BIOGEOGRAPHIC AFFINITIES OF THE NORTH ATLANTIC DEEP-WATER SCLERACTINIA

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SUMMARY

We investigated the biogeographic properties and relationships of Scleractinia in the North Atlantic. The North Atlantic was divided into 38 geographic regions and each of the 134 North Atlantic species known from deeper than 200 m was scored for each region, resulting in a data matrix of 5092 cells. The species composition of each region was then analyzed by calculating a matrix of Bray-Curtis distance coefficients and performing a cluster analysis (UPGMA) and ordination (Non-Metric Multi-Dimensional Scaling) to determine biogeographic affinities and relationships of these localities. Three major clusters (superclusters) were distinguished: western, eastern and North Atlantic. The western Atlantic supercluster consists of the tropical and warm temperate western Atlantic regions and is characterized by 58% endemic species and a relatively low percentage of deep-water species. It consists of three subordinate clusters, which represent insular, continental and warm temperate areas. The eastern Atlantic supercluster extends from the Faroe Islands to the Gulf of Guinea, and is characterized by 38% endemic species and a disproportionately high number of amphi-Atlantic and cosmopolitan species, as well as a higher than average number of deep-living species. It also consists of three subordinate clusters: a Lusitanian warm temperate group, tropical localities, and a third cluster consisting of the Cape Verde and Canary Islands. The North Atlantic supercluster is characterized not by endemic species, but rather by a high number of cosmopolitan and amphi-Atlantic species, as well as a disproportionately high number of deep-living, unattached, and flabellid species. Two subordinate clusters correspond to the cold temperate northeast and northwest Atlantic.

INTRODUCTION

There is a deep-rooted desire among people to organize data into systems of classification (e.g., clusters). This probably originates in the need to organize multi-dimensional data into smaller packets that can be visualized and manipulated by researchers, but also probably reflects a degree of real clustering in natural systems. Within natural history, if species are the objects of classification, then cladistics or phenetics may provide the algorithms used, but if zoogeography is the subject under consideration, then geographic regions are usually the units of classification and various clustering and ordination algorithms are the tools typically used to synthesize these data. According to Clarke and Warwick (1994) there are literally hundreds of clustering methods, indeed whole volumes (e.g., Hartigan, 1975) dedicated just to clustering algorithms. Cormack (1971) warned that the "availability of ... classification techniques has led to the waste of more valuable scientific time than any other 'statistical' innovation." Nonetheless, a judicious use of clustering and ordination techniques can lead to thought-provoking and valuable insights about the distribution of organisms and it is becoming increasingly common for authors of biogeographic analyses to include a clustering dendrogram and/or an ordination to explore their data set. Several examples using cnidarian taxa are presented below, in increasing order of sophistication, each with a slightly different method and purpose for the analyses, but all using the Bray-Curtis or Jaccard similarity coefficients and various clustering (typically UPGMA; Sneath and Sokal, 1973) and ordination algorithms (usually non-metric multi-dimensional scaling, MDS; Clarke and Warwick, 1994).

For instance, Veron (1995) used clustering techniques in a simple way to document patterns of geographic affinity of shallow-water Scleractinia from adjacent geographic regions. Similarly, Wallace (1999) used clustering methods to demonstrate geographic affinities among acroporid Scleractinia, but also analyzed the composition of her clusters based on the overall distribution of the component species. Ketchum and Reyes-Bonilla (1997) and Reyes-Bonilla and López-Pérez (1998), based on shallow-water Scleractinia, clustered the regions of the eastern Pacific followed by an analysis of these patterns for evidence of the presumed direction of colonization, and to test for the validity of zoogeographic barriers. In an elegant pair of papers based on shallow-water corals, Sheppard (1997, 1999) used clustering and ordination (MDS) to find the geographic affinities of various localities in the Indian Ocean and then used these results to assess the role of the Chagos Archipelago as a possible stepping stone for dispersal. Clustering and ordination can also be used for studying finer-scale ecological processes, such as assessing the relationship between a circumscribed ecological zone of occurrence versus various physical factors, such as light and substrate, as was done by Sánchez et al. (1998) and Sánchez (1999) for shallow-water Caribbean Octocorallia on selected reefs.

The current study seeks to use clustering and ordination analyses to address many of the parameters described above. First, we seek to establish how many species of Scleractinia occur in the North Atlantic below 200 m, where they occur, and at what depths. Using these data, we then try to document the relationships among the faunas of various regions, in both gross and fine detail, based on the shared presence of these taxa. We attempt to characterize these groupings based on physical characteristics of the environment and the morphological characteristics of the species, in an effort to understand why these various localities cluster in the way they do. In so doing we compare our clusters to the traditional shallow-water zoogeographic provinces. We also compare the results of traditional clustering with the results of the ordination (MDS) in an effort to better understand the clusters. Finally, we ask if those transitional localities that do not fit nicely within any single cluster may, instead, represent either stepping stones for dispersal or are simply regions for which little is known.

MATERIAL AND METHODS

Material

The taxonomy and distribution of the North Atlantic deep-water Scleractinia are fairly well known, and are based primarily on the faunistic revisions of the western Atlantic (Cairns, 1979) and eastern Atlantic (Zibrowius, 1980). These sources were updated with records from Zibrowius (1983, 1985, 1992), Cairns (1981, 2000), and Tyler and Zibrowius (1992). From these sources, a total of 134 species (Table 1) are known to occur at depths greater than 200 m in the North Atlantic, representing about 20% of the worldwide azooxanthellate fauna (Cairns, 1999). For the purpose of these analyses, the two subspecies of *Caryophyllia ambrosia* are treated as different species. Drawing on these 134 species, species lists were compiled for 38 regions (Table 2, Figure 1) in the North Atlantic, in general corresponding to those regions listed by Cairns (1979) and Zibrowius (1980) in their respective analyses; in our study, however, the additional outlying locality of Indo-Pacific was included. The only regions not covered in the analysis were the coastline of western Africa between Guinea and Ivory Coast and the New England Seamounts, areas that are still very poorly known.

Methods

The first step in any biogeographic analysis of this type is to examine the data matrix for endemic species, i.e., taxa that are restricted to a single locality in our data set. Although quite useful for documenting the diversity present in each locality, such species are not useful for showing the relationship among the various localities. Consequently, they were not used for the generation of the distance matrix used for the clustering and ordinations; fifteen taxa were noted as endemic and were removed from the data matrix, leaving a 38 x 119 matrix. We then performed an outlier analysis using the program PC-ORD4 (McCune and Mefford, 1999) to see which localities are so different from the others that they should also be removed so as not to overly affect the analyses. Two localities, St. Peter and Paul Rocks and the Arctic (Table 2), were determined to be outliers and were removed from the subsequent analyses, although they subsequently were used for the overall interpretation of the data. In preliminary cluster analyses, these two localities always joined the rest at the very end, independent from each other. The result was the 36 x 119 data matrix used for the clustering and ordination analyses (Table 3).

The next step in the process is the generation of the distance (0 = dissimilarity; 1 = similarity) matrix that serves as the starting point for the more advanced analyses. There are a great many coefficients that could be used including euclidean distance, correlation coefficients and other angle measurements, and coefficients of association such as the Jaccard or Dice (Sneath and Sokal, 1973; Clarke and Warwick, 1994; McCune and Mefford, 1999). We chose to apply the Bray-Curtis Coefficient (also known as the Sorensen or Czekanowski Coefficient; Bray and Curtis, 1957; Clarke and Warwick, 1994; McCune and Mefford, 1999), which is related to the city-block metric distance measure (Sneath and Sokal, 1973; McCune and Mefford, 1999). It has become the most commonly applied coefficient for studies in quantitative biogeographic and ecological analyses and their paleontological equivalents because it typically exhibits a little more sensitivity to trends when compared with euclidean distance. Furthermore, it is not affected by joint absences of taxa; gives more weight to abundant species than rare ones; has some theoretical support based on fuzzy-set theory (Roberts, 1986); and empirically tends to give very useful results (Clarke and Warwick, 1994; McCune and Mefford, 1999).

The Bray-Curtis distance coefficient is relatively simple to calculate for presence/absence data such as we used. The numerator is the sum of the absolute value of the differences between the equivalent entries for the two localities being compared. If a species is either present or absent in both localities, then the entry for the species is 0. If a species is present in only one locality, the entry is 1. These entries are then summed across all species to give the numerator value. The denominator is the sum of all entries for both localities, equivalent to the total number of occurrences of species at both localities. If the two localities are exactly mis-matched, the numerator equals the denominator and the distance is the maximum value of one. If the localities are exactly matched, the numerator, and thus the coefficient, equals zero; the two localities have no distance between them in space.

The final result was a 36 x 36 matrix of distance coefficients for each locality with itself and each of the other localities. The distance of a locality with itself is, of course, zero; these form the diagonal elements of the matrix. The other two sections (top and bottom) of the matrix are then symmetrical as the distance of locality 1 with locality 2 equals the distance of locality 2 with locality 1. This matrix was then used with the selected clustering algorithm to produce the dendrogram. UPGMA (Unweighted Pair-Group Method with Arithmetic Averages; Sneath and Sokal, 1973) was chosen because it has been shown to be the algorithm that produces the best clustering representation of the original distance matrix using the cophenetic correlation coefficient as an indicator (Sneath and Sokal, 1973) and is, by far, the most commonly applied clustering algorithm in natural history applications. Once the clusters were established (Figure 2, Table 4), an effort was made to characterize each cluster by annotating various biological data exhibited by the localities that make up that cluster. These include the type of distribution patterns shared by the species found at those localities, the number of deep-living species, the percentage of colonial and attached species, and the ratio of the major taxonomic groups.

However useful clustering techniques may be in establishing and helping to visualize the relationships of the entities being studied (i.e., regions), clustering also has several disadvantages that have been discussed by various authors including Sneath and Sokal (1973) and Field et al. (1982). These include

Table 1. Taxa used in the analyses. *Number*: # assigned in data matrix (Table 3); those species not assigned a number are endemic to one region, as indicated in column 2 (for abbreviations see Table 2). *Pattern*: pattern of distribution (or endemicity): w – endemic to western Atlantic; e – endemic to eastern Atlantic; aad – amphi-Atlantic with a disjunct distribution; aac – amphi-Atlantic with contiguous distribution; c – widespread (cosmopolitan) distribution. *Coloniality*: colonial (C) or solitary (S). *Attachment*: attached (A) or free-living (F). C/F/D: caryophylliid, flabellid or dendrophylliid. *Depth*: depth range in western Atlantic (w) and eastern Atlantic (e).

Number	Endemic	Taxon	Pattern	Coloniality	Attachment	C:F:D	Depth (m)
1		*Anomocora fecunda* (Pourtalès, 1871)	aad	C	F	C	w:37-640; e:130-350
2		*Anomocora marchadi* (Chevalier, 1966)	c	S	F	C	w:35-229; e:32-85
3		*Anomocora prolifera* (Pourtalès, 1871)	aad	S	F	C	w:30-329; e:110-125
4		*Anthemiphyllia patera patera* Pourtalès, 1878	w	S	F	-	w:500-700
5		*Astrangia poculata* (Ellis & Solander, 1786)	w	C	A	-	w:0-263
6		*Aulocyathus atlanticus* Zibrowius, 1980	e	S	A	C	e:450-1716
	NWC	*Balanophyllia bayeri* Cairns, 1979	w	S	A	D	w:274-311
7		*Balanophyllia cellulosa* Duncan, 1873	e	S	A	D	e:80-850
8		*Balanophyllia cyathoides* (Pourtalès, 1871)	w	S	A	D	w:45-494
9		*Balanophyllia dineta* Cairns, 1977	w	S	A	D	w:127-274
10		*Balanophyllia floridana* Pourtalès, 1868	aad	S	A	D	w:13-220; e:29-95
	SWC	*Balanophyllia hadros* Cairns, 1979	w	S	A	D	w:238-274
11		*Balanophyllia palifera* Pourtalès, 1878	w	S	A	D	w:53-708
12		*Balanophyllia thalassae* Zibrowius, 1980	e	S	A	D	e:380-1150
13		*Balanophyllia wellsi* Cairns, 1977	w	S	A	D	w:412-505
14		*Bathypsammia fallosocialis* Squires, 1959	w	S	A	D	w:213-805
15		*Bathypsammia tintinnabulum* (Pourtalès, 1868)	w	S	A	D	w:210-1115
16		*Caryophyllia abyssorum* Duncan, 1873	e	S	A	C	e:732-2000
	AZO	*Caryophyllia alberti* Zibrowius, 1980	e	S	A	C	e:76-506
17		*Caryophyllia ambrosia ambrosia* Alcock, 1898	c	S	F	C	w:1487-2286; e:1600-2300
18		*Caryophyllia ambrosia caribbeana* Cairns, 1979	w	S	F	C	w:183-1646
19		*Caryophyllia antillarum* Pourtalès, 1874	w	S	A	C	w:150-730
20		*Caryophyllia atlantica* (Duncan, 1873)	e	S	A	C	e:1100-2165
21		*Caryophyllia barbadensis* Cairns, 1979	w	S	A	C	w:129-249
22		*Caryophyllia berteriana* Duchassaing, 1850	w	S	A	C	w:99-1033
23		*Caryophyllia calveri* Duncan, 1873	e	S	A	C	e:91-340
24		*Caryophyllia corrugata* Cairns, 1979	w	S	A	C	w:183-380
25		*Caryophyllia cyathus* (Ellis & Solander, 1786)	e	S	A	C	e:70-300
	AZO	*Caryophyllia foresti* Zibrowius, 1980	e	S	A	C	e:155-950
	LA	*Caryophyllia paucipalata* Moseley, 1881	w	S	A	C	w:714-843
26		*Caryophyllia polygona* Pourtalès, 1878	w	S	A	C	w:700-1817
27		*Caryophyllia sarsiae* Zibrowius, 1974	aad	S	A	C	w:1097-1200; e:520-2200

Table 1. Taxa used in the analyses *(continued)*

Number	Endemic	Taxon	Pattern	Coloniality	Attachment	C:F:D	Depth (m)
28		*Caryophyllia seguenzae* Duncan, 1873	e	S	F	C	e:1000-1400
29		*Caryophyllia smithii* Stokes & Broderip, 1828	e	S	A	C	e:40-400
30		*Caryophyllia zopyros* Cairns, 1979	w	S	A	C	w:73-618
31		*Ceratotrochus magnaghii* Cecchini, 1914	e	S	A	C	e:7-400
32		*Cladocora debilis* ME & H, 1849	aad	C	F	C	w:32-480; e:28-100
33		*Cladopsammia manuelensis* (Chevalier, 1966)	aad	C	A	D	w:70-366; e:55-150
34		*Coenocyathus anthophyllites* ME & H, 1848	e	C	A	C	e:65-250
35		*Coenocyathus cylindricus* ME & H, 1848	e	C	A	C	e:65-500
36		*Coenocyathus parvulus* (Cairns, 1979)	w	C	A	C	w:97-399
37		*Coenosmilia arbuscula* Pourtalès, 1874	w	C	A	C	w:74-622
38		*Colangia immersa* Pourtalès, 1871	w	C	A	C	w:0.5-347
39		*Concentrotheca laevigata* (Pourtalès, 1871)	aad	S	A	C	w:183-576; e:600-772
	NWC	*Crispatotrochus* sp cf *C. cornu* Moseley, 1881	w	S	A	C	w:220-241
40		*Crispatotrochus squiresi* Cairns, 1979	w	S	A	C	w:686-822
	GSN	*Cryptotrochus carolinensis* Cairns, 1988	w	S	F	-	w:320-338
41		*Dasmosmilia lymani* (Pourtalès, 1871)	c	S	F	C	w:37-366; e:85-316
42		*Dasmosmilia variegata* (Pourtalès, 1871)	c	S	F	C	w:110-421; e:185-600
43		*Deltocyathoides stimpsonii* (Pourtalès, 1871)	aad	S	F	-	w:110-553; e:200-600
44		*Deltocyathus agassizii* Pourtalès, 1867	w	S	F	C	w:494-1115
45		*Deltocyathus calcar* Pourtalès, 1874	w	S	F	C	w:81-675
46		*Deltocyathus eccentricus* Cairns, 1979	aad	S	F	C	w:183-907; e:300-1000
47		*Deltocyathus italicus* (Michelotti, 1838)	aad	S	F	C	w:403-2634; e:1500-2300
48		*Deltocyathus moseleyi* Cairns, 1979	aad	S	F	C	w:201-777; e:200-1372
49		*Deltocyathus pourtalesi* Cairns, 1979	w	S	F	C	w:311-567
50		*Dendrophyllia alternata* Pourtalès, 1880	aad	C	A	D	w:276-900; e:450-688
51		*Dendrophyllia cornigera* (Lamarck, 1816)	e	C	A	D	e:80-600
52		*Desmophyllum dianthus* (Esper, 1794)	c	S	A	C	w:183-2250; e:230-2460
53		*Desmophyllum striatum* Cairns, 1979	w	S	A	C	w:277-823
54		*Eguchipsammia cornucopia* (Pourtalès, 1871)	aad	C	F	D	w:91-300; e:330-960
55		*Eguchipsammia gaditana* (Duncan, 1873)	c	C	F	D	w:97-505; e:73-417
56		*Enallopsammia profunda* (Pourtalès, 1867)	w	C	A	D	w:403-1748
57		*Enallopsammia rostrata* (Pourtalès, 1878)	c	C	A	D	w:300-1646; e:480-2165

Table 1. Taxa used in the analyses *(continued)*

Number	Endemic	Taxon	Pattern	Coloniality	Attachment	C:F:D	Depth (m)
58		*Flabellum alabastrum* Moseley, 1873	aac	S	F	F	w:357-1977; e:906-2000
59		*Flabellum angulare* Moseley, 1876	aac	S	F	F	w:2266-3186; e:2000-2700
60		*Flabellum atlanticum* Cairns, 1979	w	S	F	F	w:357-618
61		*Flabellum chunii* Marenzeller, 1904	e	S	F	F	e:200-700
62		*Flabellum floridanum* Cairns, 1991	w	S	F	F	e:80-366
63		*Flabellum macandrewi* Gray, 1849	aac	S	F	F	w:180-667; e:128-1260
64		*Flabellum moseleyi* Pourtalès, 1880	w	S	F	F	w:216-1097
65		*Fungiacyathus crispus* (Pourtalès, 1871)	aad	S	F	-	w:183-1115; e:340-1010
66		*Fungiacyathus fragilis* Sars, 1872	c	S	F	-	w:412-460; e:200-2200
67		*Fungiacyathus marenzelleri* (Vaughan, 1906)	c	S	F	-	w:2450-4798; e:1820-4822
68		*Fungiacyathus pusillus* (Pourtalès, 1868)	w	S	F	-	w:285-685
69		*Fungiacyathus symmetricus* (Pourtalès, 1871)	w	S	F	-	w:183-1664
70		*Gardineria paradoxa* (Pourtalès, 1868)	c	S	A	-	w:91-700
71		*Gardineria simplex* (Pourtalès, 1878)	w	S	A	-	w:46-241
72		*Guynia annulata* Duncan, 1872	c	S	A	-	w:30-653; e:28-200
73		*Javania cailleti* (Duch. & Mich., 1864)	c	S	A	F	w:30-1809; e:400-2165
74		*Javania pseudoalabastra* Zibrowius, 1974	aad	S	A	F	w:625-1234; e:1070-1275
75		*Labyrinthocyathus facetus* Cairns, 1979	w	S	A	C	w:385-402
76		*Labyrinthocyathus langae* Cairns, 1979	w	S	A	C	w:695-810
77		*Leptopenus discus* Moseley, 1881	c	S	F	-	w:2842-3475
	SHE	*Leptopsammia britannica* (Duncan, 1870)	e	S	A	D	e:459-665
	MAU	*Leptopsammia chevalieri* Zibrowius, 1980	e	S	A	D	e:70-500
	AZO	*Leptopsammia formosa* Gravier, 1915	e	S	A	D	e:375-1385
78		*Lophelia pertusa* (L, 1758)	c	C	A	C	w:146-1200; e:50-1440
79		*Madracis asperula* ME & H, 1849	c	C	A	-	w:24-311; e:0-95
80		*Madracis myriaster* (ME & H, 1849)	w	C	A	-	w:37-1220
81		*Madracis pharensis pharensis* (Heller, 1868)	c	C	A	-	w:11-333; e:6-40
82		*Madracis profunda* Zibrowius, 1980	e	C	A	-	e:112-327
83		*Madrepora carolina* (Pourtalès, 1871)	w	C	A	-	w:53-801
84		*Madrepora oculata* L, 1758	c	C	A	-	w:300-1391; e:295-1550
85		*Oxysmilia rotundifolia* (ME & H, 1848)	w	S	A	C	w:46-640
86		*Paracyathus arcuatus* Lindström, 1877	e	S	A	C	e:201-343
87		*Paracyathus pulchellus* (Philippi, 1842)	aad	S	A	C	w:17-250; e:40-1260

Table 1. Taxa used in the analyses *(continued)*

Number	Endemic	Taxon	Pattern	Coloniality	Attachment	C:F:D	Depth (m)
88		*Peponocyathus folliculus* (Pourtalès, 1868)	aad	S	F	-	w:284-457; e:300-732
89		*Phacelocyathus flos* (Pourtalès, 1878)	w	C	A	C	w:20-355
90		*Placotrochides frustum* Cairns, 1979	aad	S	F	F	w:497-907; e:1300
91		*Polycyathus mayae* Cairns, 2000	w	C	A	C	w:137-309
92		*Polymyces fragilis* (Pourtalès, 1868)	w	S	A	F	w:75-822
93		*Polymyces wellsi* Cairns, 1991	c	S	A	F	w:549-1682
94		*Pourtalocyathus hispidus* (Pourtalès, 1878)	w	S	A	-	w:349-1006
95		*Pourtalosmilia anthophyllites* (E. & S., 1786)	e	C	A	C	e:250-300
96		*Premocyathus cornuformis* (Pourtalès, 1868)	aac	S	F	C	w:137-1290; e:1300-2360
97		*Premocyathus dentiformis* (Alcock, 1902)	c	S	F	C	w:231-258
98		*Rhizosmilia gerdae* Cairns, 1978	w	C	A	C	w:123-549
99		*Rhizosmilia maculata* (Pourtalès, 1874)	w	C	A	C	w:0.5-508
100		*Schizocyathus fissilis* Pourtalès, 1874	aad	S	F	-	w:88-640; e:410-1300
101		*Solenosmilia variabilis* Duncan, 1873	c	C	A	C	w:220-1383; e:860-2165
102		*Stenocyathus vermiformis* (Pourtalès, 1868)	c	S	F	-	w:165-835; e:110-1229
103		*Stephanocyathus coronatus* (Pourtalès, 1867)	c	S	F	C	w:543-1250
104		*Stephanocyathus crassus* (Jourdan, 1895)	e	S	F	C	e:400-1557
105		*Stephanocyathus diadema* Moseley, 1876	w	S	F	C	w:795-2553
106		*Stephanocyathus laevifundus* Cairns, 1977	w	S	F	C	w:300-1158
107		*Stephanocyathus moseleyanus* (Sclater, 1886)	e	S	F	C	e:1000-2000
108		*Stephanocyathus nobilis* (Moseley, 1873)	e	S	F	C	e:1300-2200
109		*Stephanocyathus paliferus* Cairns, 1977	w	S	F	C	w:220-715
110		*Tethocyathus cylindraceus* (Pourtalès, 1868)	w	S	A	C	w:183-649
111		*Tethocyathus recurvatus* (Pourtalès, 1878)	w	S	F	C	w:320-569
112		*Tethocyathus variabilis* Cairns, 1979	aad	S	A	C	w:250-576; e:269-860
	FLA	*Thalamophyllia gombergi* Cairns, 1979	w	C	A	C	w:188-220
113		*Thalamophyllia riisei* (Duch. & Mich., 1860)	w	C	A	C	w:4-914
114		*Thecopsammia socialis* Pourtalès, 1868	w	S	A	D	w:214-878
	CUB	*Trematotrochus corbicula* (Pourtalès, 1878)	w	S	F	-	w:400-576
	NWC	*Trochocyathus fasciatus* Cairns, 1979	w	S	A	C	w:238
115		*Trochocyathus fossulus* Cairns, 1979	w	S	A	C	w:205-775
	BZL	*Trochocyathus laboreli* Cairns, 2000	w	S	A	C	w:130-240
116		*Trochocyathus rawsonii* Pourtalès, 1874	w	S	A	C	w:55-700
117		*Trochocyathus spinosocostatus* Zibrowius, 1980	e	S	A	C	e:1575-1650
118		*Trochopsammia infundibulum* Pourtalès, 1878	w	S	A	D	w:532-1472
119		*Vaughanella concinna* Gravier, 1915	c	S	A	C	e:1022-3018
	CTC	*Vaughanella margaritata* (Jourdan, 1895)	w	S	A	C	w:1267

Table 2: Description and abbreviations of the 38 North Atlantic regions used in cluster analysis, ordered clockwise from west to east. Number of deep-water (over 200 m) species listed in parentheses for each region. Two outlier regions omitted from ordination are bracketed.

[SPP]	St. Peter and Paul Rocks (6 species)
BZL	Tropical coast of Brazil, including coast south of equator to Rio de Janeiro (32)
GUY	Guyana, Suriname, French Guiana (22)
SC	Southern Caribbean: coasts of Venezuela and Colombia (29)
SWC	Southwestern Caribbean: offshore islands and banks from Panama to Nicaragua (30)
NWC	Northwestern Caribbean: offshore islands and banks from Honduras to Yucatan Channel (45)
WGM	Western Gulf of Mexico (36)
EGM	Eastern Gulf of Mexico (45)
LAV	Lesser Antilles (off Venezuela): Los Testigos to Aruba (27)
LA	Lesser Antilles: Virgin Islands to Trinidad (71)
HPR	Hispaniola and Puerto Rico (35)
CUB	Cuba and Cayman Islands (70)
JAM	Jamaica (43)
BAH	Bahamas (64)
FLA	Eastern Florida and Florida Keys (53)
GSN	Southeastern U.S: Georgia, S. Carolina, N. Carolina to Cape Hatteras (40)
BER	Bermuda and Muir Seamount (19)
CTU	Cold temperate U.S. coast from Cape Hatteras to Gulf of Maine, including Georges Bank (15)
CTC	Cold temperate Canadian coast from Bay of Fundy to Cape Breton Island, including: Browns Bank, Sable Bank, Grand Bank and Orphan Knoll (10)
[ARC]	Arctic: off Labrador, Newfoundland, Greenland (3)
ICE	Iceland, Reykjanes Ridge (9)
SCA	Scandinavia: coast of Norway (6)
SHE	Shetland, Faroe, Orkney, New Hebrides Islands; Rockall Bank (19)
GB	North Sea and coasts of Great Britain, Ireland and France (Bay of Biscay) to 45°N (29)
SPA	Southern Bay of Biscay (northern coast of Spain) (34)
POR	West coast of Spain and Portugal (43°-37°N) (34)
IMG	Ibero-Moroccan Gulf (37°-33°N) (33)
MED	Mediterranean (21)
MWS	Morocco and Western Sahara (33°-22°N) (31)
AZO	Azores (51)
MAD	Madeira (41)
CAN	Canary Islands (15)
CVI	Cape Verde Islands (14)
SMA	Seamounts and banks south of Azores: Pluto, Atlantis, Cruiser, Irving, Hyeres, Great Meteor (17)
SMP	Seamounts and banks between Portugal and Madeira: Gorringe, Gettysburg, Ampere, Seine, Josephine (22)
MAU	Coasts of Mauritania and Senegal (22°-13°N) (15)
GG	Gulf of Guinea (18)
IP	Indo-Pacific: species having distributions outside Atlantic Ocean (23)

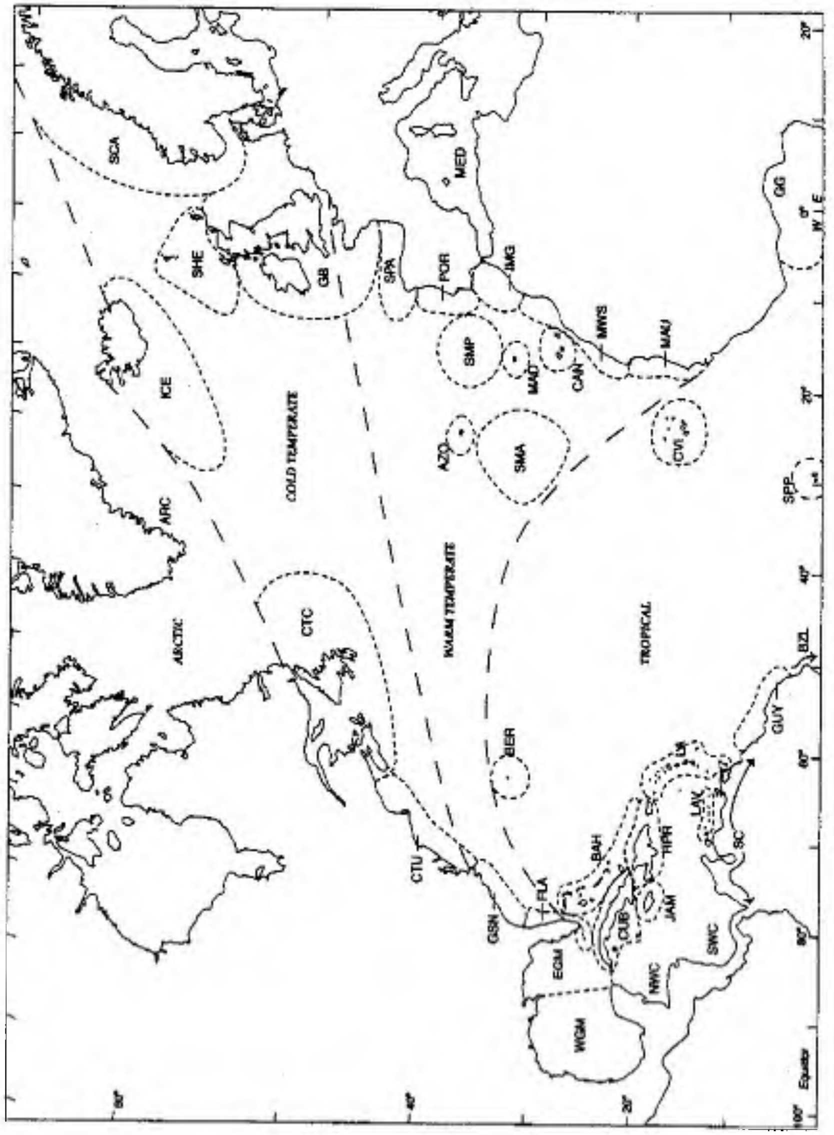


Figure 1. Locator map of North Atlantic showing 37 of the 38 regions scored in the analysis. Indo-Pacific region not mapped.

Table 3. The data matrix. The 38 rows correspond to the localities listed in Table 2. The 119 columns correspond to the species listed in Table 1.

Locale/Taxa	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	28	29	30
1 BER	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
3 FLA	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
5 WGM	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
7 CUB	1	0	0	1	0	0	0	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1	0	1	0	1	0	0	0	1
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
9 JAM	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
11 LAV	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
13 SWC	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
15 GUY	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
17 SPP	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
19 CTC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21 SCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
23 SHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
25 SPA	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
27 MED	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
29 MWS	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
31 GG	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
33 SMA	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
35 MAD	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
37 CVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 3. The data matrix *(continued)*

Locale/Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1 BER	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
3 FLA	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	1	0	1	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
5 WGM	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
7 CUB	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
9 JAM	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
11 LAV	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
13 SWC	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
15 GUY	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
17 SPP	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
19 CTC	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21 SCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
23 SHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
25 SPA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
27 MED	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
29 MWS	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
31 GG	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
33 SMA	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
35 MAD	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	1	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
37 CVI	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 3. The data matrix *(continued)*

Locale/Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
1 BER	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
3 FLA	0	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
5 WGM	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
7 CUB	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
9 JAM	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0	0	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
11 LAV	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
13 SWC	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
15 GUY	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
17 SPP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
19 CTC	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21 SCA	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
23 SHE	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
25 SPA	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
27 MED	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
29 MWS	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
31 GG	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
33 SMA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
35 MAD	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	0	1	1	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
37 CVI	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 3. The data matrix *(continued)*

Locale/Taxa	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
1 BER	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
3 FLA	0	1	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
5 WGM	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
7 CUB	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1	1	0	0	1	0	1	1	1	0	1	1	0	1	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
9 JAM	1	0	0	1	0	1	0	0	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
11 LAV	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
13 SWC	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
15 GUY	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
17 SPP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
19 CTC	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21 SCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
23 SHE	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
25 SPA	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
26 BOR	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
27 MED	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
29 MWS	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
30 MAU	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
31 GG	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
32 AZO	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
33 SMA	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34 SMP	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
35 MAD	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
36 CAN	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
37 CVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

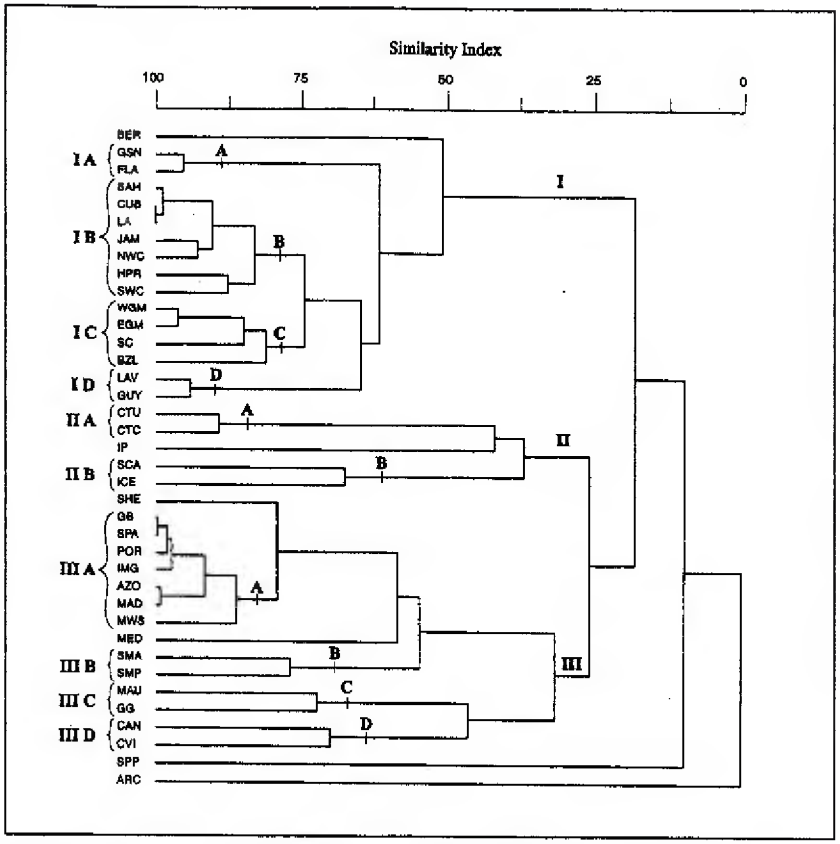


Figure 2. The dendrogram of the 38 regions produced by the UPGMA clustering, the superclusters indicated by Roman numerals, the component clusters by upper case letters. Percent chaining = 19.9. Percent similarity indicated on scale at top.

the progressively less useful values to the right of the dendrogram that result from averaging together values for more and more localities, the arbitrary fashion in which dissimilar regions may be placed adjacent to one another (the brackets can rotate freely at each junction), and the fact that a cluster analysis will generate a cluster regardless of the strength of the connection (it is, as always, up to the researcher to recognize the usefulness of the result). In order to better visualize the relationships between the groups identified using the dendrograms and to seek an independent confirmation of those results (an indication of the robustness of those patterns), it is common, and recommended, to perform an ordination on the same data and using the same distance matrix.

An ordination presents the data in the original distance matrix, here 36 dimensional data, in a very reduced number of dimensions, typically two or three, depending on the patterns of variation present. Although this tends to introduce some distortion from reducing the dimensionality of the data, and also tends to lose some of the information present in the distance matrix, most analyses will produce ordinations that account for most of the variance present in the data, and will also show the major trends that are present. This was the case for our analyses. The two types of analyses are also complementary in that the groupings indicated by the cluster analysis can be superimposed on the continuously distributed ordination results. If the clusters can be superimposed with relatively little effort, then the results are considered relatively robust. If the clusters cross each other and are very distorted, the results are given less weight.

Many different methods are available for ecological/biogeographic ordinations, including Principal Components Analysis (PCA), Correspondence Analysis (CA), and Detrended Correspondence Analysis (DCA) (Sneath and Sokal, 1973; Clarke and Warwick, 1994). The ordination algorithm chosen to analyze these data was Non-Metric Multi-Dimensional Scaling (MDS, sometimes NMS or NMMDS). Simply stated, MDS produces a map (usually of two or three dimensions) of the analyzed samples (i.e., regions) that best represents the dissimilarity among all samples. It does this in a non-metric way, in that it converts all the Bray-Curtis similarity values to rank values, not absolute values, and produces the plot on this basis. It starts out with a configuration of the data in space and progressively moves points around. At each step it measures the goodness of fit of the data with the structure of the starting distance matrix and stops when the fit is no longer improved with additional movement. According to Clarke and Warwick (1994) and McCune and Mefford (1999), MDS is undoubtedly the best ordination technique to use for ecological data, and it is becoming increasingly popular in biogeographic analyses, especially now that computing power has increased so greatly over the past decade and has caught up with the needs of researchers. One of the few disadvantages of using MDS in the past was the long computation time needed to apply it. However, the software used in these analyses for both clustering and ordination, PC-ORD4 (McCune and Mefford, 1999), handled the data expediently. The MDS analysis, run on the autopilot mode on the "slow and thorough" option, took approximately 11 minutes, which included 400 iterations and 90 runs through the data: 40 with real data and 50 with randomized data.

RESULTS

The total starting data matrix of 38 localities by 134 taxa (5092 cells) is presented in Table 3. The number of species-presence records (1's in the matrix) is 1127, or 22.1% of the total. Although this is thought to be a good approximation of the distribution of these species, this percentage will certainly rise with additional collection as will the number of taxa. Table 1 presents data for each species: its general pattern of distribution, depth range in the west-

Table 4. Some of the characteristics of the various clusters, unclustered regions and outlying regions, as determined by Bray-Curtis clustering and MDS. The first number of every pair is the absolute number of species in the cluster having this quality, the second number the percentage this number constitutes of the total number of species in this cluster. Numbers in brackets are total numbers for the cluster or region; numbers in parentheses are endemic species. Abbreviations as in Table 1; cos – cosmopolitan.

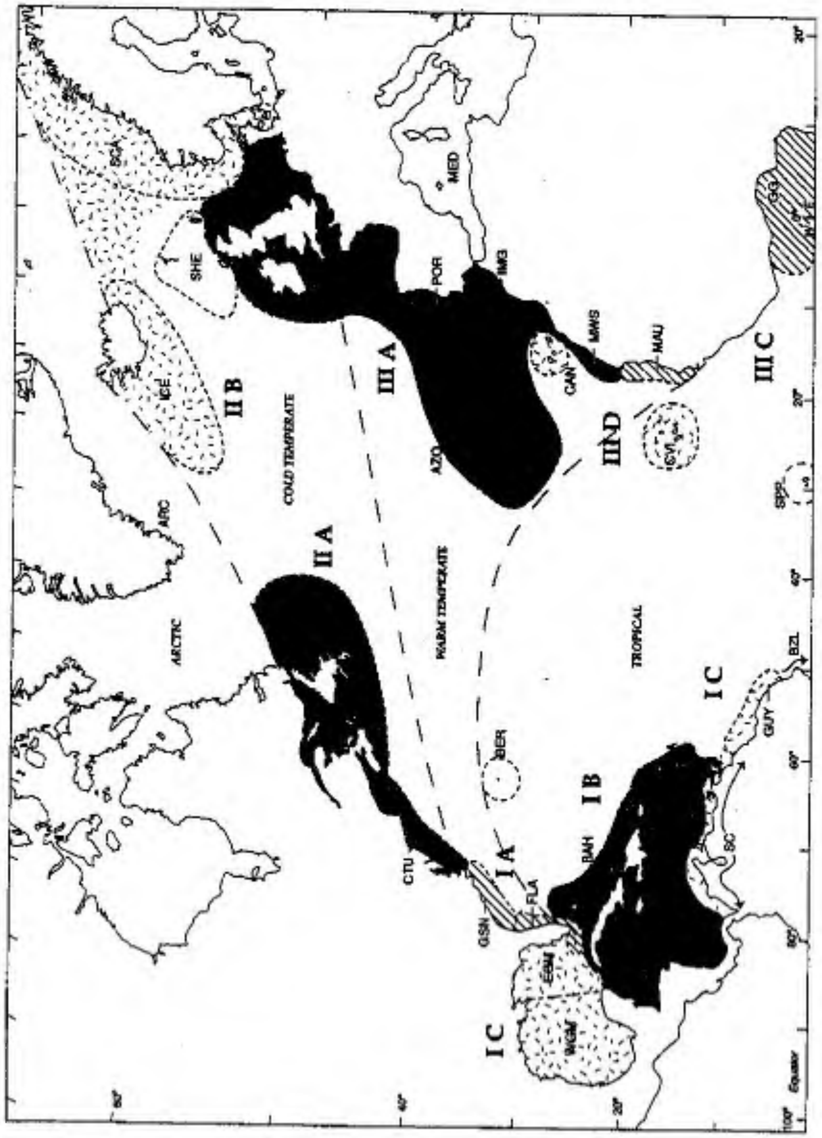
	Zoogeographic Pattern								CFD Ratio		
Superclusters/Clusters	w	e	aad	aac	cos	over 1000 m	Colonial	Attached	C	F	D
North Atlantic [134]	61/46	26/19	20/15	4/3	23/17	50/37	30/22	86/64	75/56	12/9	23/17
Super cluster I: Western Atlantic [104]	60(60)/58	-	20/19	4/4	20/19	18/17	21/20	62/60	54/52	10/10	18/17
Cluster ID [32]	15/47	-	6/19	1/3	10/31	3/6	10/31	15/47	22/69	2/6	3/9
Cluster IB ("insular") [92]	54(19)/59	-	19/21	1/1	18/20	18/20	20/22	55/60	47/51	7/8	18/20
Cluster IC ("cont.") [60]	29(1)/48	-	15/25	1/ 2	15/25	4/7	18/30	34/57	32/53	4/7	2/20
Cluster IA [60]	29(4)/48	-	15/25	4/7	12/20	7/12	13/22	29/48	29/48	7/12	10/17
Bermuda [19]	7/37	-	5/26	1/5	6/31	5/26	6/32	12/63	13/68	1/5	1/5
Supercluster II: North Atlantic [22]	4(1)/18	3/14	1/5	4/18	10/45	16/73	6/27	10/45	12/55	4/18	2/9
Cluster IIA [17]	4(1)/24	-	1/6	4/22	8/47	12/71	5/29	8/47	9/53	5/29	2/12
Indo-Pacific [22]	-	-	-	-	22/100	8/36	6/27	10/45	10/45	2/9	2/9
Cluster IIB [11]	-	3/27	0/0	2/18	6/55	5/45	7/27	5/45	7/64	1/9	0/0
Supercluster III: Eastern Atlantic [68]	-	26(26)/38	20/29	4/6	18/26	32/47	17/25	38/56	36/53	7/10	13/19
Shetland [19]	-	7(1)/37	0/0	3/16	9/47	11/58	3/16	8/42	10/53	3/16	2/11
Cluster IIIA [62]	-	22(4)/35	18/29	4/6	18/29	32/52	16/26	31/50	33/53	7/11	9/15
Mediterranean [21]	-	10/48	3/14	0/0	8/38	3/14	8/38	17/81	12/57	1/5	2/10
Cluster IIIB [28]	-	12(1)/43	7/25	1/4	8/29	8/29	8/29	15/54	15/53	2/7	5/18
Cluster IIID [21]	-	6/29	6/29	1/5	8/38	6/29	9/43	11/52	13/62	1/5	2/10
Cluster IIIC [24]	-	10(1)/42	4/17	2/8	8/33	9/38	11/46	14/58	14/58	2/8	6/25
Outliers											
[St. Peter & Paul Rocks] [6]	1/17	0/0	2/33	0/0	3/50	1/17	4/67	2/33	3/50	0/0	1/17
[Arctic] [3]	0/0	0/0	0/0	1/33	2/67	3/100	1/33	1/33	1/33	0/0	1/33

ern and eastern Atlantic, coloniality, attachment, and whether the species is a caryophylliid, a flabellid, or a dendrophylliid, the three major taxonomic groups that occur at these localities.

The results of the UPGMA clustering are illustrated in Figures 2-3. After segregating the two outlier regions of St. Peter and Paul Rocks and the Arctic, the dendrogram shows three superclusters: western Atlantic, eastern Atlantic, and cold temperate North Atlantic. The western Atlantic grouping is the most highly supported supercluster, containing four discrete clusters and one unclustered outlier: Bermuda. The North Atlantic supercluster contains two component clusters. The least well-supported supercluster, the eastern Atlantic, contains four clusters and two outliers: the Shetland Islands and the Mediterranean. Table 4 lists various biological parameters that characterize those clusters and superclusters, as well as the outlier regions. Each cluster can be compared to the North Atlantic average (Table 4), i.e., the 134 species of deep-water scleractinians known from the North Atlantic. For instance, among all the North Atlantic deep-water corals, 46% are endemic to the western Atlantic, 19% endemic to the eastern Atlantic, 15% are disjunct amphi-Atlantic, 3% are continuous amphi-Atlantic, and 17% are widespread outside the Atlantic, if not cosmopolitan. Furthermore, 37% of this general group occur at depths greater than 1000 m (the deepest record being at 4822 m), 22% are colonial, 64% are attached, and the ratio of caryophylliids:flabellids:dendrophylliids is 56:9:17.

The results of the MDS ordination, done using the program PC-ORD4 (McCune and Mefford, 1999), are illustrated in Figure 4, with the clusters from the UPGMA cluster analysis overlain on the plot. The outliers (St. Peter and Paul Rocks, and the Arctic) are not shown and were not used in this analysis as they would have had an overly large effect on the results; the outlier analysis already indicated they are very different from the other localities and each other and we have interpreted the results with this in mind. The plot was also rotated 190° from the PC-ORD4 output to optimize the graphic representation of the results, a cosmetic change that has no effect on the inter-relationships of the points but makes the results graphically more congruent with the geography. The resultant two-dimensional ordination plot clearly shows the three superclusters and component clusters in a more graphic way than that obtained from the dendrogram. This combined presentation of the results forms the basis of much of the discussion that follows. In general, however, one can immediately see certain relationships that bear further analysis. For example, the component regions of cluster ID are not contiguous; Bermuda is placed closest to cluster IA; the outlier Mediterranean is central to the eastern Atlantic region; the North Atlantic is closer to the eastern than western Atlantic; and the Shetland Islands, although clustering with the eastern Atlantic, are transitional between the North and eastern Atlantic superclusters. All of these results are discussed in further detail below, resulting in the slightly modified MDS plot of Figure 5.

Figure 3. Map of the three major superclusters of North Atlantic deep-water Scleractinia and their component clusters, as explained in the text and Figure 5



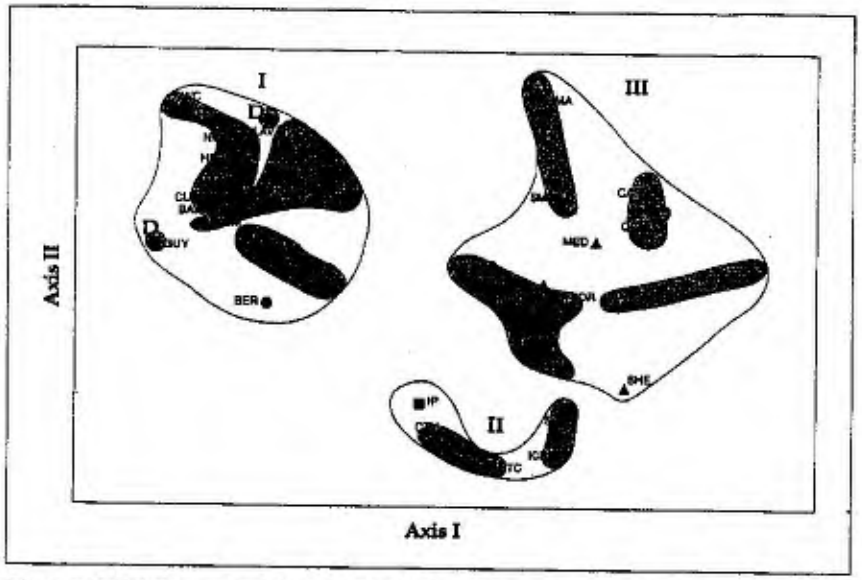


Figure 4. Multi-Dimensional Scaling plot of 36 regions, emphasizing the three superclusters and all component clusters of the UPGMA dendrogram (Figure 2)

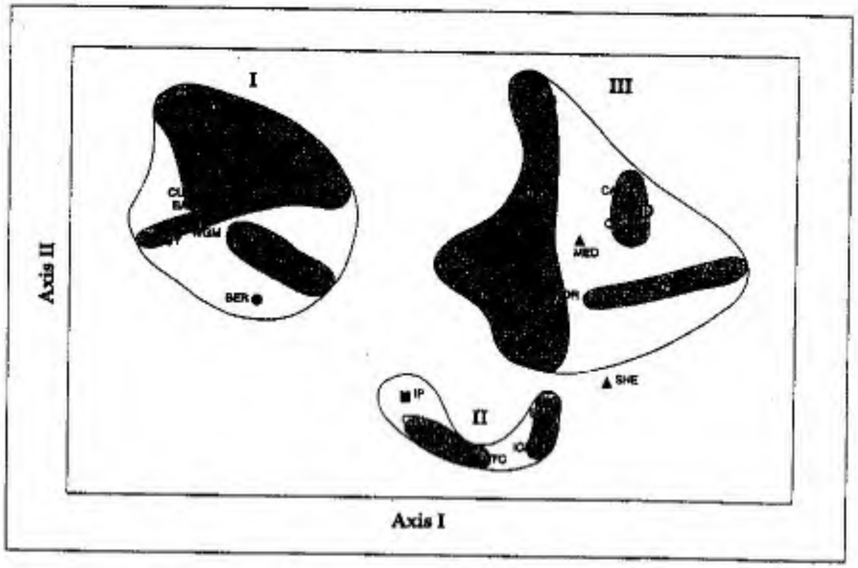


Figure 5. Multi-Dimensional Scaling plot of 36 regions, emphasizing three superclusters and a revised interpretation of the component clusters in superclusters I and III

DISCUSSION

Analysis of Clusters

The western Atlantic supercluster (I), consisting of 104 species that occur deeper than 200 m, is the best supported of the three major clusters in the analysis, containing 60 species (58%) endemic to the region (Table 4). Zoogeographically, it consists of the tropical and warm temperate western Atlantic realm (Briggs, 1974). Statistically it approximates the North Atlantic averages for most parameters, except for depth of capture; only 17% of its species occur deeper than 1000 m.

In an earlier analysis, Cairns (1979:205) distinguished several patterns of distribution of the deep-water corals of the western Atlantic, but stopped short of delimiting zoogeographic subregions characterized by endemic species, stating that the entire western Atlantic deep-water fauna was primarily one Caribbean province with depauperate extensions to the north and south. However, these analyses suggest that there are four deep-water subregions in the western Atlantic that can be defined and distinguished by species composition and various other parameters, as quantified in Table 4.

For instance, the largest cluster (IB), consisting of 92 species (including 19 species endemic to this cluster), unites the Greater and Lesser Antilles, as well as the far offshore islands and banks of the western Caribbean. Like the main cluster it belongs to, it is average in most parameters, including having a paucity of deep-water species, but geographically it consists of species that occur off islands. Even the records in the western Caribbean are found on the slopes of islands or banks often hundreds of km offshore (e.g., Arrowsmith Bank, Roatán, Rosalind Bank, Serrana Bank, Serranilla Bank). This insular pattern of distribution is similar to Ekman's (1953) Antillean region, Briggs' (1974) West Indian Province, Antillean pattern 2A of shallow-water azooxanthellates (Cairns, 2000), and deep-water coral distribution patterns 2 and 3 of Cairns (1979). It is also similar to the insular distribution pattern of stylasterids in the western Atlantic (Cairns, 1992), and may have a similar etiology, i.e., composed of species than require full oceanic salinity and clear water (not interrupted by low-salinity, sediment-laden water from riverine runoff) and an abundance of hard substrate (not muddy soft substrate).

A closely related cluster (IC), consisting of 60 species, groups the disjunct regions of the continental margins of Brazil, northern South America, and the Gulf of Mexico (Figures 2-3). It is essentially a subset of cluster IB, having only four species different from that cluster (*Astrangia poculata, Dasmosmilia lymani, D. variegata* and *Trochocyathus laboreli*, the last endemic to the subregion), and statistically (Table 4) is similar to cluster IB, except in having an even lower percentage of deep-living species. This pattern does not correlate well with traditional zoogeographic regions based on shallow-water organisms, for instance including three provinces described by Briggs (Brazilian, Caribbean and Carolinian), but does correspond to continental pattern 3B of shallow-water azooxanthellate corals (Cairns, 2000). It is suggested that the species of this "continental cluster" are more resistant to salinity and sediment fluctuations and perhaps more able to exist on soft substrates, conditions that are more common off continental margins than an insular setting.

Cluster ID groups two disjunct and disparate geographic areas (the islands off Venezuela and the continental slope off Guyana and Suriname), regions not only separated geographically but ecologically. Logically, the islands off Venezuela should group with the insular cluster, and in fact have a complete overlap in species except for two, and the Guyana/Suriname region should cluster with the continental cluster, and in fact all the species from that region do occur in the continental cluster. Thus, cluster ID is considered to be invalid, a mathematical anomaly of the clustering algorithm perhaps created by the relative low number of species in these regions and perhaps reflecting inadequate sampling of those regions. Based on their geography and species composition, we would thus prefer to place these two geographic regions adjacent to the clusters suggested above.

Cluster IA consists of 60 species, including four endemic to the cluster (*Labyrinthocyathus squiresi, L. facetus, Cryptotrochus carolinensis* and *Thalamophyllia gombergi*), and zoogeographically corresponds to the warm temperate western Atlantic Carolinian Province. It is thus a fairly well differentiated group in both the cluster and ordination analyses, characterized by having species that have a relatively high amphi-Atlantic component, few species occurring deeper than 1000 m, and a higher than average percentage of free-living species. It corresponds to Briggs' (1974) Atlantic coast section of the Carolinian Province, pattern 4 of Cairns (1979) based on deep-water corals, and pattern 5 (Carolinian) of Cairns (2000) based on shallow-water azooxanthellates. Bermuda, having a deep-water fauna of only 19 species, does not cluster with any other region, but does fall within the domain of the western Atlantic (I) supercluster by standard clustering and ordination analyses. It has no distinctive endemic species, but does have an unusually high percentage of amphi-Atlantic and cosmopolitan species at the expense of a relatively low number of endemic western Atlantic species. In fact, one species, *Caryophyllia sarsiae*, is known only from the warm temperate eastern Atlantic and Bermuda, an indication of the independent nature of the Bermudian deep-water corals from the tropical western Atlantic. These faunistic components ally it closer to cluster IA (warm temperate w. Atlantic) and even to the North and eastern Atlantic superclusters instead of the tropical western Atlantic region (e.g., cluster IB), where conventional shallow-water zoogeography would place it.

The eastern Atlantic supercluster (III), consisting of 68 species, is also well supported by 26 species (38%) endemic to the region, although it is less well defined than the western Atlantic supercluster. Zoogeographically, it extends from the Faroe Islands to the Gulf of Guinea and thus includes the cold and warm temperate and tropical eastern Atlantic realms. As indicated in Table 4, this supercluster has a disproportionately high number of amphi-Atlantic and cosmopolitan species as well as a higher than average number of deep-living species, a phenomenon discussed below. Although conventional zoogeography (Briggs, 1974) based on shallow water fauna would indicate two major provinces within this supercluster, a warm temperate Lusitanian and a tropical West African, the cluster and ordination analyses suggest four clusters and several outliers.

The largest cluster (IIIA), consisting of 62 species, extends from Great Britain to Senegal, including the Azores and Madeira; Briggs (1974) calls this cluster the Lusitanian Province. Statistically, it resembles the larger eastern Atlantic supercluster in which it sits, having high components of amphi-Atlantic, cosmopolitan, and deep-living species, but also having four species endemic to the cluster, three of which are endemic to the Azores: *Leptopsammia formosa*, *Caryophyllia alberti* and *C. foresti*. Although the Azores lie far off the coast of Europe, this region strongly clusters within the Lusitanian region, as do most Azorean shallow water organisms (Briggs, 1974). The region consisting of the Shetland, Orkney and Faroe Islands, including 19 species, is an outlier, not strongly clustering with any other; it clusters most closely to the Lusitanian region, but aspects of its high component of amphi-Atlantic, flabellid, and unattached species, as well as its transitional placement between the North and Eastern Atlantic superclusters on the ordination analysis and its position in the cold temperate region, favours an interpretation that this region belongs with the North Atlantic supercluster but forms a faunistic transition between the two superclusters. It has one endemic species: *L. brittanica*. The 21 species occurring in the Mediterranean do not strongly cluster with any other regions, but only loosely to the Lusitanian cluster, with which it is normally associated (Briggs, 1974). The Mediterranean has no endemic deep-water species, the fauna being characterized as having a very high cosmopolitan component, few deep-living species, and a disproportionately high number of colonial and attached species (Table 4). Its central, but isolated, position on the ordination graph suggests that it might have served as a Tethyan centre of distribution for the surrounding regions.

It is difficult to understand why the cluster and ordination analyses distinguished cluster IIIB: the 28 species found on the seamounts south of the Azores and off Portugal. Whereas this cluster has one endemic species (*Paracyathus arcuatus*), the remaining 27 species are all found in the Lusitanian cluster (IIIA) and the statistics for this small cluster are unexceptional. It is suggested that this cluster be combined with the larger Lusitanian cluster (IIIA).

Cluster IIID consists of 21 species found off the Canary and Cape Verde Islands, the former island group in the warm temperate region, the latter at the northern edge of the tropical region. Although this cluster has no endemic species and is quite similar to the Lusitanian cluster in species composition, it is distinguished by having a very high cosmopolitan component, a high proportion of colonial species, and a low proportion of deep-living species. It also contains the species *Cladopsammia manuelensis*, which does not occur in the Lusitanian region.

Cluster IIIC consists of 24 species and represents the tropical eastern Atlantic realm, although very few if any species are known from a large part of this region from the continental slope off Dakar to the Gulf of Guinea. In general, this cluster falls near that of the Canary and Cape Verde Islands (IIID), but contains one endemic deep-water species (*L. chevalieri*) and two species not known from the Lusitanian region or Canary/Cape Verde regions: *Balanophyllia floridana* and *Ceratotrochus magnaghii*. This cluster has a high component of cosmopolitan species, and a high percentage of colonial and dendrophylliid species.

Whereas it is clear that both the western and eastern Atlantic superclusters (I and III, respectively) are each distinguished by a significant number of endemic species (Table 4), the boreal North Atlantic supercluster (II) contains only one endemic species (*Vaughanella margaritata*), but is nonetheless fairly well differentiated from the other two clusters. Instead of endemics, this region, which oceanographically corresponds to the cold temperate North Atlantic, is characterized by having an unusually high percentage of widespread (cosmopolitan) species, as well as all four contiguous amphi-Atlantic species; deep-living species; and an unusually low percentage of attached species. For instance, cluster IIA (cold temperate U.S. and Canada) consists of 47% widespread species and 28% amphi-Atlantic species, both numbers well above the North Atlantic average. Furthermore, this region is characterized by having many deep-living species, 71% of the 17 species from cluster IIA occurring deeper than 1000 m. Taxonomically, the fauna is heavily weighted towards flabellids (i.e., *Flabellum alabastrum*, *F. angulare* and *F. macandrewi*, three of the four contiguous amphi-Atlantic species) and the dendrophylliids are poorly represented. Cluster IIB (cold temperate northeastern Atlantic) is characterized by an even greater proportion of widespread species (i.e., 55%) and a relatively high amphi-Atlantic component, although including only two of the contiguous amphi-Atlantic species. This cluster also contains a higher than average number of deep-living species and a paucity of dendrophylliids. Although the Arctic region was considered to be an outlier in the cluster and ordination analyses, probably based on its low number of species, Table 4 indicates it is related to the other cold temperate regions of cluster II, being composed of a high percentage of widespread and contiguous amphi-Atlantic, deep-living, solitary species.

The fauna of St. Peter and Paul Rocks, two very small islands just north of the equator on the axis of the mid-Atlantic Ridge, is very poorly known; Briggs (1974) does not even commit to a zoogeographic placement. Because only six deep-water corals are known from these islands, it was treated as an outlier in the cluster analysis and not plotted in the ordination. Befitting its intermediate geographic position, its coral fauna also has largely intermediate affinities (50% cosmopolitan and 33% amphi-Atlantic), but one species, *Madrepora carolina*, indicates a western Atlantic affinity; its larvae are presumably transported by the Equatorial Counter Current.

Only three species are known from the New England Seamounts (*Desmophyllum dianthus*, *Solenosmilia variabilis* and *Enallopsammia rostrata*), not enough to formulate a meaningful analysis. All three species are deep-living cosmopolitan species, suggesting an affinity with the North Atlantic supercluster rather than the warm temperate region.

Amphi-Atlantic Depth Distributions

Zibrowius (1980: 221) noted that in general, the upper bathyal (200-1000 m) azooxanthellate corals of the eastern Atlantic were often found in deeper water than those in the western Atlantic, lamenting the fact that he had to trawl deeper in the east to get the same species Cairns obtained at shallower depths in the west. He hypothesized that each coral species has a temperature range preference and that corresponding isotherms were deeper in the eastern Atlantic. This is a logical explanation with which we agree, but we would like to elaborate. Azooxanthellate corals need not only the proper temperature range, but also a certain minimum amount of space (substrate) to populate and within which to evolve. The largest, most diverse, and most favorable region in the western Atlantic for deep-water azooxanthellate corals is the tropical Caribbean, some subregions of this province (e.g., Cuba, Lesser Antilles) having as many as 70-71 deep-water species. The warm temperate western Atlantic region is geographically compressed, does not have many offshore islands, and has a much smaller species diversity. In the eastern Atlantic, the region having the greatest geographic complexity, volume and species diversity is the warm temperate Lusitanian Province. In this case, the eastern Atlantic tropical region is latitudinally constricted, has narrow shelf and slopes, few islands and seamounts, and is thus less favourable for marine life, including deep-water azooxanthellate corals. Thus, if one were to consider an amphi-Atlantic species that had a temperature preference for 5-10°C, one might expect to find it at 500-1200 m in the tropical latitudes of the Antilles, but at 1300-1800 m in the warm temperate latitudes of the eastern Atlantic, the depths at which corresponding temperature ranges are found (Zibrowius, 1980). Indeed, among the 14 deep-water amphi-Atlantic Scleractinia, eight are known only from the tropical west and warm temperate east, in five cases the eastern populations occurring at significantly greater depths (no significant difference in one species); another eight species are known from the tropical and temperate west but only the warm temperate east, in four cases the eastern populations occurring at significantly greater depths (no significant difference in three species). Thus, among the 16 amphi-Atlantic species with asymmetric distributions, nine species were found at greater depths in the east, three at greater depths in the west, and there was no appreciable difference between east and west with the remaining four. The data in Table 4 also confirm that, in general, eastern Atlantic species tend to occur at greater depths than western Atlantic species.

CONCLUSIONS

The first step in conserving or managing a resource such as the deep-water corals of the North Atlantic, is to know the number of species, and their distribution and abundance within that region. Tables 1 and 2 address that issue. But knowing other biological and zoogeographic information about the species and species clusters to which they belong may also allow some predictions about the stability or vulnerability of the fauna of various regions. These factors are quantified in Table 4. For instance, one would assume that a fauna having a higher-than-average percentage of cosmopolitan and amphi-Atlantic species and a low percentage of endemic species would constitute a more stable fauna, since the extirpation of one or more species from such a region would more easily be replaced from an adjacent region, and there would be a lesser chance for an endemic to go extinct. Likewise, faunas having a higher-than-average percentage of deep-water species (over 1000 m) would be more stable than one having numerous shallow-water species. If these assumptions are correct, the most stable region in the North Atlantic is cluster IIA, specifically the cold temperate U.S. and Canada (region CTC), which has 60% cosmopolitan, 30% amphi-Atlantic and 10% endemic components, and 90% of whose species occur deeper than 1000 m. Conversely, the most vulnerable region or cluster appears to be IB (insular western Atlantic), which has a 27% endemic component, and only 20% of whose species occur deeper than 1000 m. This is somewhat ironic in that this most vulnerable region has the highest species diversity in the North Atlantic, and the CTC one of the smallest, but this may be due to a combination of a faster adaptive radiation of deep-water corals in the tropical western Atlantic than in the more temperate regions, and little or no decrease by extinction as yet.

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