted by or "predicted" from stability—predictability concepts as developed in contemporary ecologic work, if surface water masses are considered to represent unique hydrographic climates with innate stability and predictability characteristics. This concept of "hydroclimatic stability" is used to identify *fossilizable* living dinoflagellates as being environmentally adapted to unstable conditions around continental margins and comparable shallow-water environments around oceanic islands. In addition there is a tendency for the more stenotopic extant cyst-based taxa to be adaptively specialized towards more stable sectors of nearshore and offshore plankton environments which develop at the terminal and subterminal ends of temperature and salinity regimes or profiles.

One taxonomic change is introduced: *Planinosphaeridium choanum* (Reid 1974) nov. comb. is proposed from the basionym *Ataxiodinium choanum* Reid 1974.

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[1] Contribution No. 3933 from the Woods Hole Oceanographic Institution.

[2] Present address: Institute for Marine Biology, University of Oslo, Norway.

1. Introduction and objectives

The distribution of dinoflagellate cysts in modern marine sediments is of interest for two main reasons. First, it provides specialized marine biological information concerning the biogeography and ecology of the living dinoflagellate species which form resistant encysted stages during their life histories. Second, it represents a major source of information for palynologists who are concerned with dinoflagellate paleoecology and paleoenvironmental research. To this end, there have been several recent studies on the distribution of dinoflagellates in recent marine sediments of the North Atlantic Ocean (D.B. Williams, 1971), around the continental shelf of western South Africa (Davey, 1971; Davey and Rogers, 1975) and around the coastal zone of the British Isles (Reid, 1972, 1974, 1975) in recent years. These studies have demonstrated the feasibility of mapping the biogeographic distribution of dinoflagellate cysts in modern sediments and established that there exists a general relationship between species (cyst) distribution in sediments and surface water environments above.

The present study represents an extension of these earlier investigations with the same general objectives in mind. It reports on the distribution of dinoflagellate cysts from fourteen regions in the North and South Atlantic Oceans, the Caribbean and Mediterranean Seas and one area in the southeastern Pacific Ocean near Peru (see section 3 for details). However, its orientation differs from that of previous cyst studies.

It was not formulated to provide comprehensive biogeographic information on a regional basis, but rather to provide an environmental—climatic analysis of dinoflagellate cyst distribution in modern sediments leading to ecologic conclusions. Specifically, this investigation had four goals: (1) to analyze the environmental—climatic distribution of extant cyst-based dinoflagellate species in marine sediments; (2) to attempt an ecologic—environmental classification of these taxa on the basis of this analysis; (3) to identify important factors which determine the distribution of these cysts in modern sediments; and (4) to provide a quasi-theoretical model to account for the observed distribution of cysts which will be useful in the future development of paleoecological and paleoenvironmental studies with fossil dinoflagellates (cysts).

To meet these goals, dinoflagellate cyst assemblages were studied from a wide variety of physical marine environments, which ranged from estuarine to coastal (neritic) and oceanic (pelagic) across continental margins and round oceanic islands and were situated at latitudes between ca. 62°N (in Norway) to 27°S (in western South Africa). Suites of sediment samples were examined from these environments and they comprised either inshore—offshore transects (Transects 1—9), were disposed in local groups or were taken in series along coastlines. Almost all the samples were surface sediments which were from grabs or the tops of piston cores or gravity cores and they were analyzed for cyst assemblages by standard palynological methods. These samples were supplemented by a few analyses of dinoflagellate cyst assemblages in plankton samples.

Major emphasis was placed on collecting data which were relevant to the environmental—climatic distribution of extant cyst-based dinoflagellate species and genera in modern marine sediments in order to produce an ecologic classification. Such a classification has not been produced in earlier work and yet it clearly is necessary to have one if dinoflagellates are to be used effectively in environmental-ecologic palynology in the future. Thus the results of this investigation are presented in a manner which emphasizes information about individual taxa and discusses processes which determine their environmental—climatic distributions; its results are not presented as a series of regional descriptions for this reason.

Parameters which were measured included the percentage abundance of species within assemblages, species diversity in assemblages and specimen density (number of cysts per gram of sediment, dry weight). Species associations were defined with the aid of a cluster analysis technique and distributional trends were diagnosed with the help of factor analysis. These methods are described in more detail in section 2. Experimentation with methods and concepts which may prove useful in dinoflagellate paleoecologic and paleoenvironmental work was an integral part of this study and it is hoped that this work will provide a stimulus for similar experimentation in other paleontological work with dinoflagellates in older sediments.

2. Laboratory and statistical methods

Sample preparation

Sediment samples were prepared for microscopy by routine palynological methods which included digestion of minerals with hydrochloric and hydrofluoric acids after they were oven-dried and weighed. The organic residues were washed to a neutral pH with distilled water and a portion of each residue was cleaned. This cleaning was accomplished by a short sonification treatment followed by washing through a high-quality 20-μm nickel screen. An aliquot of the cleaned residue was used to compute specimen density (cysts per gram of sediment, dry weight) in many samples. Another aliquot was used to make reference microscope slides with glycerine jelly as the mounting medium in a seal of beeswax. Several plankton samples were treated by standard acetolysis to obtain cyst assemblages from them.

Statistical methods

Three methods of multivariate statistical analysis were employed to assist in the identification of trends in cyst distribution. These were factor analysis, cluster analysis and calculation of an index value for species-assemblage diversity.

(a) *Q-mode factor analysis*

A *Q*-mode varimax factor analysis was carried out using the programme CABFAC by Klovan and Imbrie (1971) on a Xerox Sigma 7 computer. This method was described in general terms by Imbrie and Van Andel (1964) and more mathematical discussions of it were presented in Cooley and Lohnes (1971) and Pielou (1969). The method employed here was the one which was recently applied to nannoplankton paleobiogeography by Haq and Lohmann (1976).

The overall objectives of *Q*-mode factor analysis are threefold: first, to determine a minimum number of end members (i.e. composite idealized assemblages) which will account for a maximum amount of the observed variation in the observed data; second, to determine the taxonomic composition of these idealized end members; and third, to resolve each sample-assemblage into the proportional contributions which it receives from different end members. This effectively reduces a large amount of complex information into a more condensed format which is more readily interpreted. The varimax rotation procedure ensures that the idealized end members (factors) have a realistic relationship to some original samples in the raw data.

(b) *Cluster analysis*

Cluster analysis combines samples with greatest similarity into groups on the basis of a pre-selected index of similarity. It begins with fusion of small groups of samples with greatest similarity and proceeds until all samples are accounted for; the results are usually expressed in dendrogram format. Various clustering strategies are available and the one used here was a hierarchical agglomerative method which employed a "flexible" strategy where a constant, β, the clustering intensity coefficient, was set at −0.25 (see W.T. Williams, 1971, p. 318).

Two indices of similarity were used. The first was a commonly employed Percentage

Similarity Index as defined by:

$$PS = 100 \cdot \sum_{i=1}^{t^{AB}} \text{MIN} \left(\frac{N_i^A}{N^A}, \frac{N_i^B}{N^B} \right)$$

where t^{AB} is the total number of species which are common to samples A and B and where N^A and N^B are the total number of individual specimens to each assemblage (sample). N_i^A and N_i^B are the numbers of individuals which represent the ith species in assemblages A and B, respectively.

The second index of similarity employed was the Normalized Expected Species Shared Index (NESS) of Grassle and Smith (1976). This method was based on the following idea. When random subsamples of size n are drawn from samples A and B, then the expected number of species which they will have in common is represented by:

$$ESS_{A,B} = \sum_{i=1}^{t^{AB}} \left[1- \frac{\binom{N^A - N_i^A}{n}}{\binom{N^A}{n}} \right] \cdot \left[1- \frac{\binom{N^B - N_i^B}{n}}{\binom{N^B}{n}} \right]$$

where N^A and N^B represent the total numbers of individuals which were counted in samples A and B, respectively; N_i^A and N_i^B represent the number of individuals of the ith species in A and B (when the species is common to both); and the value of n is a number to which sample size is rarefied according to Hurlbert's measure of diversity (species richness in his terminology).

A similarity index should be one if the two populations (assemblages) are identical and zero if they have no species in common. An estimator of similarity is formed by normalizing expected species-shared by the expected number of species in common between two subsamples of size n drawn from the same sample (see Grassle and Smith, 1976, for details).

The ESS index is based on the number of species which are common to two samples when random samples of size n are drawn. In this instance, n was set at 100 and 137 samples were clustered. The main value of this index is that it is sensitive to the presence of species which are of persistent occurrence between samples without ever becoming numerically abundant. This is important in biogeographic analysis since some important zonal indicator species in space and time are among the least abundant of specimens within assemblages.

(c) *Species diversity (richness)*

The number of species recorded in an assemblage increases as progressively larger numbers of individual specimens are counted and thus in comparing species abundance between samples it is desirable to take this into account by reducing sample size to a common number (a "rarefied" quantity). A simple method for accomplishing this was described by Hurlbert (1971, p. 581). It is achieved by estimating the number of species to be expected in a sample of n individuals which are selected at random without replacement from a collection comprising N individuals and S species, according to the following formula, where the terms have the same meaning as those given above for the ESS Index:

$$E(S_n) = \sum_{i=1}^{t} \left[1- \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

Maximum benefit is derived from the use of this index by plotting values for it at increasingly large values of n. In this study, a value of n=32 was used to compare diversity in 135 samples. These estimates of diversity with the Hurlbert Index were used to detect biogeographic trends such as increasing assemblage diversity along an inshore—offshore transect. (Diversity within assemblages of dinoflagellate cysts in sediments obviously should not be interpreted as having the same ecologic implications which diversity analyses of living communities carry in terms of food-chain interactions. It is used here simply as a numerical measure which is preferable to non-rarefied lists of species for each sample.)

Smith and Grassle (1977) have demonstrated that this expected species-shared measure of diversity is unbiased and have derived sampling variance for it.

3. Sample distribution, bathymetry and hydrography

Locations and depths of surface sediment samples are shown in Table I and Figs. 1—11. Additional information concerning physical environments and hydrography at the sample locations is summarized below.

Inner coastal zone of the eastern United States (Region 1)

Gulf of Maine to Delaware (Fig. 1)
Samples: 1—25; depths from 4 to 48 m.
Environment: Predominantly estuarine with neutral coastal areas in between major rivers. Northern shores rocky with high tidal range, southern shores fringed by marshes and coastal plains with drowned river valleys.
Hydrography: Highly variable seasonal thermal regime; winter values 3—6° C with little latitudinal variation over a wide distance; summer temperatures near 12—15° C in the Gulf of Maine, from 20° to 25° C in the inshore Middle Atlantic Bight. Annual range of mean monthly temperature greater than 20° C in the northern Middle Atlantic Bight, from 10° to 15° in the Gulf of Maine inshore. Salinity below $32^0/_{00}$ close to $30^0/_{00}$ at river mouths and becoming increasingly fresher upstream. Salinity minimum in spring (due to run-off) and a maximum in summer. Strong seasonal thermocline alternating with thorough vertical mixing in winter. Often a weak year-round halocline with salt wedge formation at river mouths.
Climate: Cool temperate (north) to mild temperate (south) *sensu* Hall (1964).
Sources: Parr (1933); Bumpus (1957, 1973); U.S. Coast and Geodetic Survey (Anonymous, 1960); Pease (1969); Emery and Uchupi (1972); Churgin and Halminski (1974).

Pamlico Sound, Cape Hatteras (Fig. 1)
Samples: 26—28; 6—7 m depth.
Environment: Barrier island lagoon (estuary) with a high degree of enclosure. Flat hinterland.
Hydrography: Highly variable temperature regime seasonally; winter values near 6° C, summer maximum around 29° C; salinity with strong lateral gradient from river mouths (around $9^0/_{00}$) across the lagoon to entrances to the sea (near $35^0/_{00}$). Too shallow for stratification.
Climate: Almost subtropical (inner tropical *sensu* Hall, 1964) but with cool winters.
Sources: Roelofs and Bumpus (1953); Pickett and Ingram (1969).

South Atlantic Bight (Fig. 1)
Samples: 29—42; depths from 4 to 41 m.
Environment: Estuarine with low relief and extensive salt-marsh hinterland.
Hydrography: Seasonal temperature regime (despite low latitude) with winter values near 11° and summer values near 28° C. Brackish to low salinities in locations where samples were collected ($21—33^0/_{00}$). Extremely sharp lateral gradient with silinities of $36^0/_{00}$ close to shore. No stratification.
Climate: Almost tropical but with cool winters.
Sources: Reports of the M/V *Theodore N. Gill* (Anderson et al., 1956; Anderson and Gehringer, 1957); the "Inner Shelf Zone" therein.

Offshore Middle Atlantic Bight (Region 2)

Inner zone (Figs. 1, 24).
Samples: 44—47, 51—56, 61—62 and *67*, representing Transects 1—4 respectively. All less than 200 m depth.
Environment: Continental shelf, widening towards the northeast from ca. 25 km near Chesapeake Bay to more than 200 km south of Cape Cod. Floored with sandy sediments (glacio-fluvial and relict) with one band of mud and silt south of Nantucket.
Hydrography: Shelf water of Labrador Coastal Current origin plus local run-off. Pronounced seasonal variation in the annual cycle of temperature from 5° to 7° in winter to 20—25°C range in summer. Vernal warming noticeably lags in shoal areas near Nantucket to form a local gradient of ecologic consequence; persistence of cold bottom water in the summer. Salinity at surface across the middle and outer shelf zone from $32^0/_{00}$ to $35.5^0/_{00}$. Strongly stratified in summer and early fall, isothermal in winter. Haloclinal year round with most saline water at depth.
Climate: Generally temperate.
Sources: Bigelow (1933); Bigelow and Sears (1935); Ketchum and Corwin (1964); Bumpus (1973); Milliman (1973); Churgin and Halminski (1974).

Outer zone (Figs. 1, 24)
Samples: 48—50, 57—60, 63—66, and *68—72*, representing the seaward sectors of Transects 1—4, respectively. Transects terminated in general regions of Veatch, Block and Atlantic, northeast Hudson and Wilmington Canyons. Maximum depth 2975 m.
Environment: Continental slope (declivity 3—5°) and adjacent continental rise zone (declivity around 1°), rough topography dissected by gulleys and can-

TABLE I

Locations and water depths for quantitatively-treated samples

Sample	Cruise station	Latitude	Longitude	Depth (m)
Inner coastal zone, eastern U.S.A. (Region 1)				
1	Asterias 6-175	44°38.9′N	67°20.5′W	17
2	Asterias 6-174	44°37′N	67°21′W	23
3	Asterias 6-169	44°19′N	68°18.6′W	16
4	Asterias 6-167	44°01.1′N	68°30.1′W	32
5	Asterias 6-150	43°45.4′N	69°56.3′W	14
6	Asterias 6-149	43°41.1′N	70°02.6′W	38
7	Asterias 6-140	42°41.7′N	40°33.6′W	58
8	Asterias 6-136	41°57.7′N	70°27′W	40
9	Asterias 5-1	41°31′N	70°58.2′W	6
10	Asterias 5-3	41°29.3′N	71°14.3′W	4
11	Local, Woods Hole	41°29′N	70°54′W	10
12	Asterias 5-10	41°26.3′N	71°24′W	22
13	Asterias 5-11	41°18.6′N	71°42.2′W	26
14	Asterias 5-21	41°12.7′N	72°51.1′W	15
15	Asterias 5-132	41°07.5′N	72°10.3′W	10
16	Asterias 5-27	40°27.1′N	72°02′W	7
17	Asterias 5-30	40°02.6′N	74°01.4′W	19
18	Asterias 5-32	39°35′N	74°11.9′W	11
19	Asterias 5-35	39°03.5′N	74°59′W	8
20	Asterias 5-127	39°01.2′N	74°44.7′W	13
21	Asterias 5-126	38°57.6′N	74°48′W	12
22	Asterias 5-125	38°47′N	74°57′W	15
23	Asterias 5-124	38°17′N	75°02.5′W	19
24	Asterias 5-54	37°14.7′N	76°11.2′W	12
25	Asterias 5-117	37°01.7′N	75°53.8′W	10
26	Asterias 5-61	35°24.2′N	75°41.8′W	7
27	Asterias 6-62	35°22′N	75°53′W	6
28	Asterias 5-66	35°07.5′N	76°14.7′W	7
29	Asterias 5-74	33°02.3′N	79°32.7′W	6
30	Asterias 5-82	32°27.6′N	80°15′W	10
31	Asterias 5-83	32°20.7′N	80°19.5′W	10
32	Asterias 5-100	32°16′N	80°42.3′W	7
33	Asterias 5-99	32°09.8′N	80°48.3′W	10
34	Asterias 5-86	31°52.1′N	80°51.8′W	12
35	Asterias 5-97	31°44′N	81°08′W	7
36	Asterias 5-96	31°32.4′N	81°13.7′W	41
37	Asterias 5-95	31°31.7′N	81°16.9′W	6
38	Asterias 5-94	31°24.5′N	81°18.5′W	10
39	Asterias 5-93	31°19.8′N	81°19.4′W	4
40	Asterias 5-90	31°13.5′N	81°13.6′W	10
41	Asterias 5-91	31°11.2′N	81°15.9′W	8
42	Asterias 5-92	31°10′N	81°24.7′W	8
Offshore Middle Atlantic Bight, eastern U.S.A. (Region 2)				
43	Gosnold 49-2189	40°18.2′N	67°00.3′W	2235
Transect 1				
44	Delaware 7-N4A	40°28′N	69°31′W	66
45	Delaware 7-N5A	40°17′N	69°31′W	85
46	Delaware 7-N6A	40°06′N	69°30′W	103
47	Delaware 7-N7A	39°58′N	69°30′W	147

TABLE I (*continued*)

Sample	Cruise station	Latitude	Longitude	Depth (m)
48	Gosnold 49-2152	39°46.6'N	69°30.3'W	1865
49	Gosnold 49-2153	39°30'N	69°28.9'W	2335
50	Gosnold 49-2154	39°08.3'N	69°27.8'W	2840
Transect 2				
51	Delaware 7-N43A	40°54'N	70°45'W	53
52	Delaware 7-42A	40°43'N	70°45'W	60
53	Delaware 7-N41A	40°34'N	70°45'W	73
54	Delaware 7-N40A	40°23'N	70°45'W	92
55	Delaware 7-N39A	40°13'N	70°44'W	129
56	Delaware 7-N38A	40°07'N	70°45'W	138
57	Atlantis 283-E15	39°58'N	70°40'W	300
58	Atlantis 263-E5	39°42'N	70°39'W	2086
59	Atlantis 273-E6	39°25'N	70°35'W	2500
60	Gosnold 49-2144	38°59.2'N	70°29.3'W	2850
Transect 3				
61	Gosnold 13-1076	39°49'N	72°14.5'W	89
62	Gosnold 13-1077	39°40'N	72°14'W	121
63	Gosnold 13-1079	39°35.2'N	72°00'W	292
64	Gosnold 49-2128	39°26.3'N	71°45.2'W	1605
65	Gosnold 49-2134	39°15.5'N	71°21.9'W	2590
66	Gosnold 49-2135	39°10.5'N	71°5.4'W	2722
Transect 4				
67	Gosnold 45-1416	38°19.7'N	73°59.5'W	66
68	Gosnold 49-2112	38°24.7'N	73°19'W	1060
69	Gosnold 49-2111	38°19.8'N	73°6.5'W	2225
70	Gosnold 49-2116	38°18.2'N	72°42'W	2680
71	Gosnold 49-2117	38°15.6'N	72°29'W	2910
72	Gosnold 49-2118	38°14.4'N	72°16'W	2975
Bermuda (Region 3)				
73	Local	32°19.4'N	64°43'W	22
74	Local	32°22.5'N	64°40.75'W	13
75	Local	32°22.1'N	64°39.8'W	10
76	Local	32°22.1'N	64°39.8'W	10
77	Local	32°21.1'N	64°42.1'W	13
78	Local	32°21'N	64°41'W	13
79	Local	32°20.5'N	64°40.9'W	15
80	Local	32°15.4'N	64°50'W	2
81	Local	32°22.1'N	64°42'W	2
Bahamas (Region 4)				
82	Gosnold 154-2	24°12'N	77°57'W	2
83	Gosnold 154-3	24°11.5'N	78°00'W	2
84	Gosnold 154-5	24°12.5'N	78°09'W	3
85	Gosnold 154-8	25°56'N	77°15.5'W	1
86	Gosnold 154-10	25°58'N	77°21'W	1
87	Gosnold 154-11	25°04'N	77°18.5'W	5
Yucatan Channel, British Honduras (Region 5)				
88		21°13.2'N	85°31'W	2600
89		20°17'N	86°22.5'W	500
90		20°10.5'N	86°03.6'W	3000

TABLE I (*continued*)

Sample	Cruise station	Latitude	Longitude	Depth (m)
Jamaica (Region 6)				
91	Local	17°57′N	76°44′W	7
92	Gosnold 97-31	18°01.8′N	76°14.8′W	370
93	Gosnold 97-30	18°04.1′N	76°15′W	680
94	Gosnold 97-6	17°47.1′N	76°17′W	720
Puerto Rico and Isla de Vieques (Region 7)				
95	Gosnold 114-1	18°25′N	67°11.2′W	16
96	Gosnold 114-3	18°17.5′N	67°12.2′W	13
97	Gosnold 114-7	18°13.2′N	67°10.8′W	10
98	Gosnold 114-8	18°12.5′N	67°9.7′W	10
99	Gosnold 114-9	18°13.3′N	67°11.5′W	30
100	Gosnold 114-11	18°7.1′N	67°12.8′W	17
101	Gosnold 114-19	18°1.2′N	67°11.1′W	5
102	Gosnold 114-20	18°1.3′N	67°12.2′W	15
103	Local	17°58.5′N	67°0.9′W	3
104	Gosnold 114-24	17°58.2′N	66°55.5′W	4
105	Gosnold 114-25	17°57.7′N	66°54.7′W	10
106	Gosnold 114-28	18°00′N	66°45.6′W	5
107	Gosnold 114-29	17°59.6′N	66°46.4′W	17
108	Gosnold 114-30	17°58.5′N	66°37.2′W	10
109	Gosnold 114-31	17°58.2′N	66°38.7′W	16
110	Gosnold 114-33	17°56.7′N	66°13.4′W	7
111	Gosnold 114-35	18°7.5′N	65°20.9′W	12
Gulf of Paria, Trinidad (Region 8)				
112	Gosnold 96-26	10°29.6′N	62°30′W	10
113	Gosnold 96-28	10°24.6′N	62°19.8′W	14
114	Gosnold 96-30	10°21.2′N	61°48.3′W	28
115	Gosnold 96-32	10°24.5′N	62°45.6′W	24
116	Gosnold 96-34	10°27.7′N	61°43′W	22
117	Gosnold 96-36	10°31.5′N	62°40.4′W	20
118	Gosnold 96-38	10°34.8′N	61°37.8′W	18
Peru (Region 15)				
119	Local, Callao	11°40′S	75°30′W	6
120	Local, Callao	11°40′S	75°30′W	5
Transect 5				
121	Gosnold 140-218	14°52.5′S	75°39.1′W	100
122	Gosnold 140-219	14°59.7′S	74°45.7′W	200
123	Gosnold 140-220	15°03.2′S	75°49.7′W	520
124	Gosnold 140-221	15°05′S	75°50.7′W	1000
125	Gosnold 140-223	15°13.6′S	75°59.2′W	3350
Transect 6				
126	Gosnold 140-214	15°04′S	75°28.2′W	85
127	Gosnold 140-215	15°10.2′S	75°34.2′W	300
128	Gosnold 140-216	15°11′S	75°35′W	1025
129	Gosnold 140-217	15°22′S	75°45.5′W	2700

TABLE I (*continued*)

Sample	Cruise station	Latitude	Longitude	Depth (m)
Offschore Rio de la Plata, Argentina (Region 9)				
Transect 7				
130	Atlantis II 60-236	36°27.0'S	53°31.0'W	500
131	Atlantis II 60-237	36°32.6'S	53°23.0'W	1000
132	Atlantis II 60-264	36°12.7'S	52°42.7'W	2045
133	Atlantis II 60-259	37°13.3'S	52°45.0'W	3320
134	Atlantis II 60-258	37°31.3'S	52°11.1'W	3910
135	Atlantis II 60-249	39°31.4'S	51°43.3'W	5024
Southern Norway, Scandinavia (Region 10)				
136	Chain 13-(VV11)	62°09.5'N	5°59.8'E	673
137	Chain 13-(PC6)	62°10.2'N	5°58.7'E	680
138	Local, Korsfjord	60°11.3'N	5°13'E	680
139	Local, Raunefjord	60°16.1'N	5°08.35'E	240
140	Chain 13-5(Baltic)	57°03.7'N	17°37'E	113
Mediterranean Sea (Region 11)				
141	Chain 21-9	42°16'N	7°10.5'E	2687
142	Chain 61-19	34°47'N	13°09'E	1474
143	Chain 61-29	33°55.9'N	19°38.8'E	3955
144	Chain 61-37	35°45'N	25°15'E	1792
145	Chain 61-43	32°33'N	25°15.2'E	2780
146	Chain 61-51	36°26'N	28°50.2'E	2304
147	Chain 61-53	34°11.9'N	28°57.8'E	2469
148	Chain 61-62	36°01.5'N	31°46.5'E	2447
149	Chain 61-59	35°52.1'N	33°17.2'E	2158
150	Chain 61-65	35°32'N	35°26'E	1342
151	(1560/1, U. Jerusalem)	32°02'N	34°49'E	183
Eastern Equatorial Atlantic (Regions 12, 13)				
152	Local, San Miguel	37°44'N	25°41'E	3
154	Local, Las Palmas	28°09'N	15°25'E	6
153	Chain 21, Core 1	29°00'N	47°28'W	3802
155	Chain 17-9	01°29'N	19°43'W	3474
156	Local, Abidjan	05°00'N	03°45'W	30
157	Local, Abidjan	0.5°00'N	03°45'W	60
158	Atlantis II 42-1199	06°08'S	09°02'E	3586
South Africa (Region 14)				
Transect 9				
159	SANCOR-3166	27°07'S	15°07.6'E	123
160	SANCOR-3169	27°07'S	14°52'E	202
161	SANCOR-3171	27°05'S	14°31'E	349
162	SANCOR-3172	27°07'S	14°18'E	403
163	SANCOR-3175	27°12'S	13°24'E	2060
Transect 8				
164	SANCOR-2746	29°55'S	17°01'E	110
165	SANCOR-2748	29°55'S	16°39'E	160
166	SANCOR-2740	29°54'S	16°10'E	176
167	SANCOR-2737	29°57'S	15°36'E	195
168	SANCOR-2730	29°55'S	14°22'E	730

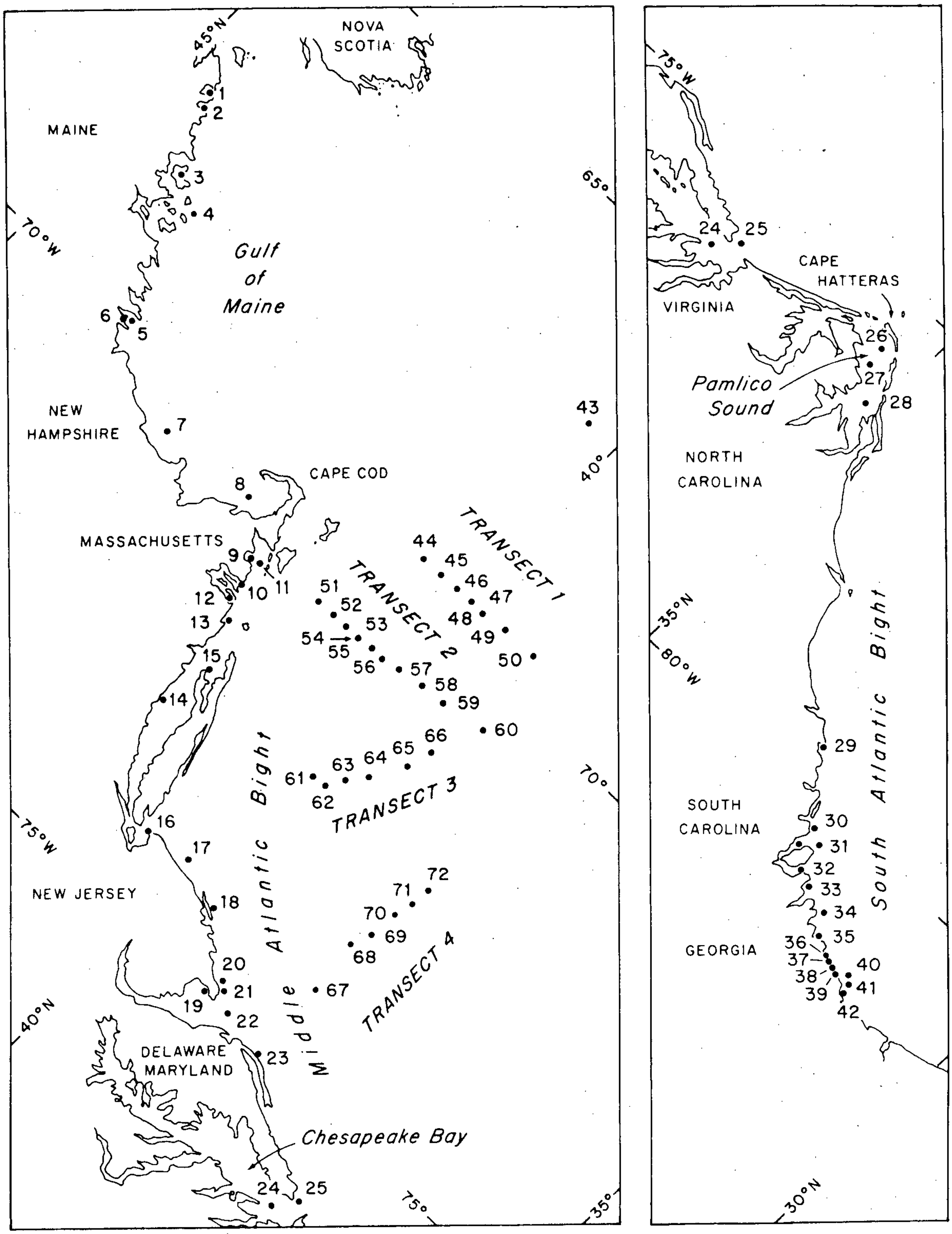


Fig. 1. Sample locations in Regions 1 and 2, the coastal zone and offshore Middle Atlantic Bight area of the eastern United States.

yons, smooth bottom with silty and muddy sediments, including a pelagic biogenic component not seen on the shelf to the landward.

Hydrography: Slope water, intermediate in composition between shelf water and Sargasso Sea—Gulf Stream water. Persistent enough to warrant its own name, occurring in a band which widens to the northeast from around 100 km near Chesapeake Bay offshore to 275 km south of Nova Scotia. Seasonal temperature changes experienced to depths (in water column) near 150 m. Winter surface temperatures ca. 12° to 26.8°C in summer. Surface salinities from $34^{0}/_{00}$ to $36.3^{0}/_{00}$ or higher. Water structure complex with extensive vertical and horizontal mixing, including warm-water eddies and intrusion of cold water from the shelf at mid-depths. Seasonal thermocline, semi-permanent halocline. Saline slope water sometimes indrafted over the outer edge of the continental shelf near bottom as a compensatory inflow to offshore surface movements. Slope water forms an important oceanographic front (convergence) at its boundary with shelf (coastal) water.

Climate: Warm temperate to subtropical, no major winter cold period.

Sources: Bigelow (1933); Bigelow and Sears (1935); Iselin (1936); Miller (1950); Grice and Hart (1962); Colton et al. (1968); Emery and Uchupi (1972); Milliman (1973); Schlee (1973).

Bermuda Islands (Region 3, Fig. 2)

Samples: 73—81; depths from 2 to 22 m.

Environment: Lagoonal estuarine "sounds" of intra-insular nature, fringed with carbonate reefs and some marshy terrain.

Hydrography: Moderately seasonal range of temperatures from 14.4° to 30°C with a mean annual value near 22.5°C. Relatively rapid seasonal increase in late April—early May, slower cooling in late summer and fall. Salinities of sound waters from $33.8^{0}/_{00}$ to $37.6^{0}/_{00}$ with an average near $36.6^{0}/_{00}$, with very little seasonal change. Sound waters strongly pycnoclinal in summer.

Climate: Tropical with cool winters.

Sources: Anonymous (1960); Neumann (1965); records from the Bermuda Marine Biological Station.

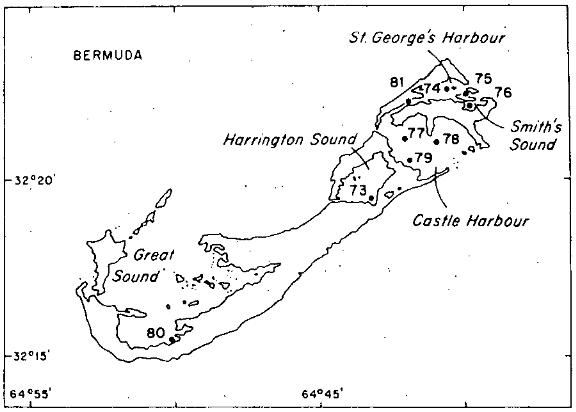


Fig. 2. Sample locations in Region 3, the Bermuda Islands.

Bahamas Islands (Region 4, Fig. 3)

Samples: 82—87; depths 1—5 m.

Environment: Carbonate platform shoals close to shore of islands, low relief and marshy.

Hydrography: Water temperatures from 20.4° to 25.4°C in winter, reaching as high as 31.5°C in summer. Salinities generally very high, from $37^{0}/_{00}$ to as high as $42^{0}/_{00}$ or greater over the carbonate banks.

Climate: Tropical

Sources: Smith (1940), Busby and Dick (1964).

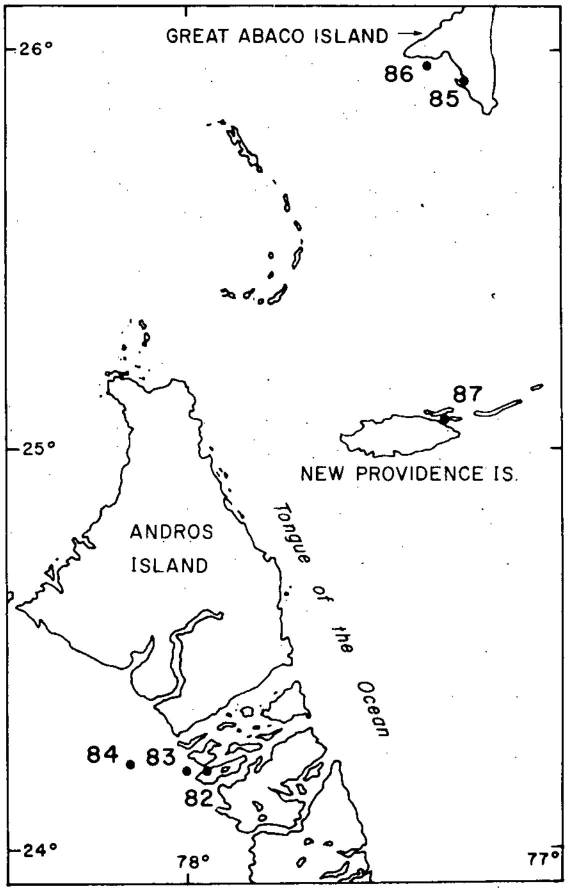


Fig. 3. Sample locations in Region 4, the Bahamas Islands.

Yucatan Channel, British Honduras (Region 5)

Samples: 88—90; depths 500—3,000 m.
Environment: Pelagic intercontinental sea environment above continental slope and rise zone with carbonate fine-grained sediments.
Hydrography: Water temperatures with mean monthly values from 25.8° in winter to 29° C in summer (September). Surface salinities in excess of 36‰.
Climate: Tropical.
Sources: Robinson (1973), Emery and Uchupi (1972, p. 264, 265).

Jamaica (Region 6, Fig. 4)

Samples: 91—94; depths 7—720 m.
Environment: Sheltered man-made harbor (Kingston) and pelagic intercontinental sea environment above carbonate-reef and lutite facies along the continental slope zone (eastern and southeastern Jamaica).
Hydrography: Kingston Harbor has temperatures from 23.3° to 31.1°C with a mean annual value of 27.6°C. Salinities vary from brackish during monsoon periods in May to July and October to November, when they are as low as 23.8‰ (the mean monthly minimum), and 8.9‰ (the extreme low individual value) to as high as 36.4‰ (mean monthly maximum) and 37.1% (extreme high individual reading) in between. The mean annual salinity value is 34.7‰. The offshore water temperatures vary from around 25° to 28°C and salinities are always greater than 36‰.
Climate: Tropical.
Sources: Anonymous (1960); Goodbody (1961).

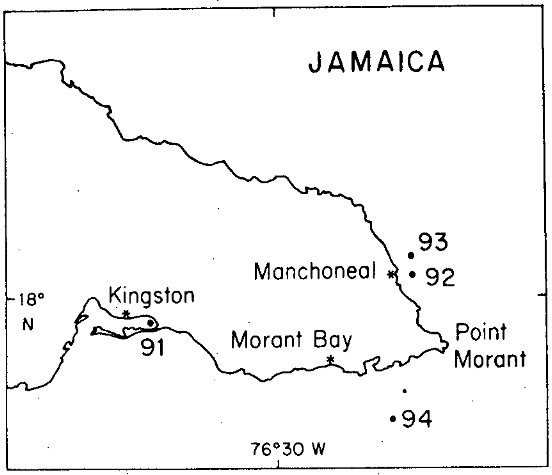


Fig. 4. Sample locations in Region 6, Jamaica.

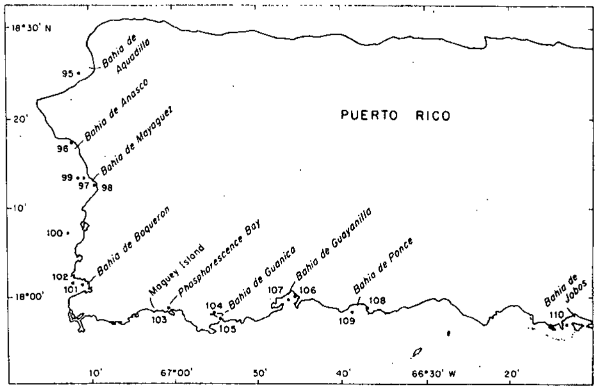


Fig. 5. Sample locations in Region 7, coastal areas of Puerto Rico.

Puerto Rico and Isla de Vieques (Region 7, Fig. 5)

Samples: 95—111; depths from 3 to 30 m.
Environment: Small bays and intervening shoal-water coastal areas with carbonate sediments adjacent to volcanic islands.
Hydrography: Data from Phosphorescence Bay, Puerto Rico and nearby Maguey Island are typical for this region. Water temperatures range from 27.3° to 30.5°C (mean monthly values) and the annual mean is 28.9°C. Salinities vary between 34.1‰ and 37.1‰ and have a mean annual value of 36.0‰. Salinities fall below 36‰ only in September to October.
Climate: Tropical.
Sources: Anonymous (1960); Burkholder and Burkholder (1958); and Seliger et al. (1971).

Gulf of Paria, Trinidad (Region 8, Fig. 6)

Samples: 112—118; depths from 10 to 28 m.
Environment: Large coastal embayment within the influence of a major delta (Orinico Delta) and coastal waters.

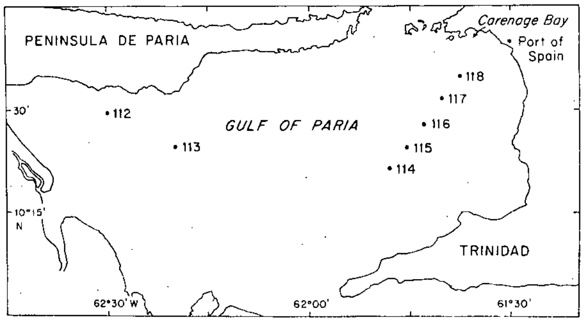


Fig. 6. Sample locations in Region 8, the Gulf of Paria, Trinidad.

Hydrography: Data from Carenage Bay, Port of Spain indicate that surface temperatures vary from 26.6° to 28.8°C (mean monthly values) and average 27.7°C per annum. Extreme values recorded from 1949 to 1955 were 25° and 31.1°C. Temperatures exceed 28°C from August through November. Salinities are low and vary from 26.6‰ to 28.8‰ (mean monthly values) and average 27.1‰ per annum. Extreme values have reached 10.6‰ and 37.7‰ from June through January. Greatest fluctuations occur in July to December and are coincident with warmest water temperatures.
Climate: Tropical monsoonal.
Sources: Van Andel and Postma (1954); Muller (1959); Anonymous (1960).

Offshore region southeast of Rio de la Plata, Argentina (Region 9, Fig. 7)

Samples: 130—135; depths from 500 to 5024 m.
Environment: Offshore pelagic environment at the approximate summer northern limit of a subtropical convergence involving the mixed subtropical waters of the Brazilian Current and northward-flowing cool waters of the Malvinas Current. Also influenced environmentally at times by detached parcels of shelf water from the Argentina Coastal Current which invade the offshore region. Continental slope-rise zone.
Hydrography: Surface temperatures vary from around 11° to 13°C in winter (August, September) to 18° to 22°C in summer (January, February). An inshore temperature gradient develops in summer with cooler water offshore and warm water offshore, but it disappears in winter. Water associated with the Brazilian Current has surface salinities between 35.6‰ and 36.4‰ and water associated with the Malvinas Current has values closer to 34.7‰. Lenses of coastal water have even lower values near 33‰—33.5‰.
Climate: Subtropical to warm temperate.
Sources: Data Files, Woods Hole Oceanographic Institution; Anonymous (1960); Boltovskoy (1965, p. 408; 1968).

Southern Norway (Region 10)

Samples: 136—139; depths from 240 to 680 m.
Environment: Glaciated fjords, including Voldenfjord, Korsfjord and Raunefjord.
Hydrography: Highly seasonal temperature ranges from less than 4°C in winter to ca. 15°C in summer, but occasionally as high as 20°C in the innermost sectors of fjords in shoal water. Surface salinities from around 21‰ to 30‰ but with more saline water (32‰ and increasing to 35‰ near bottom) only a few meters below surface.
Climate: Cool temperate type of Hall (1964).
Sources: Anonymous (1967); various plankton monographs.

Mediterranean Sea (Region 11, Fig. 8)

Samples: 141—151; depths 183—3,995 m.
Environment: Pelagic intercontinental sea environment above continental slope and rise zones.
Hydrography: Eastern Basin—surface temperatures from 15°C in winter to 28.3°C in summer and salinity values from 36‰ to 39.5‰. Western Basin — surface temperatures (in the vicinities of the Tunisia—Sicily gap and Ligurian Sea near sample locations) from 12.8° to 23°C, surface salinities 36‰—38‰.
Climate: Tropical to subtropical.
Sources: Parker (1955); Anonymous (1967).

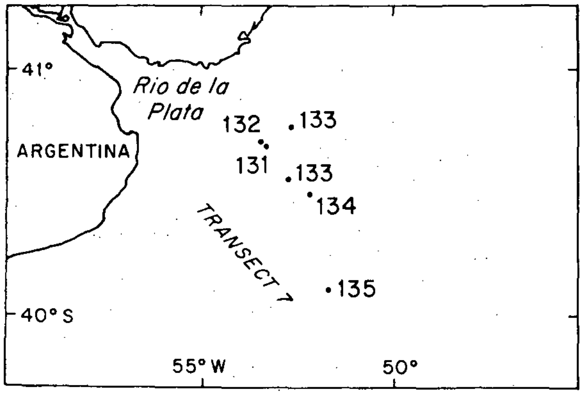


Fig. 7. Sample locations in Region 9, offshore Rio de la Plata, Argentina.

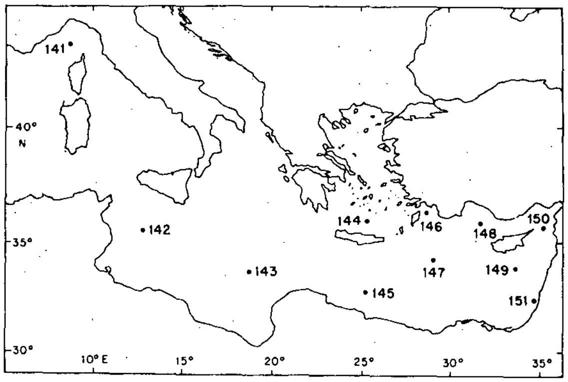


Fig. 8. Sample locations in Region 11, the Mediterranean Sea.

Ivory Coast near Abidjan, Gulf of Guinea (Region 12, Fig. 9)

Samples: 156, 157; depths 30 and 60 m.
Environment: Inshore continental shelf—coastal water environment near low-lying coast with large bar-built lagoons. Some coastal upwelling.
Hydrography: Surface water temperatures generally high, from 22°C in July through October to 28°C in March to June. Salinities moderate, from $32^{0}/_{00}$ to $34^{0}/_{00}$. Annual hydrographic climate involves two cool seasons (January to February and July through October) with intervening hot seasons. Coastal upwelling in the cool seasons associated with activity of the Guinea Current.
Climate: Tropical.
Sources: Reyssac (1970).

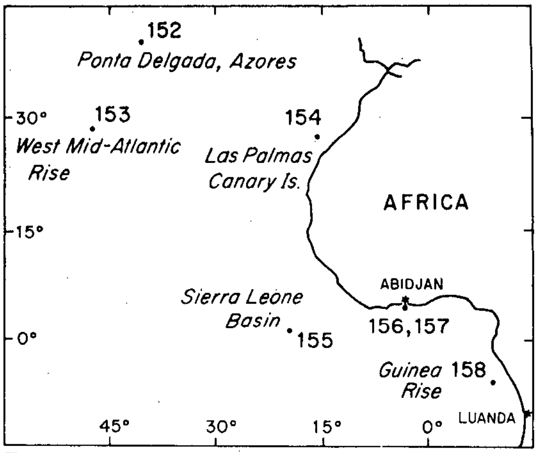


Fig. 9. Sample locations in Regions 12 and 13, the Ivory Coast near Abidjan and the Eastern and Equatorial Atlantic.

Eastern and Equatorial Atlantic Region (Region 13, Fig. 9)

Samples: 152—155; depths from 3 to 3,802 m.
Environments: Harbors in oceanic island environments at Ponta Delgada, Sao Miguel Island (Azores) and Las Palmas (Canaries); open ocean pelagic environments above the western flank of the Mid-Atlantic Ridge, north of the Romanche Trench and Guinea Rise off Angola. Influenced by the North Atlantic Drift, Canaries Current and South Equatorial Current.
Hydrography: Surface temperatures for the harbor environments ranged from 15.3° to 22.6°C (Ponta Delgado) and from 17.8° to 21.9°C (Las Palmas) in mean monthly values. Comparable values for the mid-oceanic and oceanic stations ranged from 20.2° to 26.5°C (Middle Atlantic Rise station), 24.3—27.2°C (Romanche Trench Station) and 20.6—26.5°C (Guinea Rise station). Salinity data indicate values for oceanic stations were above $36^{0}/_{00}$; none were available for the two harbor stations.
Climate: Tropical to subtropical.
Sources: Anonymous (1944, 1967).

Western South Africa (Region 14, Fig. 10)

Inshore zone

Samples: 159, 160 (Transect 9); *164—167* (Transect 8); depths from 110 to 202 m.
Environment: Western continental margin shelf environment with coastal upwelling (Benguelan upwelling system) adjacent to an arid hinterland. Some estuarine influence near the Orange River, but otherwise a neutral coastal environment.

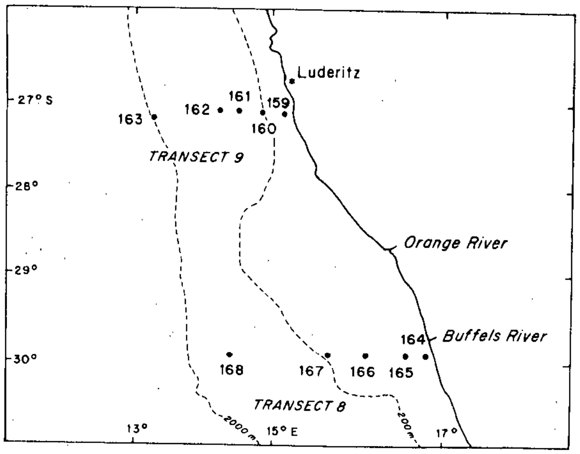


Fig. 10. Sample locations in Region 14, western South Africa.

Hydrography: Involves strong inshore—offshore zonation; nearshore zones include one of spasmodic upwelling and an outer zone of previously upwelled coastal water (see Fig. 26). Surface water temperatures of coastal waters vary from 12—15°C in the north (near latitude 27°S) to 14—16°C (near 30°S). Salinities vary between $34.8^{0}/_{00}$ and $35^{0}/_{00}$ excepting in the vicinity of the Orange River where they are as low as $33.4^{0}/_{00}$.
Climate: Subtropical to warm temperate.
Sources: Stander (1964); Shannon (1966); Bang (1971); Jones (1971).

Offshore zone

Samples: 161—163, 168; depths 349—2,060 m.
Environment: Offshore pelagic environment with an interior zone of divergence marked by a strong temperature—salinity discontinuity and an exterior oceanic zone which is part of the anticyclonic South-East Trade Wind Drift (Fig. 26). Site of the discontinuity

shifts further offshore to the north and centers around the $35^{0}/_{00}$ isohaline.
Hydrography: Surface temperatures range from 14—18°C in the north (around latitude 27°S) to 18—20°C in the south. Salinities are consistently around 35—$35.5^{0}/_{00}$.
Climate: Subtropical but tending towards temperate.
Sources: Stander (1964); Shannon (1966); Bang (1971); Jones (1971).

Coastal and offshore areas near Peru, South America (Region 15, Fig. 11)

Inshore zone near Callao and Pisco, Peru
Samples: 119—122; depths from 5 to 200 m.
Environment: Coastal embayments with nutrient-rich waters.
Hydrography: Surface water temperatures range from 15° to 23°C and salinities are slightly less than $35^{0}/_{00}$.
Climate: Subtropical
Sources: Instituto del Mar, Lima.

Offshore zone, near Pisco, Peru
Samples: 123—125 (Transect 5) and *127—129* (Transect 6); depths from 300 to 3,350 m.
Environment: Offshore pelagic environment in a region which experiences upwelling (Peruvian upwelling system) and also is a zone of offshore divergence between subtropical water (Peru Oceanic Current, part of the South Pacific East Trade Wind Drift) and subantarctic water (Peruvian Coastal Current) near 15°S.
Hydrography: Offshore surface water temperatures range from around 15.8° to 18°C and surface salinities vary from $35.0^{0}/_{00}$ to $35.5^{0}/_{00}$.
Climate: Cool subtropical.
Sources: Wyrtki (1966); Smith et al. (1971); Walsh et al. (1971).

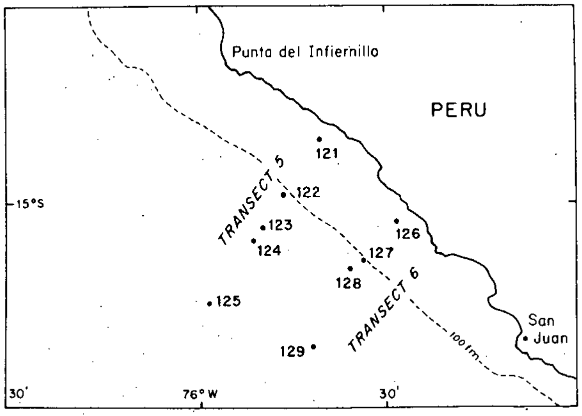


Fig. 11. Sample locations in Region 15, offshore areas of Peru near 15° S.

4. Results

The results of this study comprised in effect seven matrices of species-distributional data. These were the original sample counts, percentage data from them, a factor analysis matrix (including factor scores), a cluster analysis matrix (dendrogram) based on the Grassle—Smith Index, a cluster analysis matrix (dendrogram) based on the percentage similarity index, a species diversity matrix based on Hurlbert's Index and a specimen density matrix.

These results are summarized in Tables II, IV—VII, Appendices I—III and are dealt with below under the following five headings: assemblage composition in relation to environment and latitude, individual species distributions (mainly the results of percentages and factor analysis), species association definition and distribution (mainly the results of cluster analysis with the Grassle—Smith Index), species diversity and specimen density distributions.

Environmental and climatic distribution of assemblages

A moderately formal classification of marine environments was devised to facilitate the description and analysis of cyst-assemblage distributions. This classification divided marine environments into four systems, which were termed estuarine, coastal, transitional coastal—oceanic and oceanic and subdivided each according to criteria such as local surface water temperatures ("climate"), degree of stratification of the water column and vertical mixing (which are important among the factors which are known to influence the compositions of phytoplankton communities).

Each system in this classification represented a surface water hydrographic zone combined with a corresponding physiographic (topographic) unit beneath it. The hydrographic zones were based on broadly defined surface water types *sensu* Miller (1950), Bary (1963a), Laevastu (1963), Dodimead et al.

(1963), and others and included estuarine, coastal (shelf), transitional coastal—oceanic and oceanic types. The corresponding physiographic units were the familiar ones of estuaries, continental shelves, continental slope-rise and abyssal zones, respectively. Together they represent a series of marine environments which often are broadly referred to as estuarine, neritic, transitional neritic—oceanic and oceanic (pelagic) in literature. This type of classification, which recognized a mutual relationship between surface water and bottom topographic zones was necessary because dinoflagellate cysts originate in surface or near surface plankton but eventually accumulate as a thanatocoenosis in bottom sediments. Moreover, the surface water—bottom topography interrelationship is not merely fortuitous or passive in terms of phytoplankton ecology. The proximity of the sea floor to the euphotic zone in estuarine and inner neritic environments for example, strongly influences nutrient levels and rates of renewal, water clarity and other features to which phytoplankton are known to respond, whereas conversely, the greater distance between topographic bottom and the euphotic zone in pelagic realms means that the former exerts little or no influence on epipelagic communities.

This classification is presented below as a framework within which environmental—climatic variations in the species compositions of cyst assemblages can be described. These data are summarized in Table II for the most commonly seen cyst-based species.

A. Estuarine systems

Estuarine systems develop within topographic estuaries (drowned river valleys, fjords, bar-built lagoons, etc.) in which seawater is measurably diluted according to Pritchard's (1967) definition. They have certain characteristic circulation patterns (see Bowden, 1967) and may be brackish (positive) but also can be highly saline (inverse) at low latitudes. They develop over a wide range of thermal zones and have varying climates, which the subdivisions below represent in part.

A1. *Cool temperate, brackish, stratified estuaries*

Examples studied: Norwegian fjords (Voldenfjord, Korsfjord, Raunefjord).
Assemblages: Dominated by *Operculodinium centrocarpum* with smaller proportions of *Spiniferites bulloideus*, *Peridinium* species (including grouped *Peridinium* species as defined below), *P. conicum* and *P. pentagonum* with minor numbers of *Nematosphaeropsis balcombiana* and *Tectatodinium pellitum.*

A2. *Mild to cool temperate, low salinity, moderately stratified to vertically homogeneous estuaries*

Examples studied: Estuaries of the drowned river valley type along the northeastern coast of the United States from Maine to Cape Hatteras, including Machias Bay, Penobscot Bay, Cape Cod Bay, Buzzards Bay, Narragansett Bay, Long Island Sound, Raritan Bay, Delaware Bay and Chesapeake Bay.
Assemblages: Dominated either by *Operculodinium centrocarpum* or grouped *Peridinium* species with *P. conicum*, *Spiniferites elongatus* and *S. mirabilis* in smaller proportions (Fig. 12). In Somes Sound, Maine, a semi-enclosed fjord-like embayment, *S. elongatus*, *Bitectatodinium tepikiense* and *S. membranaceus* (*sensu* Reid, 1974) were unusually abundant compared with adjacent areas. In the Buzzards Bay region, a short-spined morphotype of *Spiniferites bentori* was present and *S. bulloideus* was more abundant than elsewhere along this section of coast excepting New Jersey.

A3. *Cool subtropical, brackish, vertically homogeneous estuaries*

Examples studied: Pamlico Sound, a shallow bar-built lagoon in the vicinity of Cape Hatteras, eastern United States.

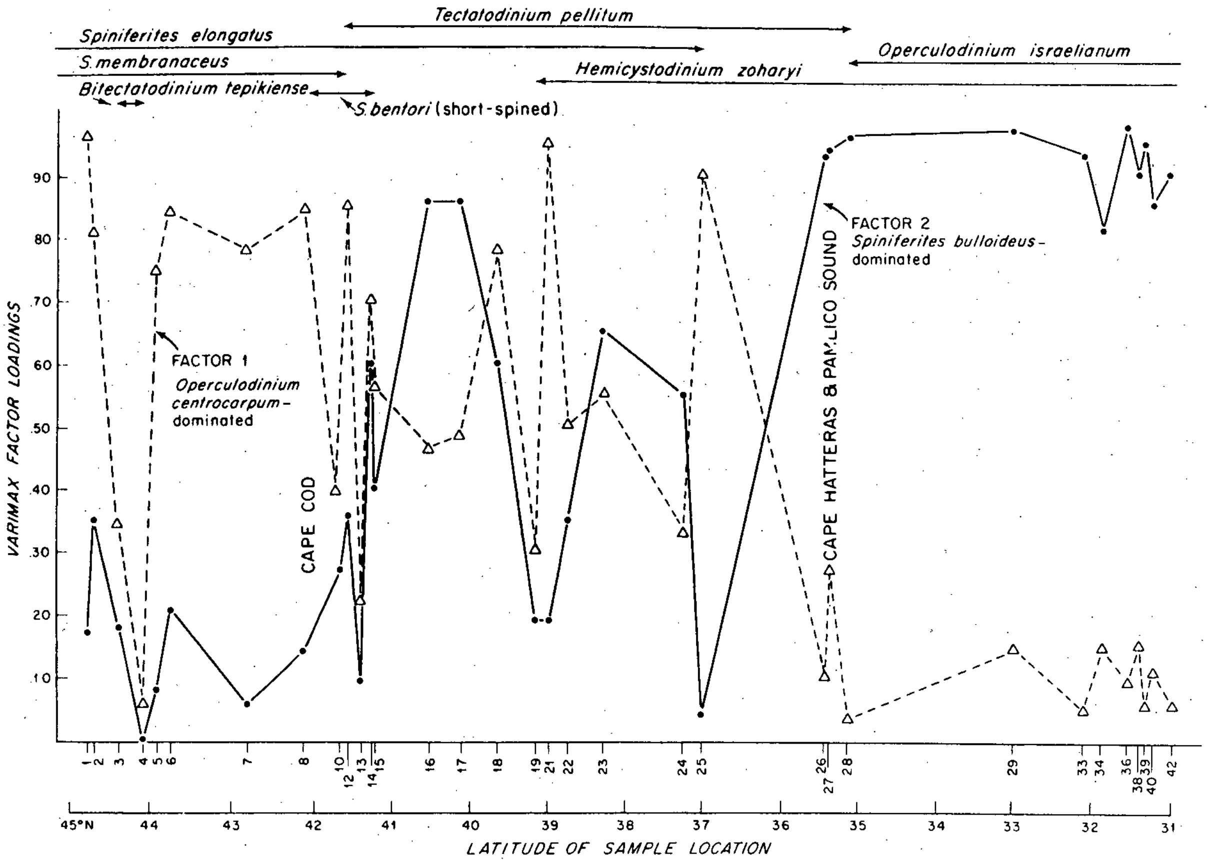


Fig. 12. Latitudinal variation in varimax factor loading values for principal components Factor 1 (*Operculodinium-centrocarpum*-dominated) and Factor 2 (*Spiniferites bulloideus*-dominated) along the coastal zone of the eastern United States. The local latitudinal ranges for selected taxa also are indicated at the top of the diagram.

Assemblages: Dominated by *S. bulloideus* with smaller proportions of *O. centrocarpum*, grouped *Peridinium* species, *Nematosphaeropsis balcombiana*, *Lingulodinium machaerophorum* and *Hemicystodinium zoharyi*. (Similar assemblages also were found adjacent to lagoons along the coast of New Jersey in the contiguous warm temperate climatic zone).

A4. *Subtropical—tropical, brackish to saline, vertically homogeneous estuaries*

Examples studied: Open coastal bight estuarine environments in the South Atlantic Bight from St. Helena Sound to Lanier Island.

Assemblages: Dominated by *Spiniferites bulloideus* with subdominant grouped *Peridinium* species. Minor proportions of *Lingulodinium machaerophorum*, *S. mirabilis*, *P. conicum*, *Operculodinium centrocarpum* and *Tuberculodinium vancampoae* (Fig. 12).

A5. *Tropical, low salinity estuarine-coastal subsystem with alternating periods of upwelling and stratification annually*

Example studied: Innermost shelf zone near Abidjan on the Ivory Coast of West Africa

TABLE II

Summary of the distribution of common cyst-based species (values are percentage-ranges for groups of assemblages single sample values)

Species cyst-based / Environmental subsystem	Estuarine and estuarine—neritic						
	Spiniferites elongatus	*S. membranaceus* (*sensu* Reid 1974)	*Bitectatodinium tepikiense*	*Planinosphaeridium choanum*	*Hemicystodinium zoharyi*	*Tuberculodinium vancampoae*	*Operculodinium israelianum*
Estuarine							
A1. Southern Norway	1—3	-	1—2	1	-	-	-
A2. United States Northeast Coast	38	9	11	P	8	1	-
A3. Pamlico Sound	-	-	-	-	8—14	2	1
A4. South Atlantic Bight	-	-	-	-	5	1—8	16
A5. Abidjan	-	-	-	-	-	-	-
A6. Gulf of Paria	-	-	-	-	-	1	1
A7. Azores, Canary Islands	-	-	-	-	-	-	-
A8. Bermuda	-	-	-	-	18—98	1	5
Bahamas	-	-	-	-	20	1	1—8
Puerto Rico	-	-	-	-	55	5	21
Jamaica	-	-	-	-	-	-	(30)
Coastal							
B1. Middle Atlantic Bight	3	-	-	-	-	-	-
B2. Peru near 15°S	-	-	-	-	-	-	-
western South Africa	-	-	-	-	-	-	-
Transitional coastal—oceanic							
C1. Argentina	-	-	-	-	-	-	-
Middle Atlantic Bight	1—3	-	P	P	-	1	1
C2. Peru	-	-	-	-	?3	1	-
western South Africa	-	-	-	-	-	-	-
Oceanic							
D1. Equatorial Atlantic	-	-	-	-	-	-	-
D2. Mediterranean Sea	-	-	-	-	18	1	4
Caribbean Sea, Yucatan Channel	-	-	-	-	10	-	1

(which is adjacent to several large bar-built lagoons inshore).

Assemblages: Diverse with *Spiniferites bulloideus* and *S. ramosus* ("African variety") as the most common taxa but moderate proportions of *S. mirabilis*, *Operculodinium centrocarpum* and *Tuberculodinium vancampoae* also present. Varied selection of *Peridinium* species.

A6. *Tropical, brackish, stratified estuaries*
Example studied: Gulf of Paria, Trinidad; a large, semi-enclosed embayment adjacent to a large river mouth delta, the Orinoco.

within environmental subsystem; a single value assumes a range of zero to the number indicated; parentheses indicate

					Neritic		Neritic—Oceanic		Oceanic
Spiniferites ramosus	*Spiniferites bentori* (two types)	*S. bulloideus*	*Lingulodinium machaerophorum*	Peridinioid taxa combined	*Operculodinium centrocarpum*	*Spiniferites mirabilis*	*Nematosphaeropsis balcombiana*	*Tectatodinium pellitum*	*Leptodinium* (*L. aculeatum*, *L. paradoxum*, *L. patulum*, *L. strialatum*, *L. sphaericum*)
1–2	-	2–18	1–2	2–18	62–77	2	1–8	2	-
4	1–29	2–58	7	3–90	5–62	6	5	2	-
1	-	47–63	3–7	9–17	3–15	2–8	3–11	1	-
3	3	33–58	2–17	4–43	1–6	2–8	3	-	-
7–30	-	19–27	1	15–16	9–13	6–9	1	-	-
20–42	-	8–20	15–56	5–24	1	1	1–6	-	-
-	40	1–17	12	5	8	1	-	-	-
2	-	1–18	1–52	5	7	1			
4	2	28–71	11	-	12–71	6	1	3	-
5	5	4–50	58	1–14	21	1	1	-	-
(1)	-	(12)	(17)	(39)	-	(1)	-	1	-
6	-	3–16	-	27–74	11–44	1–9	1	1	1
1	-	3–30	-	44-94	1	-	1	-	-
1	-	15–43	-	1–67	7–72	1	6	-	1
1–10	-	11–56	-	2–7	33–71	2–5	1–8	-	1–2
6	1	5–13	1	11–52	20–56	6	1–17	1–9	2–16
	-	2–9	-	36–95	1	1	2	16	2
1	-	10–32	1	1–4	57–80	2	2–13	1	1
43	-	1–3	2	4	2–46	1	1–7	1	2–96
8	1	1–44	1–18	15	1–26	1–5	1–49	2	8–55
2–4	-	39–63	1–8	3	8–21	2–8	1	1	3–17

Assemblages: Dominated mostly by *Spiniferites ramosus* ("Bermuda" type, *sensu* Wall and Dale, 1970), *Lingulodinium machaerophorum* and to a lesser extent, *S. bulloideus*. Small proportions of grouped *Peridinium* species, *P. conicum* and *Nematosphaeropsis balcombiana*.

A7. *Subtropical, saline stratified estuaries in oceanic islands*

Examples studied: Harbors in the Azores and Canary Islands; small embayments adjacent to volcanic terrain with precipitous slopes.

Assemblages: One assemblage from Ponta Delgado was dominated by calcareous cysts of the *Peridinium trochoideum* type and another from Las Palmas was dominated by long-spined specimens of *Spiniferites bentori. Lingulodinium machaerophorum* was common in the latter assemblage.

A8. *Tropical—subtropical, highly saline, stratified estuaries in oceanic islands*

Examples studied: Numerous small bays, lagoons and shallow carbonate platforms in Bermuda, the Bahamas Islands, Puerto Rico, Isla de Vieques and Jamaica.
Assemblages: Assemblages varied locally to a considerable extent (see Table II), but important species included *Hemicystodinium zoharyi*, which in places was strongly dominant, *Spiniferites bulloideus, Lingulodinium machaerophorum, Operculodinium israelianum* and *O. centrocarpum* (a type referred to as the "Abaco" variety below). *Spiniferites mirabilis, S. ramosus* (*sensu* Wall and Dale, 1970) and *Tuberculodinium vancampoae* were present in small numbers.

B. Coastal systems

Environmental systems comprising coastal or shelf water overlying the topographic continental shelf, characterized by variability in their temperature—salinity (T/S) properties with latitude but usually with increasing salinity and decreasing temperatures at greater depths in the water column. Systems sensitive to short-term phenomena such as wind stress and with both tidal and non-tidal circulation. Upwelling common in subsystems on the western margins of major landmasses.

B1. *Temperate, low to medium salinity, seasonally stratified subsystems*

Example studied: Continental shelf in the Middle Atlantic Bight region of the eastern United States, Cape Hatteras to Cape Cod.
Assemblages: Dominated either by *Operculodinium centrocarpum* or by grouped *Peridinium* species, with minor numbers of *Spiniferites bulloideus, S. mirabilis* and *Peridinium conicum* (Figs. 13—16).

B2. *Warm temperate, medium salinity subsystem with major upwelling*

Examples studied: Coast of Peru near Pisco in the Peruvian upwelling system and the coast of western South Africa in the Benguelan upwelling system.
Assemblages: Peruvian assemblages dominated by species of *Peridinium* including grouped *Peridinium* species and others (see Association VIII below) and South African assemblages containing high amounts of *Peridinium* inshore but dominated by *Operculodinium centrocarpum* and *Spiniferites bulloideus* elsewhere on the shelf (Transects 8 and 9, Figs. 18,19). A new species called Form A was found in association with upwelling systems both in Peru and South Africa.

C. Transitional Coastal—Oceanic System

The system comprising a band of surface water of intermediate hydrographic composition between coastal and oceanic waters which occur either side of it, overlying primarily the continental slope topographic-zone, but also extending over the outer continental shelf and continental rise zones. In some regions this intermediate water forms a near-surface permanent wedge-shaped mass known as *slope water* and its junction with coastal water is a major temperature—salinity discontinuity (convergence or oceanographic front). The coastal—oceanic transitional zone is frequently characterized by vertical turbulence in the upper hundred meters and it is hydrodynamically complex with current shearing, eddy formation and detachment.

C1. *Temperate-subtropical, eastern continental margin subsystems with hydrodynamic convergence*

Examples studied: The outer continental shelf, slope and rise zones of the Middle Atlantic Bight, eastern United States; continental rise off the coast of Argentina, southeast of the Rio de la Plata.
Assemblages: Middle Atlantic Bight assemblages dominated by *Operculodinium centro-*

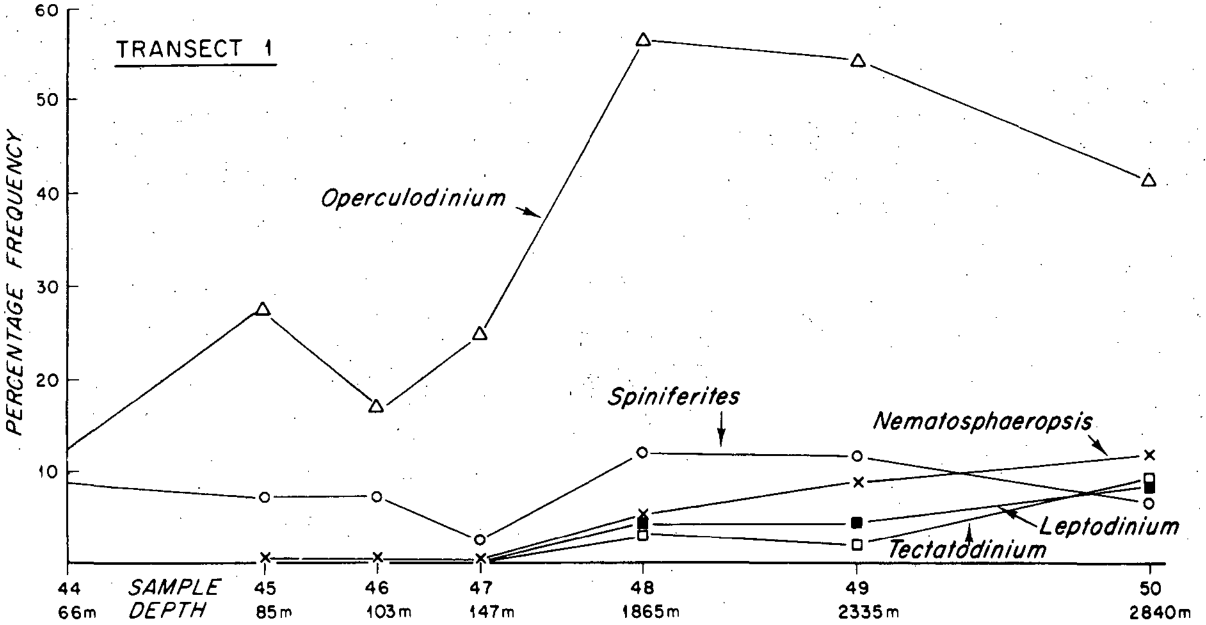


Fig. 13. Percentage frequency distributions for selected cyst-based genera along Transect 1, Middle Atlantic Bight.

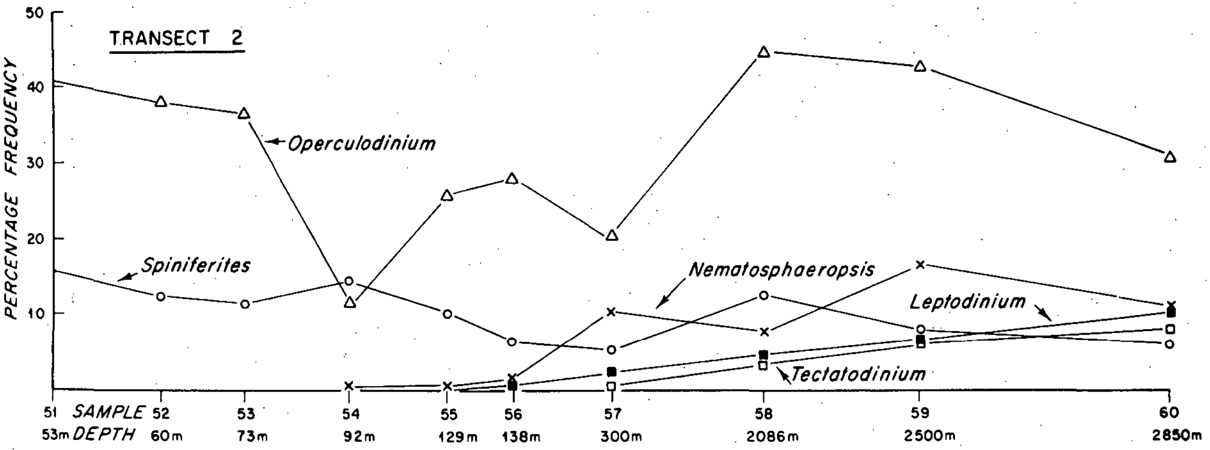


Fig. 14. Percentage frequency distributions for selected cyst-based genera along Transect 2, Middle Atlantic Bight.

carpum and grouped *Peridinium* species with significant occurrences of *Nematosphaeropsis balcombiana*, *Leptodinium sphaericum*, *Tectatodinium pellitum*, *Spiniferites bulloideus*, *S. mirabilis* and a few specimens of *S. elongatus*. Assemblages in the Argentina region very similar with *Operculodinium centrocarpum* dominant, *S. bulloideus* common in a few instances but lesser numbers of *Peridinium* species, *L. sphaericum*, *N. balcombiana* and *S. mirabilis* (Fig. 17).

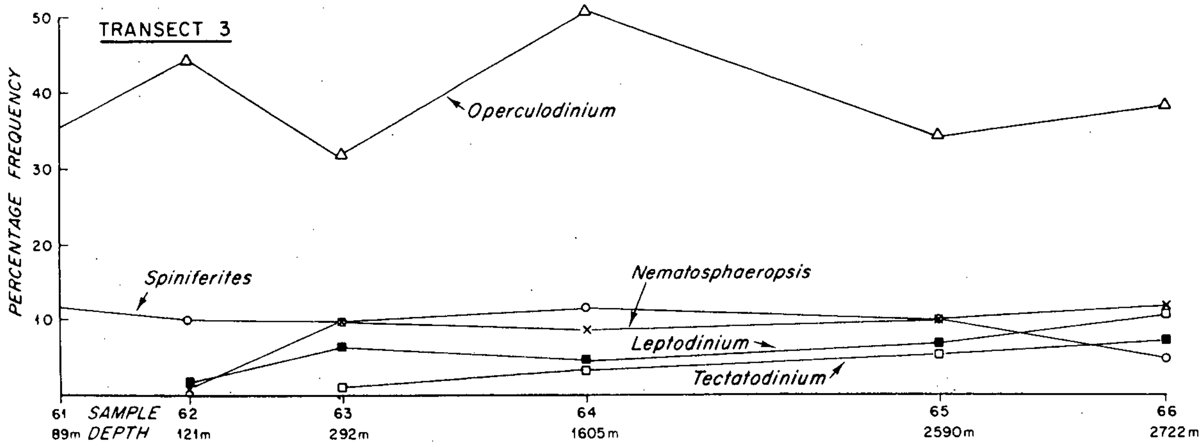


Fig. 15. Percentage frequency distributions for selected cyst-based genera along Transect 3, Middle Atlantic Bight.

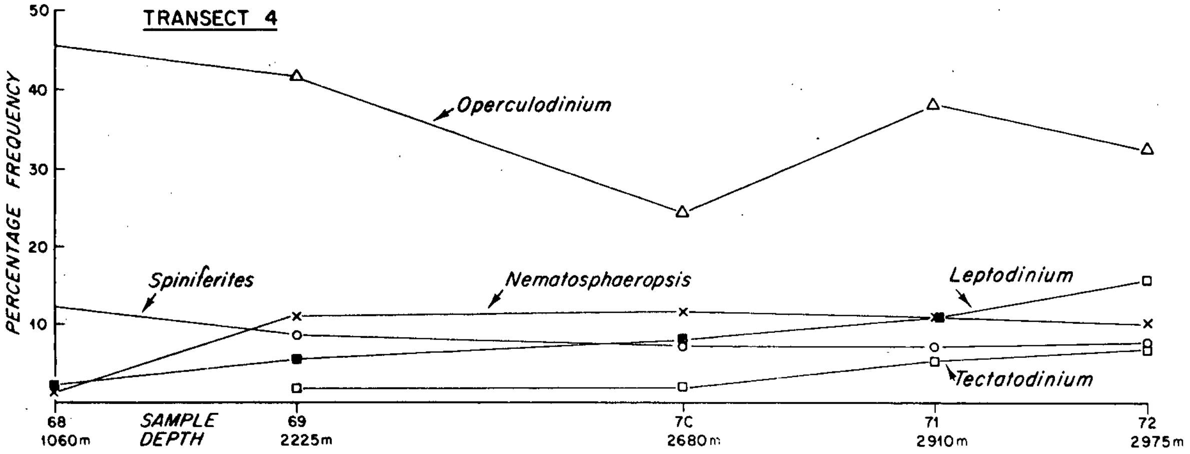


Fig. 16. Percentage frequency distributions for selected cyst-based genera along Transect 4, Middle Atlantic Bight.

C2. *Warm temperate, western continental margin subsystems with hydrographic divergence*

Examples studied: Outer continental shelf and slope off the western coast of South Africa and the outer shelf and slope-rise zone off Peru near 15°*S*.

Assemblages: Assemblages from the Peruvian region were dominated by *Peridinium* species which included grouped *Peridinium* species (Fig. 21) and *P. excentricum* as notable constituents. *Operculodinium centrocarpum* was present but less abundantly than in other slope-rise zones examined. *Nematosphaeropsis* and *Leptodinium* species were present only at very low relative frequencies. *Tectatodinium pellitum* was abundant in one assemblage. The dominant species in the South African slope-rise zone assemblages was *O. centrocarpum; Spiniferites bulloideus* was subdominant with *Nematosphaeropsis balcombiana* and species of *Peridinium* and *Leptodinium* were present in very low numbers (Figs. 18, 19).

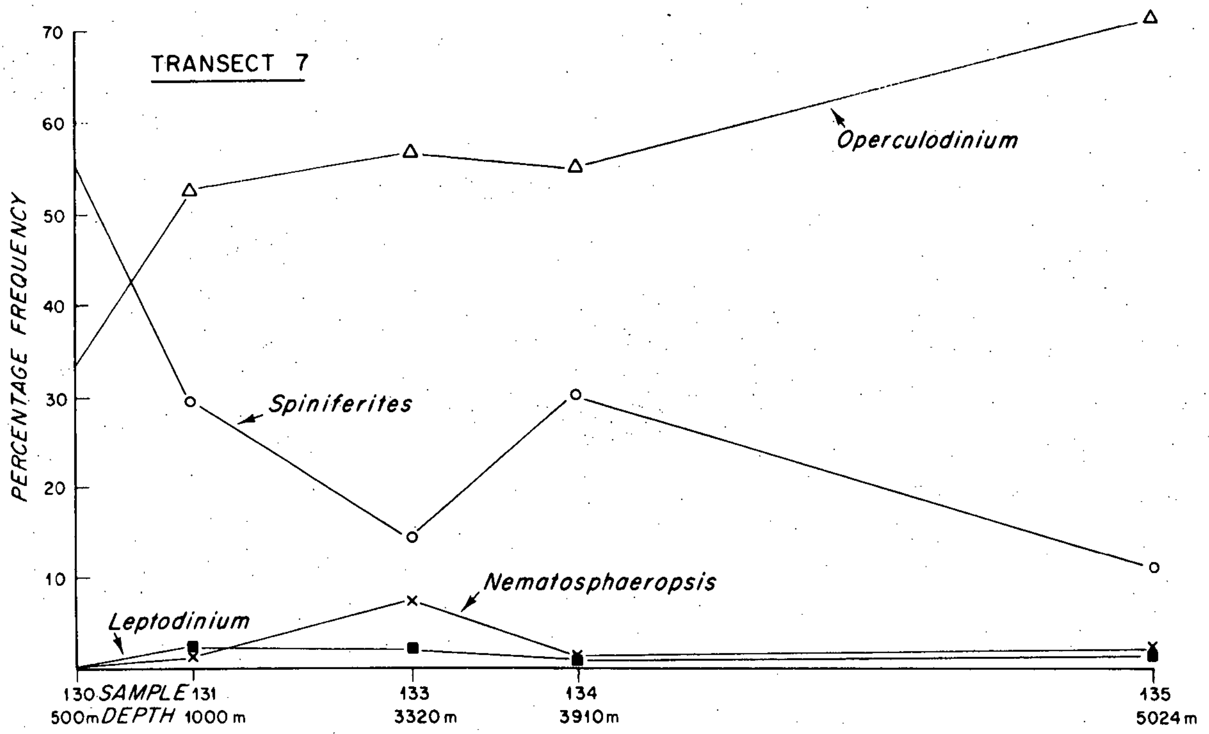


Fig. 17. Percentage frequency distributions for selected cyst-based genera along Transect 7, offshore Rio de la Plata, Argentina.

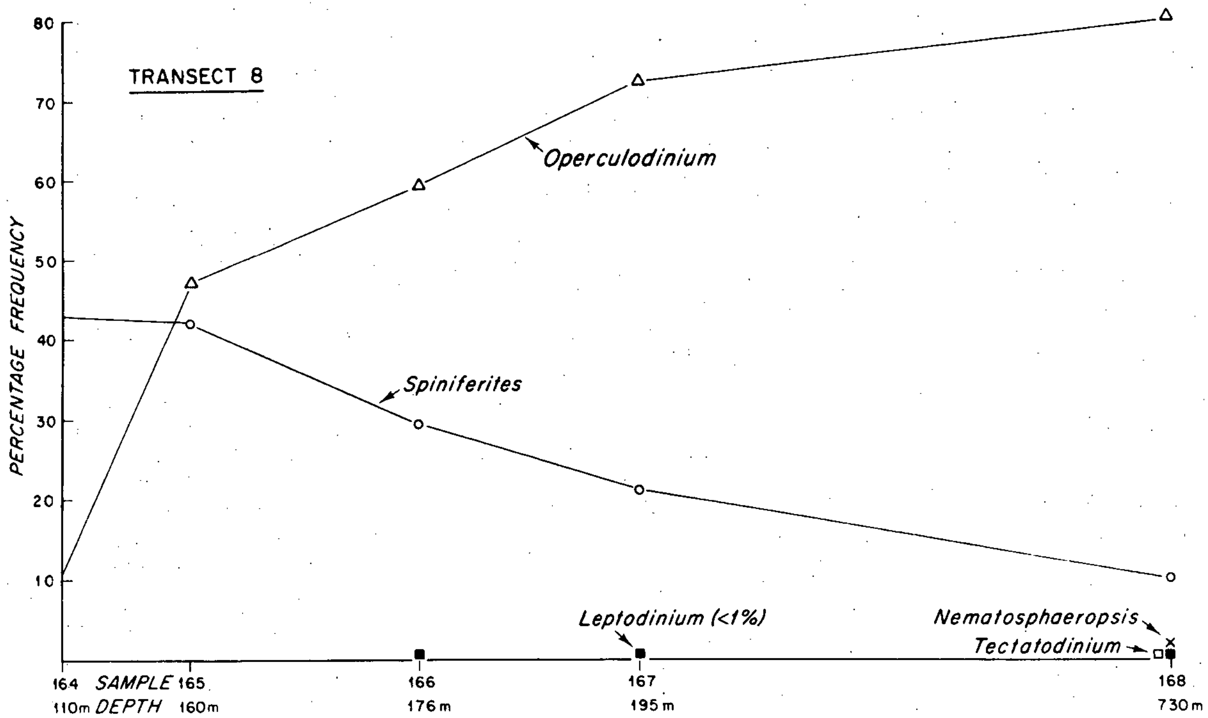


Fig. 18. Percentage frequency distributions for selected cyst-based genera along Transect 8, western South Africa

D. Oceanic systems

These comprise open ocean surface water environments which are part of major gyral circulation systems, overlying pelagic sediments on abyssal plains and continental rise zones. Intercontinental sea subsystems were incorporated here as "oceanic" (rather than transitional) because they possess highly saline surface waters and do not show features which appear in coastal—oceanic "slope water" systems of the types which were described above. Nonetheless, intercontinental sea samples were from continental rises and not from abyssal plains.

D1. *Tropical-subtropical open ocean subsystems in major oceans*

Examples studied: Mid-ocean pelagic sediments from the Middle Atlantic Rise, Sierra Leone Rise and Basin in the North and South Atlantic Oceans.

Assemblages: Dominated by species of *Leptodinium (L. aculeatum, L. strialatum, L. paradoxum, L. sphaericum* and *L. patulum)* with *O. centrocarpum* and *Spiniferites ramosus* common in samples from the vicinity of continental rises.

D2. *Tropical—subtropical open ocean subsystems in intercontinental seas*

Examples studied: Continental rise zone sediments from the Mediterranean Sea and Caribbean Sea (Yucatan Basin and eastern Jamaica).

Assemblages: Assemblages dominated either by species of *Leptodinium*, by *Nematosphaeropsis balcombiana* or *Spiniferites bulloideus* in the Mediterranean Sea. *Operculodinium centrocarpum*, *Lingulodinium machaerophorum* and *Hemicystodinium zoharyi* present in moderate proportions in some assemblages. Assemblages from the Caribbean Sea dominated by *S. bulloideus* with lesser proportions

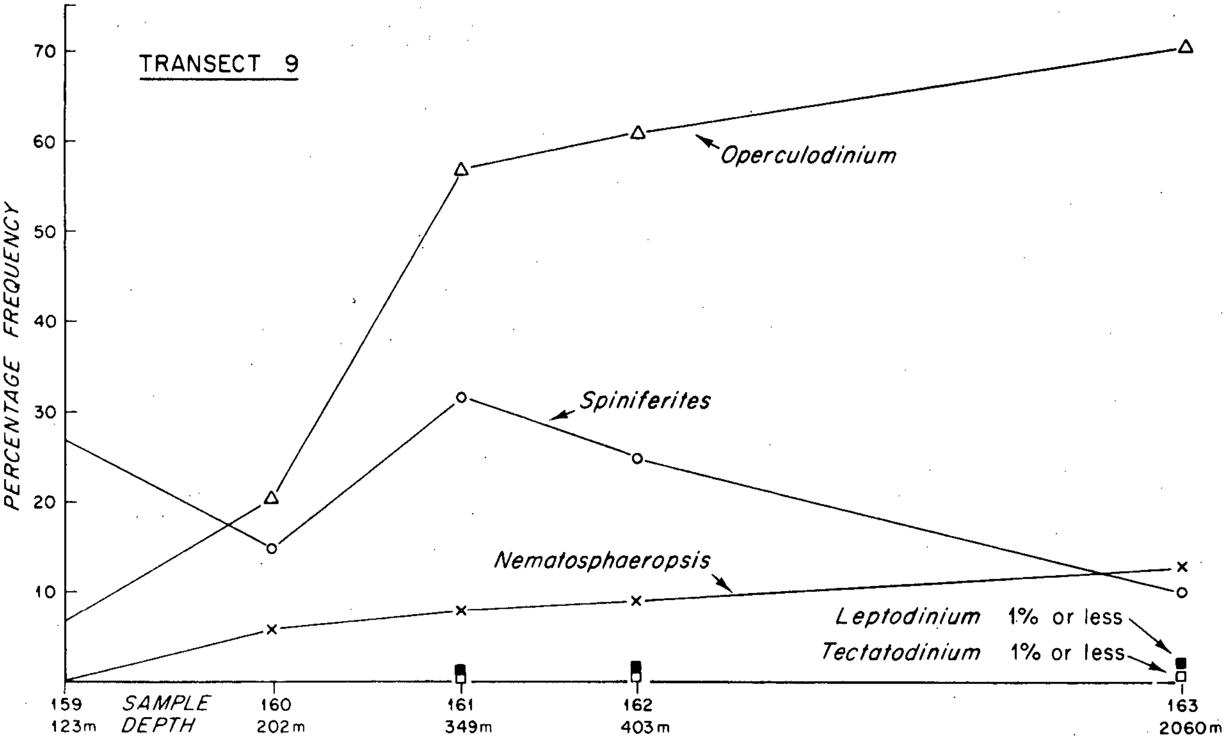


Fig. 19. Percentage frequency distributions for selected cyst-based genera along Transect 9, western South Africa.

of *O. centrocarpum* and *Leptodinium* species; *Nematosphaeropsis balcombiana* rare.

Distribution of selected individual species

Distributions as observed for some selected cyst-based taxa are described below because they largely comprise the basis for development of an ecologic classification (section 6) and because they embody the results of factor analysis which was instrumental in recognition of distributional trends of an environmental and climatic nature (section 5).

Factor scores (Appendix I) which corresponded to Factors 1 to 9 in that analysis, clearly were each dominated by a single high value for a different species (with the exception of Factor 5 and its respective factor scores). This indicated that factor loading values (Appendix II) for these first nine factors were, in their turn, heavily influenced by the numerical presence of a single different species. The results of factor analysis therefore were considered to be mainly a reflection of species distributions on the part of a few dominant or common taxa and are discussed in this context. This mode of treatment is similar to that adopted by D.B. Williams (1971), who recognized single species-dominated "biofacies".

A concept of "centers of distribution" for individual species is used below for convenience. A center of distribution was defined simply as a site (set of samples) wherein a species was the most abundant member of one or more assemblages. This coincidentally denoted samples (assemblages) wherein that species had factor loading values greater than 0.7, and in practice, this meant that the first ranked species comprised between 30 and 98% of the assemblage. The taxonomic nomenclature used here is that previously applied to dinoflagellate cyst-based taxa in palynological literature. A summary of known taxonomic equivalences between cyst- and theca-based entities is given in Table III. Eighty-six cyst morphotypes were identified during this study and unfortunately, nineteen of these are not described in previous literature but it is beyond the scope of this paper to describe them here. A few illustrations of the most environmentally significant ones are given (Plate I). Descriptions of other cyst-based taxa referred to here can be found in Rossignol (1964), Wall (1967), Wall and Dale (1968a), Davey and Rogers (1975) and Reid (1975). A few miscellaneous taxonomic notes are appended to species descriptions where there is significant departure from earlier treatments, but in general, the nomenclature used here is conservative and direct reference to names in other literature can be made from it.

Operculodinium centrocarpum (Deflandre and Cookson) Wall 1967

This was the single most abundant species in 31% of the samples and locally it was dominant in assemblages to the level of 80% (southwestern South Africa). It attained a maximum single-species specimen density value of 24.4×10^3 per g (Argentina). It ranked second in ubiquity and occurred in 90% of the samples. In factor analysis, it was an almost monospecific component of Factor 1, with a corresponding factor score of 0.994; this factor accounted for 32.8 of the variance in the compositional data. In many respects therefore *O. centrocarpum* was the single most important species in the study.

Centers of its distribution (as defined above) were located within a range of estuarine, coastal and transitional coastal—oceanic environmental systems at temperate and subtropical latitudes in the main. Specifically, these centers were as follows: in estuarine systems (type A1, Norway, 62—77%; type A2, northeastern United States above Cape Hatteras, 33—62%), in coastal subsystems (type B1, Middle Atlantic Bight, 41—44%; type B2, southwestern South Africa, 47—72%), and transitional coastal—oceanic subsystems (type C1, Middle Atlantic Bight, 31—56%; Argentina, 53—71%; and type C2, southwestern

TABLE III

Taxonomic equivalence between cyst-and theca-based nomenclature (where dual nomenclature exists)

Cyst-based taxon	Theca-based taxon
Spiniferites all extant species *Nematosphaeropsis* *N. balcombiana* *Tectatodinium* *T. pellitum* ? other extant species *Bitectatodinium* *B. tepikiense* *Planinosphaeridium* *P. choanum* *Leptodinium* probably all extant species	*Gonyaulax spinifera*-group (*G. spinifera, G. digitalis, G. scrippsae*, others)
Operculodinium all extant species	*Protoceratium reticulatum*-group *(= Gonyaulax grindleyi)*
Lingulodinium *L. machaerophorum*	*Gonyaulax polyedra*-group
Hemicystodinium *H. zoharyi*	*Pyrodinium* *P. bahamense*
Tuberculodinium *T. vancampoae* *(= Pyrophacus vancampoae)*	*Pyrophacus* *P. vancampoae*

South Africa, 57—80%).

The species was notably less abundant (and significantly so in view of its tendency to be cosmopolitan) in other environmental subsystems where it failed to develop centers. These "negative" subsystems for *O. centrocarpum* included estuarine subsystems (types A3—A8 above), coastal and transitional coastal—oceanic subsystems (types B2 and C2 in the Peruvian region) and oceanic subsystems (types D1 and D2 above). These subsystems represent tropical environments in general (from nearshore to mid-ocean), environments with extensive coastal upwelling and estuaries with brackish, non-stratified waters. Percentage values for *O. centrocarpum* in these and other environments are shown in Table II.

One small and unusual center of distribution was located near southern Great Abaco Island (Bahamas), in a tropical-estuarine environment (type A8). The specimens from this site were larger than elsewhere (vesicle diameter 47—66 μm compared with ca. 40 μm elsewhere) and they had fewer stronger spines. Consequently they may represent a distinct local ecophenotypic race whose ecologic preferences depart from the species norm (see section 7).

Two trends were recognizable in the overall distribution of *O. centrocarpum*. First, its relative abundance tended to increase offshore to a maximum in the continental slope and upper rise zone, beyond which it again decreased. This trend was seen in transects across the Middle Atlantic Bight region of the United States (Figs. 13—16), in the Argentina region (Fig. 17) and South African regions

(Figs. 18, 19). Second, its abundance tended to decrease tropicwards. An example of this was along the eastern coast of the United States (Fig. 12) where its percentage abundance decreased from an average value of 35% north of Cape Hatteras to 7% to the south of it. [This is the reverse of a latitudinal relationship which was encountered by Davey (1971) along the western coast of South Africa, and is discussed later.]

Operculodinium israelianum (Rossignol) Wall 1967

This species occurred in only 20% of the samples and its distribution was limited to the Caribbean region, Bermuda, the Bahamas, the southeastern coast of the United States and Mediterranean. Its maximum representation was 54% (Bahia de Guayanilla, Puerto Rico) and its specimen density values did not exceed 138 per gram. It was represented as Factor 8 in the factor analysis with a matching factor score of 0.928 but this accounted for only 1.4% of the variance in the data, and so reflects the species' general lack of abundance.

It had only two small, localized centers of distribution, indicating a very patchy distribution. These centers were both in tropical-estuarine subsystems (type A8), namely, in Bahia de Guayanilla, Puerto Rico and Kingston Harbor, Jamaica (30% of the assemblage). Other occurrences of the species were in Bermuda (up to 5%) and the Bahamas (up to 8%) in the same type of environment.

Spiniferites bulloideus (Deflandre and Cookson) Sarjeant 1970

This was the second most abundantly encountered species in the study. It occurred in all the samples and was the most abundant species in 25% of the assemblages. It often was dominant in the latter and it reached a maximum of 71% in an assemblage from the Bahamas (Table II). Its specimen density attained a maximum of 3.46×10^3/g in a sample from Raunefjord, Norway, but elsewhere its values were typically less than one half of this. In factor analysis, *S. bulloideus* was the major contributor to Factor 2 with a corresponding factor score of 0.99. This factor accounted for 21.2% of the variance in compositional data.

Centers of distribution of the species were mainly located in estuarine environments and especially in subsystems where brackish, nonstratified hydrographic conditions prevailed, as in (or near entrances to) bar-built lagoons. However, the centers were not exclusively located in this type of environment and two small centers were situated in more saline, tropical sites. These estuarine centers and percentage values for *S. bulloideus* within them were as follows: type A2 (northeastern United States, 30—58%, mainly bar-built lagoons along the coast of New Jersey), type A3 (Pamlico Sound, 47—63%), type A4 (South Atlantic Bight, 33—58%), type A5 (Abidjan region, 19—27%, adjacent to large coastal lagoons), and type A8 (Bahamas, 39—71%, Puerto Rico, 29—50%).

This species was not the dominant one in all estuarine subsystems: for instance, it was not the most abundant species in assemblages from Norwegian fjords, the Gulf of Paria or in Bermuda sounds. However, it was always present in them and in some instances its specimen density values were high, even though its percentages were modest: for instance, it had density values from 407 to 2,260 specimens/g in Norwegian fjords even though it did not exceed 18% of any assemblage there. This contrasted with the South Atlantic Bight where its percentages reached between 36 and 58 but its specimen densities were only 214/g at their maximum.

Overall, the species was ubiquitous in all estuarine subsystems, despite some low percentage values in places. However, *S. bulloideus* was not an important constituent of coastal and transitional coastal—oceanic environmental systems in the Middle Atlantic Bight, Argentina, Peruvian or South African regions in terms of being dominant, although it was often a common subdominant species. It did not develop many centers in these non-estuarine sites, but there were isolated ones in continental rises of the intercontinental sea subsystem (type D2) from the Mediterranean region, the Yucatan Basin and Jamaican Caribbean regions. These D2-type centers were not considered to be important in the overall distribution pattern of the species.

Spiniferites ramosus (Ehrenberg) Loeblich and Loeblich 1966

Specimens identified as *S. ramosus* occurred in 63% of the samples (see note below) and locally it was dominant in assemblages to the level of 42% (Gulf of Paria). However, it was the most abundant species in only three samples in sharp contrast to other "ubiquitous" species (*S. bulloideus, O. centrocarpum*) which were first ranked in 40—50 samples. It was an important member of Factor 5 with a corresponding factor score of 0.437 (together with *Lingulodinium machaerophorum*) and Factor 5 accounted for 5.9% of the variance in the compositional data.

Only one center of distribution for *S. ramosus* was encountered in this study. This was in the Gulf of Paria estuarine subsystem (A6) where the species was the most abundant one in two samples (*112*, *113*) (maximum 42%); its percentage range for the entire Gulf of Paria was 20—42%. Elsewhere it was found in small numbers (5% maximum) in a few samples from Bermuda, the Bahamas, Puerto Rico and Jamaica in estuarine subsystems of type A8.

It must be noted that the name *S. ramosus* almost unavoidably was used for a range of very similar morphotypes which did not necessarily comprise a single "biologic unit"; nor is it theoretically certain what systematic status such a "unit" should have (e.g., species, subspecies, or race) if it was recognizable. The particular morphotype which occurred in the Gulf of Paria and the Caribbean—Bahamas—Bermuda region in general was one which was described and cultured by Wall and Dale (1970). Its distribution apparently is limited (within this study) to tropical—subtropical estuarine subsystems (A6, A8). It apparently is morphologically and perhaps ecologically different from *S. ramosus* as it was defined by Davey (1971) and Davey and Rogers (1975) from assemblages in the South African region in two respects. First, we probably identified small specimens of this general morphology as *S. bulloideus* (although not solely on the basis of size as was stated by Davey and Rogers, 1975, p. 233 in their footnote). Second, specimens which we referred to *S. ramosus* from the eastern Atlantic region, the Mediterranean Sea and Black Sea, had a weakly micropunctate wall which the Gulf of Paria specimens lacked. Informally we referred to the eastern Atlantic—South African specimens as the "African" variety during this work. *Spiniferites ramosus sensu* Davey ("African" variety) attained local abundances which exceed those which we observed for *S. ramosus sensu* Wall and Dale and it appeared to occur in shelf and slope sediments rather than estuarine sediments (but see later discussion).

Spiniferites mirabilis (Rossignol) Sarjeant 1970

This species was widespread geographically and environmentally, with occurrences in 72% of the assemblages but it was consistently present only in small proportions with a maximum of 9% in samples from Abidjan (subsystem A5) and the Middle Atlantic Bight shelf zone (subsystem B1). It was not important in the factor analysis. The only definitive aspect of its distribution was its cosmopolitanism.

Spiniferites membranaceus (Rossignol) Sarjeant 1970

Specimens identical with those illustrated by Reid (1975, his plate 3, figs. 28—30) from Britain were found in four samples from the northeastern coastal zone of the United States from Buzzards Bay to Maine. They were most abundant in an assemblage near Mount Desert Island, from a fjord-like estuary called Somes Sound (subsystem A2) where they represented 9% of the count and had a specimen density of 342/g.

Spiniferites membranaceus as described by Reid (op. cit) is probably not conspecific with *S. membranaceus* as described by Rossignol (1964) and Wall (1967) from Quaternary sediments of the Mediterranean and Carribbean. A few of the latter type were found in surface sediments from the Mediterranean Sea and Bahamas during this study, but they were rare.

Spiniferites elongatus Reid 1975

This distinctive species was found in 30% of the samples and had a distribution which was limited to the northeastern coastal zone of the United States, the Middle Atlantic Bight and Scandinavia. Its southernmost occurrence was in Chesapeake Bay (Fig. 12). It was the most abundant species in one assemblage from Somes Sound, Maine (38%, 1.43×10^3 specimens/g) and it reached 7% in Buzzards Bay, but elsewhere did not exceed 4%. Its only center of distribution was in Somes Sound (subsystem type A2) but it was persistent at a low level of abundance in other assemblages from the same subsystem along the eastern United States and in shelf and slope-rise sediments from the Middle Atlantic Bight (subsystems B1 and C1).

Spiniferites bentori (Rossignol) Wall and Dale 1970

Two distinctive morphotypes of *S. bentori* were recognized during this study. The first corresponded to the holotype (Rossignol, 1964, plate 1, figs. 3, 7, 8). It was found in abundance at only one locality, namely, Las Palmas Harbor in the Canary Islands (40% of the assemblage) in estuarine subsystem A7. Elsewhere it occurred only in low relative frequencies (5% maximum) in small bays along the coast of Puerto Rico, Isla de Vieques and Bahamas (estuarine subsystem A8), rarely in the South Atlantic Bight (subsystem A4) and in the Mediterranean Sea (subsystem D2) in insignificant quantities.

The second morphotype was a short-spined variant which was described by Wall (1965, figs. 1, 2) and used in laboratory culture experiments. It had a highly localized distribution and was restricted to five assemblages between eastern Long Island Sound and Buzzards Bay in the inshore zone of the northern sector of the Middle Atlantic Bight (samples *11—15* in Fig. 1). It reached a maximum of 29% in sample *11* from Buzzards Bay (430 specimens/g) and did not exceed 3% in the other four.

Bitectatodinium tepikiense Wilson 1973

This species was encountered in Norwegian fjords, in Maine along the eastern United States and in one sample from the Mediterranean Sea north of Crete. In Norwegian fjords it never exceeded 2% of the four assemblages which contained it but it reached 320 specimens/g in one sample. In the inshore Gulf of Maine area it occurred in Somes Sound (11% and 425 specimens/g) and Blue Hill Bay (3%). Its environmental association was with estuarine subsystems of type A1 and A2 which are similar in many respects. (Live specimens from Somes Sound were cultured to produce thecae of the general *Gonyaulax spinifera* type and this will be reported in detail elsewhere.)

Reid (1964) recorded this species as *Caledonidinium vermiculatum* sp. nov. from its occurrences around the British Isles but Wilson's (1973) name takes priority.

Planinosphaeridium choanum (Reid 1974) nov. comb. Wall 1977

Reid's new genus *Ataxiodinium* (type species: *Ataxiodinium choanum*, sp. nov., Reid, 1974, p. 588, plate 1, figs. 1, 2; Nova Hedwigia, 25 has precisely the generic characteristics of *Planinosphaeridium* Eisenack 1965 (p. 151), and hence Reid's new species *Ataxiodinium choanum* is changed to *Planinosphaeridium choanum* (Reid 1974) nov. comb. Wall 1977.

The species was rare and was found only in Norwegian fjords, Somes Sound in the western Gulf of Maine and in four samples (*52, 53, 64, 65*) from the Middle Atlantic Bight region at a very low level (1% or less of assemblages). It is of interest because of its unusual morphology and because its distribution appears to be very similar to that of *Bitectatodinium tepikiense* with which it often occurs. It also was isolated live from Somes Sound and cultured to produce thecae of the *Gonyaulax spinifera*-type.

Nematosphaeropsis balcombiana Deflandre and Cookson 1955

This species occurred in 58% of the assemblages and so was generally common. It was absent or rare only in shallow-water oceanic island assemblages from parts of the Caribbean, Bahamas and Bermuda Islands. However, it was the dominant species in only two samples, which both were from the Mediterranean region (*141, 145*) where it represented 49 and 47%, respectively. Elsewhere it never exceeded 17%. Its maximum observed specimen density was 1.12×10^3/g in sample *64* from the offshore Middle Atlantic Bight. In factor analysis it was the most important contributor to Factor 7 with a corresponding factor score of 0.977; Factor 7 accounted for only 1.7 of the variance in the compositional data. The species was ranked the sixth most important species in overall abundance and the seventh in terms of representation in samples.

It was present over a wide range of latitude (southern Norway to South Africa) and in all environmental systems examined (Table II). Its only center was diffuse and sample-poor, being that comprising the two samples cited above from north of Corsica in the Ligurian Sea and northeast of Libya in the southern central Mediterranean (subsystem type D2). However, in some regions it showed a clear trend towards increasing in relative abundance offshore in slope-rise sediments as compared with adjacent shelf and estuarine assemblages (Figs. 13—17, and 19). For example, in the eastern United States region it averaged 1.1% in estuarine subsystems (A2, A3, and A4); it averaged 5.5% in shelf sediments of the coastal subsystem (B1); and it averaged 9.6% in slope-rise zone sediments of the transitional coastal—oceanic system. Corresponding increases in its specimen density values were observed alongside these percentage increases (from mean values of 8, to 210 and 388 specimens/g, respectively). A comparable set of observations was collected from the Argentina, Peru and South African transects (Transects 6—9) but the trend was not so pronounced.

Tectatodinium pellitum Wall 1967

This species occurred in only 38% of the samples and did not exceed 9% of any individual assemblage or more than 530 specimens/g. It was present in small numbers in each of the four systems examined and represented geographically in the eastern United States, Bermuda, the Bahamas, Peru, South Africa and the Mediterranean, but not in Argentina, Scandinavia and parts of the Caribbean (Table II). It was not very important in the factor analysis, but it made a small contribution to Factor 7 in conjunction with *Nematosphaeropsis balcombiana*, whose overall pattern of distribution it closely followed.

The species was only common in offshore sediments from the outer continental shelf and the slope-rise zone of the Middle Atlantic Bight in the transitional coastal—oceanic "slope" system there (type C2). In Transects 1—4 in this area it systematically increased seawards to maxima of 9%, 8%, 7% and 6%, respectively, from around 1% or less in shelf sediments. Like *N. balcombiana*, it also occurred in estuarine sediments, but in the eastern United States was detected only between Buzzards Bay and Pamlico Sound (in six samples) and it apparently was not present along the entire coastline.

Leptodinium aculeatum Wall 1967 (and related species)

The five species of *Leptodinium* which are known to occur in modern sediments can be dealt with together because they all have essentially the same type of distribution. These species are *L. aculeatum*, *L. paradoxum*, *L. patulum*, *L. sphaericum* and *L. strialatum* (Wall 1967). They occurred in 31% of the assemblages and in sum, comprised the most abundant genus present in six of the samples. *Leptodinium* (as a genus) attained a maximum percentage abundance of 96% (sample *153*, Mid-Atlantic Rise) but did not exceed 632 specimens/g. In factor analysis, *L. aculeatum* was a major contributor to Factor 6 with a factor score for this factor of 0.952; Factor 6 accounted for 3.86 of the variance in compositional data.

The environmental pattern of distribution for *Leptodinium* species was highly distinctive. All five species were restricted to outermost continental shelf, slope, rise and abyssal sediments representing primarily oceanic and transitional coastal—oceanic systems in the central North and South Atlantic Oceans (type D1), the Mediterranean and Caribbean (type D2), the offshore Middle Atlantic Bight and offshore Argentina sections (type C1) and offshore areas in southwestern South Africa and Peru (type C2). Specimens of *Leptodinium* were not found in any of the eight estuarine subsystems which were examined and were absent from all shelf sediments in coastal subsystems excepting for low-level occurrences (1% or less) in six samples near the shelf edge in the Middle Atlantic Bight and South African regions. The minimum bathymetric depth at which *Leptodinium* occurred was close to 100 m in the Middle Atlantic Bight area and 175 m in South Africa.

Species of *Leptodinium* were (collectively) most abundant in three assemblages from the southern Aegean and Cyprus areas of the Mediterranean Sea (49—66%), one assemblage from south of Sicily (55%) and in two oceanic assemblages (samples *153*, *155*) in the Atlantic equatorial zone (96 and 89%, respectively). These six together constituted its only two centers of distribution. Elsewhere it was well represented in offshore samples at the seaward sectors of Transects 1—4 in the Middle Atlantic Bight (maximum 16%) and in the Yucatan Channel region of the Caribbean Sea (10—17%). It was present at percentage abundances of only 2% or less in the South African, Argentinian and Peruvian regions in slope-rise zone sediments there.

In the Middle Atlantic Bight and Yucatan regions, species of *Leptodinium* collectively developed a clear trend involving increasing relative abundance offshore (i.e. with increasing sample depth). In the former area (Fig. 20), the species of *Leptodinium* present increased from 1% or less at the edge of the continental shelf to 8—16% in terminal assemblages along Transects 1—4 (Figs. 13—16) at depths close to 3000 m. (This trend apparently continues to develop further seawards because some mid-ocean samples have over 95% *Leptodinium* as noted above.) In the Yucatan Channel area, the percentage representation increased from 10 to 17% offshore between depths of 370—720 m. The genus was too weakly represented in the other regions for the detection of any trends.

Leptodinium aculeatum was the single most abundant species in the genus in sediments from the Mediterranean Sea, Yucatan Channel and equatorial Atlantic regions. *L. sphaericum* was most common in sediments from the Middle Atlantic Bight region. All five species were present in the Middle Atlantic Bight, Yucatan, central Atlantic and Mediterranean region but *L. strialatum* was not seen in the Argentina and South African regions and three species (*L. aculeatum*, *L. paradoxum* and *L. sphaericum*) were apparently absent from the Peruvian region. This was unusual because these three species were the most commonly encountered ones elsewhere.

Lingulodinium machaerophorum (Deflandre and Cookson) Wall 1967

This species occurred in 51% of the assemblages and was the most abundant species in twelve of them. It reached a maximum of 58% (sample *105*, Bahia de Guanica in Puerto

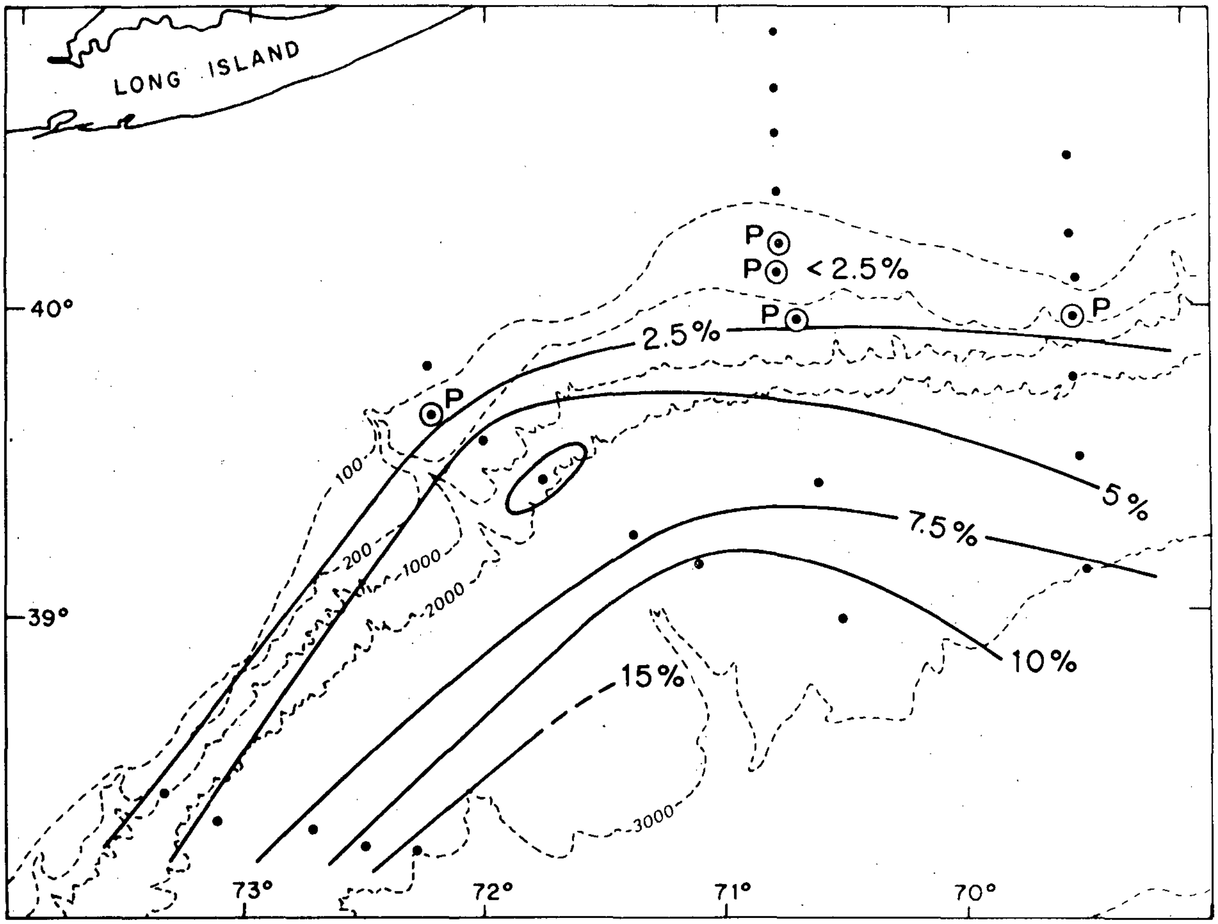


Fig. 20. Percentage frequency distribution for the cyst-based genus *Leptodinium* in the region of the Middle Atlantic Bight showing increasing representation offshore. (*P* = present at less than 1%; depths in meters).

Rico) and a specimen density maximum of 345 per gram (sample *116*, Gulf of Paria). In factor analysis it made an important contribution to Factor 5 together with *S. ramosus* and had a corresponding factor score of 0.895.

Its distribution was limited almost entirely to estuarine systems. Its main center of distribution was in the Gulf of Paria (subsystem A6) and here it ranged from 34 to 56% of five assemblages in this center. It had a more diffuse center in four samples along the coast of Puerto Rico (*96*, *98*, *99*, *105*) and reached 58% in the last mentioned, but its specimen densities were very low (3—23 per gram for the first three, unknown in the last). A very minor, single-sample center was found in Bermuda (sample *73* with 52%). These latter two centers were within the estuarine subsystem of type A8.

The species was extremely uncommon or absent in coastal and transitional coastal—oceanic system environments in the eastern United States, Argentina, South Africa and Peru and in the mid-oceanic subsystem (pelagic environment) of type D1. However, in slope-rise zone sediments within the intercontinental sea subsystem (type D2) as represented by the Mediterranean Sea and Yucatan Channel assemblages, *L. machaerophorum* was always present and reached as high as 18% of one assemblage (sample *150*). This type of distribution is discussed later.

As noted elsewhere (Wall and Dale, 1968a), *L. macherophorum* in modern environments is represented by cysts with three different types of archeopyles, namely, types 3P, 5P and $\overline{\mathrm{AIP}}$ (an equatorial suture). These three morphotypes did not appear to be evenly represented in different environments. The morphotype with a 3P archeopyle was found mainly in Norwegian fjords (subsystem A1) whereas the other two morphotypes with 5P and $\overline{\mathrm{AIP}}$ archeopyles occurred in Bermuda lagoons, in coastal Puerto Rico (both type A8 subsystems) and in the Gulf of Paria (type A6). However, the species was not abundant enough to permit more detailed resolution of this distribution.

Hemicystodinium zoharyi (Rossignol) Wall 1967

This species had a highly localized distribution and occurred in only 32% of the samples. It was the most abundant and dominant species in eight assemblages and in one (sample *78*, Bermuda) comprised 98% of the specimens. In factor analysis it was the virtual monospecific member in Factor 4 (factor score of 0.999) and this factor accounted for 6.3 of the variance in the total compositional data. (The specimen density per gram was not determined.)

The species had two centers of distribution where it was statistically of maximum importance: first, in lagoons in the Bermuda Islands, it ranged from 67 to 98% of seven assemblages; and second, in a single-sample center in Phosphorescence Bay, Puerto Rico (55% in sample *103*). It also was moderately abundant in two other small bays in the same region, namely, in Bahia de Guanica (23%) and Bahia de Jobos (20%). All of these centers and sites of moderate abundance for *H. zoharyi* were in the estuarine subsystem of type A8.

Other occurrences of note included the coastal zone of the United States south of the Delaware River (Fig. 12) and in offshore assemblages in the Mediterranean and Caribbean Sea regions (subsystem D2, from 8 to 18%). It was absent in continental shelf and slope-rise zone sediments from the Middle Atlantic Bight, South Africa, Argentina and Peru and from mid-ocean pelagic sediments in the equatorial Atlantic.

Tuberculodinium vancampoae (Rossignol) Wall 1967

This distinctive cyst-based taxon occurred in only 19% of the samples and generally was uncommon. It did not exceed 11% of any assemblages and had a maximum observed specimen density of only 33 per gram (sample *29*). It was not important in the factor analysis. It was notable in two samples from Abidjan which represented estuarine subsystem type A5 (from 4 to 11%) and in two assemblages from similar estuarine environments (type A8) in coastal Puerto Rico (5% in Phosphorescence Bay, 4% in Bahia de Guayanilla). It also was consistently present along the southern coast of the eastern United States from Pamlico Sound to Georgia (subsystem types A3, A4) where it attained 8% as a maximum value. It was very rare north of Cape Hatteras inshore and was never more than 1% in sediments from coastal, transitional and oceanic systems in any other region investigated.

Species of *Peridinium* Ehrenberg 1830 and related forms

The cysts of many marine species of *Peridinium* (used here taxonomically in the broader sense of Ehrenberg and not limited to *Protoperidinium* Bergh 1881) are subspherical, brownish cells with an apparently single-layered wall without projections (Wall and Dale, 1968a). They can be identified to species level under controlled laboratory conditions, but not so in sediments, where cysts of this type often are damaged and hence critical morphological features, such as the precise shape of the archeopyle, are obscured. Cysts of this simple type thus were treated collectively as an entity which will be referred to here as "grouped *Peridinium* species". Species which are known to have contributed to this entity included *P. conicoides* Paulsen 1905, *P. punctulatum* Paulsen 1907, *P. denticulatum* Gran and Braaud 1935, *P. avellana* (Meunier) Lebour 1925 and *P. excentricum* Paulsen. In some assemblages, other peridinioid dinoflagellates such as *Diplopsalis lenticula* Bergh and even *Diplopeltopsis minor* (Paulsen) Pavillard 1913 and *Diplopsalopsis orbicularis* (Paulsen) Lebour 1922 possibly were included as "grouped *Peridinium* species", although under favorable circumstances they could be distinguished from *Peridinium* and were counted separately.

Grouped *Peridinium* species was represented in 82% of the assemblages and was the first ranking category in 33 samples. It was strongly dominant in some assemblages to a maximum observed value of 87% (sample 128, Peru) and had a maximum observed specimen density value of 12.8 $\times 10^3$/g in this same sample. It was important in the factor analysis as the major contributor to Factor 3 with a corresponding factor score of 0.997. This factor accounted for a sizeable amount of variation in the compositional data with a variance of 22.8.

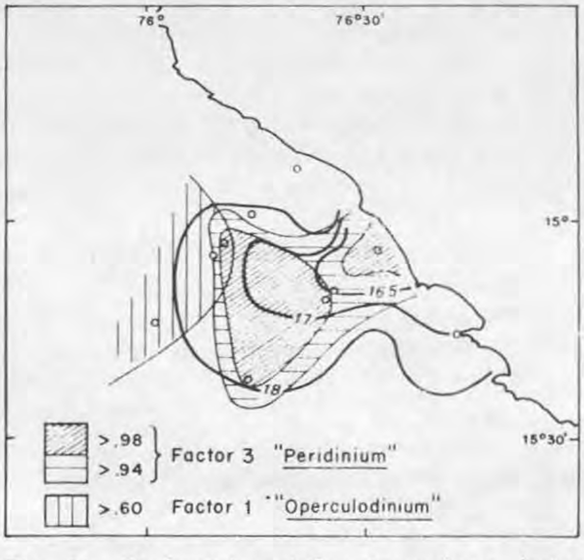


Fig. 21. Horizontal variation in varimax factor loading values for the principal components Factors 1 (*Operculodinium centrocarpum*-dominated) and 3 (*Peridinium*-species-dominated) along Transects 5 and 6 in the Peruvian region. High factor loading values for Factor 3 correspond with upwelling water. Base map after Walsh et al. (1971, fig.4); surface water temperature °C.

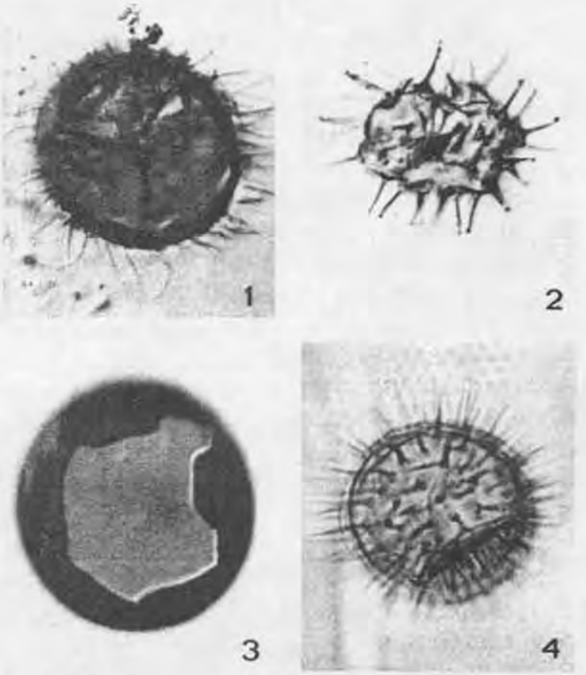


PLATE I

1. Dinoflagellate cyst Form A, body diameter 48 μm, spines simple and curved, maximum length of 15 μm. Sample 122.
2. Dinoflagellate cyst Form B, maximum body length 36 μm, spines blade-like with clavate tips. Sample 122.
3. Dinoflagellate cyst Form C, maximum body length 48 μm, sediment from Independence Bay, near Pisco.
4. Dinoflagellate cyst Form D, maximum body length 41 μm, spines straight, pointed and simple, maximum length 10 μm. Sample 122.

It had centers of distribution in estuarine, coastal and transitional coastal–oceanic systems, the most important of which were located along the eastern United States (including the Middle Atlantic Bight) and in the Peruvian region (Figs. 21, 22). The individual centers and the percentage values of grouped *Peridinium* species within them were as follows: in the estuarine subsystem of type A2 (northeastern United States, 30–84%), in the coastal subsystem B1 (Middle Atlantic Bight, 39—67%), in coastal subsystem B2 (Peruvian region near Callao and inner sectors of Transects 5 and 6, 25—82%), in the transitional coastal—oceanic subsystem of type C1 (a minor center with only two samples in the slope-rise zone of the Middle Atlantic Bight, 42—50%) and in subsystem type C2 (the continental slope-rise zone in Transects 5 and 6 near Pisco, 30—87%). Grouped *Peridinium* species also were significant within three assemblages from coastal subsystem B2 in the South African region. The inshore assemblage in sample *164* (Transect 8) had 40% grouped *Peridinium* species and samples *159* and *160* (the inshore end of Transect 9) had 27 and 36%, respectively.

Grouped *Peridinium* species was not a major statistical component of assemblages in estuarine subsystems other than type A2, but single samples occasionally had a strong localized imput. It was not an important entity in the Argentina region (subsystem C1) or in any of the oceanic systems (type D1, D2).

Cysts of other species of *Peridinium* were identified individually and they included *P. conicum* (Gran) Ostenfeld and Schmidt 1902, *P. claudicans* Paulsen 1907, *P. latissimum* Kofoid 1907, *P. oblongum* (Aurivillius) Cleve 1900, *P. leonis* Pavillard 1916, *P. subinerme* Paulsen, *P. nudum* Meunier 1919, *P. pentagonum* Gran 1902, *P. compressum* (Abe) Nie 1939 and *P. minutum* Kofoid 1907. In addition to this there were other morphotypes of unknown systematic affinity which may be peridinioid: these were designated Form A to D (Plate I).

The above listed species invariably occurred in too small proportions to provide any definitive environmental—geographic distribution patterns. Among them, *P. conicum* was most prevalent; it occurred in 60% of the assemblages but never exceeded 10% in any and was widely distributed. *Peridinium pentagonum* represented 9% of the assemblages in two samples from fjords in Norway (samples *137*, *139*) but it also occurred in contrasting tropical environments such as the Gulf of Paria and like *P. conicum*, was cosmopolitan.

Definition and distribution of species associations

Eleven species associations of cyst-based taxa were defined on the basis of cluster analysis with the Grassle-Smith (ESS) Index (see section 2). It was preferred to define them by this method rather than from percentage-similarity cluster analysis or from factor analysis because the ESS Index minimized the influence of dominance of many assemblages by just one or two species, which was its desired effect.

The results are displayed in dendrogram format in Fig. 23, together with notations which refer to the environments and geographic locations wherein assemblages originated. The species compositions of individual species associations were determined simply by re-ordering the original sample-species matrix according to the results of cluster analysis so that the most similar assemblages were placed in adjacent columns. The species compositions of different associations are given below. "Ubiquitous" species are those which were present in all assemblages within a given association; "common" species were present in one-half or more of assemblages; and "uncommon" species were present in less than half of them. Within each category (ubiquitous, common, uncommon), species were ranked in order of decreasing mean abundance within each association. An asterisk by a species name indicates that it had a center of distribution (see above) within that association or domain and that it was an important member of it numerically. The environmental distribution of associations is summarized in Table VI (p. 162).

Association I

Ubiquitous species: *O. centrocarpum**, grouped *Peridinium* species*, *S. bulloideus*.

Common species: *S. elongatus*, *P. conicum*, *S. mirabilis*, *N. balcombiana*, *L. machaerophorum*.

Uncommon species: *B. tepikiense*, *S. bentori* (short-spined morphotype), *P. choanum*, *S. membranaceus* (*sensu* Reid 1974), *P. leonis*, *P. pentagonum*.

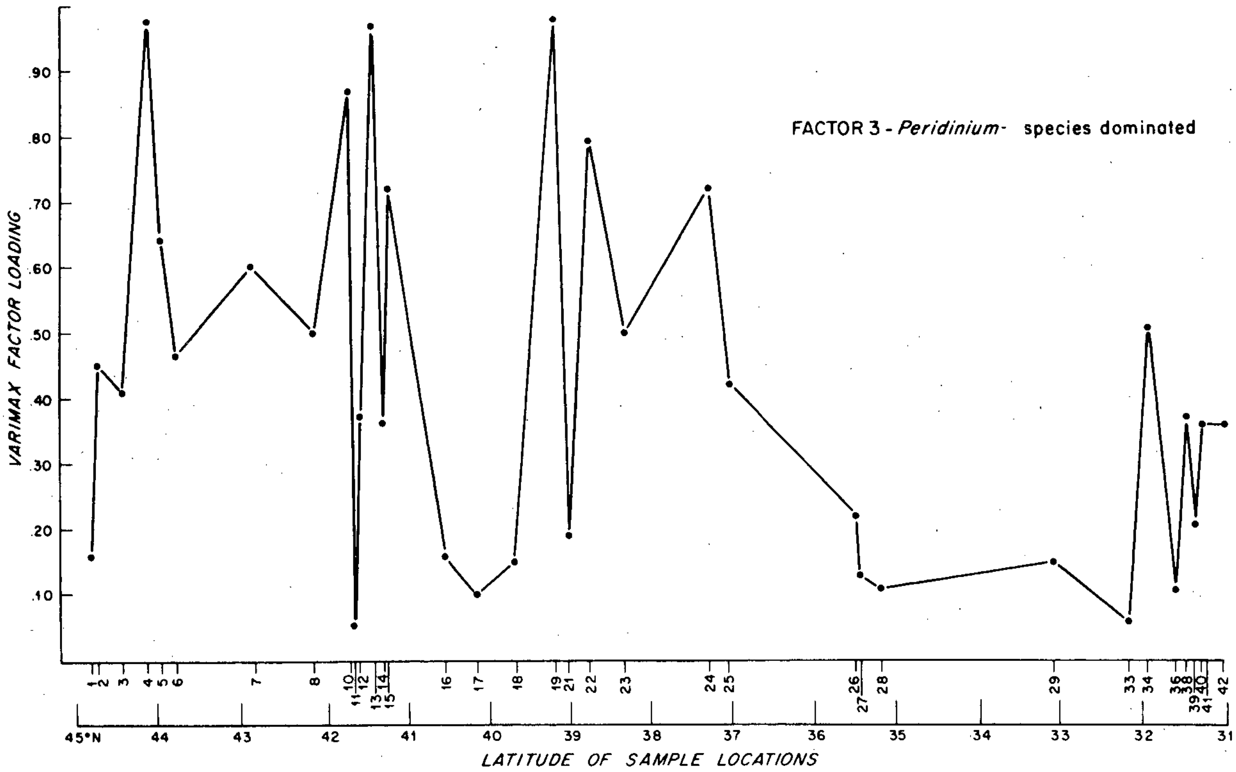


Fig. 22. Latitudinal variation in Varimax Factor 3 (*Peridinium*-dominated) along the coastal zone of the eastern United States.

Distribution: Southern Norway, eastern coast of United States (Somes Sound, Buzzards Bay, Narragansett Bay, Long Island Sound, Cape May, Delaware Bay). Environments represented: Temperate estuarine environments of types A1, A2.

Association II

Ubiquitous species: Grouped *Peridinium* species*, *O. centrocarpum**, *S. bulloideus**, *S. mirabilis*, *P. conicum*.

Common species: *S. elongatus*, *S. ramosus*.

Uncommon species: *N. balcombiana*, *P. nudum*, *P. conicoides*, *G. tamarensis*.

Distribution: Eastern coast of United States north of Cape Hatteras (Machias Bay to Chesapeake Bay), Middle Atlantic Bight (inner sectors of Transects 1—3), Las Palmas Harbor. Environments represented: Temperate estuarine and continental shelf environments of types A2 and B1.

Association III

Ubiquitous species: *S. bulloideus**, *L. machaerophorum**, grouped *Peridinium* species*, *H. zoharyi*, *S. mirabilis*, *P. conicum*.

Common species: *O. centrocarpum*, *N. balcombiana*, *T. vancampoae*.

Uncommon species: *O. israelianum*.

Distribution: Eastern United States (Delaware Bay, Chesapeake Bay, Pamlico Sound, South Atlantic Bight), Bermuda (Harrington Sound), southern Puerto Rico (Bahia de Jobos, Bahia de Guayanilla, Bahia de Guanica).

Environments represented: Warm temperate to tropical estuarine environments of types A3, A4 and A8 primarily.

Association IV

Ubiquitous species: *H. zoharyi**, *S. bulloideus**.

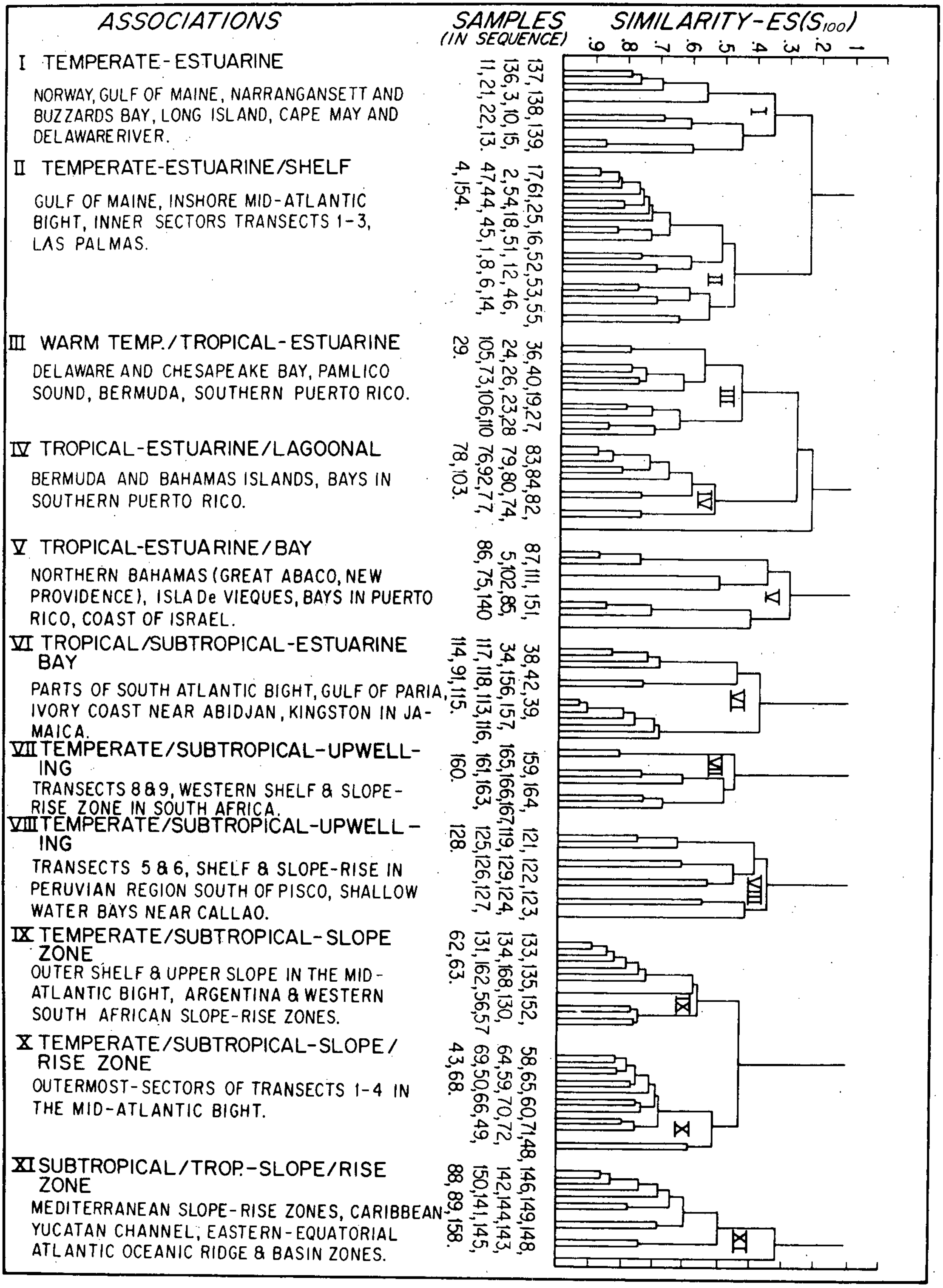


Fig. 23. Cluster analysis dendrogram of assemblages from all Regions (1—15) using the Grassle—Smith expected species-shared index. Species compositions of assemblages that comprise Associations I—XI are detailed in the text.

Common species: *L. machaerophorum*, *S. ramosus*, *S. mirabilis*, *O. israelianum*, *O. centrocarpum.*
Uncommon species: *T. vancampoae*, *T. pellitum.*
Distribution: Bermuda Island, Bahamas Islands (west of Andros Island), Phosphorescence Bay in Puerto Rico.
Environments represented: Tropical to subtropical estuarine—lagoonal environments of type A8.

Association V
Ubiquitous species: *S. bulloideus**, *O. centrocarpum** (including Abaco morphotype).
Common species: *O. israelianum*, *S. ramosus*, *L. machaerophorum*, *O. psilatum.*
Uncommon species: *H. zoharyi.*
Distribution: Bahamas Islands (Great Abaco and New Providence Islands), Isla de Vieques and Bahia de Boqueron in Puerto Rico, coast of Israel.
Environments represented: Mainly tropical climate estuarine environments of type A8.

Association VI
Ubiquitous species: *S. bulloideus**, *L. machaerophorum**, *S. ramosus**, grouped *Peridinium* species, *P. conicum*, *P. subinerme.*
Common species: *P. leonis*, *O. centrocarpum*, *T. vancampoae*, *S. mirabilis*, *N. balcombiana.*
Uncommon species: *Diplopsalopsis orbicularis*, *O. israelianum*, *P. pentagonum.*
Distribution: South Atlantic Bight, Gulf of Paria, Ivory Coast, Jamaica · (Kingston Harbor).
Environments represented: Tropical to subtropical estuarine environments of types A4, A5, A6.

Association VII
Ubiquitous species: *O. centrocarpum**, *S. bulloideus.*
Common species: Grouped *Peridinium* species, Form A, *P. leonis.*
Uncommon species: *N. balcombiana*, *S. scabratus.*
Distribution: South Africa (inner sector of Transect 8 over the continental shelf, Transect 9 excepting one sample, *162*).
Environments represented: Coastal environments of type B2, transitional coastal—oceanic environments of type C2.

Association VIII
Ubiquitous species: Grouped *Peridinium* species*, *S. bulloideus*, Form A.
Common species: Form B, Form C, *P. leonis*, *Peridinium* sp. I Davey and Rogers 1975, *P. subinerme.*
Uncommon species: *O. centrocarpum*, *P. excentricum*, *Peridinium*, sp. I Wall and Dale 1968, Form D.
Distribution: Peru Transects 5 and 6, and inshore region near Callao.
Environments represented: Coastal system environments (type B2), transitional coastal—oceanic systems environments (type C2).

Association IX
Ubiquitous species: *O. centrocarpum**, *S. bulloideus**, grouped *Peridinium* species, *N. balcombiana*, *L. sphaericum*, *S. mirabilis.*
Common species: *S. ramosus*, *S. scabratus.*
Uncommon species: *T. pellitum*, *S. elongatus*, *P. conicum.*
Distribution: Middle Atlantic Bight (outer continental shelf and upper slope zone), Argentina (slope and rise zones), South Africa (slope zone).
Environments represented: Transitional coastal—oceanic environments (types C1 and C2).

Association X
Ubiquitous species: *O. centrocarpum**, grouped *Peridinium* species, *S. bulloideus*, *N. balcombiana*, *L. sphaericum*, *T. pellitum*, *S. elongatus.*
Common species: *S. ramosus*, *S. mirabilis*, *S. scabratus*, *L. aculeatum*, *L. paradoxum*, *L. patulum*, *P. conicum.*
Distribution: Middle Atlantic Bight, outermost sectors of Transects 1—4, upper slope and rise zones (1,000—3,000 m depths).

Environments represented: Transitional coastal—oceanic environments (type C1).

Association XI

Ubiquitous species: *L. aculeatum**, *N. balcombiana**, *S. bulloideus**, *O. centrocarpum*, *L. machaerophorum*.
Common species: *S. bentori* (long-spined morphotype), *S. mirabilis*, *S. ramosus*, *L. paradoxum*, *L. sphaericum*, *L. patulum*, *H. zoharyi*, grouped *Peridinium* species.
Uncommon species: *S. scabratus*, *L. strialatum*.
Distribution: Mediterranean Sea (slope and rise zones), Yucatan Channel (slope and rise zones), central and eastern Atlantic Ocean (abyssal zone, Middle Atlantic Rise, Sierra Leone Rise).
Environments represented: Tropical to subtropical oceanic and transitional coastal—oceanic environments, mainly types D1 and D2.

Species diversity

The Hurlbert Index of species richness or diversity, $E(S_n)$ was computed for 135 samples which were rarefied to n=32. In these samples, actual N varied between 72 and 1,201 and the maximum number of species which occurred in any single sample was twenty. The total range for the computed values for this index ranged from 1.4 to 12.1. The results are summarized in Table IV where they are arranged in an environmental sequence from estuarine to oceanic according to the classification above. Values for the index were most varied in estuarine environments where they ranged from 1.4 to 10.5. Corresponding ranges for coastal (shelf), transitional (slope-rise) and oceanic (intercontinental sea) environments were from 3.6 to 8.0, 3.7 to 9.2 and 7.7 to 12.1, respectively, so that the span for each of them was approximately one half of that for the estuarine assemblages.

Highest values for the index were encountered in warmer-water environments in general, either in estuarine or estuarine-neritic inshore situations such as the tropical Ivory Coast near Abidjan, the subtropical South Atlantic Bight and the Bahamas—Caribbean region, or in offshore areas along slope-rise zones in the Caribbean and Mediterranean Seas and the Middle Atlantic Bight. More moderate values were found in assemblages from temperate estuarine and coastal environments such as those in southern Norway, the eastern coast of the United States north of Cape Hatteras and in coastal to offshore zones which were influenced by cool current systems or experienced some upwelling, such as in the Argentina, South Africa and Peruvian areas. Extreme low values occurred in assemblages from Bermuda.

Further discussion of trends which were observed in species diversity is given in section 5.

Specimen density

Specimen density, measured as the number of cysts per gram of sediment (section 2), was determined for 123 samples from the eastern United States, including its offshore area, Jamaica, Puerto Rico, the Gulf of Paria, offshore Argentina, Norwegian fjords and from Peru and South Africa. Values for cysts/g are summarized in Table V.

Specimen density clearly was higher in slope-rise zone sediments than in all others. Samples from the Argentina, Middle Atlantic Bight, Peru and South African slope-rise zones often had more than 3.0×10^3 cysts per gram and almost all contained more than 1.0×10^3 per gram. Other environments where comparably high density values were encountered included the outer and middle continental shelf (relict) sediments of the Middle Atlantic Bight and modern bottom sediments in fjords from Norway.

More moderate values, averaging less than 2.0×10^3 and individually not exceeding 5.0×10^3 per gram were observed in estuarine and inner shelf sediments along the northeastern coast of the United States and in compa-

TABLE IV

Summary of diversity values for Hurlbert's Index $E(S_n)$ rarefied to $n = 32$

Environmental subsystem		Range of values	Mean	Number of samples	Mode
Estuarine					
A1	southern Norway	4.6—6.3	5.7	3	6
A2	United States east coast	3.8—8.8	5.9	22	5
A3	Pamlico Sound	6.7—8.8	7.9	3	—
A4	South Atlantic Bight	7.7—9.9	8.6	8	7,9
A5	Abidjan, Ivory Coast	9.2—10.5	9.9	2	9
A6	Gulf of Paria	4.9—7.2	6.0	6	5,7
A8	Bermuda	1.4—6.3	3.8	8	3
	Bahamas	3.3—8.0	5.9	5	—
	Puerto Rico	4.1—8.2	6.1	6	6
Coastal					
B1	Middle Atlantic Bight	4.6—6.1	5.3	12	5
B2	Peru near Pisco	4.8—8.0	6.6	5	—
	western South Africa	3.6—6.3	4.9	6	—
Transitional coastal—oceanic					
C1	Argentina	4.6—6.3	5.5	5	5
	Middle Atlantic Bight	6.9—8.5	7.6	16	7
C2	Peru	4.6—9.2	6.6	6	—
	South Africa	3.7—4.4	4.1	4	4
Oceanic					
D2	Mediterranean Sea	7.7—12.1	8.7	9	8
	Caribbean Sea	6.8—8.1	7.3	3	—

TABLE V

Summary of specimen density values (cysts per gram dry weight of sediments)

Environmental subsystem		Range of values	Mean value	Number of samples
Estuarine				
A1	southern Norway	3,416—16,106	10,032	4
A2	United States northeast coast	30—3,822	897	25
A3	Pamlico Sound	105—2,236	917	3
A4	South Atlantic Bight	5—776	189	14
A6	Gulf of Paria	63—695	300	7
A8	Puerto Rico	8—288	98	15
	Kingston, Jamaica	672	—	1
Coastal				
B1	Middle Atlantic Bight	33—8,326	1,928	13
B2	Peru near Pisco	584—2,030	1,169	3
	western South Africa	728—4,999	1,997	6
Transitional coastal—oceanic				
C1	Argentina	1,501—18,257	6,352	5
	Middle Atlantic Bight	725—12,888	3,728	16
C2	Peru	2,285—14,700	6,321	3
	South Africa	1,582—11,200	5,116	4
Oceanic—intercontinental sea				
D2	Jamaica	370—720	590	3

rable shelf sediments from Peru and South Africa. [However, Davey (1971) previously found that there is large local variation in cyst abundance in shelf sediments of southwestern South Africa, and he encountered some much higher values than we did in our two transects.]

Estuarine samples from the South Atlantic Bight, Puerto Rico and Gulf of Paria were noticeably lower in specimens than estuaries along the northeastern coast of the United States. This was part of the considerable amount of local variation which was encountered in nearshore environments as a whole. Trends in specimen density distributions are discussed in section 5.

5. Analysis of cyst distributions and controlling factors

Major trends in cyst distribution

The predominant feature of cyst distribution in modern marine sediments is the development of two concurrent distributional trends. The first of these lies in the inshore to offshore direction while the second is latitudinal. Both trends can be identified according to several independent criteria which include changes in species compositions of assemblages (individual species distributions), the distribution and composition of species associations (groups of co-occurring species), changes in species diversity between assemblages and changes in specimen density (cysts per gram) between samples.

Identification of these two trends is of major importance for its intrinsic value and because their existence raises the possibility that identical trends can be identified in paleobiogeographic cyst data.

The inshore to offshore trend

Changes in the species composition of assemblages which developed in the inshore—offshore direction were of two kinds. First, a few species were limited in distribution to offshore assemblages (i.e., they did not occur in sediments inshore of the outer continental shelf). Second, all assemblages showed proportional changes in species composition in going from nearshore to offshore sediments and environments.

With respect to the first, all five species of *Leptodinium (L. aculeatum, L. patulum, L. paradoxum, L. sphaericum* and *L. strialatum)* were restricted to outer shelf, slope, rise and abyssal zone sediments. With respect to the second, different species attained their peak abundances in either estuarine, shelf, slope-rise or abyssal zone sediments or within any contiguous pair of them. For example, *Hemicystodinium zoharyi, Tuberculodinium vancampoae, Operculodinium israelianum, Spiniferites ramosus* (*sensu* Wall and Dale 1970), *S. elongatus, S. membranaceus* (*sensu* Reid 1974), *S. bulloideus, S. bentori, Lingulodinium machaerophorum, Bitectatodinium tepikiense* and *Planinosphaeridium choanum* nov. comb. reached their respective maximum abundances in estuaries or the innermost shelf zone. *Operculodinium centrocarpum* had its maximum abundances in shelf and slope-rise zone sediments. *Nematosphaeropsis balcombiana* and *Tectatodinium pellitum* had their respective peaks in continental slope and rise zones and all five species of *Leptodinium* (see above) reached their maxima in mid-oceanic pelagic sediments in the abyssal zone. (Details are given in section 4, Table II, Figs. 13—20 and Appendices I and II).

The spatial distribution of distinctive species associations (as defined by cluster analysis) also showed an inshore—offshore trend which involved a seaward succession, but with overlap (Table VI). Associations I—IV were located in shelf and slope-rise zones; Associations IX and X were located exclusively in slope-rise zones and Association XI was found only in abyssal and slope-rise zone sediments. This seaward succession was best exemplified within a single region in the Middle Atlantic Bight (Fig. 24) by Associations II, IX and X but a similar pattern was seen in the South African region too, where Association VII occurred mainly in shelf sediments (along

TABLE VI

Environmental distribution of species associations

Environmental subsystem		Associations										
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Estuarine												
A1	southern Norway	+										
A2	United States northeast coast	+	+	+								
A3	Pamlico Sound			+								
A4	South Atlantic Bight			+			+					
A5	Abidjan, Ivory Coast						+					
A6	Gulf of Paria						+					
A7	Canary Islands		+									
A8	Bermuda, Bahamas,			+	+	+						
	Puerto Rico			+								
Coastal												
B1	Middle Atlantic Bight		+							+		
B2	Peru near Pisco								+			
	western South Africa							+				
Transitional coastal—oceanic												
C1	Argentina									+		
	Middle Atlantic Bight									+	+	
C2	Peru								+			
	South Africa							+		+		
Oceanic												
D1	Equatorial Atlantic											+
D2	Mediterranean Sea											+
	Caribbean Sea											+

Transects 8 and 9) and Association IX was limited to the local slope and rise zone sediments. An inshore to offshore trend in species diversity was shown by a tendency for values of the Hurlbert Index to increase in offshore assemblages and for them to be more uniformly high offshore. For example, in the Middle Atlantic Bight area, the mean value for 15 estuarine samples was 5.97 and individual values ranged widely from 3.3 to 8.8. In adjacent shelf sediments, diversity for 13 assemblages had a mean value of 5.46, which was not significantly different but the range of values was only between 4.6 and 6.9. In the slope-rise zone, the mean value for 15 assemblages increased to 7.72 and individual values ranged between still narrower limits of 7.0—8.5 (Fig. 25). The same trend was seen in other regions with generally warmer climatic conditions. For example, the mean value for 39 estuarine assemblages from the Caribbean, Bermuda, Bahamas and southeastern United States was 6.45 and it ranged from 1.4 to 10.5 for individual assemblages. The mean value for 12 offshore assemblages from slope and rise zones was 8.35 and it varied from 5.9 to 12.1 for individual extreme values.

The inshore—offshore trend in specimen densities (cysts/g) was established as a tendency for values to be highest in slope-rise zone sediments as noted earlier. The mean value for 31 slope-rise zone samples (from all areas included in this study) was 5.27×10^3 cysts/g and this contrasted with values of 1.82×10^3 for 23 shelf samples and 1.06×10^3 for 68 estuarine samples, representing roughly a mean five-fold increase offshore. Samples from slope-rise zones also were consistently richer in cysts than others and hence the only samples to have cyst quantities in the

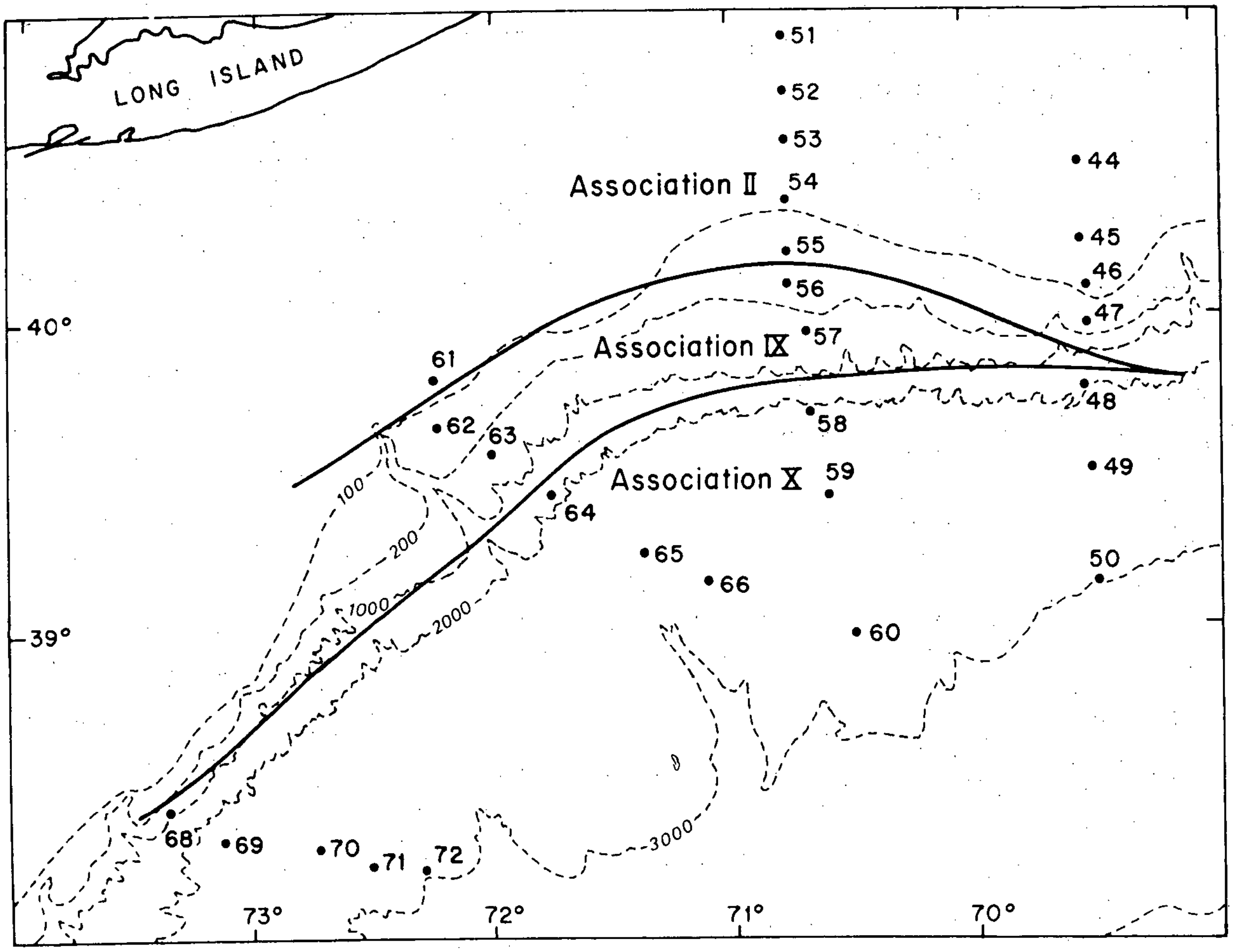


Fig. 24. Horizontal distribution of assemblages that comprise Associations II, IX and X in the continental shelf and slope-rise zones of the Middle Atlantic Bight.

order of 10^4 per gram were from depths of 1,000 m or more. Similarly all samples with densities in the order of 10^3 cysts/g were from depths of 200 meters or more and all samples with less than 100 cysts/g were from shoal depths not in excess of 70 m.

The tendency for values to increase sea-

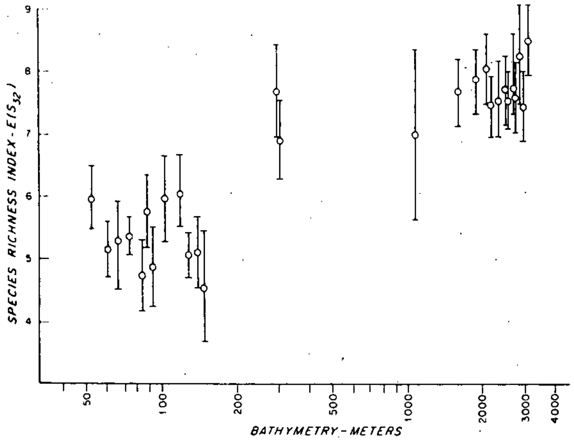


Fig. 25. Diagram to illustrate increasing species richness ("diversity") in the Hurlbert $E(S_n)$ Index (n= 32) with increasing depth and distance from shore in the Middle Atlantic Bight area. The samples represented are those from Transects 1—4 (see Fig. 24). The vertical bars represent 95% confidence limits.

wards towards the slope-rise zone was observed in Transects 1—4 in the Middle Atlantic Bight, Transects 6 and 7 in the Peruvian region and Transect 8 off southwestern South Africa. In five of these (Transects 1—4 and 6), cyst densities reached their peaks between 403 m and 2500 m and then began to decline seawards, which indicates that this trend towards higher values away from shelf edges does not continue uninterruptedly into mid-oceanic domains. Little is known to date about cyst density values in pelagic sediments, but the data in D.B. Williams (1971, his figs. 14.1, 14.2) indicate that they are lower than those for slope-rise zone values.

The latitudinal trend

Latitudinally detectable changes in the species composition of assemblages, like those in the inshore—offshore direction, included both restricted range distributions and fluctuations in species ratios.

Spiniferites elongatus, *S. membranaceus* (*sensu* Reid 1974), *S. bentori* (short-spined type), *Bitectatodinium tepikiense* and *Planinosphaeridium choanum* were limited to temperate latitudes. In contrast, *Hemicystodinium zoharyi*, *Tuberculodinium vancampoae*, *Operculodinium israelianum* and *S. ramosus* (*sensu* Wall and Dale 1970) were restricted to tropical and subtropical latitudes in nearshore assemblages, whereas species of *Leptodinium* were restricted to offshore assemblages either at lower latitudes or at middle latitudes where warm-water currents occurred offshore (such as in the Middle Atlantic Bight where the Gulf Stream and warm slope water occur).

Similarly, species associations also showed a latitudinal component of spatial variation. Associations I and II were found in temperate latitudes between 35° and 62°N. Associations III, IV, V and VI were found only at latitudes below 35°N (in nearshore environments) and Associations IX, X and XI, which contained *Leptodinium*, were found only equatorwards of ca. 40°N in the Middle Atlantic Bight and 42°N in the Mediterranean Sea.

The climatic—latitudinal trend in species diversity was shown by increased values for the Hurlbert Index in assemblages from low latitudes in general and in assemblages from sediments beneath warm-water surface environments offshore. For example, north of Cape Cod along the eastern coast of the United States, the mean value for 8 estuarine assemblages was 5.26. It increased to 6.24 for 18 assemblages in the Middle Atlantic Bight and further to 8.63 for 8 assemblages in the inshore South Atlantic Bight. This trend was also exemplified by mean values for all estuarine sediments from either temperate or tropical—subtropical latitudes. The average value for 27 temperate zone assemblages (from all regions) was 5.72 and it was 6.45 for 39 tropical—subtropical zone assemblages.

Similarly, offshore assemblages from slope-rise zones in areas which were influenced by warm-water currents (the Middle Atlantic Bight, Mediterranean and Caribbean Seas) had higher diversity than offshore assemblages where surface waters above were cooler (South Africa, Peru, Argentina) (see Table IV).

The latitudinal trend as it was manifested in specimen density values consisted of a decline in values towards low latitudes, mainly within inshore environments from which most of our samples were collected. This equatorwards decrease is shown by Table V under the heading "Estuarine Systems". The subsystems are arranged with the highest latitude stations listed first (A1—A8) and the tropical stations last. Thus it is clear that mean values for sets of samples within the subsystems from different latitudes and the extreme maximum values for individual samples within them, both decreased equatorwards.

The data for specimen densities in offshore samples at different latitudes, or beneath warm versus cool surface currents, are insufficient to determine if the same trend is found away from shore. Information such as now exists (D.B. Williams, 1971) indicates that it probably does.

Factors which determine trends in cyst distribution in sediments

Surface water environments

Trends in the inshore to offshore and latitudinal distribution of cysts in sediments can be empirically correlated with the spatial configuration of surface water environment, whose physico-chemical componental variables (e.g. temperature and salinity) and associated biotas (e.g. plankton communities) likewise vary in these two directions. This broad type of empirical correlation was first noted in earlier publications by D.B. Williams (1971), Davey (1971), Davey and Rogers (1975) and Reid (1972, 1975) and it hinges on two observations; First, that limits to the distributions of some cyst-based species and species associations generally conform to boundaries between different surface waters above them, and second, that different cyst-based taxa attain their respective peak abundances in sediments which lie beneath different surface water environments. Examples of both are discussed below here and have been cited in this earlier literature.

This type of empirical correlation necessitates that two inferences are drawn regarding the interrelationship between the dinoflagellate biocoenosis and thanatocoenosis. One is that the distribution of cyst-based species in bottom sediments corresponds reasonably well with the distribution of cysts and their parental dinoflagellates as they occur in surface water environments (i.e. as members of phytoplankton communities). A second is that the primary distribution of cyst-producing dinoflagellate species in plankton itself is related in like manner to contrasting surface water types. These inferences represent a normal type of relationship in the marine biogeography of plankton (see McGowan, 1971) but nonetheless are inferences to date because they are not substantiated by solid data.

These postulated and empirical relationships between the dinoflagellate biocoenosis and thanatocoenosis are similar to those which have been previously established in studies of other planktonic microfossils. Studies on coccolithophorids (McIntyre and Bé, 1967), diatoms (Kanaya and Koizumi, 1966; Round, 1967) and planktonic foraminifera for example, indicate that species distributions within the marine thanatocoenosis provide a good facsimile of their respective distributions in near-surface water environments above. Dinoflagellates therefore do not emerge as an exception to the rule despite their unique mode of fossilization as cysts which must introduce some abnormally restrictive taxonomic selectivity into the number of species which is present in the cyst thanatocoenosis.

A logical extension of this reasoning is that oceanographic factors which basically control the distribution of (fossilizable) dinoflagellates in surface water also must play a major role in determining the composition of assemblages in sediments too and therefore, the trends which species exhibit within them. These oceanographic factors can be divided into a biological set, which determines biotic interactions between a species-population, its surrounding aquatic medium and other organisms; and a hydrodynamic set, which determines the spatial configuration of the medium itself and the communities which it supports. The biologic set (evolutionary—ecologic factors) is discussed in section 7 and only the hydrodynamic set is considered further in this section.

Hydrodynamic factors which contribute to trend development by cysts

Hydrodynamic boundaries

The overall pattern of distribution of cysts in bottom sediments can be considered to represent a vegetational continuum with two predominant trends which are detectable because species replace one another as the dominant member of local assemblage, or reach their individual peak abundances beneath some surface water environment which is optimal for them. The cyst thanatocoenosis thus is comparable with a two-trend ecocline along a corresponding two-trend environmental gradient by analogy with land vegetation (see Pianka, 1974, p. 247). Locations where important changes occur in assemblage compositions in bottom sediments are closely coincident with hydrodynamic boundaries in the surface water circulation pattern which are usually marked by temperature—salinity discontinuities. Thus, these boundaries are of major importance to cyst biogeography and the effects which they have on the composition of assemblages need to be defined. The ecologic classification which is presented in the following section is based largely on observation of cyst distributions with respect to major hydrodynamic boundaries.

Among hydrodynamic boundaries which are relevant to marine cyst studies, two are outstanding. The first is the boundary between estuarine and coastal (shelf) water and the second is the boundary between coastal water and oceanic water. These can be referred to as the estuarine—neritic and neritic—oceanic boundaries.

An attempt is made in the following paragraphs to identify significant motions which develop at these boundary sites and to describe the explicit effects which they have on the compositions of cyst assemblages in sediments.

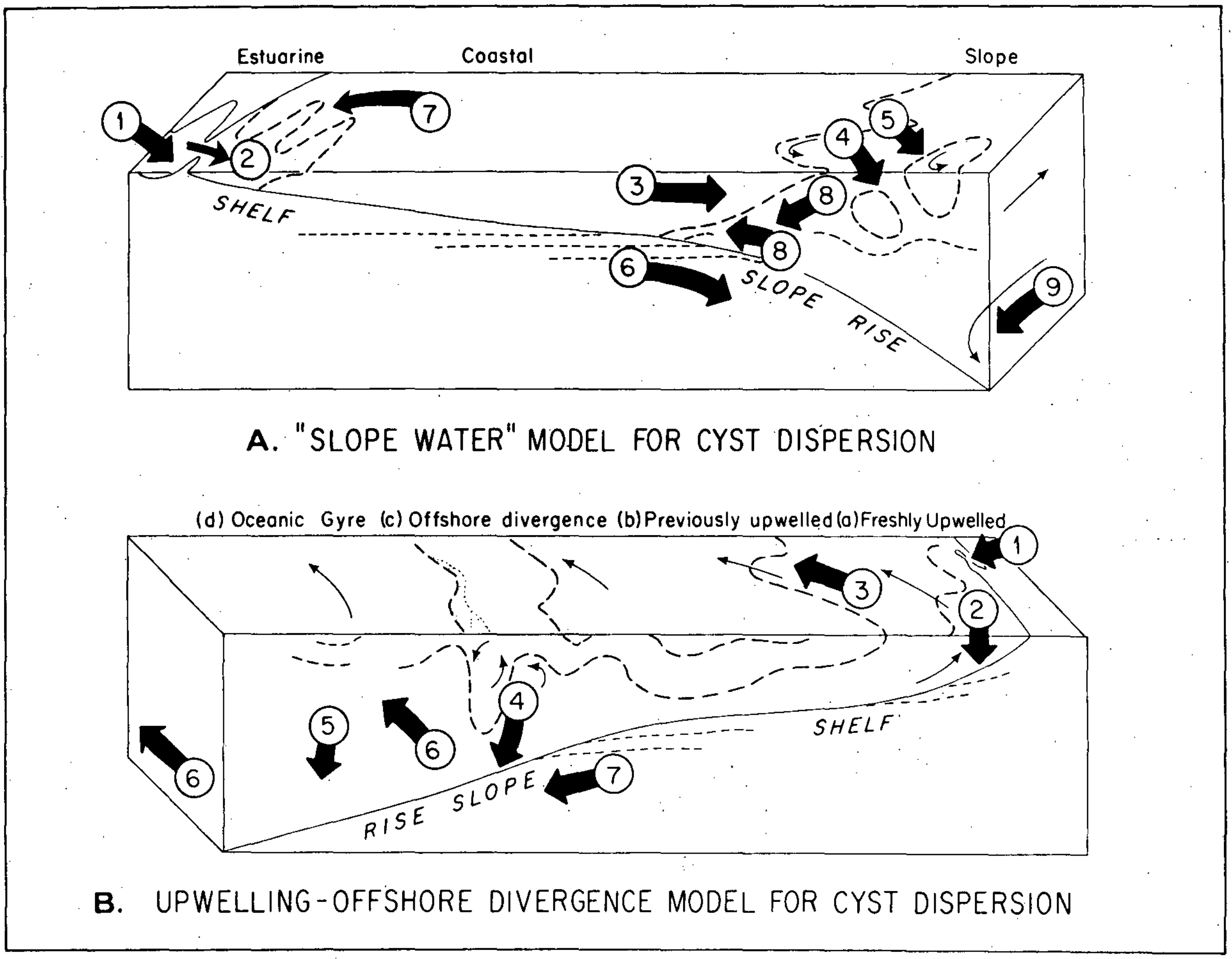
Estuarine—neritic boundary

Confinement of terrestrial run-off. Physical and hydrographic barriers both can limit the mixing and exchange between terrestrial run-off and coastal waters and this maximizes the ecologic impact of land drainage on the shallow-water marine ecosystem. This has the effect (indirectly) of creating special environments in which some cyst-based taxa attained their relative maximum abundances; these environments included bar-built lagoons, coastal embayments and the innermost reaches of coastal bights. Cysts which were abundant in them included *Spiniferites bulloideus* in Pamlico Sound and the inshore South Atlantic Bight; *S. elongatus*, *S. membranaceus* (*sensu* Reid) and *Bitectatodinium tepikiense* in Somes Sound, Maine, *Lingulodinium machaerophorum* in the Gulf of Paria and small bays in southern Puerto Rico; *Operculodinium israelianum* and *Hemicystodinium zoharyi* in small bays and sounds around Puerto Rico, the Bahamas and Bermuda. Often these environments were brackish, but in tropical island areas in particular, run-off results only in temporarily lower salinities and these small bays are highly saline for most of the year.

Outwash from lagoons. Plumes of estuarine water which flow out of bar-built lagoons, such as those described by Pease (1969) along the coast of New Jersey, probably carry with them sediments and suspended matter which includes cysts. This probably results in enhanced frequencies of estuarine cyst-types such as those mentioned above, in the inner neritic zone. Examples of this included *Spiniferites bulloideus* in nearshore sediments along the coast of New Jersey and *Tuberculodinium vamcampoae* in nearshore sediments along the Ivory Coast near Abidjan, which also is flanked by several large bar-built lagoons.

Coastal water entering estuaries. Many estuaries along the northeastern coast of the United States and fjords in Scandinavia contain substantial proportions of coast water, either in vertically mixed or stratified subsystems (see section 3). Their plankton thus comprises a mixture of estuarine and neritic organisms and this appears to be true of their cyst assemblages. Relatively strong representation of *Operculodinium centrocarpum* in such environments can be related to this neritic influence. In addition, an outer neritic or neritic—oceanic influence (see below) is added by the minor presence of species such as *Nematosphaeropsis balcombiana* and *Tectatodinium pellitum.*

Coastal upwelling. Coastal upwelling represents a special condition (which is similar to that above) where cooler, more saline and nutrient-rich coastal waters invade either the coastal or estuarine environment from a near-bottom source (Fig. 26). The upwelling may



A. "SLOPE WATER" MODEL FOR CYST DISPERSION

B. UPWELLING-OFFSHORE DIVERGENCE MODEL FOR CYST DISPERSION

Fig. 26. Diagram to illustrate some dynamic motions which are postulated to contribute to cyst dispersal. Model A. *1* = estuarine-lagoonal confinement; *2* = outwash from lagoons; *3* = offsetting coastal waters; *4* =eddies of coastal water migrating seawards into offshore zones; *5* = detached parcels of coastal water containing neritic microfloras; *6* = winnowing of relict shelf deposits; *7* = intrusion of coastal-shelf water into estuaries by mixing or bottom intrusions; *8* = mixing, sinking and bottom indrafting of oceanic water with shelf water across the continental slope and the outer shelf zones; *9* = alongslope subsurface currents of subpolar origin in intermediate waters. Model B. *1* = localized inflows of estuarine water; *2* = vertical sinking of the products of nearshore plankton blooms in upwelling areas; *3* = seaward dispersal of nearshore bloom products by wind-driven transport; *4* = vertical sinking of cells from the offshore zone of divergence; *5* =vertical sinking from surface oceanic waters; *6* = alongslope subsurface countercurrents at intermediate depths; *7* = winnowing of outer shelf and slope deposits during submarine erosion.

occur in "neutral" coastal stretches which are almost entirely free of estuaries (e.g. many areas of western South Africa and Peru) or in the proximity of river mouths (e.g. some areas in the Gulf of Maine). In each situation, the effect on cyst assemblages was an enrichment in peridinioid cysts, such as those which were referred to earlier as the "grouped *Peridinium* species" and related taxa such as *Diplopeltopsis minor* and *Diplopsalopsis orbicularis.* This influence was seen mostly profoundly in the Peruvian region near Pisco where peridinioid cysts, in parallel with the extent of the upwelling water, were found in high relative abundances from the inner shelf into the adjacent continental rise zone (Fig. 21). The Factor 3 loading isolines were superimposed on a surface water temperature map of this region to demonstrate this relationship. In the South African region, which included part of the Benguelan upwelling system, enrichment of assemblages in peridinioid cysts was limited to the immediate coastal zone (innermost sectors of Transects 8 and 9). This was in accord with Bang's (1971) analysis of the Benguelan upwelling system in this region where he drew a distinction between upwelled water *sensu stricto* in the nearshore inner neritic zone and vertically mixed but not strictly upwelled waters at the continental shelf edge divergence (see Fig. 26B). Both in the Peru and South African regions, a cyst morphotype called Form A was found in assemblages which were influenced indirectly by upwelling and this species (of unknown affinity) apparently is in its optimum environment under these conditions. It was not found in estuarine assemblages in the Gulf of Maine or Middle Atlantic Bight, but several of them, like the assemblages from Peru, were rich in peridinioid cysts.

Neritic—oceanic boundary

Inshore penetration of warm oceanic water. The inshore limit to the penetration of warm oceanic waters at low and middle latitudes generally represents the landward limit to the distribution of tropical and subtropical oceanic plankton. In the Middle Atlantic Bight region for instance, the landward edge of the slope water (Fig. 26), which has an oceanic component, represents the inshore limit to the occurrence of oceanic plankton from the Gulf Stream and Sargasso Sea biomes (Grice and Hart, 1962). The landward extension to the distribution of *Leptodinium* cysts in this region (in bottom sediments) can be related to this landward limit of oceanic water, i.e. the neritic—oceanic boundary (Fig. 20). The species associations to which it contributes (Associations IX and X in this region) show a similar limit to their landward extents (Fig. 24) which lie beneath the slope water—coastal water junction above. The small amount of information which is available concerning occurrences of *Leptodinium* in plankton samples (Table VII) indicates that it occurs in slope waters of the Middle Atlantic Bight and to date, it has not been found in coastal waters. This indicates *Leptodinium* is of oceanic derivation and the landward limits to its distribution are determined by the extent to which oceanic waters penetrate shorewards.

However, the precise mechanism by which *Leptodinium* cysts eventually stabilize their position in sediments may be a complex process involving both vertical settling from plankton and further re-distribution along the bottom by internal wave motions near the shelf edge. It is curious for example, that an organism of planktonic origin should have a distribution in bottom sediments which lies almost exactly parallel to the isobaths (see Fig. 20). In the Middle Atlantic Bight region, the limit to *Leptodinium* occurrences is close to the known limit to bottom indrafts of saline water (Bigelow and Sears, 1935, p. 50) at approximately 100 m depth. This also is the approximate depth of the top of a semi-permanent halocline. This represents a water stratum where internal wave motions may be concentrated (see Miller, 1950) and thus they may be responsible for the shoreward movement of fine resuspended bottom material where they intersect the local topography. This type of situation is not unique to the Middle Atlantic Bight: similar circumstances are known to develop on the Pacific coast of North America for example (see Dodimead and Pickard, 1967, p. 2219).

Poleward flow of subtropical oceanic water. The outer or landward neritic—oceanic boundary of the slope water system in the western North Atlantic can be traced laterally to the northeast along isohalines and isotherms towards mid-ocean as a weak subtropical convergence (Defant, 1961). Its northern limit is approximately coincident with the extent of the North Atlantic Drift and marked

TABLE VII

Percentage composition of dinoflagellate cysts in acetolysed plankton net (35 μm mesh size) samples from estuarine (1—2), coastal (3—7) and slope waters (8—11) (Locations at foot of table)

	1	2	3	4	5	6	7	8	9	10	11
Spiniferites											
S. bentori			0.4	0.7							
S. bulloideus	2.4	0.5	10.9	1.4	1.0	2.0	2.6				
S. elongatus	39.5	1.5	1.3	2.1							
S. mirabilis			0.4			3.9	2.6				4.7
S. membranaceus	5.4	2.0	2.2								
S. scabratus										0.9	
S. sp. of *ramosus*			2.7	1.4							
Bitectatodinium											
B. tepikiense	40.7										
Planinosphaeridium											
P. choanum	1.8										
Nematosphaeropsis											
N. balcombiana			0.4					91.4	95.1		
Leptodinium											
L. paradoxum											20.0
L. patulum								0.3	P	0.9	12.3
L. sphaericum								5.4	3.2	0.9	57.1
L. strialatum									P		2.9
Operculodinium											
O. centrocarpum			71.3	87.5	5.7	80.4	92.0				
Lingulodinium											
L. machaerophorum										0.9	
Peridinium											
P. sp. of *trochoideum*	10.1	94.5			92.3						
Other *Peridinium* spp.		1.5	9.5	6.9	1.0	13.7	2.6	2.9	0.8	96.4	0.9
Total cysts counted	167	201	220	143	105	153	113	294	122	111	105

Sample locations: 1 = Somes Sound, Maine, VIII-11-72, surface; 2 = Somes Sound, Maine, VI-2-73, surface; 3 = Vineyard Sound, V-28-73, surface; 4 = Buzzards Bay, V-28-73, surface; 5 = Cape Cod Bay, V-28-73, surface; 6 = 38° 25'N, 73° 50'W, 18 m, IX-23-75, near Wilmington Canyon; 7 = 38° 09'N, 73° 46'W, IX-23-75, near Baltimore Canyon, 20 m; 8 = 39° 56'N, 70° 59'W, IX-21-75, continental slope, South of Cape Cod, 300 m; 9 = 37° 54'N, 73° 42'W, IX-23-75, near Baltimore Canyon, 212 m; 10 = 23° 30'N, 17° 00'W, X-30-72, offshore West Africa, 100 m; 11 = 35° 32'N, 9° 08'W, XII, 1974, west of Gibraltar, 225 m.

by the 36‰ isohaline and 15°C summer isotherm. It lies with the Transitional III coccolithophore zone of McIntyre and Bé (1967). The northern limit to the distribution of *Leptodinium* in pelagic sediments as determined by D.B. Williams (1971) appears to be coincident with this convergence. Thus it is in accordance with its inshore distribution as discussed above.

Near-surface mixing of coastal and oceanic waters. The horizontal and vertical turbulent mixing of cooler coastal and warm oceanic waters, especially at middle latitudes, creates waters of intermediate composition between these two source waters from the surface to a depth of 100 m or more. It creates a transitional or ecotone environment (see Pianka, 1974, p. 245; McGowan, 1971, p. 3) whose corresponding plankton is a combination of neritic and oceanic elements. For example, as noted above, in the slope water zone of the Middle Atlantic Bight the epizooplankton is a blend of species from Labrador Coastal Water and the Gulf Stream—Sargasso Sea Water (Grice and Hart, 1962). This combination of neritic and oceanic elements likewise can be seen in slope-rise zone cyst assemblages beneath this surface water ecotone in areas such as the Middle Atlantic Bight, South Africa and Argentina. The cyst assemblages there contain species which are abundant in adjacent shelf sediments, such as *Operculodinium centrocarpum*, plus species such as those of *Leptodinium* which represent an oceanic element. In addition, species such as *Nematosphaeropsis balcombiana* and *Tectatodinium pellitum* attained their peak abundances in these slope-rise zone assemblages. The transitional ecotone thus apparently represents their optimum surface water environment.

Hart and Currie (1960, p. 251, their fig. 95B) recorded a distribution pattern for a species of *Gonyaulax* which was centered in the transitional (outer neritic—oceanic) zone off western South Africa. This type of planktonic distribution is precisely that which can be postulated for cyst-based species such as *N. balcombiana* and *T. pellitum.* Reid (1974, p. 593) drew attention to Lohmann's observation (1910) that *Pterosperma labyrinthus* Ostenfeld 1903 (which Reid considers to be a senior synonym for *N. balcombiana*) was found in an area of mixed cold and warm water along the northern edge of the Gulf Stream and in the Irminger Sea. This seems to further confirm its preference for a transitional-ecotone type of habitat.

TABLE VIII

Encystment temperature data for *Operculodinium centrocarpum* (cysts of *Protoceratium reticulatum* = *Gonyaulax grindleyi*) from diverse sources

Site and water depth, date and cruise	Temperature (°C)
1. Skagerrak, Oslo, Surface May, 1948, Station #3 (Braarud, Gaarder, Grønntved, 1953)	6.3
2. Woods Hole Dock, Surface April-May, 1965 (Wall and Dale, 1968a)	10—14
3. Cape Cod Bay, Buzzards Bay Surface, May 1973 R/V *Westward* (original)	10.5—13.0
4. Elands Bay, South Africa Surface December 1966 (Grindley and Nel, 1970)	14.0—17.5
5. Middle Atlantic Bight (original)	
(a) Surface, 38° 25′N, 73° 50′W, September 1975 R/V *Gosnold* 185-322	23.1
(b) Surface, 38° 09′N, 73° 46′W, September 1975 R/V *Gosnold* 185-323	23.6
(c) Surface, 37° 22′N, 74° 38′W, September 1975 R/V *Gosnold* 185-326	23.7
6. Laboratory cultures (Braarud, 1944)	10—20

Offsetting of coastal waters. While the greatest mass of coastal water (by definition) occurs immediately above the continental shelf, it also can extend seawards as a thin surface layer which reaches out above the slope and rise zones. This offsetting develops especially when the water column is highly stratified, as at the end of summer and under the favorable influence of offshore wind stress. Its potential importance with respect to the composition of cyst assemblages, is to enrich slope-rise zone assemblages (along with other mechanisms) in the neritic element, and in particular, to enrich them in specimens of *O. centrocarpum.* As indicated in Tables VII and VIII, cysts of this type were found in outer neritic—coastal water plankton along the eastern coast of the United States in September 1975 under these hydrographic conditions. Similarly, Grindley and Nel (1970) recorded high numbers of these cysts (as cysts of *Gonyaulax grindleyi*) in coastal waters between 32° and 33°S along the coast of western South Africa. This is a region where strong winds frequently blow the surface waters seawards as part of the upwelling mechanism (see Bang, 1971, p. 223) and this may be another example of surface transport of neritic cysts seawards before their eventual deposition in slope sediments.

Non-ecologic factors which indirectly affect trend development

In addition to these foregoing oceanographic—ecologic factors which mainly determine trends in cyst distribution in sediments, there are "geological" factors which apparently indirectly contribute to them under special circumstances. These factors are non-ecologic because they pertain to non-living cyst material and are independent of cyst biogenesis in plankton. Rather they include mechanisms such as recycling of specimens of extant species from older marine sediments, allochthonous displacements of cysts from inshore to offshore environments and the presence of non-equilibrium assemblages in late Pleistocene—early Holocene relict sediments with submarine outcroppings. Since a major objective of this study was to classify living cyst-based taxa on an ecologic—environmental basis, it clearly was important to distinguish "modern" from "relict" or other non-equilibrium assemblages.

Recycling of specimens from continental sources

This problem arose mainly with respect to occurrences of *Hemicystodinium zoharyi* and *Operculodinium israelianum* along the southeastern coast of the United States. The former occurred as far north as the Delaware River mouth, and the latter as far north as Pamlico Sound. Elsewhere both had centers of distribution in small tropical bays in the Caribbean region and in the Bermuda and Bahamas Islands. It is uncertain whether they live in modern plankton as far north as Delaware or Pamlico Sound respectively, where the waters are cooler, more brackish and more eutrophic than in Caribbean bays. Recycling of specimens from Tertiary or even Quaternary interglacial sediments along the coastal plain seems likely.

Submarine erosion

Species of *Spiniferites*, *Lingulodinium*, *Hemicystodinium*, *Tuberculodinium* and *Operculodinium israelianum*, which were found in estuarine environments and less commonly in shelf sediments, sometimes were "secondarily" abundant in some slope and rise zones. This was especially true of slope-rise assemblages from the Mediterranean and Caribbean Seas, but not limited to them. These "secondary" occurrences are interpreted here as allochthonous and due to displacement of shallow-water organisms into offshore sediments (or redeposition from older estuarine—neritic sediments which today are stranded along the outer continental shelf and slope zones).

The high relative and per gram abundances of *Operculodinium centrocarpum* which were encountered in slope-rise zone sediments from the Middle Atlantic Bight, the Argentina region and South Africa are probably due in part to derivation of specimens from such sedimentary sources and not entirely from surface water plankton. Sedimentological studies suggest three sources for redeposited cysts of *O. centrocarpum* in slope-rise and abyssal zones. First, they may be derived by penecontemporaneous erosion of neighboring shelf sediments (see Milliman, 1973; Emery and Uchupi, 1972; Schlee, 1973) due to storm-induced motions, resuspension of fine material by benthos, winnowing by bottom currents, gravity slumping and downslope creep. Second, some specimens may have been derived by erosion of the bevelled edges of early Holocene—late Pleistocene relict sediments along the outer edge of continental shelf, especially during the post-glacial rise in sealevel. Third, some specimens may have been transported alongslope by nearbottom countercurrents flowing equatorwards, along with clays. Emery and Uchupi (1972, p. 389) and others have suggested that silty clays in the slope-rise zone of the Middle Atlantic Bight were derived from the Labrador region by this mechanism and Wyrtki (1966) and Hart and Currie (1960) have described comparable countercurrents in the Peruvian and South African regions.

Relict sediments

Sediments which were deposited during the early Holocene to late Pleistocene and have subsequently remained unburied are called relict (Emery, 1968). They contain microfossils which are not in equilibrium with modern oceanographic—ecologic conditions. However, since these relict deposits often are marine and contain only extant species, it is difficult to determine what proportion of the specimens in them are ancient versus modern. (Modern planktonic material will likely reach these relict surfaces even when there is no non-biogenic deposition.) Clearly a predominance of early Holocene—late Pleistocene dinoflagellate cysts is possible in relict deposits and potentially this can be misleading in an ecologically orientated investigation.

Dinoflagellate assemblages from the Middle Atlantic Bight continental shelf and upper slope zone almost certainly fall in this category to some degree (Association II above). Sediments in this region have been determined as relict by Emery and Garrison (1967), Schlee (1973), Milliman (1973) and others and in particular, a patch of fine-grained sediments south of Martha's Vineyard has attracted attention in this regard. It differs from adjacent sediments in color, by a higher proportion of benthic foraminifera, its heavy-mineral and clay-mineral compositions and organic carbon and nitrogen contents (Milliman, 1973 and others). Radiocarbon ages for all relict sediments in the Middle Atlantic Bight show that there is a seaward increase so that older sediments now outcrop at greater bathymetric depths near the outer shelf and upper slope zone (Fig. 27, from radiocarbon dates in Emery and Garrison, 1967, table 1). In the patch of fine-grained sediments mentioned above, radiocarbon dates of 9,150 ± 200 and 13,420 ± 210 were determined in the vicinity of our samples *51* and *56* (Transect 2).

The dinoflagellate content of assemblages from within this fine-grained sediment patch and adjacent to it, were dominated by grouped *Peridinium* species (44—77% in Transect 1; 41—67% in Transect 2) and they contained very robust specimens of *Spiniferites mirabilis* plus much pollen and spore material. These features can be attributed to the fact that they are relict assemblages which apparently were deposited in a paleoestuarine environment during the early Holocene and late Pleistocene. Similar modern assemblages (with a dominance of *Peridinium*) were found in estuarine sediments between Cape Hatteras and the Gulf of Maine.

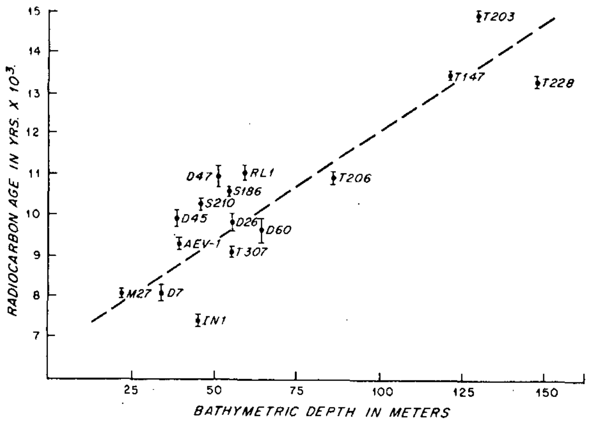


Fig. 27. Diagram to illustrate increasing age of sediments at the water—sediment interface with increasing bathymetric depth across the Middle Atlantic Bight relict sediment region. Radiocarbon ages from Emery and Garrison (1967).

To what extent relict sediments were encountered in other regions which were studied is unknown. However, it is likely that assemblages from western South Africa are partly relict. For example, two areas in the middle and inner shelf to the west and southeast of Danger Point where Davey (1971, p. 333, his fig. 3) found exceptionally high abundances of cysts may be sites of fine-grained relict sediments (personal communication, Dr. Colin Summerhayes). Thus the distribution of cysts which Davey described in this general area may not be in equilibrium with the modern oceanographic conditions. This is discussed further in section 6.

Interpretation of trends in assemblage diversity

There were three intrinsic causes of variations in species diversity between assemblages which created inshore—offshore and latitudinal trends as described above. First, diversity was increased by the addition of a small group of more stenotopic species to a "background" of cosmopolitan forms. For example, offshore assemblages had *Leptodinium* species present in addition to others; tropical estuarine assemblages had a few warm-water estuarine species (e.g. *Hemicystodinium zoharyi*) present in addition to cosmopolitan forms; and cool temperate estuarine assemblages had colder water stenotopic species present (e.g. *Spiniferites elongatus*, *Bitectatodinium tepikiense*) in addition to cosmopolitan species. Second, diversity was increased (within samples of equal numbers of individuals) by failure of one of the three most abundant and cosmopolitan taxa (*Spiniferites bulloideus*, *Operculodinium centrocarpum* and grouped *Peridinium* species) to materialize to a substantial level within localized assemblages. Third, an environmentally restricted species, such as *H. zoharyi*, would simply dominate so strongly that diversity was reduced almost to the monospecific level, as in Bermuda Sounds.

These intrinsic reasons can be interpreted as caused by combinations of biological and sedimentological phenomena. Localization of certain species to specific environments (e.g., *Leptodinium* species, *H. zoharyi*, *S. elongatus*) clearly is a biological contribution to increased diversity. Similarly, strong dominance by a species within some preferred optimum environment which locally reduces assemblage diversity, also is a biological cause. In contrast, the presence of many estuarine and neritic cysts in slope sediments, according to the interpretation which was given above, is a sedimentological phenomenon and yet its overall effect also is to increase the diversity of assemblages. (If these possibly allochthonous occurrences were discounted, the diversity of pelagic cyst assemblages could not exceed 5.0 since there are only five species of *Leptodinium*.) Similarly, entrapment of fine-grained sediments within semi-enclosed embayments (such as Somes Sound, Pamlico Sound and others) in the nearshore zone apparently tended to increase assemblage diversity, probably because larger total numbers of individuals were isolated from these samples and hence the number of species encountered also tended to increase. This type of diversity increase (a statistical bias) also can be termed sedimentological. It may have been an additional factor in producing greater diversity values for slope-rise zone assemblages which frequently were extracted from fine-grained sediments (see below).

Interpretation of trends in specimen density values

Inshore to offshore and latitudinal trends in specimen densities also must be interpreted as due to the combined influence of biological (productivity-related) and sedimentological (rates of deposition, grain-size distributions, age of surfaces) factors.

The trend for specimen densities to decrease in lower-latitude inshore environments by comparison with high and middle latitudes parallels a trend in declining rates of biological primary productivity towards equatorial environments (see Parsons and Takahashi, 1973, p. 19; Odum and Copeland, 1974; Koblentz-Mishke et al., 1970). This trend thus is biological in genesis, at least in part, and differences for example between cyst densities in Norwegian fjords versus the Gulf of Paria, both of which have fine-grained sediments (see below), apparently are related to differing rates of production of cysts in surface water environments.

In contrast, rates of biological primary productivity (and presumably rates of cyst production), decrease in the offshore direction in areas such as the Middle Atlantic Bight (Emery and Uchupi, 1972, p. 306; Smayda, 1973) while the numbers of cysts per gram in the sediments increase strongly. Biological productivity thus cannot be invoked to explain this trend and this observation tends to confirm the hypothesis that many cysts in slope-rise zone sediments are of "non-biological" origin.

Sedimentological factors are clearly important in creating this offshore trend and this is exemplified through a statistical positive correlation between cyst densities and increasing proportion of the clay plus silt-size particles in sample grain-size distributions (Fig. 28). These data for samples from the Middle Atlantic Bight area and western South Africa indicate that cyst density increased semi-logarithmically with increasing percentages of the combined clay and silt-sized mineral fraction to the level where this comprised 50—60% of the sediment: beyond this plateau, no further increase occurred. This relationship, which probably is almost universal for palynomorphs, means that conditions which favor the accumulation of finer-grained sediments (of varying lithology) simultaneously tend to favor higher accumulations of cysts.

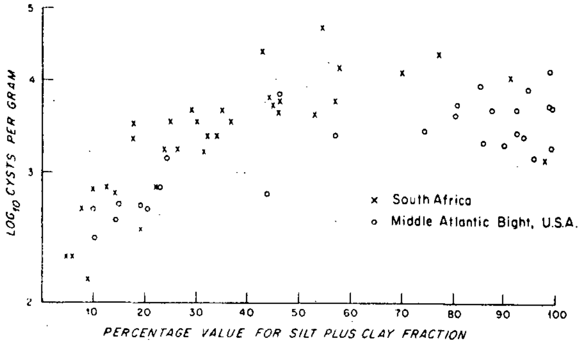


Fig. 28. Diagram to illustrate statistical trend for dinoflagellate cyst density values (number of cysts per gram of sediment, dry weight) to increase semi-logarithmically with increasing proportions of silt and clay-sized components of sediment lithology. Data for samples from the Middle Atlantic Bight, U.S.A., and southwestern South Africa.

Unfortunately there are no data for rates of cyst production in surface waters or their corresponding rates of supply to sediment surfaces below and therefore it is impossible to evaluate the relative importance of biological and sedimentological factors. Rates of sedimentation frequently are ten times lower for continental slope zones than they are in estuaries and thus they could easily account for the mean five-fold increase in cyst density which occurred offshore in the Middle Atlantic Bight (see above) assuming other variables remained constant. However, it is extremely doubtful whether rate of sedimentation was the only factor involved. It may be that a large proportion of cyst material in slope sediments is of pre-Recent origin and thus the rate of supply of cysts (and other biogenic material) to the bottom would be only one co-factor which controlled the observed densities. A large amount of work on cyst distribution and production within the water column is required to resolve a complex issue such as this raises.

6. An ecologic—environmental classification of cyst-based taxa

Content and format

An attempt is made in this section to classify extant cyst-based dinoflagellate taxa into environmental—ecologic groups and to classify associations along similar lines. This represents an attempt to synthesize the biogeographic results and discussions of them which were presented in section 5 and to provide a framework which can be used as a model to classify extinct dinoflagellates too. It will be obvious from foregoing remarks that there are inherent problems in attempting to formulate this type of classification, but as noted in the introductory notes, such a classification is mandatory for future progress.

The classification of species which is presented below is based mainly on the results of this study, but it considers other results too. These include those published by D.B. Williams (1971), Davey (1971), Davey and Rogers (1975) and Reid (1972, 1974, 1975), preliminary results of cyst distribution in plankton (Table VII), literature which describes the biogeography and ecology of dinoflagellate thecate stages in plankton, results of life studies on theca—cyst relationships and existing schemes of classification for phytoplankton and zooplankton in oceanographic literature. Potentially allochthonous occurrences of cysts in sediments and occurrences due to possible recycling of older specimens, were ignored in this compilation.

The results of cyst distribution studies concerning plankton samples were particularly useful in confirming deductions which were based on assemblages from bottom sediments, but unfortunately as yet these results are limited to but a few stations (Table VII).

A binary scheme was used to classify marine cyst-based taxa according to (a) their inshore—offshore distributions and (b) their latitudinal distributions, in a fashion which is similar to existing classifications for marine phytoplankton and zooplankton in Gran (1902), Gran and Braarud (1935), Colebrook et al. (1961), and Bary (1963b, c, 1964). The use of this type of scheme was dictated by the existence of dual trends in cyst distribution as detailed above and the empirical correlation between cyst distributions in sediments and surface water environments. Its adoption is intended to emphasize that an interrelationship exists between ecologic groups of species (cysts) and water types rather than between species and any single "controlling" factor such as temperature. A conceptual basis for the origination of this type of classification is presented in section 7.

The inshore—offshore component of the classification is recognized by five divisions, namely, estuarine, estuarine—neritic, neritic, neritic—oceanic and oceanic. These terms and divisions are used in direct equivalence with the estuarine, estuarine—coastal, coastal, transitional coastal—oceanic and oceanic subsystems which were described in section 4 as physiographic—hydrographic units. The latitudinal component is recognized by temperate (cool water), tropical—subtropical (warm water) and cosmopolitan (unrestricted distribution relative to climate) terms and divisions.

The main basis for allocating a cyst-based taxon to a particular subdivision of this classification was its peak abundance within a corresponding environmental subsystem or its limitation to one subsystem. The centers of distribution which were described for individual species above in section 4 were of special importance in this regard, but they were not the sole criterion. An asterisk is used to mark species whose distributions were restricted to the environmental—climatic unit to which they are allocated below to distinguish them from more cosmopolitan taxa. The restricted species obviously are the ones with greatest potential value in paleoenvironmental studies.

Classification of cyst-based taxa

Estuarine group
(1) Temperate estuarine species
    *Spiniferites elongatus**
    S. membranaceus (sensu Reid, 1974)*
    *Bitectatodinium tepkiense**
    *Planinosphaeridium choanum**

(2) Tropical—subtropical estuarine species
    *Hemicystodinium zoharyi**
    *Tuberculodinium vancampoae**
    *Operculodinium israelianum**
    Spiniferites ramosus (sensu Wall and Dale, 1970)*
    S. membranaceus (sensu Rossignol, 1964; Wall, 1967)
    S. scabratus
    S. bentori (long-spined morphology)

(3) Cosmopolitan estuarine species
    Spiniferites bulloideus
    Lingulodinium machaerophorum

Estuarine—neritic group
(4) Temperate estuarine—neritic species
    Spiniferites bentori (short-spined morphology)*
(5) Tropical-subtropical estuarine—neritic species
    Spiniferites ramosus (sensu Davey, 1971)
(6) Cosmopolitan estuarine—neritic species
    grouped *Peridinium* species (see text)
    Diplopsalis lenticula
    Diplopsalopsis orbicularis
    Diplopeltopsis minor
    Peridinium conicum
    P. pentagonum

Neritic group
(7) Cosmopolitan neritic species
    Operculodinium centrocarpum
    Spiniferites mirabilis

Neritic—oceanic group
(8) Cosmopolitan neritic—oceanic species

Nematosphaeropsis balcombiana
Tectatodinium pellitum

Oceanic group
(9) Tropical—subtropical oceanic species
*Leptodinium aculeatum**
*L. patulum**
*L. paradoxum**
*L. sphaericum**
*L. strialatum**

Classification of species associations

The eleven species associations which were defined by cluster analysis with the ESS Index of Similarity (Fig. 23) also were classified in similar manner. They were categorized as estuarine, neritic, neritic—oceanic and oceanic associations and subdivided according to their respective occurrences in temperate, subtropical and tropical climatic zones. This effectively reduced them to five groups (see below) as identified by arabic numerals within each of which the included associations were very similar in composition. Differences between associations within each of these five groups tend to be small and may prove to be statistically insignificant when more data are gathered. Details of these compositional differences can be found in section 4.

Estuarine group
(1) Temperate estuarine and estuarine—neritic

Association I.	Temperate estuarine
Association II.	Temperate estuarine—neritic

(2) Tropical—subtropical estuarine and estuarine-neritic

Association III.	Tropical to warm temperate estuarine
Association IV.	Tropical estuarine—lagoonal
Association V.	Tropical estuarine small embayment
Association VI.	Tropical—subtropical estuarine—neritic bay

Neritic group (in upwelling regions)
(3) Subtropical to warm temperate neritic-upwelling

Association VII.	Subtropical—temperate upwelling (South Africa)
Association VIII.	Subtropical—temperate upwelling (Peru)

Neritic—oceanic group
(4) Subtropical to warm temperate neritic—oceanic transitional

Association IX.	Subtropical—temperate transitional (Middle Atlantic Bight, South Africa, Argentina)
Association X.	Subtropical—temperate neritic—oceanic transitional (Middle Atlantic Bight only)

Oceanic group
(5) Tropical—subtropical oceanic—pelagic

Association XI.	Tropical—subtropical pelagic (Mediterranean and Caribbean Seas, Equatorial Atlantic)

Discrepancies in interpretation with earlier literature

There is no comprehensive classification of cyst-based living dinoflagellates in previous literature, but ecologic—environmental interpretations were presented for several taxa in brief discussions of biogeographic data (D.B. Williams, 1971; Davey, 1971; Davey and Rogers, 1975; Reid, 1975; Wall and Dale, 1968b) Some important discrepancies exist between these earlier interpretations and the classification for cyst-based species which was presented above and they require comment.

Operculodinium centrocarpum
Davey (1971) and Davey and Rogers (1975) interpreted *O. centrocarpum* as a warm-water species (cyst) on the basis of its strong occurrence in sediments beneath the Agulhas Current. In our classification it is considered to be a cosmopolitan neritic species. We believe that representation of it as a warm-water organism is erroneous for several reasons. First *Operculodinium centrocarpum*, while indisputably abundant in sediments beneath warm-water currents, certainly is not limited to them and in fact it is equally abundant in sediments in northern temperate regions such as the northeastern coast of the United States (Fig. 12) and Scandinavian fjords below cool waters. The only assemblages wherein *O. cen-*

trocarpum was not a dominant species in this study were tropical indicating, if anything, its tolerance for all except the warmest water conditions (above 25°C).

Second, a survey of literature and some previously unpublished data showed that cysts of this type, as produced by *Protoceratium reticulum (= Gonyaulax grindleyi)* form over a wide range of temperatures from as low as 6.3°C to as high as 23.7°C (Table VIII, see p. 170).

Operculodinium centrocarpum was interpreted as a neritic (coastal water) species in our classification for several reasons. The parental species *(Protoceratium reticulatum)* for example, usually is considered to be a neritic dinoflagellate (Schiller, 1937, p. 323) and cysts correspondingly were found most abundantly only in sediments beneath surface waters with a major coastal water component. Initial observations on cysts within modern plankton confirm this affinity for coastal waters (Table VII) in nearshore and outer neritic hydrographic zones. It was not classified as neritic—oceanic, despite its strong presence in many continental slope and rise zone sediments because we believe these occurrences are related (a) to the coastal and not the oceanic component of "slope" or transitional waters and (b) to the penecontemporaneous displacement of specimens from nearby shelf sediments plus submarine erosion of others from Pleistocene and relict sediments.

Spiniferites ramosus

Davey (1971) and Davey and Rogers (1975) considered *S. ramosus* to be a cold-water species. In our interpretation, *S. ramosus sensu* Davey (and Davey and Rogers) is a tropical—subtropical, estuarine—neritic species. This interpretation is advanced largely because we believe that *S. ramosus* in western South African shelf and slope-rise zone sediments probably is correlated with relict paleoestuarine sediments and that its present-day (observed) distribution, therefore, does not accurately represent its ecology. (The same comment may apply to *O. centrocarpum* in shelf and slope-rise zone sediments, not only in the South African regions, but at many glaciated latitudes.) Similarly, the observed tendency for *S. ramosus* to become "secondarily" abundant in slope-rise sediments along western South Africa is interpreted here as due to erosion of submarine outcrops of paleoestuarine relict (or older) sediments along the outer continental shelf edge zone so that again this distribution is not a true reflection of the species ecology. Specimens which were extremely similar to the "African" variety of *S. ramosus* were found in sediments at low latitudes (Gulf of Aden) and apparently they are widespread in the eastern central Atlantic region, the Mediterranean Sea region and Black Sea to Red Sea provinces. This at least partly substantiates our classification of it and means that its ecology is comparable with that of *S. ramosus sensu* Wall and Dale (1970) in having an affinity for warmer waters. Apparently it differs from the latter in being less tolerant of brackish conditions.

The *Operculodinium—Spiniferites* ratio

It follows from the above that we believe the ratio of *Operculodinium centrocarpum* to *Spiniferites ramosus* as observed by Davey and Rogers in the western South Africa region is not a direct reflection of present-day warm-water versus cold-water current systems but is better explained by other means. We believe that a high ratio of *O. centrocarpum: S. ramosus* in shelf sediments from western South Africa is the result of stronger neritic over estuarine influence in local hydrography at a time when cyst formation occurred and that this took place mainly before present-day hydrographic conditions were established in this region.

It also follows that in our opinion the ratio between *O. centrocarpum* and *S. ramosus* (or other species of *Spiniferites*) as it develops in continental slope and rise sediments often has little ecologic significance in terms of overlying surface waters and the local plankton biocoenosis. Its significance lies more in the direction of sediment provenance: a high ratio reflects derivation of sedimentary fine-grained material from neritic depositional or paleodepositional sites whereas a low ratio reflects derivation of the cysts from paleoestuarine silts and clays. Similarly the ratio of these two species to others such as *Nematosphaeropsis balcombiana* and species of *Leptodinium* in assemblages from outer shelf, slope, rise and abyssal zones is considered to have no ecologic significance because it also is dependent on sedimentation-related and not strictly biologic processes.

Spiniferites mirabilis

This species is mentioned briefly because it was difficult to categorize it. It was interpreted as neritic and cosmopolitan because its distribution seemed to parallel that of *Operculodinium centrocarpum* rather than any other species. However, it never reached the same level of abundance as the former in our samples and unlike other species of *Spiniferites*, did not have detectable centers of distribution in estuarine environments. Specimens of the species from some offshore assemblages were noticeably larger and more robust than specimens in nearshore assemblages (e.g., Argentina region, Middle Atlantic Bight) and its preferred environment may be the outer neritic zone, including part of the transitional coastal—oceanic system. It is clearly cosmopolitan but it may have some preference for a warm temperate climatic regime. D.B. Williams (1971) found centers of distribution for it in the north-eastern North Atlantic Ocean near the Bay of Biscay which occur in the warm temperate Lusitanian province (See Hall, 1964). This climatic zone is absent along the eastern coast of the United States and this may explain why no centers of distribution for *S. mirabilis* were encountered in our study.

Lingulodinium machaerophorum

D.B. Williams (1971, p. 237) noted that his Facies VIII, which was almost exclusively composed of *L. machaerophorum*, was restricted to the Straits of Gibraltar region and interpreted this as an allochthonous facies which was associated with outflows of highly saline water from the Mediterranean Sea. We believe this should not be interpreted as evidence that *L. machaerophorum* shows a preference for highly saline surface waters. On the contrary, it is common in estuarine environments including coastal bays with estuarine influences as Reid (1972, p. 943) pointed out. Its parental thecate dinoflagellate, *G. polyedra*, is cosmopolitan and occurs in estuaries and inner neritic waters (Eppley and Harrison, 1975, p. 12) and it is tolerant of brackish waters, as evidenced by its abundance in the modern Black Sea (see references in Wall and Dale, 1974). For this reason it is classified here as estuarine or estuarine—inner neritic.

Operculodinium israelianum

The present data indicate that *O. israelianum* is a tropical estuarine or possibly estuarine—neritic species (cyst) with centers of distribution erratically distributed through the Caribbean region and nearby Bahamas Islands. This is completely contrary to its ecology as deduced from its occurrences in early Pleistocene Thurnian sediments of Stage L2 in the Royal Society Borehole at Ludham in East Anglia, Britain (see Wall and Dale, 1968b). These sediments were characterized as deposited during "glacial" climatic conditions and as containing pollen which was representative of an "oceanic heath" vegetation (see references in Wall and Dale, 1968b). These sediments contained assemblages with over 90% *O. israelianum*, which was almost monospecific in them.

There are no obvious dissimilarities in specimen morphology between these Pleistocene and modern specimens (some have been cultured in the laboratory) and this virtually eliminates any possibility that they belong to different species, although not finally. One possible explanation is that the paleoclimatic interpretation was in error for assemblages with *O. israelianum* in the borehole. It is now known that the Thurnian (Tiglian) interval included some rapid and pronounced shifts in climatic conditions (Zagwijn, 1974) and the borehole was so situated that its site probably received alternating influxes of cold and warm water from the North Sea and English Channel—Mediterranean sides during the Pleistocene. Thus in retrospect it appears that as far as *O. israelianum* was concerned, the connotations "glacial and oceanic" both may be inappropriate. However, it still seems unlikely that the marine climate was warm enough to be tropical and it is possible that the present-day distribution of *O. israelianum* is not restricted to tropical—subtropical regions. Modern assemblages comprising 96% of this species (thus being strictly comparable with the Thurnian assemblages) were not discovered in this study: should they ever be found, this could change the status of *O. israelianum* in our classification of living cysts.

7. Evolutionary—ecologic considerations

Importance of species—water type relationships

The distribution of cysts in modern sediments can be interpreted as being mainly a function of the distribution of their parental dinoflagellates in relationship to contrasting surface water types (even though non-ecologic factors interject their influence). It follows that the distribution of cysts in sediments is indirectly determined by the complex set of ecologic factors which controls the distribution of dinoflagellates within and between water types. The broader problem of phytoplankton species distributions in relationship to water types (or water masses) which is paramount in almost all aspects of marine plankton biogeography and ecology (see McGowan, 1971), thus is also highly relevant to cyst biogeography. The future development of dinoflagellate paleoecology and related paleoenvironmental studies are closely allied in this way with this universal problem in biological oceanography and will be served by formulation of a concept which interprets the genesis of cyst assemblages in terms of water types—species relationships.

Such a concept is formulated below as a combination of several others which are cited in existing ecologic literature. This composite concept involves two postulations. First, that cyst assemblages originate as various combinations of ecologic species-groups, such as those defined in our classification, in accordance with a hydrographic mixing model which was developed by Barry (1964). Second, that the evolution of these ecologic species-groups themselves can be explained or "predicted" by quasi-theoretical models in contemporary ecology which invoke environmental—climatic stability and predictability as master factors in the control of species compositions of communities, their diversities, complexities and organization. These stability—predictability concepts further can be used as background to identify some types of environmental adaptations that are shown by living cyst-based taxa.

Cyst assemblages as combinations of ecologic species-group components

Cyst assemblages, as they are observed in sediments, can be conceptualized as comprising various combinations of the environmental—ecologic groups of species (ecologic components) which were defined in our classification above. Precisely which of these ecologic components is represented in any given assemblage can be considered as a function of hydrographic mixing, i.e. the nature of local surface waters. Naturally occurring surface water types invariably have some degree of mixing and exchange with neighboring types and thus there is a corresponding mixing and interchange between their respective ecologic components. The basic assumption is that our classification of cyst-based taxa expresses species preferences for source water types with reasonable accuracy.

Typically the overall composition of many cyst assemblages in sediments involves a combination of a few species with restricted environmental occurrences together with one or more cosmopolitan elements. The former are drawn from only three subgroups (cool temperate/estuarine, tropical—subtropical/estuarine and tropical—subtropical/oceanic) whereas the latter are drawn from estuarine, neritic and neritic—oceanic larger groups; the last two comprise exclusively cosmopolitan taxa.

There are important precedents in marine biology both for the type of classification which we adopted and for our conceptualization of assemblages as comprising mixtures of species-groups which are indigenous to contrasting water types (source or primary types). For example, the format of our classification of cyst-based taxa, is clearly analogous with the classical "plankton element" classification of Gran (1902) and Gran and Braarud (1935) and the more recently constructed schemes of Colebrook et al. (1961), Colebrook (1964) and Bary (1963b, c, 1964). In each instance the classification recognized environmental—ecologic groups of species according to their inshore—offshore distributions (i.e. occurrences in hydrographic zones which lie parallel to the coast) in conjunction with their latitudinal—climatic distributions, although the exact terminology and definition of groups varied between authors.

Bary (1964) also proposed a qualitative model which described the mixing of ecologic species-groups in relation to surface water types in the North Atlantic region west of Britain. He suggested that ecologic species-groups were essentially indigenous to specific water types which occurred in this region and that they mixed in proportion to physical hydrographic mixing to create unique local associations of species. His concept is clearly very similar to the one which we suggest to explain the genesis of cyst assemblages. Bary's (1964) model is particularly appropriate because it deals with species distributions across the neritic—oceanic boundary which was of special interest here.

Biologic—ecologic relationships between phytoplankton species and surface water types

Combining ecologic components (species-groups), which are indigenous to surface water types, according to a physical hydrographic mixing model to produce unique assemblages provides only a mechanical explanation of the species—water type problem. It leaves unanswered the question of why species show differential affinities for contrasting water types.

Bary (1964) hypothesized that "unspecified properties" of water types, other than their temperature—salinity characteristics (which were used to define them in the first instance), were responsible for locating species within them. He was unable to identify these "properties" but merely noted that the fidelity of the water type—species relationship varied according to hydrographic mixing in a "dilution" ratio. Johnston (1964) and others have suggested that the properties of natural waters which control phytoplankton species affinities for them include trace metal concentrations and chelating substances and that these supersede temperature and salinity in importance. This viewpoint is typical of that held by many contemporary phytoplankton ecologists who believe that phytoplankton species distributions are determined by complex sets of variables in synergistic and antagonistic combinations which may be colligative with temperature and salinity (i.e. co-vary with them) but are not limited to them. For example, Guillard and Kilham (1977) recently reviewed marine diatom biogeography and ecology and provided a comprehensive list of variables which are known to influence phytoplankton growth and reproduction. These variables included physical factors (temperature, light, water density distributions), chemical factors (inorganic substances such as iron, nitrogen, phosphates, silicon, oxygen, etc.; organic substances such as vitamins, chelating agents, etc.), biological factors (extracellular metabolites, "clock" mechanisms, life history processes, symbiosis, zooplankton grazing, sinking rates) and human factors ("pollution"). However, the fact remains that the exact set of factors which controls the distribution (defines the niche) which is occupied by any single phytoplankton species still is not definable to date and it is difficult to reconcile the biologic activity of complex sets of variables with biogeographic data. Guillard and Kilham (1977) commented that the traditional approach of attempting to define the fundamental niche of individual species really has met with limited success in this regard.

This strictly biological approach to the species-water type problem thus is not amenable to direct use in most paleontological studies and for this reason (plus the fact that all paleontological studies do have inherent limitations), a more generalized approach is required towards its practical resolution and applications from it. We suggest that the stability—predictability class of ecologic hypotheses provides this alternative approach if stability and predictability are viewed as properties of hydrographic climates. This theme is pursued after a brief generalized resume of stability—predictability concepts is provided to accommodate the later discussion.

Stability—predictability concepts in ecology and marine biogeography

Many marine and terrestrial ecologists consider that environmental—climatic stability, predictability and severity determine patterns of species-community diversity, niche breadths, rates of speciation and complexity within food-chains (ecosystems). The most widely offered generalization is that species diversity, rates of speciation and complexity in community organization increase under the influence of more stable and predictable environments in non-severe habitats (provided that time was sufficient to establish a climax or equilibrium condition). It is adjunct to this, that the stability and predictability-related properties of environments comprise sets of proximate and ultimate factors whose total fluxes control the biogeographic distributions of species within and between communities. This follows because the measurable parameters (indices), such as diversity and community complexity in the biota, are based directly on the presence and proportional abundances of their component species. Thus major marine biomes (Zenkevitch, 1949, in Hedgpeth, 1953, p. 195) of the worlds oceans, major marine ecosystems and environments with contrasting stability—predictability properties all show gross distributional conformity (Fig. 29). This figure, from Odum and Copeland (1974) with slight modification, demonstrates this and the concomitant development of the two ubiquitous interacting inshore—offshore

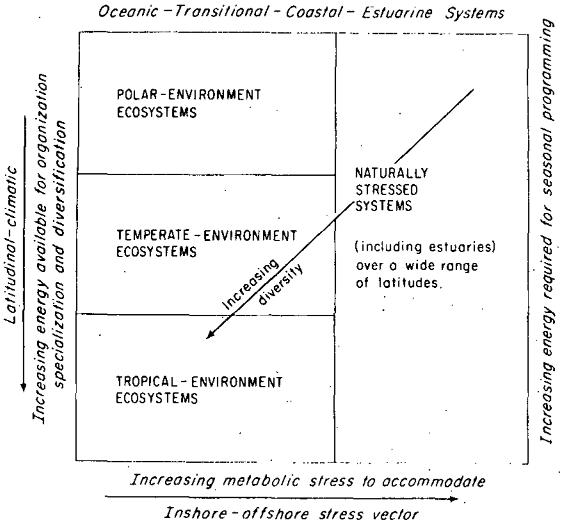


Fig. 29. Diagram to illustrate the global scale relationship between ecosystem distributions, various biological stress vectors and trends in species diversity, after Odum and Copeland (1974, p. 44). Increasing environmental—climatic stability generally parallels increasing species diversity so that the diagram also reflects global distributions of corresponding stability—instability regimes.

and latitudinal trends, which Odum and Copeland (1974) referred to as "salinity" and "latitudinal" stress factors in their discussion of coastal ecosystems.

Concepts which relate to environmental stability, predictability and severity have been formulated over a period of several years and independently by several ecologists. These concepts include some divergent viewpoints within their overall framework. They are dealt with by MacArthur (1960), MacArthur and Wilson (1967), Fischer (1960), Levins (1968), Pianka (1974), Grassle (1972), Sanders (1968), Slobodkin and Sanders (1969), Valentine (1973), Odum and Copeland (1974) in various contexts and the reader is referred to them for detailed discussions. A generalized and paleontologically orientated treatment was presented by Bretsky and Lorenz (1970) and it is paraphrased here.

Organisms which typically occur in stable, predictable or "benign" types of environments show an observed and predictable tendency to be stenotopic and are intolerant of conditions which develop outside narrow ranges of fluctuation in many environmental variables. They have limited geographic ranges and are provincial, specialist types of organisms with narrow niches and a high level of speciation. They occur in diverse communities with a high ratio of species to individual specimens and it is postulated that they possess evolutionary characteristics such as low homeostasis, low genetic variability, low polymorphism and tend to be "*K*-selected" (see Pianka, 1974, p. 90).

Organisms which typically occur in unstable, unpredictable or severe environments essentially possess contrasting characteristics. They tolerate a broader spectrum of ambient conditions by virtue of intrinsically broader niches and they become cosmopolitan-generalist species with wide-ranging biogeographic distributions. They do not speciate highly and occur often in communities of low diversity with a low ratio of species present to number of individual specimens. It is postulated that these organisms possess high homeostasis, high genetic variability within species-populations, are highly polymorphic and tend towards being "*r*-selected" in evolution.

Stable environments in the present context are definable as those which experience a minimum of seasonal change. Predictable environments are those wherein conditions repeat themselves regularly, even though annual ranges of change may be high. Severe environments are those where ambient conditions approach the cardinal limits to continuation of physiological cellular processes and therefore threaten the existence of biological life. All environments innately possess stability, predictability and severity properties independently since these properties are not mutually exclusive. Moreover, individual sets of ecologic factors also exhibit some independence with respect to each; for example temperature may be stable (invariate) annually, at the same time that humidity or salinity is unstable (variable). It is impossible therefore to generalize very far about the interrelationships between stability, predictability and severity in differing environments and the influences which they exert on biological communities. Each facet may be limiting under certain critical circumstances, but severity for example, generally will supersede stability and/or predictability in importance in extreme environments and unstable environments naturally have a greater propensity towards being unpredictable than stable ones because total deviation from mean conditions is innately greater within them.

Stability—predictability concepts as applied to the species—water type problem

Concepts of climatic stability and predictability have been applied widely in benthic marine ecology (Sanders, 1968; Slobodkin and Sanders, 1969; Bretsky and Lorenz, 1970) but seldom used in application to the biogeography and ecology of phytoplankton or the species--water type distribution problem. However, in broad application to this problem they have the outstanding merit that they alleviate any necessity to explain species distributions in terms of single variables, but rather emphasize the total variability around mean climatic conditions as a master ecological controlling factor. This is consistent with the *n*-dimensional hypervolume ecologic niche concept which is held by most modern ecologists (Pianka, 1974, p. 190; Valentine, 1973, p. 59).

It is suggested here that contrasting water types at the ocean surface zone have unique stability—predictability properties and that these fluctuate sufficiently between water types to act as an ecological master factor which controls planktonic species distributions. The stability and predictability characteristics of water types can be evaluated from the temperature—salinity data which are used to define them when these data are plotted on a seasonal (monthly) basis and for successive years. A technique along these lines was introduced by Hedgpeth (see Hedgpeth, 1951, 1953); it involved plotting for each month of the annual climatic cycle, T/S data pairs for extreme minimum and maximum values, mean monthly maximum and minimum values and mean monthly values in five separate blocks on a "hydroclimatic" diagram. [Similar diagrams were subsequently called T/S polygons by Emery and Uchupi (1972, p. 261) and climographs by Pianka (1974, p. 36).] Diagrams for a single year thus indicate the extent of climatic stability by the deviation of extreme and maximum to minimum mean monthly values around the mean monthly values and indicate at a glance whether this deviation is due mainly to temperature or salinity fluctuations. Climatic severity is indicated by the external locus of data points in the T/S field. Climatic predictability is indicated by coincidence of points representing the same month in different years (or lack of it). Hedgpeth (1953) emphasized that climographs of this nature were necessary to describe hydrographic climate as *combinations of their paired temperature and salinity properties.* Pianka (1974, p. 36) noted that the same principle could be extended to any other biologically important variables and used to predict the responses by organisms to changing physical environments.

Hydrographic measurements which are comprehensive enough for this technique to be applied usually are limited to coastal stations but not entirely so, and Bary (1964) for instance, provided T/S polygons for coastal, transitional and oceanic water types in the North Atlantic region which he studied. Sufficient is known about surface water types to permit several generalizations which develop in their stability—predictability characteristics. First, water types conserve their hydrographic—climatic identities even though their geographic positions alter seasonally as oceanographic fronts migrate alongside changing current patterns. Second, hydrographic climates in estuarine environments are less stable, less predictable and more severe (especially in littoral to sublittoral zones) than those in oceanic domains while those in coastal and coastal—oceanic transition zones are intermediate along an environmental—climatic gradient. Unstable and unpredictable hydrographic climates in estuaries conserve their characteristics over a wide range of latitude (Fig. 29). Third, hydrographic climates in low latitudes generally are more stable, more predictable and less severe than at higher latitudes, both inshore and offshore. Fourth, transitional zones (ecotones) have hydrographic climates which are less stable and less predictable but not more severe than climates in contiguous zones.

There are many features of modern plankton biogeography which are in accord with this interpretation of hydrographic climates as units with unique stability and predictability characteristics. For instance, species diversity tends to be higher in plankton communities at lower latitudes and in equivalent warm-water current systems than in high latitude or other colder-water environments

(Graham, 1941; Hulburt, 1963; Honjo and Okada, 1974). In addition, the more highly specialized, stenotopic species in modern plankton tend to be localized in stable hydrographic climatic zones, such as the open ocean domain in general and in particular its stable cool and warm water sectors. Transitional, unstable zones in contrast carry few or no indigenous species but are populated by the more tolerant migrants from contiguous tropical and subpolar zones (see Graham, 1941, with reference to the dinoflagellate genus *Ceratium*). Moreover, there now is evidence that physiological traits as developed by morphologically similar species-populations in contrasting environments, such as coastal and oceanic domains, represent explicit evolutionary adaptations to ambient conditions (Carpenter and Guillard, 1971; Murphy and Guillard, 1976). Finally, estuarine phytoplankton do show characteristics of "*r*-selected" organisms (i.e., less efficient resource utilization, broad niches, opportunistic and rapid growth in plankton blooms) whereas open ocean species have some traits of "*K*-selected" organisms (efficient resource utilization in oligotrophic waters, narrow niches, low growth rates) according to Guillard and Kilham (1977) and Fisher (1977).

These statements are generalizations but they provide some justification that the stability—predictability and severity characteristics of water types are reasonably invoked as ecologic master factors which control modern phytoplankton species distributions. Thus indirectly they are responsible for the distribution of cysts in sediments to a substantial degree via the intermediary of water type—species relationships within surface plankton.

A central theme in this water type—species relationship is adaptive specialization in response to environmental stability. This phenomenon is manifest at the basal systematic level of species-populations to the upper level of major marine biomes. The adoption of a "plankton element" mode of classification can be considered as an extension of this thesis because recognition of environmentally specialized (restricted) adaptations is foremost among its goals. Thus this thesis within stability—predictability hypotheses can be used as background to identify some specific types of environmental adaption among living cyst-based dinoflagellates which are of paleoecologic—paleoenvironmental interest.

Environmental adaptations by living cyst-based taxa

A definitive pattern of environmental adaptation on the part of modern cyst-based dinoflagellate taxa emerges when they are interpreted according to the above thesis. It is that modern fossilizing dinoflagellate species primarily represent adaptations to unstable—unpredictable hydrographic regimes which are typical of shallower-water environments along continental margins and around oceanic islands. Superimposed on this basic pattern, there is some adaptive specialization towards the relatively more stable and predictable subsectors of this unstable macroenvironment and it is within these subsectors that the more morphologically distinctive and stenotopic species are found. The relative stability of these subsectors may be created by limited seasonal variation in either temperature- or salinity-related environmental variables.

This predominant trend in adaptation towards the unstable—unpredictable continental margin environment is readily appreciated from an inventory of cyst-producing taxa which fossilize. These mainly comprise estuarine—neritic species of the theca-based genera *Gonyaulax*, *Protoceratium*, *Pyrophacus*, *Peridinium* (or *Protoperidinium* according to some authors), *Diplopsalis*, *Diplopsalopsis*, *Diplopeltopsis* and others which are common in nearshore waters. In contrast, almost all oceanic dinoflagellates (including for example, large suites of *Ceratium* species from all latitudes as described by Graham, 1941), find no representation at all as cysts in bottom sediments. The only exception to this bias is the cyst-based genus *Leptodinium* which has an "oceanic" distribution in bottom sediments. However, it is the "oceanic" end-member of a large complex of species, the *Gonyaulax spinifera*-complex, whose predominant locus lies with the estuarine—neritic environment. Thus *Leptodinium* is only an "oceanic subcomponent" of a large estuarine—neritic complex which itself is primarily adapted to the unstable continental margin environment.

Other features of fossilizing modern dinoflagellates are consistent with this interpretation as corollaries to stability—predictability hypotheses as discussed above. For example, their predominant type of distribution tends towards cosmopolitanism and assemblages of cysts generally are of low diversity with a high specimen: species ratio. They also show only a weak tendency towards latitudinal zonation and that which exists is developed among species which inhabit the inshore rather than the offshore domain. Weak latitudinal zonation is predictable for inshore species according to terms of stability—predictability hypothesis because the unstable—unpredictable shallow-water realm extends over a wide range of latitude without major modification in its gross nature (Fig. 29).

The production of (fossilizing) cysts by living dinoflagellates thus in itself can be considered as an adaptive life history feature which fits them for survival in unstable—unpredictable hydrographic climatic regimes. As a fossilizing group, the dinoflagellates thus are predominantly planktonic estuarine—neritic organisms although in total, the living dinoflagellates as a group do include a large oceanic component too.

The general characteristics of the most abundant cyst-based taxa in modern sediments are consistent with those of organisms which are adapted to unstable—unpredictable regimes. Thus species such as *Operculodinium centrocarpum*, *Spiniferites bulloideus*, *Lingulodinium machaerophorum* and *Nematosphaeropsis balcombiana* occur as cosmopolitan opportunistic types of organisms which have a tendency to dominate assemblages. They represent the most eurythermal, euryhaline cyst-based taxa with broad ecologic niches and accordingly they contribute little to the development of precise zonal schemes in biogeography. They have only weakly developed thermal preferences (see Table VI) and only slight differentiation in the inshore—offshore direction although they can be categorized broadly as estuarine (*S. bulloideus*, *L. machaerophorum*), neritic (*O. centrocarpum*) and neritic—oceanic (*N. balcombiana*) according to peak abundances.

They also show one further feature, namely, incipient speciation, which is a feature of organisms adapted to unstable—unpredictable regimes (Slobodkin and Sanders, 1969). This is manifest in subtle changes in cyst morphology which are superimposed on otherwise constant configurations. For example, *Spiniferites bulloideus* shows considerable variation in its ornamentation; *Operculodinium centrocarpum* shows some regional variation in its cell size and spine length as evidenced by the "Abaco morphotype" as described in section 4; *Lingulodinium machaerophorum* shows variation in its archeopyle form which varies from an epitractal type to a 3P type; and *Nematosphaeropsis balcombiana* sometimes appears to be separable into "large" and "small" forms. These features are logically interpreted as part of an incipient trend towards speciation at a very low taxonomic level and perhaps some of these individual morphologic populations with restricted geographic ranges are systematically analogous with the ecophenotypic races of diatoms which were described on the basis of physiological traits by Carpenter and Guillard (1971). The cumulative effect of many weakly differentiated local "races" being developed within the framework of a single cosmopolitan species presumably is to increase the overall variability in its gene pool, which Grassle (1972) suggested is a feature of opportunistic species.

The least cosmopolitan of modern cyst-based dinoflagellate taxa appear to represent a more pronounced trend in adaptive specialization towards some relatively stable sectors of marine environments. (Taxa which show this tendency are marked by an asterisk in the species ecologic classification.) These species were localized to three environmental subsystems, namely, small bays and inshore areas at cool temperate latitudes, in comparable bays in tropical—subtropical latitudes and in tropical to warm temperate latitude pelagic subsystems. They were not encountered in nearshore environments which experience large fluctuations in salinity or in "high energy" environments where strong currents, turbulence and high flushing rates prevailed (e.g., Gulf of Paria, mouths of large rivers such as the Chesapeake and Delaware estuaries).

The pattern of environmental adaptation which they formed thus could be resolved as localization (specialization) to the terminal sectors (the stable sectors) of temperature and salinity regimes. These types of adaptation are of paleoecologic and paleoenvironmental interest and for this reason they are discussed in more detail.

Adaptations to thermal regimes

Adaptations by cyst-based taxa to thermal regimes can be illustrated by reference to Figs. 30 and 31 which show seasonal temperature data for the western North Atlantic coastal zone and offshore along meridian 66°W. These data for the inshore zone have been divided into three thermal regimes, I—III, in which regimes I and III are terminal and II is median. Values were plotted for mean annual temperate, the mean monthly temperature of the warmest month, and the mean monthly value of the coldest month as averaged over a multiyear period. The height of the temperature "envelope" thus represents annual range in mean monthly temperature as it varies with latitude.

Regime I, from 61 to ca. 44°N, is a cool-water sector wherein the mean annual temperature is less than 10°C and summer mean monthly values do not exceed 15°C. The annual range of values is below 10°C. Regime II extends from ca. 44 to near 23°N and within it, mean annual temperature increases from ca. 8° to 20°C, representing approximately one degree per degree of latitude. The mean monthly values for the warmest months increase from ca. 15° to 30°C and those for the coldest month from near zero in the north to 24°C in the south. The annual range in mean monthly temperature varies markedly from 6° in the south to a maximum of 22°C in the Middle Atlantic Bight region near 39°N and then begins to diminish northwards again. Regime III, from 23°N to the Equator has mean annual temperatures around 27.5°C, highest mean monthly values near 30°C and lowest mean monthly values above 25°C. The annual range in temperature is small, being less than 6°C.

Species which were classified above as cool temperate—estuarine organisms above *(S. elongatus, S. membranaceus sensu* Reid, *B. tepikiense, P. choanum)* are the most oligosthenothermal cyst-based taxa and they represent adaptations to thermal regime I. Their encystment temperatures can be estimated from data in Fig. 30 by assuming that encystment occurred during the warmest months (since these are cysts of autotrophic gonyaulacid species which are typical members of the secondary summer phytoplankton). The left-hand shaded area in Fig. 30 estimates the range of temperature over which these taxa encysted (as deduced from their observed distributions along the coast of the eastern United States), at between 3° and 15°C.

Species which were classified as tropical—subtropical estuarine and as tropical—subtropical oceanic cysts in section 6 represent the most polythermic stenotopic taxa which were found in nearshore and offshore zones, respectively. Members of the inshore group *(H. zoharyi, T. vancampoae, O. israelianum, S. ramosus sensu* Wall and Dale 1970) can be interpreted as species which are adapted to thermal regime III in Fig. 30 and it is estimated that they encysted between temperatures

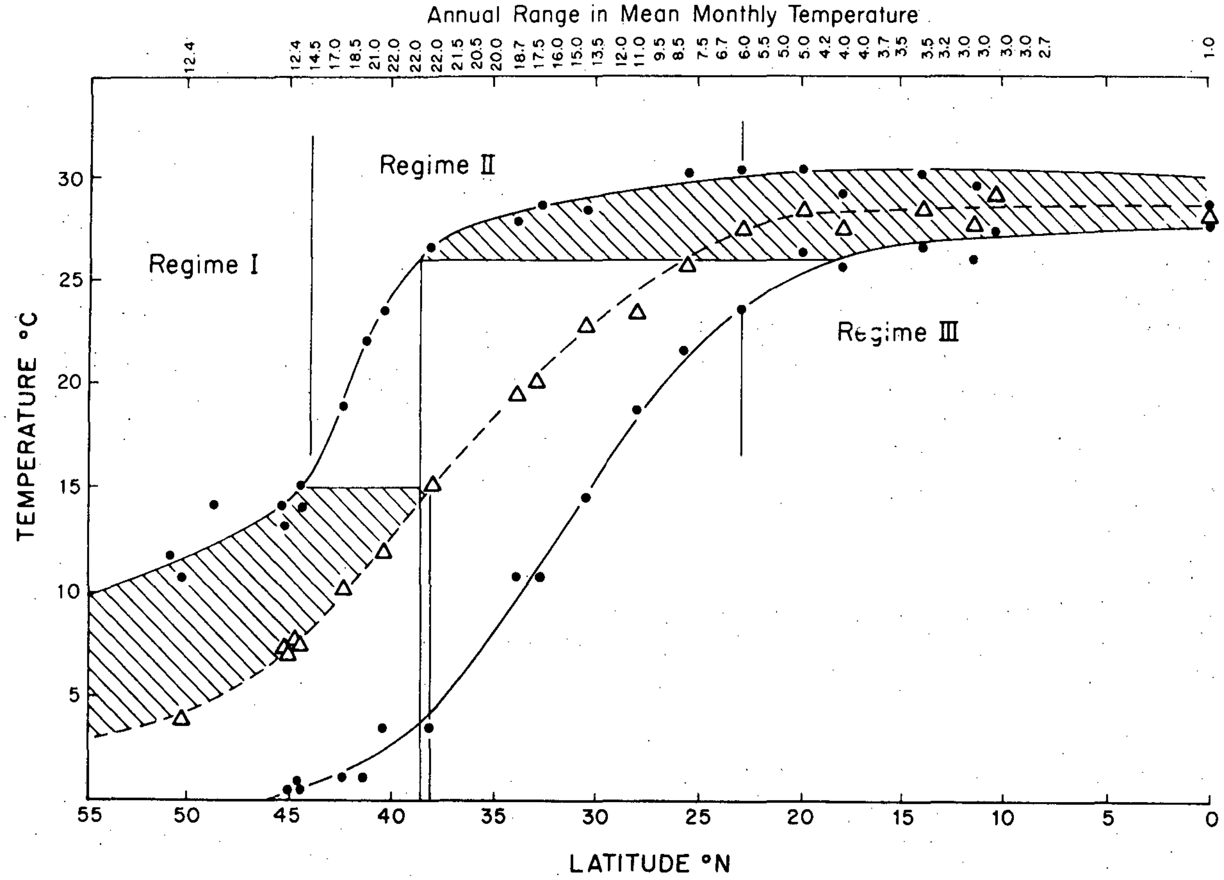


Fig. 30. Thermal regimes along the coastal zone of the western North Atlantic Ocean from the Equator to 55° N. The upper and lower temperature curves represent mean monthly values for the hottest and coldest months of the year and the intermediate curve represents mean annual temperature. The shaded zones represent Temperature—latitidinal ranges which are occupied by temperate and tropical—subtropical estuarine—neritic ecotypes (see text). Temperature data from Anonymous (1960).

of ca. 24° and 30°C, as indicated by the shaded area to the right of the figure. The offshore group, comprising five species of *Leptodinium*, can be considered as adaptations to the offshore thermal regime III indicated in Fig. 31. An estimate of their encystment temperatures (shaded area in the profile) is between 21° and 29°C. This estimate may be too conservative because the poleward distribution of *Leptodinium* reaches cooler latitudes in the eastern North Atlantic according to D.B. Williams (1971), but it may involve some post-encystment transport and would therefore overestimate the temperature range.

A more unusual type of adaptive specialization apparently is developed by the short-spined morphotype of *Spiniferites bentori*. Its occurrences along the eastern coast of the United States were limited to the northern part of the inshore Middle Atlantic Bight where the range of annual temperature is between 17° and 23°C. This suggests that this taxon is an adaptation to predictability in temperature rather than stability. (A membranous "variety" of *S. bulloideus* was co-occurrent with *S. bentori* in this area and it appears to be similarly adapted.) Independent observations indicate that *S. bentori* encysts at temperatures between 19° and 21° C in the vicinity of Woods Hole.

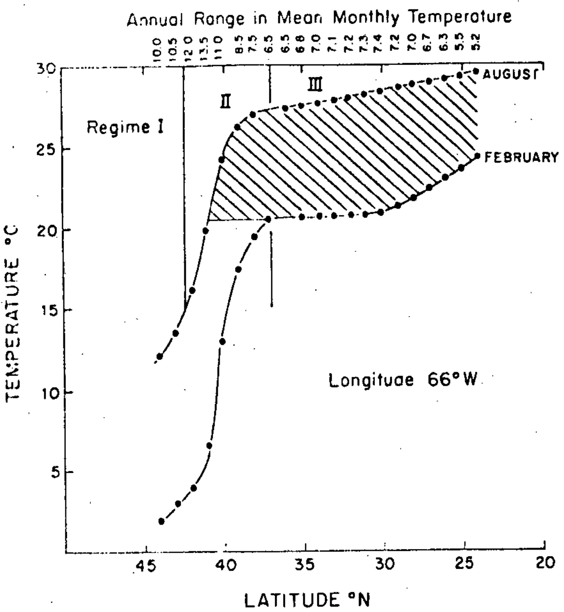


Fig. 31. Thermal regimes in the surface offshore zone of the western North Atlantic Ocean along longitude 66°W from 20° to 50°N. The temperature curves are based on mean monthly values for August and February, respectively from Schroeder (1966, Bull. Mar. Sci. 16: 307, 313). The shaded area represents the approximate temperature—latitudinal range for modern species of *Leptodinium*.

Adaptations to salinity regimes

Adaptations to salinity by fossilizable dinoflagellates appear to follow a similar pattern to their adaptations to thermal regimes in that species with restricted occurrences are localized within the terminal stable sectors of salinity regimes. The most interesting and completely expressed example concerns cyst-based taxa which are the fossilizable members of the *Gonyaulax spinifera*-complex (see Wall, 1975). To illustrate this relationship, a salinity profile was constructed (Fig. 32) to parallel the thermal profile (Fig. 30) to which reference was made above. The two terminal regimes of this salinity profile are represented by freshwater (Regime A) and saline ocean water (Regime C) and there is an intermediate brackish-water regime (Regime B) which constitutes the highly unstable estuarine sector.

There are cyst-based taxa of a stenohaline character which represent adaptations to both terminal sectors of this type of salinity profile (not explicitly to the one in Fig. 32). At the fully marine end, associated with Regime C, there are species of *Leptodinium* which are the most orthostenohaline of living cyst-based marine taxa and they are adapted to salinities of approximately $35^0/_{00}$ and above. At the freshwater end, associated with Regime A, there is the unusual oligostenohaline species *Gonyaulax apiculata* (Penard) Entz 1904, whose fossilizable cysts occur in freshwater lake sediments such as those of Lake Zurich, Switzerland.

Other cyst-based taxa appear to represent adaptations to the subterminal sectors of this salinity regime and appear as species which possess wide salinity-related tolerances but still are not completely euryhaline. For example, at the marine end of the salinity profile, there are taxa which apparently tolerate fluctuations in salinity in the range of 4—6 $^0/_{00}$ such as *Nematosphaeropsis balcombiana*, a neritic—oceanic or panthalassic taxon, and taxa such as *Spiniferites elongatus*, *S. membranaceus*, *Bitectatodinium tepikiense* and *Planinosphaeridium choanum* which occurred in semi-enclosed embayments where salinity fluctuated in this general order of a few parts per mil. *Hemicystodinium zoharyi* and *Operculodinium israelianum* also can be considered as subterminal adaptations of this type in tropical zones. [*Pyrodinium bahamense*,the parental thecate stage to *H. zoharyi*, is known to undergo short vertical migrations to avoid direct contact with inflowing freshwater (Seliger et al., 1970) and this is another manifestation of specialization towards relatively stable salinities.] At the freshwater subterminal sector of the salinity spectrum, there are two unusual early Holocene species, *Spiniferites cruciformis* and *Tectatodinium psilatum*, which according to estimates of paleosalinities in the Black Sea region, lived in surface waters with values between 2 and $7^0/_{00}$ (Wall and Dale, 1974).

There are no cyst-based taxa which are in-

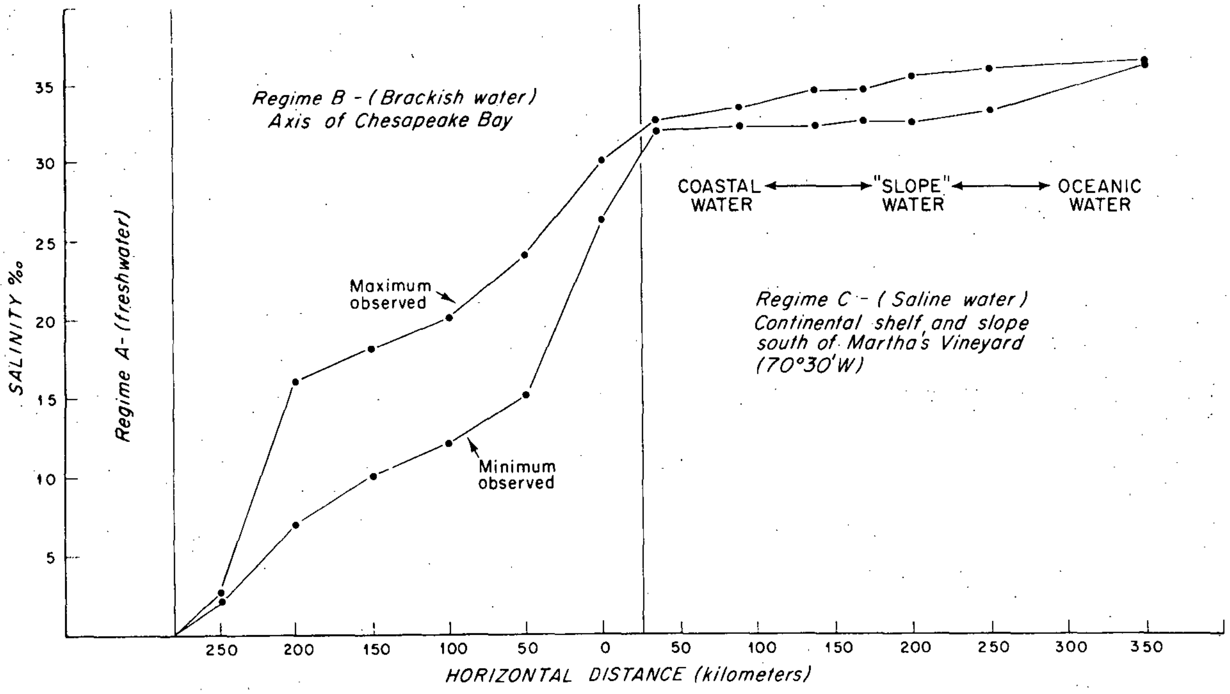


Fig. 32. Salinity regimes as developed from inshore to offshore across the general region of the Middle Atlantic Bight, eastern U.S.A. The upper and lower lines of the envelope represent some maximum and minimum observed values: those in Regime B are surface versus bottom values along the axis of Chesapeake Bay from Seliger et al. (1975, p. 195) for April, 1973 while the values in Regime C are based on surface water data for the offshore zone in Colton et al. (1968, U.S. Fish Wildl. Serv. Data Rep., 23).

digenous and restricted to the intermediate salinity Regime B, which represents an ecotone transitional environment. Assemblages from within this type of regime comprise only the more cosmopolitan members of the *G. spinifera*-complex such as *Spiniferites bulloideus.*

In sum, the salinity-related environmental distribution of the cyst-based fossilizable taxon from this species-complex spans a range from freshwater to fully marine (oceanic). Thus it replicates the halobic distribution of diatoms ("Halobiensystem") which was determined by Kolbe and later revised by Budde and Hustedt (see Gessner and Schramm, 1971 p. 809 for details). This is remarkable for the members of a single species-complex and shows considerable diversification in their adaptive specialization. It provides an important clue for approaching future work in dinoflagellate paleoecology since the fossil record contains many examples of ancient species-complexes. It is reasonable to assume that their individual taxonomic components exhibited similar types of adaptive specialization and efforts should be devoted to identifying these taxa and defining their individual adaptational characteristics by analogy with the living forms.

In this respect, it is significant that living cyst-based species which represent adaptations to the terminal and subterminal sectors of both temperature and salinity regimes are the most morphologically distinctive ones as a general rule. For instance, species of *Leptodinium,* which represent adaptations to the temperature- and salinity-stable open ocean tropical—subtropical environment are readily distinguishable from each other and show little intraspecific variation. Also, species from the generally cosmopolitan genus *Spiniferites* which represent its most environmentally specialized members, such as *S. elongatus*, also are the most morphologically distinctive ones. This phenomenon can be interpreted as representing a higher degree of speciation (genetic isolation) on the part of species in relatively stable surface water environments and this also is consistent with terms of stability—predictability hypotheses.

8. Conclusions

The distribution of dinoflagellate cysts in modern marine sediments varies both in the inshore—offshore direction and with latitude and thus shows "environmental" and "climatic" trends. These two trends are complementary to some extent, especially along eastern continental margins where warm-water currents occur offshore, such as in the Middle Atlantic Bight region of the United States.

Both trends involve changes in the species compositions of cyst assemblages in sediments in the distribution of (statistically defined) species associations and in the additional parameters of species diversity and specimen density.

The inshore--offshore trend mainly involves different taxa attaining their peak abundances (relative to each other) in a seaward succession which parallels changing hydrographic and bottom topographic conditions. *Spiniferites*, *Lingulodinium*, *Hemicystodinium* and *Tuberculodinium*, for example, are most abundant close to shore in estuarine environments; *Operculodinium* and *Peridinium* tend to be most abundant in shelf sediments (although they are cosmopolitan and abundant in some estuarine and continental slope-rise zones too); *Nematosphaeropsis* attains its maximum abundance in continental slope and rise sediments below the transitional neritic—oceanic hydrographic zone and *Leptodinium* is limited to (and most abundant within) pelagic sediments which occur near the outer continental shelf and beyond it. Species associations naturally reflect this arrangement of individual taxa on a cumulative basis and thus their distributions also have an inshore—offshore trend which incorporates a general seaward progression. Similarly, species diversity has an inshore—offshore trend in some regions and tends to increase seawards, partly because an oceanic suite of species *(Leptodinium)* is added to others in assemblages from continental slope, and many abyssal zone sediments. This increase in diversity is not due entirely to biological factors, however, because may cysts which occur in slope-rise zone sediments probably are not Recent in age, or are allochthonous estuarine—neritic modern specimens. Cyst density values per gram of sediment also tend to increase offshore, but again not primarily because of biological factors but rather because of sedimentological factors (more fine-grained sediments, lower rates of sedimentation, presence of recycled material) which cannot be evaluated individually.

The latitudinal trend in distribution is seen best in nearshore environments where some taxa are restricted to tropical and subtropical regions *(Hemicystodinium zoharyi*, *Tuberculodinium vancampoae*, *Operculodinium israelianum)* and a few others are limited to cool to warm temperate regions *(Spiniferites elongatus*, *Bitectatodinium tepikiense*, the rare taxon *Planinosphaeridium choanum)*. This trend also involves some changes in relative species abundance too, but these changes are not entirely due to temperature and at least partly reflect changing estuarine and neritic influences along coastlines at different latitudes. Species associations also show a latitudinal trend in their distributions; some are limited to tropical—subtropical regions whereas others are found only at temperate latitudes. Species diversity tends to increase towards low latitudes and thus parallels the situation in many marine biological communities. Specimen densities are higher by and large at temperate latitudes, so they also show a trend which parallels the normal biological pattern with higher primary productivity in cooler climatic zones.

There is also a latitudinal trend in the distribution of offshore cyst assemblages, which largely transpires because species of *Leptodinium* are limited to warmer-water latitudes, equatorwards of subpolar oceanographic frontal systems. Higher-latitude pelagic sediments appear to contain only cyst-based taxa (e.g., *O. centrocarpum*, *N. balcombiana*) which also occur in shelf sediments and therefore are not exclusively oceanic species.

The main factor which determines cyst distribution in sediments probably is the species—water type relationship which varies between taxa, since the distribution of cysts in sediments bears an empirical relationship to surface water types (in parallel with other planktonic microfossils, such as coccolithophorids, diatoms and foraminifera). Hydrodynamic motions (currents) which produce and conserve the physical arrangement of water types, thus play a major role together with respective biologic—ecologic properties of the water types themselves, in determining cyst distributions in the bottom sediment thanatocoenoses. Current actions along the estuarine—neritic and neritic—oceanic boundaries or "fronts" have a strong influence on individual species and species association distributions in sediments below. Some specific motions in this "boundary" category include confinement of land run-off, coastal waters penetrating into estuaries, coastal upwelling, inshore movements of oceanic water (indrafting), poleward movement of warm surface waters, mixing of warm and cold waters to form ecotone or transitional environments, offsetting of coastal waters above shelf breaks, and others. An attempt was made in the text to identify how several of these various motions have influenced special aspects of species distributions in sediments.

In accordance with the development of inshore—offshore and latitudinal trends in distribution, modern cyst-based taxa can be classified "ecologically" into species-groups which resemble the classical "plankton elements". It is possible to recognize temperate—estuarine, tropical—subtropical estuarine and tropical—subtropical oceanic groups of species which include some with restricted distributions, and estuarine, neritic, estuarine—neritic, and neritic—oceanic species-groups which solely comprise more cosmopolitan taxa. Commonly seen extant cyst-based taxa are classified into these groups and eleven species associations were classified in parallel fashion in the main text.

It is suggested that evolution of "plankton element" species-groups is consistent with some quasi-theoretical concepts which are developed as a class of stability—predictability hypotheses in contemporary ecologic work. These concepts have not been applied very extensively to plankton biogeography but an attempt is made to show their relevance. This is, that water types can be interpreted as comprising unique series of hydrographic climates, each of which has its own particular stability, predictability and severity characteristics as innate properties. Following this interpretation, it is possible to discern that there is a predominant and "predicted" tendency for planktonic organisms to show adaptive specialization towards the most stable and predictable sectors of marine surface water environments (which are not so extreme (severe) to be abiotic).

This notion can be adopted as a working hypothesis to interpret the essential features of environmental adaptations among living cyst-based dinoflagellates. The conclusion which emerges from this is that living *fossilizable* dinoflagellates (in contrast to the group as a whole), mainly are biologic adaptations to the unstable and often unpredictable class of marine climates which typify shallow-water environments along continental margins and around oceanic island archipelagos. However, within this total framework, there is the omnipresent tendency for individual species to be adapted selectively to relatively stable sectors of environment and this is shown by the localization of the more stenotopic cyst-based taxa within the terminal or subterminal sectors of temperature and salinity regimes. Species which show this type of localization are those of greatest interest from paleoecological and paleoenvironmental viewpoints and often these species also are the most distinctive morphologically. Their counterparts in older sediments thus should be of particular concern in future paleoecological work with fossil dinoflagellates.

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Appendix I

Factor scores for ten varimax factors identified from a *Q*-mode factor analysis of the data listed in Appendix III. These values indicate the taxonomic compositions of the Varimax Factor assemblages which are expressed in Appendix II. The coding of the 27 species used in this analysis in Appendices I—III is as follows:

1 = *Spiniferites bulloideus*; 2 = *Spiniferites ramosus*; 3 = *Spiniferites mirabilis*; 4 = *Spiniferites scabratus*; 5 = *Spiniferites elongatus*; 6 = *Nematosphaeropsis balcombiana*; 7 = *Leptodinium aculeatum*; 8 = *Leptodinium paradoxum*; 9 = *Leptodinium sphaericum*; 10 = *Leptodinium patulum*; 11 = *Leptodinium strialatum*; 12 = *Tectatodinium pellitum*; 13 = *Operculodinium centrocarpum*; 14 = *Operculodinium israelianum*; 15 = *Hemicystodinium zoharyi*; 16 = *Lingulodinium machaerophorum*; 17 = grouped *Peridinium* species; 18 = *Peridinium conicum*; 19 = *Peridinium subinerme*; 20 = *Peridinium* sp. cf. *leonis*; 21 = *Peridinium pentagonum*; 22 = *Peridinium* sp. cf. *pentagonum*; 23 = Form A; 24 = species similar to Form A; 25 = *Peridinium? americanum*; 26 = Form C, *Peridinium* sp. cf. *excentricum*; 27 = *Tuberculodinium vancampoae.*

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VARIMAX FACTOR SCORE MATRIX

   VAR.        1      2      3      4      5      6      7      8      9     10


     1       .042   .990   .025  -.024  -.037   .026  -.006  -.052   .022   .021
     2       .032  -.020   .004   .004   .437   .024  -.046  -.143   .860   .025
     3       .012   .077   .025   .006  -.014   .046  -.015  -.019   .042  -.146
     4       .026   .029  -.017   .006   .004  -.001  -.012   .047  -.093  -.043
     5       .023   .007   .016   .002  -.008  -.000  -.022   .026   .159  -.152
     6       .041   .007  -.002  -.021   .002   .035   .977   .011   .049  -.010
     7      -.049  -.023   .006   .005  -.023   .952  -.048   .007  -.020   .016
     8      -.005  -.006   .004  -.000  -.007   .160   .001   .008   .005   .001
     9       .020  -.019   .011  -.007  -.008   .115   .148   .022   .041  -.015
```

VAR.	1	2	3	4	5	6	7	8	9	10
10	-.009	-.011	.004	.002	-.010	.184	-.001	.017	.009	.008
11	-.007	-.006	.003	.002	-.010	.116	-.011	.014	.010	.004
12	.026	-.006	.011	.000	-.004	-.007	.122	.004	-.005	-.027
13	.994	-.041	-.003	.019	.006	.044	-.045	.021	-.040	.024
14	-.013	.031	-.003	.018	-.054	-.008	-.017	.928	.129	.012
15	-.016	.023	.013	.999	-.017	-.005	.022	-.017	.005	-.003
16	-.023	.053	-.013	.017	.895	.020	.021	.115	-.412	-.018
17	.002	-.028	.997	-.012	.011	-.009	.001	-.006	-.021	-.009
18	.001	.044	.036	-.009	.024	-.019	-.016	.266	.125	-.067
19	-.004	.007	.008	-.001	.020	-.001	-.001	.026	.053	.018
20	-.009	.011	.018	-.007	.008	-.005	-.010	.149	.093	.060
21	.012	-.004	-.004	.000	.011	-.002	-.008	-.001	.010	.004
22	-.000	.001	.000	-.000	-.000	-.000	-.000	.000	.001	-.001
23	-.011	.001	.028	-.001	-.003	.002	-.008	-.007	-.014	-.010
24	-.018	.000	.017	.004	.003	-.012	.013	.011	.003	.968
25	-.007	.004	.015	-.001	-.003	.001	-.003	-.002	-.004	-.006
26	-.012	.005	.025	-.002	-.005	.001	-.007	-.011	-.016	-.016
27	-.009	.042	.005	.003	-.015	-.010	.003	.054	.057	-.071

Appendix II

Factor loading values for ten varimax factors identified in a *Q*-mode factor analysis of the data in Appendix III. Values indicate the Varimax Factor assemblage compositions of 141 samples which were treated quantitatively. Samples are identified in Table I and section 3 in the text.

VARIMAX FACTOR MATRIX

		COMM.	1	2	3	4	5	6	7	8	9	10
1	001	.9962	.9663	.1711	.1642	.0108	.0006	.0462	-.0460	.0220	-.0299	.0205
2	002	.9931	.8113	.3537	.4514	-.0002	.0239	.0419	-.0432	.0128	.0386	.0123
3	003	.3763	.3374	.1787	.4148	-.0020	.0322	.0155	-.0387	.0234	.2021	-.1198
4	004	.9971	.0631	-.0025	.9962	-.0113	.0108	-.0055	-.0028	.0063	-.0157	-.0135
5	005	.9918	.7528	.0797	.6450	.0026	.0169	.0303	-.0188	.0314	-.0099	.0056
6	006	.9781	.8437	.2108	.4662	.0033	.0114	.0405	-.0261	.0447	.0097	-.0064
7	007	.9919	.7868	.0607	.6043	.0055	.0072	.0350	-.0384	.0241	-.0267	-.0057
8	008	.9953	.8467	.1457	.5026	.0058	.0028	.0407	-.0406	.0128	-.0319	.0049
9	010	.9957	.3959	.2706	.8743	-.0104	-.0006	.0179	-.0194	-.0099	-.0186	.0014
10	011	.9784	.8275	.5372	.0396	.0009	-.0167	.0514	-.0188	-.0026	.0118	.0012
11	012	.9968	.8517	.3564	.3745	.0017	.0026	.0450	-.0436	.0106	.0025	.0103
12	013	.9953	.2241	.0955	.9668	-.0102	.0200	.0037	-.0111	.0067	-.0174	-.0123
13	014	.9954	.7035	.6000	.3625	-.0078	.0489	.0483	.0647	.0028	-.0103	.0108
14	015	.9967	.5616	.4009	.7206	-.0088	-.0064	.0324	-.0090	.0006	-.0039	-.0088
15	016	.9938	.4672	.8633	.1609	-.0155	-.0215	.0420	-.0114	-.0276	.0226	.0204
16	017	.9921	.4867	.8604	.1041	-.0131	.0061	.0442	-.0285	-.0252	.0185	.0094
17	018	.9957	.7789	.6003	.1544	-.0021	-.0188	.0527	-.0362	-.0134	-.0065	.0084
18	019	.9967	.3034	.1943	.9300	.0205	.0038	.0123	.0335	.0082	-.0122	-.0050
19	021	.9979	.9469	.1911	.1908	.1496	.0100	.0462	-.0412	.0064	-.0393	.0209
20	022	.9961	.4989	.3508	.7883	.0279	.0116	.0270	-.0242	-.0076	-.0228	.0012
21	023	.9900	.5516	.6512	.4995	.1015	-.0175	.0377	-.0027	-.0053	.0081	.0060
22	024	.9963	.3286	.5512	.7247	.1724	.1331	.0308	.0837	.0049	-.0612	-.0110
23	025	.9984	.9021	.0393	.4216	.0100	.0065	.0385	-.0418	.0160	-.0385	.0147
24	026	.9953	.1041	.9307	.2244	.1308	.0717	.0374	.2095	-.0153	-.0092	-.0060
25	027	.9956	.2696	.9480	.1327	.0404	.0140	.0380	.0443	-.0304	.0158	.0149
26	028	.9948	.0370	.9620	.1166	.2149	.0656	.0315	.0511	-.0058	-.0073	-.0112
27	029	.9971	.1457	.9738	.1515	.0144	-.0085	.0321	-.0126	.0502	.0234	.0044
28	033	.9715	.0545	.9336	.0601	.0842	.0869	.0282	.0276	.2776	-.0078	-.0058
29	034	.9910	.1518	.8069	.5094	-.0184	.2275	.0294	-.0088	.0247	-.0593	-.0145
30	036	.9970	.0875	.9752	.1081	.0133	.1439	.0339	.0291	-.0220	-.0571	.0075
31	038	.9905	.1543	.5024	.3741	-.0036	.1011	.0296	.0064	-.0147	.0304	.0012
32	039	.9614	.0576	.9505	.2082	-.0241	.0734	.0272	-.0121	.0180	.0631	-.0138
33	040	.9760	.1139	.8508	.3639	.0268	.2981	.0290	.0180	.0322	-.1216	-.0159
34	042	.9772	.0585	.8994	.3602	.0887	.1300	.0321	.0572	.0545	.0491	-.0262
35	043	.9955	.8386	.0547	.5305	.0051	.0131	.0584	.0616	.0102	-.0162	.0087
36	044	.9950	.1816	.0981	.9755	-.0117	.0208	.0017	-.0100	.0065	.0098	-.0060
37	045	.9962	.4370	.0648	.8944	-.0049	.0220	.0140	-.0198	.0028	-.0051	.0027
38	046	.9967	.2699	.0741	.9574	-.0089	.0291	.0072	-.0136	.0035	.0216	-.0074
39	047	.9975	.3604	.0039	.9308	-.0053	.0114	.0096	-.0147	.0073	-.0275	-.0026
40	048	.9988	.9662	.1595	.1750	.0098	.0126	.0751	.0465	.0272	.0025	.0179
41	049	.9973	.9537	.1633	.2133	.0076	.0143	.0747	.0958	.0139	.0084	.0143
42	050	.9779	.8589	.0949	.4132	.0020	.0049	.0658	.2355	.0153	-.0170	.0049
43	051	.9977	.7788	.2551	.5680	.0011	.0148	.0401	-.0380	.0022	.0127	-.0014
44	052	.9944	.6860	.1747	.7004	.0000	.0118	.0338	-.0343	.0049	-.0108	-.0056
45	053	.9935	.6576	.1769	.7263	-.0010	.0104	.0325	-.0310	.0040	-.0117	-.0043
46	054	.9963	.1719	.1742	.9674	-.0128	.0092	.0079	-.0079	-.0120	-.0051	-.0097
47	055	.9916	.4399	.1330	.8827	-.0056	.0121	.0208	-.0209	.0008	-.0095	-.0135
48	056	.9957	.4550	.0595	.8854	-.0044	.0083	.0195	-.0040	.0112	-.0235	-.0104
49	057	.9910	.3750	.0596	.9044	-.0091	.0310	.0258	.1636	.0078	-.0037	-.0182
50	058	.9970	.8975	.2085	.3574	.0031	.0153	.0633	.1250	.0096	.0203	.0021

		COMM.	1	2	3	4	5	6	7	8	9	10
51	059	.9918	.8809	.1242	.2914	.0016	.0014	.0860	.3283	.0145	-.0105	-.0016
52	060	.9633	.7256	.0895	.5948	-.0035	.0130	.0822	.2599	.0219	.0109	-.0044
53	061	.9977	.6571	.1780	.7258	-.0009	.0426	.0326	-.0365	-.0057	.0558	-.0025
54	062	.9803	.8380	.1508	.4952	.0063	.0498	.0501	-.0251	-.0078	.0667	-.0051
55	063	.9921	.6955	.1706	.6628	-.0054	.0129	.0543	.1901	.0231	.0110	-.0033
56	065	.9931	.7465	.1676	.6030	-.0034	.0105	.0565	.2016	.0085	.0030	-.0001
57	066	.9839	.8029	.0554	.5208	.0001	.0074	.0659	.2446	.0207	-.0152	.0006
58	068	.9972	.8408	.1664	.5096	.0043	.0171	.0469	-.0138	.0013	-.0004	.0134
59	069	.9978	.8452	.1290	.4756	.0009	.0216	.0593	.1905	.0112	.0127	.0079
60	070	.9929	.4928	.0935	.8323	-.0092	.0231	.0605	.2095	.0050	.0205	-.0014
61	071	.9803	.8187	.0974	.4887	-.0001	.0318	.0892	.2253	.0169	.0416	.0028
62	072	.9130	.7916	.1416	.4121	-.0011	.0597	.1132	.2583	-.0047	.1161	-.0006
63	073	.9924	-.0126	.3682	.0035	.3172	.7787	.0225	.0202	.1846	-.3382	-.0181
64	074	.9998	-.0141	.0687	.0140	.9968	.0104	-.0026	.0213	-.0095	.0180	-.0031
65	075	.9996	-.0031	.0978	.0138	.9940	.0331	-.0017	.0222	.0092	-.0140	-.0018
66	076	.9995	.0734	.1095	.0144	.9897	.0417	.0031	.0183	-.0138	-.0099	-.0011
67	077	.9996	-.0160	.0336	.0130	.9986	-.0080	-.0047	.0226	-.0152	.0013	-.0026
68	078	.9996	-.0154	.0431	.0134	.9981	-.0175	-.0046	.0224	-.0178	.0056	-.0023
69	079	.9996	.0025	.1908	.0164	.9803	.0388	.0019	.0209	-.0077	-.0047	-.0015
70	080	.9987	.0007	.1341	.0429	.9767	.1539	.0042	.0232	.0056	-.0232	-.0101
71	082	.9780	.2769	.8339	.0228	.4088	.1755	.0407	-.0077	.0236	-.0716	-.0067
72	083	.9754	.3322	.8514	.0206	.2943	.2106	.0419	-.0048	.0495	-.0671	.0026
73	084	.9783	.5203	.8120	.0182	.1687	.1153	.0475	-.0002	.0246	-.0566	.0122
74	085	.9928	.8956	.4086	.0091	.0712	-.0054	.0496	-.0432	.1132	-.0156	.0318
75	086	.9957	.9559	.2671	.0051	.0117	-.0095	.0493	-.0461	.0668	-.0227	.0303
76	087	.9948	.2223	.9683	.0250	-.0190	-.0007	.0377	-.0178	-.0398	.0564	.0163
77	088	.9935	.4457	.8490	.0263	.1900	.0777	.1743	-.0065	-.0172	.0205	.0116
78	089	.9932	.1959	.9487	.0285	-.0179	-.0130	.2220	-.0212	-.0479	.0374	.0071
79	091	.9134	-.0074	.3338	.0904	.0058	.3239	-.0007	-.0164	.8287	.0418	-.0077
80	092	.9919	.1612	.9671	.0712	.1046	.0999	.0431	-.0093	-.0445	.0194	.0176
81	102	.9929	.6725	.7306	.0184	-.0048	-.0044	.0492	-.0360	-.0286	.0321	.0317
82	103	.9935	-.0144	.1194	.0344	.9839	-.0260	-.0049	.0198	.0887	.0290	-.0069
83	105	.9922	-.0222	.1867	.0128	.3753	.7993	.0191	.0390	.2279	-.3504	-.0166
84	106	.9191	.0134	.1194	.0286	.1053	.3205	.0031	-.0055	.8873	-.0520	.0008
85	110	.9872	.2034	.7275	.1690	.4752	.2381	.0235	-.0040	.3174	-.0644	-.0006
86	111	.9831	.0979	.8126	.0296	-.0032	.5034	.0363	-.0060	.2080	-.1199	.0053
87	113	.9786	.0390	.3370	.2325	-.0050	.6332	.0362	.0810	-.0625	.6295	.0199
88	114	.9994	.0162	.1656	.0114	.0132	.9835	.0321	.0277	.0474	.0126	-.0032
89	115	.9955	.0086	.2181	.0317	.0125	.9618	.0342	.0065	.0153	.1419	.0057
90	116	.9969	.0079	.1595	.0125	.0125	.9695	.0329	.0040	.0127	.1729	.0002
91	117	.9963	.0100	.1894	.0546	.0099	.9479	.0318	.0017	.0231	.2390	-.0024
92	118	.9717	.0179	.4673	.1417	-.0011	.8429	.0330	.0526	.0706	.1167	-.0040
93	119	.9961	.0043	.0322	.9972	-.0132	.0085	-.0074	.0004	-.0070	-.0181	-.0069
94	120	.9967	.0052	.0579	.9964	-.0141	.0087	-.0074	-.0003	.0023	-.0114	-.0069
95	121	.6876	.0037	.2298	.7957	-.0164	-.0042	.0008	-.0061	-.0246	-.0218	-.0122
96	122	.9834	.0244	.5317	.8354	-.0237	-.0119	.0083	.0151	-.0341	-.0040	.0025
97	123	.9627	.0008	-.0008	.9807	-.0122	.0092	-.0077	-.0008	-.0078	-.0214	-.0097
98	124	.8778	.5928	.1675	.6987	.0664	.0028	.0289	.0621	.0112	-.0298	-.0037
99	125	.9942	.6149	.1916	.7592	-.0015	.0024	.0263	-.0287	-.0043	-.0358	.0124
100	126	.9956	.0050	.0475	.9963	-.0138	.0078	-.0071	.0004	-.0027	-.0168	-.0090
101	127	.9524	.0095	.2258	.9491	-.0183	.0014	-.0028	-.0040	.0084	-.0039	-.0015
102	128	.9957	.0145	-.0057	.9975	-.0006	.0146	-.0059	-.0001	-.0078	-.0117	-.0084
103	129	.9927	.0436	.0244	.9946	-.0132	.0095	-.0054	.0229	.0053	-.0111	-.0033
104	130	.9968	.5430	.8328	.0371	-.0108	-.0095	.0505	-.0277	-.0397	.0384	.0207
105	131	.9980	.8826	.4501	.1091	.0034	-.0057	.0567	-.0235	-.0073	-.0123	.0208
106	132	.9980	.9414	.3230	.0374	.0083	.0246	.0560	-.0169	-.0073	.0355	.0255
107	133	.9960	.9605	.1899	.0878	.0093	.0695	.0619	.0818	-.0142	.1164	.0213
108	134	.9970	.8906	.4394	.0752	.0045	.0077	.0578	-.0280	-.0136	.0184	.0191
109	135	.9976	.9888	.1118	.0296	.0143	.0364	.0551	-.0081	.0020	.0369	.0211
110	136	.9960	.9920	.0738	.0134	.0137	.0073	.0502	.0531	.0150	-.0152	.0198
111	137	.9804	.9779	.1076	.0923	.0125	.0056	.0464	-.0031	.0249	-.0256	.0209
112	138	.9943	.9774	.1361	.1207	.0120	.0353	.0476	-.0034	.0288	-.0286	.0213
113	139	.9816	.9585	.2377	.0210	.0114	.0380	.0513	-.0329	.0128	-.0091	.0205
114	140	.9971	.9784	.1784	.0027	.0135	.0194	.0491	-.0451	.0120	-.0445	.0279
115	141	.9862	.3252	.1639	.1526	.0005	.0812	.0978	.9021	.0209	-.0023	-.0083
116	142	.9735	.2434	.2593	.0165	.0036	.0486	.9120	-.0333	-.0186	.1048	.0140
117	143	.9907	.1772	.9001	.0617	.0043	.2462	.2530	.1414	-.0206	-.0090	.0113
118	144	.9842	.7593	.2767	.4141	.0894	.1890	.2820	.1178	-.0151	.1492	-.0037
119	145	.9561	.0347	.0302	.0032	.3271	.0738	.2905	.8700	.0166	.0011	-.0067
120	146	.9809	.1869	.4595	.0404	.0192	.0937	.8485	.0482	.0012	-.0412	.0068
121	148	.9578	.3413	.1645	.0098	.0074	.0781	.8984	.0133	.0036	.0129	.0215
122	149	.9654	.0667	.1588	.0095	.0057	.1139	.9563	.0416	.0212	-.0755	.0125
123	150	.9964	.3833	.8373	.0370	.0331	.3248	.1830	-.0056	-.0031	-.0810	.0153
124	151	.9885	.0051	.1144	-.0101	.0166	.9005	.0244	.0174	.1086	-.3884	-.0206
125	152	.9971	.8441	.0542	.5260	.0072	.0066	.0350	-.0383	.0093	-.0426	.0181
126	153	.6706	.0150	-.0304	.0113	.0027	-.0277	.8138	.0713	.0294	.0108	.0113
127	154	.9935	.0215	.8366	.1123	-.0112	.4841	.0328	.0052	.0423	-.2077	-.0013
128	155	.9628	-.0348	.0309	.0116	-.0001	-.0297	.9719	.1205	.0178	.0049	.0108
129	156	.8043	.5046	.7122	.1785	-.0093	-.0216	.0412	-.0271	.0534	.0579	-.0365
130	157	.9542	.3176	.8201	.3346	-.0151	.1041	.0484	-.0322	-.0552	.2255	-.0217
131	158	.5702	.7427	.0068	-.0125	.0190	.0355	.0479	-.0271	.0551	-.1027	-.0122
132	159	.9890	.1475	.5051	.5527	-.0143	-.0104	.0066	-.0009	-.0097	.0035	.6372
133	160	.9952	.4485	.2746	.7623	-.0099	.0020	.0200	.1042	.0099	-.0082	.3550
134	161	.9952	.8851	.4474	.0098	.0024	.0008	.0553	.0775	-.0037	-.0242	.0440
135	162	.9969	.9327	.3361	.0224	.0054	-.0078	.0554	.0907	.0011	-.0204	.0404
136	163	.9951	.9807	.0950	.0416	.0109	.0019	.0558	.1301	.0153	-.0271	.0375
137	164	.9937	.2298	.7948	.0298	-.0139	-.0264	.0235	-.0074	-.0256	.0160	.5531
138	165	.9977	.7671	.6285	.0626	-.0023	-.0190	.0494	-.0384	-.0098	-.0160	.0723
139	166	.9942	.9076	.3987	.0682	.0061	-.0033	.0505	-.0445	-.0013	-.0224	.0412
140	167	.9969	.9663	.2381	.0170	.0115	.0014	.0511	-.0446	.0072	-.0268	.0263
141	168	.9980	.9931	.0841	.0130	.0153	.0063	.0494	-.0217	.0131	-.0258	.0224
		VARIANCE	32.778	21.215	22.807	6.330	5.890	3.864	1.730	1.336	.886	.629
		CUM. VAR	32.778	53.993	76.800	83.130	89.021	92.885	94.615	95.952	96.838	97.468

Appendix III

Species percentage compositions of 141 assemblages for the 27 most common taxa which were selected from 86 in the raw data and used in the *Q*-mode factor analysis. The taxa are numbered as in Appendix I and details of sample locations were given in Table I.

			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
	SAMPLE	TOTAL	SBUL	SFUR	SMIR	SCRA	SH49	NBAL	LACU	LPAR	LSPH	LPAT	LSTR	TPEL	BCEN	BISR	MZBM	LING	PROB	PMM6	PM30	PM31	PM66	PM77	P106	P06C	P110	P115	TUBE
1	001	80.	15.0	.0	1.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	67.5	.0	.0	.0	11.2	3.7	.0	.0	1.2	.0	.0	.0	.0	.0	.0
2	002	88.	21.6	3.4	1.1	.0	1.1	.0	.0	.0	.0	.0	.0	.0	43.2	.0	.0	.0	23.9	5.7	.0	.0	.0	.0	.0	.0	.0	.0	.0
3	003	87.	10.3	4.6	.0	.0	43.7	.0	.0	.0	.0	.0	.0	.0	16.1	.0	.0	.0	20.7	3.4	.0	1.1	.0	.0	.0	.0	.0	.0	.0
4	004	97.	2.1	.0	2.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	5.2	.0	.0	.0	86.6	4.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
5	005	94.	7.4	1.1	1.1	.0	.0	1.1	.0	.0	.0	.0	.0	.0	44.7	.0	.0	.0	38.3	6.4	.0	.0	.0	.0	.0	.0	.0	.0	.0
6	006	98.	13.3	1.0	4.1	.0	2.0	1.0	.0	.0	.0	.0	.0	.0	44.9	.0	.0	.0	24.5	9.2	.0	.0	.0	.0	.0	.0	.0	.0	.0
7	007	100.	6.0	.0	6.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	47.0	.0	.0	.0	36.0	4.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
8	008	96.	11.4	.0	5.2	.0	.1	.0	.0	.0	.0	.0	.0	.0	51.0	.0	.0	.0	30.2	2.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
9	C10	94.	19.1	.0	1.1	.0	2.1	.0	.0	.0	.0	.0	.0	.0	23.4	.0	.0	.0	53.2	.0	.0	1.1	.0	.0	.0	.0	.0	.0	.0
10	011	72.	34.6	.1	1.4	.0	9.7	1.4	.0	.0	.0	.0	.0	1.4	48.5	.0	.0	.0	1.4	1.4	.0	.1	.0	.0	.0	.0	.0	.0	.0
11	012	99.	22.2	1.0	2.0	.0	3.0	.0	.0	.0	.0	.0	.0	.0	46.5	.0	.0	.0	20.2	3.0	1.0	1.0	.0	.0	.0	.0	.0	.0	.0
12	013	99.	9.1	.0	.0	.0	4.0	.0	.0	.0	.0	.0	.0	.0	15.2	.0	.0	1.0	67.7	3.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
13	014	97.	32.0	1.0	1.0	1.0	2.1	5.2	.0	.0	.0	.0	.0	.0	34.0	.0	.0	3.1	17.5	3.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
14	015	93.	22.6	.0	4.3	.0	3.2	1.1	.0	.0	.0	.0	.0	.0	28.0	.0	.0	.0	36.6	2.2	.0	1.1	.0	.0	.0	.0	.0	.0	1.1
15	016	102.	56.9	1.0	1.0	.0	1.0	1.0	.0	.0	.0	.0	.0	.0	27.5	.0	.0	.0	8.8	2.9	.0	.0	.0	.0	.0	.0	.0	.0	.0
16	017	100.	55.0	1.0	2.0	.0	5.0	.0	.0	.0	.0	.0	.0	.0	28.0	.0	.0	2.0	5.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
17	018	101.	36.6	.0	5.9	.0	2.0	.0	.0	.0	.0	.0	.0	2.0	43.6	.0	.0	.0	7.9	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
18	019	101.	13.9	.0	2.0	.0	.0	3.0	.0	.0	.0	.0	.0	.0	17.8	.0	2.0	.0	56.4	4.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0
19	021	100.	15.0	.0	1.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	61.0	.0	9.0	1.0	12.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
20	022	99.	21.2	.0	3.0	.0	2.0	.0	.0	.0	.0	.0	.0	.0	26.3	.0	2.0	1.0	42.4	.0	.0	2.0	.0	.0	.0	.0	.0	.0	.0
21	023	93.	32.2	.0	2.1	1.1	3.2	1.1	.0	.0	.0	.0	.0	1.1	24.7	.0	5.4	.1	22.6	1.1	.0	4.3	.0	.0	.0	.0	.0	.0	1.1
22	024	96.	25.0	.0	4.2	.0	1.0	4.2	.0	.0	.0	.0	.0	1.0	13.5	.0	8.3	7.3	31.3	2.1	.0	1.0	1.0	.0	.0	.0	.0	.0	.0
23	025	100.	6.0	.0	1.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	62.0	.0	.0	.0	29.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
24	C26	95.	49.5	.0	5.3	.0	.0	11.6	.0	.0	.0	.0	.0	1.1	3.2	.0	8.4	6.3	10.5	4.2	.0	.0	.0	.0	.0	.0	.0	.0	.0
25	027	103.	61.2	1.0	1.9	.0	.0	3.9	.0	.0	.0	.0	.0	.0	14.6	.0	3.9	2.9	6.8	2.9	.0	.0	.0	.0	.0	.0	.0	.0	1.0
26	028	101.	55.4	.0	7.9	.0	.0	3.0	.0	.0	.0	.0	.0	1.0	.0	1.0	13.9	6.9	5.0	4.0	.0	.0	.0	.0	.0	.0	.0	.0	2.0
27	029	86.	64.0	.0	5.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	7.0	5.8	2.3	2.3	8.1	3.5	.0	.0	.0	.0	.0	.0	.0	.0	1.2
28	033	99.	47.5	.0	4.0	9.1	.0	2.0	.0	.0	.0	.0	.0	.0	1.0	16.2	5.1	8.1	2.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	3.0
29	034	84.	39.3	1.2	4.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	6.0	.0	.0	13.1	23.8	6.0	1.2	1.2	.0	.0	.0	.0	.0	.0	3.6
30	036	88.	65.9	.0	3.4	.0	.0	2.3	.0	.0	.0	.0	.0	.0	3.4	.0	2.3	13.6	5.7	1.1	1.1	.0	.0	.0	.0	.0	.0	.0	1.1
31	C38	96.	49.0	3.1	2.1	.0	.0	1.0	.0	.0	.0	.0	.0	.0	6.3	.0	1.0	6.3	18.8	4.2	3.1	.0	.0	.0	.0	.0	.0	.0	5.2
32	039	97.	55.7	3.1	6.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0	.0	.0	5.2	10.3	14.4	2.1	.0	.0	1.0	.0	.0	.0	.0	1.0
33	040	96.	40.6	.0	2.1	2.1	.0	1.0	.0	.0	.0	.0	.0	.0	4.2	.0	2.1	17.7	16.7	4.2	1.0	.0	.0	.0	.0	.0	.0	.0	8.3
34	042	98.	40.8	3.1	8.2	.0	.0	3.1	.0	.0	.0	.0	.0	.0	1.0	3.1	5.1	7.1	15.3	4.1	1.0	1.0	.0	.0	.0	.0	.0	.0	7.1
35	043	100.	6.0	1.0	.1	.1	2.0	5.0	1.0	.1	2.0	.0	.0	5.0	47.2	.0	.0	.0	30.1	.1	.0	.0	.1	.0	.0	.0	.0	.0	.1
36	044	95.	9.5	2.1	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	12.6	.0	.0	.0	70.5	5.3	.0	.0	.0	.0	.0	.0	.0	.0	.0
37	045	98.	7.1	2.0	.1	1.0	.0	.1	.0	.0	.0	.0	.0	.0	28.5	.0	.0	.0	59.1	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
38	046	95.	7.4	3.2	2.1	.0	.1	.1	.0	.0	.0	.0	.0	.0	17.9	.0	.0	.0	65.1	4.2	.0	.0	.0	.0	.0	.0	.0	.0	.0
39	047	96.	3.1	.1	1.0	.1	.0	.1	.0	.0	.0	.0	.0	.1	25.9	.0	.0	.0	67.4	2.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
40	048	98.	12.2	2.0	1.0	1.0	1.0	5.1	1.0	1.0	2.0	1.0	.0	3.1	57.1	1.0	.0	.0	10.2	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
41	049	99.	12.1	2.0	.0	1.0	3.0	8.1	1.0	1.0	1.0	1.0	.1	2.0	54.4	.1	.0	.0	12.1	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
42	C50	99.	7.1	.1	.0	.1	2.0	12.2	.1	3.0	4.1	.1	.0	9.1	41.6	.0	.0	.1	20.3	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
43	051	99.	16.1	2.0	4.0	.0	3.0	.0	.0	.0	.1	.0	.0	1.0	41.3	.0	.0	.0	30.2	2.0	.1	.0	.0	.0	.0	.0	.0	.0	.0
44	052	99.	12.1	1.0	6.0	.1	1.0	.0	.0	.0	.0	.0	.0	.1	38.2	.0	.0	.1	39.2	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.1
45	053	97.	12.3	1.0	6.2	.1	.1	.1	.0	.0	.0	.0	.0	.1	36.9	.0	.0	.0	41.0	2.1	.0	.1	.0	.0	.0	.0	.0	.0	.0
46	054	97.	14.4	1.0	4.1	.0	.1	.1	.1	.0	.0	.0	.0	.0	11.3	.0	.0	.0	67.7	1.0	.1	.0	.0	.0	.0	.0	.0	.0	.1
47	055	100.	10.0	1.0	7.0	1.0	.1	.1	.0	.0	.1	.0	.0	.0	25.9	.0	.0	.0	52.8	2.0	.0	.1	.0	.0	.0	.0	.0	.0	.0
48	056	99.	6.0	.0	5.0	.1	.1	1.0	.0	.0	1.0	.0	.0	.0	28.2	.0	.0	.0	55.4	3.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
49	057	97.	5.1	1.0	6.2	.0	.1	10.3	.0	.0	2.1	.0	.0	.1	20.6	.0	.0	1.0	51.4	2.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
50	C58	102.	12.7	2.0	2.0	1.0	2.9	7.8	.1	1.0	3.9	.0	.0	2.9	44.1	.0	.0	.0	17.6	1.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0
51	059	98.	8.1	.0	4.1	.0	1.0	17.3	1.0	.1	5.1	.0	.0	6.1	42.6	.0	.0	.1	14.2	.1	.1	.0	.1	.0	.0	.0	.0	.0	.0
52	060	97.	6.2	1.0	1.0	.0	1.0	11.3	1.0	.0	9.3	.1	.0	8.2	31.9	.0	.0	.0	26.7	2.1	.1	.0	.0	.0	.0	.0	.0	.0	.0
53	061	99.	12.1	5.0	4.0	.1	2.0	.0	.0	.0	.0	.0	.0	.0	35.3	.0	.0	.0	39.4	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
54	062	99.	10.1	6.0	9.1	1.0	.1	1.0	.0	.1	1.0	.0	.0	.1	44.3	.0	.0	.0	26.2	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
55	063	99.	10.1	1.0	3.0	.0	.1	10.1	.0	1.0	5.0	.1	.0	1.0	32.3	.0	.0	.0	31.3	4.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
56	065	98.	10.2	1.0	2.0	.1	1.0	10.2	.0	1.0	5.1	.0	.0	5.1	34.6	.0	.0	.0	28.5	1.0	.0	.0	.1	.0	.0	.0	.0	.0	.0
57	066	99.	5.0	.1	1.0	.1	1.0	12.1	.1	2.0	7.0	.0	.0	7.0	38.2	.0	.0	.1	25.2	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
58	C68	99.	12.1	2.0	1.0	.0	1.0	1.0	.0	.0	2.0	1.0	.0	2.0	46.5	.0	.0	.0	28.3	.0	1.0	.0	1.0	.0	.0	.0	.0	.0	1.0
59	C69	99.	9.0	2.0	1.0	1.0	1.0	11.1	.1	.1	5.0	.0	.1	2.0	42.2	.0	.0	.1	24.1	1.0	.0	.0	.1	.0	.0	.0	.0	.0	.0
60	070	100.	7.0	2.0	.0	1.0	1.0	11.0	1.0	1.0	6.0	.0	.0	2.0	24.0	.0	.0	.0	42.0	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
61	C71	102.	6.8	2.9	1.0	.0	1.0	10.8	1.0	1.0	8.8	.0	.0	4.9	37.2	.0	.0	.1	22.5	2.0	.1	.0	.0	.0	.0	.0	.0	.0	.0
62	072	100.	8.0	6.0	2.0	1.0	1.0	10.0	1.0	1.0	14.0	.1	.1	7.0	31.9	.0	.0	.0	16.9	.0	.1	.0	.0	.0	.0	.0	.0	.0	.0
63	C73	100.	18.0	.0	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	5.0	18.0	52.0	.0	8.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
64	074	100.	4.0	2.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0	90.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
65	075	97.	6.2	.1	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0	2.1	85.4	5.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.C
66	076	102.	6.9	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	6.9	.0	78.4	4.9	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
67	C77	99.	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.1	97.9	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
68	C78	100.	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	98.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
69	079	99.	13.1	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0	1.0	77.7	5.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.1
70	080	98.	7.1	3.1	3.1	.0	.0	.0	.0	.0	.0	.0	.0	1.0	1.0	1.0	68.4	12.2	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0
71	C82	99.	39.4	1.0	6.1	8.1	.0	.0	.0	.0	.0	.0	.0	.0	12.1	2.0	20.2	11.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
72	083	98.	39.8	2.0	3.1	8.2	.0	.0	.0	.0	.0	.0	.0	3.1	14.3	3.1	14.3	12.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
73	084	101.	41.6	1.0	2.0	8.9	.0	1.0	.0	.0	.0	.0	.0	2.0	24.8	2.0	8.9	7.9	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
74	085	97.	28.9	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	57.7	8.2	4.1	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
75	086	99.	23.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	71.7	5.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
76	087	97.	73.2	4.1	4.1	3.1	.0	.0	.0	.0	.0	.0	.0	.0	13.4	1.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
77	088	101.	42.6	3.0	5.9	.0	.0	1.0	5.9	1.0	.0	1.0	2.0	1.0	20.8	1.0	9.9	5.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
78	089	99.	59.6	2.0	8.1	1.0	.0	.0	11.1	2.0	1.0	.0	3.0	1.0	10.1	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
79	091	99.	12.1	1.0	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	30.2	.0	17.1	3.0	21.2	3.0	12.1	.1	.0	.0	.0	.0	.0	.0
80	072	99.	63.6	4.0	2.0	.0	.0	.0	.0	2.0	.0	1.0	.0	.0	8.1	.0	8.1	8.1	3.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
81	102	96.	52.0	3.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	43.7	.0	.1	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
82	103	74.	6.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	8.1	74.3	.0	1.4	1.4	1.4	.0	.0	.0	.0	.0	.0	.0	6.8
83	105	102.	7.8	.0	1.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	8.8	22.5	56.9	1.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
84	106	100.	4.0	.0	.0	2.0	.0	.1	.0	.0	.0	.0	.0	.0	2.0	53.9	5.0	25.0	2.0	.0	.0	2.0	.0	.0	.0	.0	.0	.0	4.0
85	110	98.	29.5	.0	.1	2.0	.0	.0	.0	.0	.0	.0	.0	.0	8.1	12.2	20.3	13.2	6.1	8.1	.0	.1	.0	.0	.0	.0	.0	.0	.1
86	111	100.	42.0	5.0	1.0	6.0	.0	.0	.0	.0	.0	.0	.0	.0	4.0	11.0	.0	30.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
87	113	101.	16.8	41.6	.0	.0	.0	5.9	.0	.0	.0	.0	.0	.0	.0	1.0	.0	14.9	10.9	2.0	2.0	3.0	1.0	.0	.0	.0	.0	.0	1.0
88	114	101.	7.9	26.7	.0	.0	.0	2.0	.0	.0	.0	.0	.0	.0	1.0	.0	.0	55.4	1.0	2.0	2.0	1.0	1.0	.0	.0	.0	.0	.0	.0
89	115	99.	11.1	32.2	.1	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.1	.0	.1	48.3	2.0	.0	2.0	3.0	.0	.0	.0	.0	.0	.0	.0
90	116	98.	8.1	36.5	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.1	.0	.0	50.8	1.0	2.0	.1	.1	.1	.0	.0	.0	.0	.0	.1
91	117	101.	8.9	34.7	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	42.6	3.0	5.9	1.0	1.0	1.0	.0	.0	.0	.0	.0	1.0
92	118	101.	19.8	19.8	.0	.0	.0	3.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	33.7	5.9	9.9	4.0	3.0	1.0	.0	.0	.0	.0	.0	.0
93	119	92.	5.4	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	89.1	.0	1.1	1.1	.0	.0	3.3	.0	.0	.0	.0
94	120	42.	7.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	83.3	2.4	2.4	2.4	.0	.0	2.4	.0	.0	.0	.0
95	121	85.	14.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	43.5	.0	.1	.0	.0	.0	8.2	.0	2.4	31.7	.0
96	122	85.	35.2	.1	.0	.1	.0	1.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	51.6	.1	.0	.0	.0	.0	4.7	.0	5.9	1.2	.0
97	123	95.	2.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	77.8	.0	2.1	.0	.0	.0	16.8	.0	1.1	.1	.0
98	124	94.	9.6	.0	1.1	2.1	.0	2.1	.0	.0	.0	.0	2.1	17.0	26.5	.0	3.2	.1	31.8	1.1	1.1	1.1	.0	.0	1.1	.0	.0	.1	.0
99	125	91.	14.3	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	36.2	.0	.1	.0	45.0	.0	.0	.1	.0	.0	3.3	.0	.0	1.1	.0
100	126	67.	5.9	.0	.0	.1	.0	.1	.0	.0	.0	.0	.0	.0	.1	.0	.0	.0	78.6	1.5	.1	1.5	.0	.0	4.5	.0	3.0	4.5	.0

			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
SAMPLE		TOTAL	SBUL	SFUR	SMIR	SCRA	SH49	NBAL	LACU	LPAR	LSPH	LPAT	LSTR	TPEL	OCEN	DISR	HZOH	LING	PROB	PMM6	PH30	PH31	PH66	PH77	P106	P06C	P110	P115	TUBE
101	127	54.	14.8	.0	.0	1.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	55.5	1.8	.2	7.4	.0	.0	3.7	.0	11.1	3.7	.0
102	128	98.	2.0	1.0	.C	1.0	.0	.0	.0	1.0	.0	.0	.0	.0	1.0	.0	1.0	.0	88.8	.0	1.0	.0	.0	.0	2.0	.0	1.0	.0	.0
103	129	98.	4.1	.0	.0	.0	.0	2.0	.0	.0	.0	.0	.0	.0	3.1	.0	.0	.0	77.6	.0	2.0	6.1	.0	.0	2.0	.0	1.0	1.0	1.0
104	130	100.	55.9	3.0	4.0	2.0	.0	.1	.0	.0	1.0	.0	.0	.0	33.0	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
105	131	99.	30.3	1.0	3.C	3.0	.0	1.0	.0	.0	2.0	.0	.0	.0	53.5	.0	.0	.0	6.1	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
106	132	99.	24.2	5.0	2.0	2.0	.0	2.0	.0	.0	1.0	.0	.0	.0	61.6	.1	.0	.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
107	133	100.	14.0	10.0	3.0	1.0	.0	8.0	.0	.1	2.0	.0	.0	.0	56.9	.0	.0	.0	5.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
108	134	100.	30.0	3.0	5.0	1.0	.0	1.0	.0	.0	1.0	.1	.0	.0	54.9	.0	.0	.0	4.0	.0	.0	.C	.0	.0	.0	.0	.0	.0	.0
109	135	99.	11.1	6.1	3.0	2.0	.0	3.0	.1	.0	1.0	.0	.0	.0	71.6	.0	.0	.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
110	136	100.	9.0	1.0	.0	.0	3.0	8.0	.0	.0	.0	.0	.0	.0	77.0	.0	.0	.0	1.0	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0
111	137	97.	10.3	.1	.0	.0	1.0	3.1	.0	.0	.0	.0	.0	.0	66.9	.0	.0	.1	6.2	3.1	.0	.0	9.3	.0	.0	.0	.0	.0	.0
112	138	100.	12.0	1.0	.C	1.0	.0	3.0	.0	.0	.0	.0	.0	.0	66.0	.0	.0	2.0	8.0	4.0	.0	.0	3.0	.0	.0	.0	.0	.0	.0
113	139	100.	18.0	2.0	2.0	.0	1.0	1.0	.0	.0	.0	.0	.0	.0	62.0	.0	.0	2.0	1.0	2.0	.0	.0	9.0	.0	.0	.0	.0	.0	.0
114	140	50.	18.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	80.0	.0	.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
115	141	99.	9.1	.0	1.0	1.0	.0	49.5	2.0	.0	4.0	1.0	.0	2.0	15.2	.0	1.0	5.1	8.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0
116	142	97.	14.4	7.2	5.2	.0	.0	1.0	44.3	4.1	4.1	2.1	2.1	.0	13.4	.0	.0	1.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
117	143	100.	43.9	5.0	2.0	4.0	.0	8.0	10.0	3.0	1.0	.0	.1	.0	7.0	.0	1.0	13.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.1
118	144	94.	11.7	8.5	3.2	.0	4.2	6.4	7.4	2.1	1.1	4.2	1.1	.0	27.6	.0	3.2	4.2	14.9	.1	.0	.0	.0	.0	.0	.0	.0	.0	.1
119	145	87.	1.1	.0	.0	.0	.0	54.0	16.1	.0	.0	1.1	.0	.0	1.1	.0	20.7	5.7	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
120	146	96.	21.9	1.0	5.2	1.0	.0	4.2	37.5	5.2	3.1	3.1	.0	.0	9.4	.0	1.0	6.3	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
121	148	95.	10.5	4.2	2.1	.0	.0	4.2	47.4	5.3	.0	2.1	.0	.0	20.0	.0	.0	4.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
122	149	97.	10.3	.1	2.1	.0	.0	5.1	55.6	4.1	2.1	5.1	.0	.0	6.2	.0	.1	9.3	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
123	150	98.	42.7	4.1	2.0	3.1	.0	1.0	7.1	.1	.0	.1	.1	.0	18.3	.0	2.0	18.3	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
124	151	95.	5.3	2.1	3.2	.0	.0	.0	.0	.0	.0	.0	.0	.0	2.1	.0	.0	87.3	.0	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
125	152	14.	7.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	57.1	.0	.0	.0	35.7	.0	.0	.C	.0	.0	.0	.0	.0	.0	.0
126	153	102.	.0	.0	.0	.0	.0	2.9	27.5	12.7	12.7	18.6	22.5	1.0	2.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
127	154	34.	50.0	.0	2.9	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	35.3	5.9	2.9	.0	2.9	.0	.0	.0	.0	.0	.0	.0
128	155	100.	3.0	.0	1.0	.0	.0	7.0	45.0	11.0	11.0	17.0	5.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
129	156	62.	30.5	.0	9.6	.0	.0	.2	.0	.0	.0	.0	.0	.0	20.9	.0	.0	.2	6.4	6.4	1.6	6.4	.0	.0	.0	.0	.0	.0	17.7
130	157	71.	38.0	11.3	12.7	.0	.0	.0	.0	.0	.0	.0	.0	.0	12.7	.0	.0	1.4	14.1	1.4	1.4	1.4	.0	.0	.0	.0	.0	.0	5.6
131	158	96.	1.0	.0	.0	44.7	.0	1.0	1.0	.1	.0	.1	.0	.0	47.8	.0	.1	2.1	.0	1.0	1.0	.C	.0	.0	.0	.0	.0	.0	.0
132	159	97.	27.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	7.2	.0	.0	.0	27.8	1.0	.0	2.1	.0	.0	.0	34.0	.0	.0	.0
133	160	101.	14.9	.0	.0	.0	.0	5.9	.0	.0	.0	.0	.0	.0	20.6	.0	.0	.0	35.6	1.0	2.0	3.0	.0	.0	.0	16.8	.0	.0	.0
134	161	99.	32.3	.0	.1	.0	.0	8.1	.0	.0	.0	.0	.0	.1	57.5	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	1.0	.0	.0	.0
135	162	99.	25.2	.1	1.0	.1	.0	9.1	.0	.0	.1	.0	.0	1.0	61.4	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	1.0	.0	.0	.0
136	163	100.	10.0	.1	.0	.1	.0	13.1	.1	1.0	.1	.0	.0	.1	71.3	.0	.0	.0	3.0	.0	.0	.0	.1	.0	.0	1.0	.0	.0	.0
137	164	86.	50.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	12.8	.0	.0	.0	.0	.0	1.2	2.3	.0	.0	.0	33.7	.0	.0	.0
138	165	102.	41.2	.0	1.0	2.9	.0	.0	.0	.0	.0	.0	.0	.0	46.1	.0	.0	.0	2.9	1.0	.0	1.0	1.0	.0	.0	2.9	.0	.0	.0
139	166	100.	28.9	1.0	.1	6.0	.0	.0	.0	.0	.1	.0	.0	.0	58.7	.0	.0	.0	4.0	.1	.0	.1	.1	.0	.0	1.0	.0	.0	.0
140	167	101.	20.8	1.0	.0	5.0	.0	.0	.0	.0	1.0	.0	.0	.0	71.3	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
141	168	97.	10.3	1.0	2.1	1.0	.0	2.1	.0	.0	.1	.1	.0	.1	82.1	.0	.0	.0	1.0	.0	.0	.0	.1	.0	.0	.0	.0	.0	.0

References

Anderson, W.W., Gehringer, J.W. and Cohen, E., 1956. Physical oceanographic, biological and chemical data—South Atlantic Coast of the United States, M/V *Theodore N. Gill*, Cruise 1 and Cruise 2. Spec. Sci. Rep. U.S. Fish Wildl. Serv., Fish., 178: 160 pp.; Ibidem, 198: 270 pp.

Anderson, W.W. and Gehringer, J.W., 1957. Physical oceanographic, biological, and chemical data—South Atlantic Coast of the United States, M/V *Theodore N. Gill*, Cruise 3 and Cruise 4. Spec. Sci. Rep. U.S. Fish. Wildl. Serv. Fish., 210: 208 pp.; Ibidem, 234: 192 pp.

Anonymous, 1944. World Atlas of Sea Surface Temperatures. United States Hydrographic Office Publication 225, 2nd ed., 49 pp.

Anonymous, 1960. Surface Water Temperature and Salinity, Atlantic Coast North and South America. United States Department of Commerce, Coast and Geodetic Survey Publication 31-1, 1st ed., 76 pp.

Anonymous, 1967. Oceanographic Atlas of the North Atlantic Ocean. Section 11, Physical Properties. United States Naval Oceanographic Office, Publ. 700.

Bang, N.G., 1971. The southern Benguela Current region in February, 1966: Part II. Bathythermography and air—sea interactions. Deep-Sea Res., 18(2): 209—224.

Bary, B. McK., 1963a. Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. I. The characterization and distribution of surface waters. J. Fish. Res. Board Can., 20(3): 789—826.

Bary, B. McK., 1963b. Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. II. The relationships between species and water bodies. J. Fish. Res. Board Can., 20(4): 1031—1065.

Bary, B. McK., 1963c. Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. III. The distribution of zooplankton in relation to water bodies. J. Fish. Res. Board Can., 20(6): 1519—1548.

Bary, B. McK., 1964. Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. IV. The species' relationship to the water body; its role in distribution and in selecting and using indicator species. J. Fish. Res. Board Can., 21(1): 183—202.

Bigelow, H.B., 1933. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. Pap. Phys. Oceanogr. Meteorol., Mass. Inst. Tech., 2(4): 1—135.

Bigelow, H.B. and Sears, M., 1935. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. II. Salinity. Pap. Phys. Oceanogr. Meteorol., Mass. Inst. Tech., 4(1): 1—94.

Boltovskoy, E., 1965. Los Foraminíferos recientes. Biología, méthodos de estudio, applicación oceanográfica. University of Buenos Aires, 510 pp.

Boltovskoy, E., 1968. Hidrologia de las aguas superficiales en le parte occidental del Atlantico Sur. Mus. Argent. Cienc. Nat., Rev. Hidrobiol., 2(6): 197—224.

Bowden, K.F., 1967. Estuaries. II. Physical Factors. Circulation and Diffusion. In: G.H. Lauff (Editor), Estuaries. Am. Assoc. Adv. Sci., Publ., 83: 15—36.

Bretsky, P.W. and Lorenz, D.M. 1970. Adaptive response to environmental stability: a unifying concept in paleoecology. North Am. Paleont. Conv., Chicago, Ill., 1969, Proc. E., pp. 522—550.

Bumpus, D.F., 1957. Surface water temperatures along Atlantic and Gulf Coasts of the United States. U.S. Dep. Inter., Fish Wildl. Serv., Spec. Sci. Rep. Fish., 214: 153 pp.

Bumpus, D.F., 1973. A description of the circulation on the continental shelf of the East Coast of the United States. In: B.A. Warren (Editor), Progress in Oceanography, 6: 11—157.

Burkholder, P.R. and Burkholder, L.M., 1958. Studies on B vitamins in relation to productivity on the Bahia Fosforescente, Puerto Rico. Bull. Mar. Sci. Gulf Caribb., 8(3): 201—223.

Busby, R.F. and Dick, G.F., 1964. Oceanography of the eastern Great Bahama Bank Part I. Temperature—salinity distribution. U.S. Naval Oceanogr. Off., Tech. Rep. TR-174, 42 pp.

Carpenter, E.J. and Guillard, R.R.L., 1971. Intraspecific differences in nitrate half-saturation constants for three species of marine phytoplankton. Ecology, 52(1): 183—185.

Churgin, J. and Halminski, S.J., 1974. Temperature, Salinity, Oxygen and Phosphate in Waters off United States. Key to Oceanographic Records Documentation No. 2, Volume 1. Western North Atlantic. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Data Center, 166 pp.

Colebrook, J.M., 1964. Continuous plankton records: A principal component analysis of the geographical distribution of zooplankton. Bull. Mar. Ecol., 6(3): 78—100.

Colebrook, J.M., Glover, R.S. and Robinson, G.A., 1961. Continuous plankton records: Contributions towards a plankton atlas of the north-eastern Atlantic and North Sea. General Introduction. Bull. Mar. Ecol., 5: 67—80.

Colton, J.B., Marak, R.R., Nickerson, S. and Stoddard, R.F., 1968. Physical, chemical and biological observations on the continental shelf, Nova Scotia to Long Island, 1964—1966. U.S. Fish. Wildl. Serv., Data Rep., 23: 190 pp.

Cooley, W.S. and Lohnes, P.R., 1971. Multivariate Data Analysis. Wiley, New York, N.Y., 364 pp.

Davey, R.J., 1971. Palynology and paleo-environ mental studies, with special reference to the continental shelf sediments of South Africa. In: A. Farinacci (Editor), Proc. Second Planktonic Conference, Roma, 1970. Tecnoscienza, pp. 331—347.

Davey, R.J. and Rogers, J., 1975. Palynomorph distribution in Recent offshore sediments along two traverses off South West Africa. Mar. Geol., 18: 213—225.

Defant, A., 1961. Physical Oceanography, 1. Pergamon Press, New York, N.Y., 729 pp.

Dodimead, A.J. and Pickard, G.L., 1967. Annual changes in the oceanic—coastal waters of the eastern Subarctic Pacific. J. Fish. Res. Board Can., 24(11): 2207—2227.

Dodimead, A.J., Favorite, F. and Hirano, T., 1963. Review of oceanography of the Subarctic Pacific Region. Bull. Int. North Pac. Fish. Comm., 13: 1—176.

Eisenack, A., 1965. Uber einige Mikrofossilien des samländischen und norddeutschen Tertiärs. Neues Jahrb. Geol. Paläontol., Abh., 123(2): 149—159.

Emery, K.O., 1968. Relict sediments on the continental shelves of the world. Bull. Am. Assoc. Petr. Geol., 52: 445—464.

Emery, K.O. and Garrison, L.E., 1967. Sea levels 7,000 to 20,000 years ago. Science, 157: 684—687.

Emery, K.O. and Uchupi, E., 1972. Western North Atlantic Ocean: Topography, rocks, structure, water, life, and sediments. Am. Assoc. Petr. Geol., Mem., 17: 532 pp.

Eppley, R.W. and Harrison, W.G., 1975. Physiological ecology of *Gonyaulax polyedra*, a red water dinoflagellate of southern California. First Int. Conf. Toxic Dinoflagellate Blooms, Proc., pp. 11—22.

Fischer, A.G., 1960. Latitudinal variations in organic diversity. Evolution, 14: 64—81.

Fisher, N.S., 1977. On the differential sensitivity of estuarine and open-ocean diatoms to exotic chemical stress. Am. Nat., in press.

Gessner, F. and Schramm, W., 1971. Environmental factors Part 2. Salinity: plants. In: O. Kinne (Editor), Marine Ecology. Wiley—Interscience, New York, N.Y., pp. 705—820.

Goodbody, I., 1961. Mass mortality of a marine fauna following tropical rains. Ecology, 42(1): 150—155.

Graham, H.W., 1941. An oceanographic consideration of the dinoflagellate genus *Ceratium*. Ecol. Monogr., 11: 99—116.

Gran, H.H., 1902. Das Plankton des Norwegischen Nordmeeres von Biologischen und Hydrographischen Gesichtspunkten behandelt. Rep. Norw. Fish.-Mar. Invest., 2(5): 1—222.

Gran, H.H. and Braarud, T., 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). J. Biol. Board Can., 1(5): 279—467.

Grassle, J.F., 1972. Species diversity, genetic variability and environmental uncertainty. In: B. Battaglia (Editor), Fifth European Marine Biological Symposium. Piccin Editore, Padua, pp. 19—26.

Grassle, J.F. and Smith, W. K., 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. Oecologia (Berl.), 25: 13—22.

Grice, G.D. and Hart, A.D., 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr., 32: 287—309.

Grindley, J.R. and Nel, E.A., 1970. Red water and mussel poisoning at Elands Bay, December 1966. S. Afric., Fish. Bull., 6: 36—55.

Guillard, R.R.L. and Kilham, P., 1977. The ecology of marine planktonic diatoms. In: D. Werner, (Editor), The Biology of Diatoms. Blackwell, Oxford, in press.

Hall, C.A., 1964. Shallow-water marine climates and molluscan provinces. Ecology, 45(2): 226—234.

Haq, B.U. and Lohmann, G.P., 1976. Early Cenozoic calcareous nannoplankton biogeography of the Atlantic Ocean. Mar. Micropaleontol., 1(2): 119—194.

Hart, T.J. and Currie, R.I., 1960. The Benquela Current. Discovery Rep., 31: 123—298.

Hedgpeth, J.W., 1951. The classification of estuarine and brackish waters and the hydrographic climate. Rep. Comm. Treat. Mar. Ecol. Paleoecol., 11: 49—56.

Hedgpeth, J.W., 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci., 3(1): 111—224.

Honjo, S. and Okada, H., 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. Micropaleontology, 20(2): 209—230.

Hulburt, E.M., 1963. The diversity of phytoplanktonic populations in oceanic, coastal and esttuarine regions. J. Mar. Res., 21: 81—93.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology, 52(4): 577—586.

Imbrie, J. and Van Andel, Tj.H., 1964. Vector analysis of heavy-mineral data. Geol. Soc. Am. Bull., 75: 1131—1156.

Iselin, C.O'D., 1936. A study of the circulation of the Western North Atlantic. Pap. Phys. Oceanogr. Meteorol., Mass. Inst. Tech., 4(4): 1—101.

Johnston, R., 1964. Sea water, the natural medium of phytoplankton. II. Trace metals and chelation, and general discussion. J. Mar. Biol. Assoc. U.K., 44: 87—109.

Jones, P.G.W., 1971. The southern Benguela Current region in February, 1966: Part I. Chemical observations with particular reference to upwelling. Deep-Sea Res., 18(2): 193—208.

Kanaya, T. and Koizumi, T., 1966. Interpretation of diatom thanatocoenoses from the north Pacific applied to study of a core V20-130 (Studies of the deep-sea core V20-130 Part IV). Sci. Rep. Tohoku Univ., Sendai, 2nd Ser., (Geol.). 37(2): 89—130.

Ketchum, B.H. and Corwin, N., 1964. The persistence of "winter" water on the continental shelf south of Long Island, N.Y. Limnol. Oceanogr., 9: 467—475.

Klovan, J.E. and Imbrie, J., 1971. An algorithm and FORTRAN-IV program for large-scale *Q*-mode factor analysis and calculation of factor scores. Math. Geol., 3(1): 61—77.

Koblentz-Mishke, O.J., Volkovinsky, V.V. and Kabanova, J.G., 1970. Plankton primary production of the world ocean. In: Scientific Exploration of the South Pacific. Standard Book No. 309-01755-6 Natl. Acad. Sci., Washington, D.C., pp. 183—193

Laevastu, T., 1963. Surface water types of the North Sea and their characteristics. Ser. Atlas Mar. Environ. Am. Geogr. Soc., 4: 1—8.

Levins, R., 1968. Evolution in changing environments. Monogr. Pop. Biol., 2: 120 pp. (Princeton Univ. Press., N.J.).

MacArthur, R.H., 1960. On the relative abundance of species. Am. Nat., 94: 25—36.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton, N.J., 203 pp.

McGowan, J.A., 1971. Oceanic biogeography of the Pacific. In B.M. Funnel and W.R. Riedel (Editors). Micropaleontology of the Oceans. Cambridge University Press, Cambridge, pp. 3—46.

McIntyre, A. and Bé, A.W.H., 1967. Modern Coccolithophoridae of the Atlantic Ocean—I. Placoliths and cyrtoliths. Deep-Sea Res., 14: 561—597.

Miller, A.R., 1950. A study of mixing processes over the edge of the continental shelf. Sears Found. J. Mar., Res., 9(2): 145—160.

Milliman, J.D., 1973. Marine geology. In: S.B. Saila (Program Coordinator), Coastal and Offshore Enventory, Cape Hatteras to Nantucket Shoals, Complement Volume. Mar. Publ. Ser., 3: 10.1—10.99 (University of Rhode Island, Kingston, R.I.).

Muller, J., 1959. Palynology of Recent Orinoco delta and shelf sediments: Reports of the Orinoco Shelf Expedition; Volume 5. Micropaleontology, 5(1): 1—32.

Murphy, L.S. and Guillard, R.R.L., 1976. Biochemical taxonomy of marine phytoplankton by electrophoresis of enzymes. I. The centric diatoms

Thalassiosira pseudonana and *T. fluviatalis*. J. Phycol., 12: 9—13.

Neumann, A.C., 1965. Processes of Recent carbonate sedimentation in Harrington Sound, Bermuda. Bull. Mar. Sci., 15(4): 987—1035.

Odum, H.T. and Copeland, B.J., 1974. A functional classification of the coastal systems of the United States. In: H.T. Odum, B.J. Copeland and E.A. McMahan, Coastal Ecological Systems of the United States, 1(1): 5—84.

Parker, F.L., 1955. Distribution of planktonic Foraminifera in some Mediterranean sediments. Papers in Marine Biology and Oceanography. Deep-Sea Res., 3 (suppl.): 204—211.

Parr, A.E., 1933. A geographic—ecologic analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic Coast of the United States. Bull. Bingham Oceanogr. Coll., 4(3): 1—90.

Parsons, T. and Takahashi, M., 1973. Biological Oceanographic Processes. Pergamon Press, London, 186 pp.

Pease, T.E., 1969. A study of temperature and salinity changes along the northern New Jersey Coast. Sci. Rep. School of Engineering and Science, Research Division, New York University, GSL-TR-69-7: 51 pp.

Pianka, E.R., 1974. Evolutionary Ecology. Harper and Row, New York, N.Y., 356 pp.

Picket, T.E. and Ingram, R.L., 1969. The modern sediments of Pamlico Sound, North Carolina, U.S. Southeastern Geol., 11(2): 53—83 (Duke University, N. C.).

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. Wiley, New York, N.Y., 286 pp.

Pritchard, D.W., 1967. Estuaries, I. Basic Considerations. What is an estuary: Physical viewpoint. In: G.H. Lauff (Editor), Estuaries. Am. Assoc. Adv. Sci., 83: 3—5.

Reid, P.C., 1972. Dinoflagellate cyst distribution around the British Isles. J. Mar. Biol. Assoc., U.K., 52: 939—944.

Reid, P.C., 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, 25: 579—637.

Reid, P.C., 1975. A regional sub-division of dinoflagellate cysts around the British Isles. *New Phytol.*, 75: 589—603.

Reyssac, J., 1970. Phytoplancton et production primaire au large de la Côte d'Ivoire. Bull. Inst. Fond. Afr. Noire, 32A(4): 869—981.

Robinson, M.K., 1973. Atlas of Monthly Mean Sea Surface and Subsurface Temperature and Depth of the Thermocline Gulf of Mexico and Caribbean Sea. Scripps Institution of Oceanography, La Jolla, Calif., Reference 73-8.

Roelofs, E.W. and Bumpus, D.F., 1953. The hydrography of Pamlico Sound. Bull. Mar. Sci., Gulf Caribbean, 3(3): 181—205.

Rogers, J., 1971. Sedimentology of Quaternary deposits on the Algulhas Bank. Bull. S. Afr. Natl. Comm. Oceanogr. Res., 1: 1—117.

Rossignol, M., 1964. Hystrichosphères du quaternaire en Méditerranée orientale, dans les sediments pléistocènes et les boues marines actuelles. Rev. Micropaleontol., 7(2): 83—99.

Round, F.E., 1967. The phytoplankton of the Gulf of California, Part I. Its composition, distribution and contribution to the sediments. J. Exp. Mar. Biol. Ecol., 1: 76—97.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. Am. Nat., 102(925): 243—282.

Schiller, J., 1937. *Dinoflagellatae (Peridineae)*. In: L. Rabenhorst, Krytogamen-Flora von Deutschland, Osterreich und der Schweiz, 10 (3): 1—589.

Schlee, J., 1973. Atlantic continental shelf and slope of the United States—Sediment texture of the northeastern part. U.S. Geol. Surv., Prof. Pap., 529-L: 1—64.

Seliger, H.H., Carpenter, J.H., Loftus, M. and McElroy, W.D., 1970. Mechanisms for the accumulation of high concentrations of dinoflagellates in a bioluminescent bay. Limnol. Oceanogr., 15: 234—245.

Seliger, H.H., Carpenter, J.H., Loftus, M., Biggley, W.H. and McElroy, W.D., 1971. Bioluminescence and phytoplankton successions in Bahia Fosforescente, Puerto Rico. Limnol. Oceanogr., 16: 608—622.

Shannon, L.V., 1966. Hydrology of the South and West coasts of South Africa. Inv. Rep. Div. Sea Fish., S. Afr., 58: 1—62.

Slobodkin, L.B. and Sanders, H.L., 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol., Proc., 22: 82—93.

Smayda, T.J., 1973. Phytoplankton. In: S.B. Saila (Program Coordinator), Coastal and Offshore Environmental Inventory, Cape Hatteras to Nantucket Shoals. Mar. Publ. Ser., 2: 3.1—3.100 (University of Rhode Island, Kingston, R.I.).

Smith, C.L., 1940. The Great Bahama Bank. I. General hydrographic and chemical features. J. Mar. Res., 3(2): 147—189.

Smith, R.L., Enfield, D.B., Hopkins, T.S., Pillsbury, R.D., 1971. The circulation in an upwelling ecosystem: the PISCO cruise. Inv. Pesq., 35(1): 9—24.

Smith, W.K. and Grassle, J.F., 1977. Sampling properties of a family of diversity measures. Biometrics, 33(2): 283—292.

Stander, G.H., 1964. The Benguela Current off South West Africa. Invest. Rep. Mar. Res. Lab., S.W. Afr., 12: 1—43.

Valentine, J.W., 1973. Evolutionary Paleoecology of the Marine Biosphere. Prentice-Hall, New Jersey, N.J., 511 pp.

Van Andel, Tj.H. and Postma, H., 1954. Recent sediments of the Gulf of Paria. Reports of the Orinoco Shelf Expedition. Volume 1. Verh. K. Akad. Wet., Afd. Natuurkd., Sect. I., 20(5): 1—245.

Wall, D., 1965. Modern hystrichospheres and dinoflagellate cysts from the Woods Hole region. Grana Palynol., 6(2): 297—314.

Wall, D., 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. Palaeontology, 10(1): 95—123.

Wall, D., 1970. Quaternary dinoflagellate micropaleontology: 1959—1969. N. Am. Paleontol. Conv., Chicago, Ill., 1969. Proc. G: 844—866.

Wall, D., 1975. Modern dinoflagellates as a standard for palentological inquiry. Proc. Dinoflagellate Forum, Anaheim, 1973. Am. Assoc. Stratigr. Palynol., Contrib. Ser., 4: 37—43.

Wall, D. and Dale, B., 1968a. Modern dinoflagellate cysts and evolution of the Peridiniales. Micropaleontology, 14(3): 265—304.

Wall, D. and Dale, B., 1968b. Early Pleistocene dinoflagellates from the Royal Society Borehole at Ludham, Norfolk. New Phytol., 67: 315—326.

Wall, D. and Dale, B., 1970. Living hystrichosphaerid-dinoflagellate spores from Bermuda and Puerto Rico. Micropaleontology, 16(1): 47—58.

Wall, D. and Dale, B., 1974. Dinoflagellates in Late Quaternary deep-water sediments of the Black Sea. In: E.T. Degens and D.A. Ross (Editors), The Black Sea: its Geology, Chemistry and Biology. Am. Assoc. Petr. Geol., Mem., 20: 364—380.

Walsh, J.J., Kelley, J.C., Dugdale, R.C. and Frost, B.W., 1971. Gross features of the Peruvian upwelling system with special reference to possible diel variation. Inv. Pesq., 35(1): 25—42.

Williams, D.B., 1971. The occurrence of dinoflagellates in marine sediments. In: B.M. Funnel and W.R. Riedel (Editors), Micropaleontology of the Oceans. Cambridge University Press, Cambridge, pp. 231—243.

Williams, W.T., 1971. Principles of clustering. Annu. Rev. Ecol. Syst., 2: 303—326.

Wilson, G.J. 1973. Palynology of the Middle Pleistocene Te Piki Bed, Cape Runaway, New Zealand. N.Z. J. Geol. Geophys., 16(3): 345—354.

Wyrtki, K., 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev., 4: 33—68.

Zagwijn, W.H., 1974. The Pliocene—Pleistocene boundary in western and southern Europe. Boreas, 3: 75—97.

Zenkevitch, L.A., 1949. La structure biologique de l'océan. C.R. XIIIe Congr. Int. Zool., pp. 522—529