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# **Spatial and Temporal Patterns of Groundfish Distribution on the Scotian Shelf and in the Bay of Fundy, 1970-1981**

R. Mahon, R.W. Smith, B.B. Bernstein, and J.S. Scott

Marine Fish Division  
Bedford Institute of Oceanography  
P.O. Box 1006  
Dartmouth, Nova Scotia B2Y 4A2

December 1984

**Canadian Technical Report of  
Fisheries and Aquatic Sciences  
No. 1300**



Government of Canada  
Fisheries and Oceans

Gouvernement du Canada  
Pêches et Océans

CAB5ΦΦ18Φ

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SPATIAL AND TEMPORAL PATTERNS OF GROUNDFISH  
DISTRIBUTION ON THE SCOTIAN SHELF AND IN THE  
BAY OF FUNDY, 1970 - 1981

by

Robin Mahon, Robert W. Smith<sup>1</sup>, Brock B. Bernstein<sup>2</sup>  
and James S. Scott<sup>3</sup>

Marine Fish Division  
Bedford Institute of Oceanography  
Dartmouth, Nova Scotia B2Y 4A2

<sup>1</sup> EcoAnalysis, Inc., 114 Fox Street, Ojai, California 93023

<sup>2</sup> Richard W. Welsford Research Group Ltd., Collins Court, Historic Properties,  
1869 Upper Water Street, Halifax, Nova Scotia B3J 1S9

<sup>3</sup> Marine Fish Division, St. Andrews Biological Station, St. Andrews, New Brunswick  
E0G 2X0

Minister of Supply and Services Canada 1984  
Cat. No. Fs 97-6/1300E ISSN 0706-6457

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## ABSTRACT

Mahon, R., R.W. Smith, B.B. Bernstein, J.S. Scott. 1984. Spatial and Temporal Patterns of Groundfish Distribution on the Scotian Shelf and in the Bay of Fundy, 1970 - 1981. Can. Tech. Rep. Fish. Aquat. Sci. 1300:

The spatial and temporal patterns of groundfish distribution on the Scotian Shelf and the Bay of Fundy were explored using cluster analysis to define site and species groups and discriminant analysis to determine which environmental variables gave the greatest amount of separation of site groups. Of 92 demersal fish species observed in the 12 year trawl survey series, 31 were included in the analysis. The environmental data used were: depth, salinity, temperature, and sediment type. A new inter-sample distance index was used and is described in detail. The inter-species distances were estimated using the two-step method based on the Bray-Curtis index.

The first approach was to carry out separate analyses for each of twelve summer, three spring and three fall surveys. Subsequent analyses were aimed at synthesizing these individual survey analyses and at gaining a temporal perspective.

The striking observation on the analyses of the summer surveys is the similarity of species and site groupings from year to year. The relative importance of environmental variables in providing site-group separation was also consistent through time, as were the relative environmental preferences of the individual species.

In the final stage of the analysis sites were aggregated within sampling strata and clustered on the basis of similar species composition within years. Groups of strata were defined on the basis of the above procedure and the geographic proximity of the strata. Then, using the stratum groups in each of the twelve years as input a further cluster analysis was carried out. In general the same stratum groups tended to cluster together through time (i.e. basins clustered with basins and banks with banks). Discriminant analysis of these stratum (year groups found the same configuration of environmental variables as had emerged in the year by year analyses. Depth and sediment particle size contributed primarily to the first discriminant axis, temperature to the second, with salinity contributing equally to both axes.

The overall picture is one of a system in which the species distributions are strongly aligned with the physical environment, and consistent through time. The possible value of this consistency in formulating a multispecies management approach is discussed.

## RÉSUMÉ

Mahon, R., R.W. Smith, B.B. Bernstein, and J.S. Scott. 1984. Spatial and Temporal Patterns of Groundfish Distribution on the Scotian Shelf and in the Bay of Fundy, 1970 - 1981. Can. Tech. Rep. Fish. Aquat. Sci. 1300:

On a exploré les structures spatiales et temporelles de la répartition des poissons de fond sur le plateau continental de Scotian et dans la baie de Fundy. Pour ce faire, on s'est servi de l'analyse par grappes pour définir les groupes d'espèces et les groupes d'endroits de prélèvement et de l'analyse discriminante pour déterminer quelles variables environnementales permettaient d'obtenir la plus importante différenciation des groupes d'endroits de prélèvement. Sur les 92 espèces de poissons benthiques observées au cours de la série de relevés par chaluts sur une période de douze ans, 31 espèces ont été touchées dans l'analyse. Les données environnementales utilisées ont été la profondeur, la salinité, la température et le type de sédiment. On s'est servi d'un nouvel index des distances entre les prélèvements d'échantillons, qui est décrit en détail. On a évalué les distances entre les espèces au moyen d'une méthode en deux temps se fondant sur l'index de Bray-Curtis.

La première étape consistait à effectuer des analyses distinctes pour chacun des relevés réalisés au cours de douze étés, de trois printemps et de trois automnes. Les analyses auxquelles on a procédé ensuite étaient axées sur la synthèse des analyses de chaque relevé et sur l'obtention d'un point de vue temporel.

L'observation frappante qui se dégage des analyses des relevés d'été est la ressemblance des groupes d'espèces et des groupes d'endroits de prélèvement d'une année à l'autre. L'importance relative des variables environnementales dans l'obtention d'une différenciation des groupes d'endroits de prélèvement se maintient elle aussi dans le temps, comme d'ailleurs les préférences environnementales relatives de chaque espèce.



## INTRODUCTION

At present Canada's Atlantic fisheries are managed on a stock-by-stock basis. There is, however, general recognition that interactions among species are an important factor which should be considered in the management of fishery resources (Hobson and Lenarz 1977, Mercer 1982). There is a variety of multi-species approaches to management, all of which are in the early developmental stages as regards their practical application. In the simplest situation there may be no biological interactions among coexisting species which are fished together, but there may still be trade-offs in optimizing the combined yield of the species or in conserving one or more of them (Murawski 1983). Another approach, analogous to a single-species surplus production model, incorporates the inter- and intra-specific responses of the coexisting populations, but does not account for them explicitly, considering only the production and yield of the assemblage as a whole (Pauly 1979, Halliday and Doubleday 1976). More detailed approaches may attempt to account explicitly for the effects of predation, competition, and environmental factors, and to develop systems of interacting single species models (Anderson and Ursin 1977, Pope 1982).

Regardless of approach, one common problem is the delineation of the community or assemblage for which the strategy should be developed. Marine systems are particularly problematic in this respect as they are largely "open systems" and it is necessary to consider both internal interactions and external influences. Ideally, the assemblage should be defined in such a way as to minimize the external influences. However, for an area such as the Scotian Shelf it is by no means obvious how to place divisions which would be both ecologically meaningful and relevant as management units.

One approach has been to look for combinations of species that consistently occur together through time. If such assemblages are found to be spatially distinct and temporally stable, then it can be assumed that the species are reacting to some common physical or biotic environmental factors, and their potential as a management unit can be further explored. Classification (or cluster) analyses are most appropriate for defining assemblages (Tyler et al. 1982) and have previously been used for demersal fishes off Oregon (Gabriel and Tyler 1980) and on Georges Bank (Overholtz 1982).

An earlier analysis of assemblages on the Scotian Shelf, based on one year's data with limited geographic distribution, was promising (Knight and Tyler 1973). In this study we will further explore the possibility that there are natural assemblages of demersal fishes on the Scotian Shelf, and the distribution and temporal stability of any such assemblages. We will also attempt to relate these findings to available information on the physical environment. The study will be based on a 12-year time series of 75 search vessel groundfish surveys on the Scotian Shelf and in the Bay of Fundy.

## METHODS

### THE STUDY AREA

The area under consideration is the entire Scotian Shelf, its slope, and the Bay of Fundy (Figure 1). The following description is summarized from Uchupi (1968) and Heezen et al. (1969). The shelf is about 690 km long and from 110 to 120 km wide. To the northeast it is separated from the Grand Banks of Newfoundland by the Laurentian Channel. To the southwest, the Northeast channel separates it from Georges Bank. The topography of the Scotian Shelf is complex, as is typical of glaciated shelves (Uchupi 1968). Along the shore is a rocky zone about 30 km wide. Seaward of this zone is a relatively flat area of intermediate depth (100-150 m) in which are several deep basins. Of these, the largest are Roseway (185 m), LaHave (269 m) and Emerald (291 m) Basins. Towards the northeast the basins are particularly dendritic. Along the outer margin of the shelf is a series of flat topped banks of various sizes, separated by low saddles.

In the Northwest the study area includes parts of the Georges and Jordan Basins, and the entire Bay of Fundy which is about 250 km long and from 50-100 km wide. Depths in the latter range from about 50 m near the head to about 150 m near the mouth where there are a few deeper holes.

The circulation and water characteristics of the Scotian Shelf are complex, in keeping with the topography, and the fact that the waters originate from three main sources: runoff from the Gulf of St. Lawrence, the Labrador Current, and North Atlantic water (Houghton et al. 1978, P. Smith pers. comm.). The last of these includes water from the Gulf Stream and the central North Atlantic. In summary, Labrador Current water enters the Gulf of St. Lawrence where it mixes with the runoff water, then flows out through the Cabot Strait and along the Scotian Shelf parallel to the coast as the Nova Scotian Current (Sutcliffe et al. 1978). The fate of this water as it moves onto the southwestern half of the shelf is poorly known. Some is apparently diverted off shore (Smith 1979) and some continues along the coast turning north west around the south west tip of Nova Scotia.

The water of the Nova Scotian Current is relatively cold and fresh. As it moves along the shelf it mixes with warm saline water from the shelf slope, particularly in the region of the Scotian Gulf at mid-shelf (Houghton et al. 1978).

In the Bay of Fundy, water from the Gulf of Maine enters on the south side and exits along the north shore towards Cape Cod (Bigelow 1927). One of the most prominent features of the Bay of Fundy is extensive tidal mixing.

This account is intended only to introduce the reader to the study area. Further details of the physical oceanography of the region are available in, and in references cited by, Sutcliffe et al. (1976).

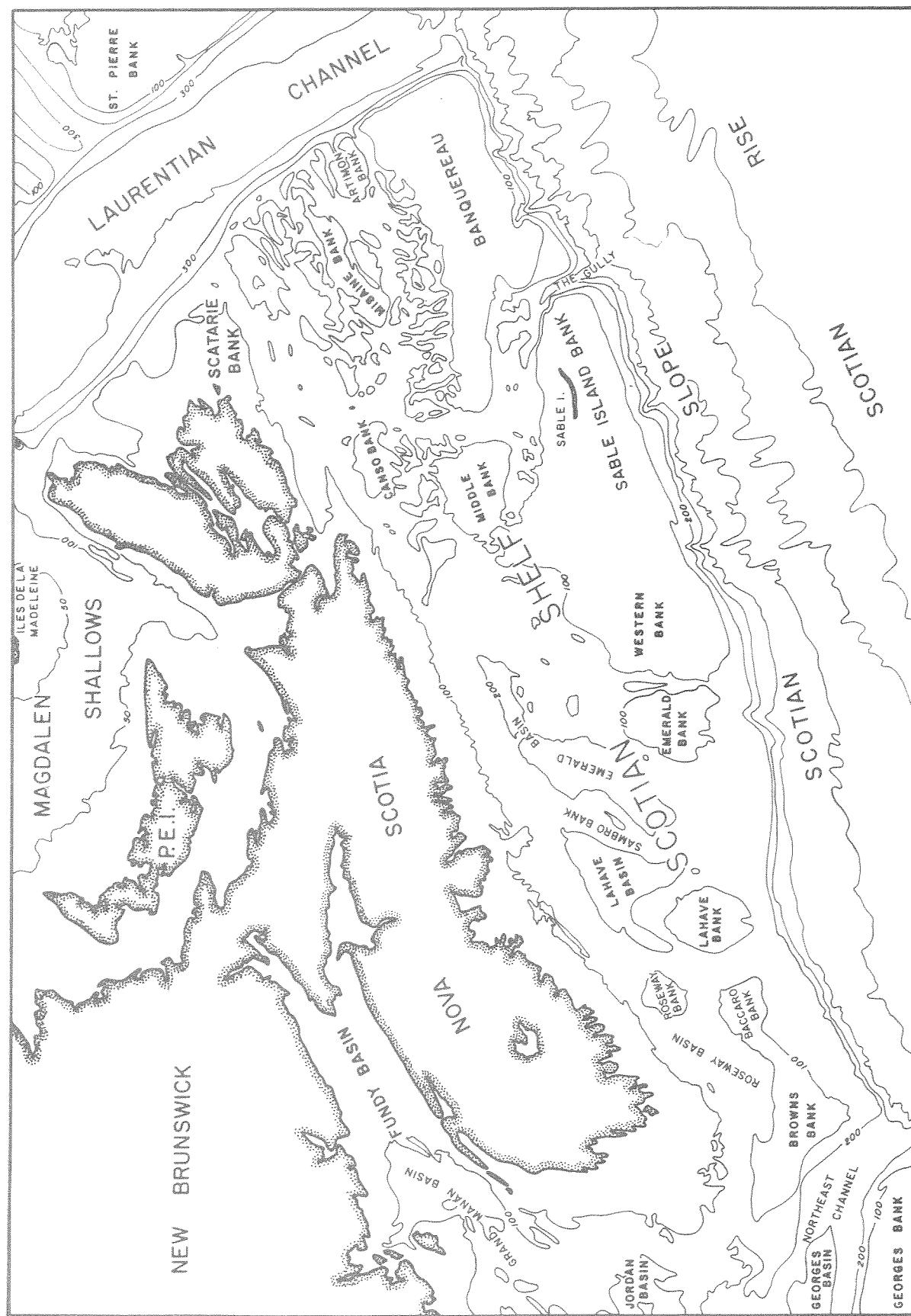


Fig. 1. Bathymetric map of the Scotian Shelf and Bay of Fundy.

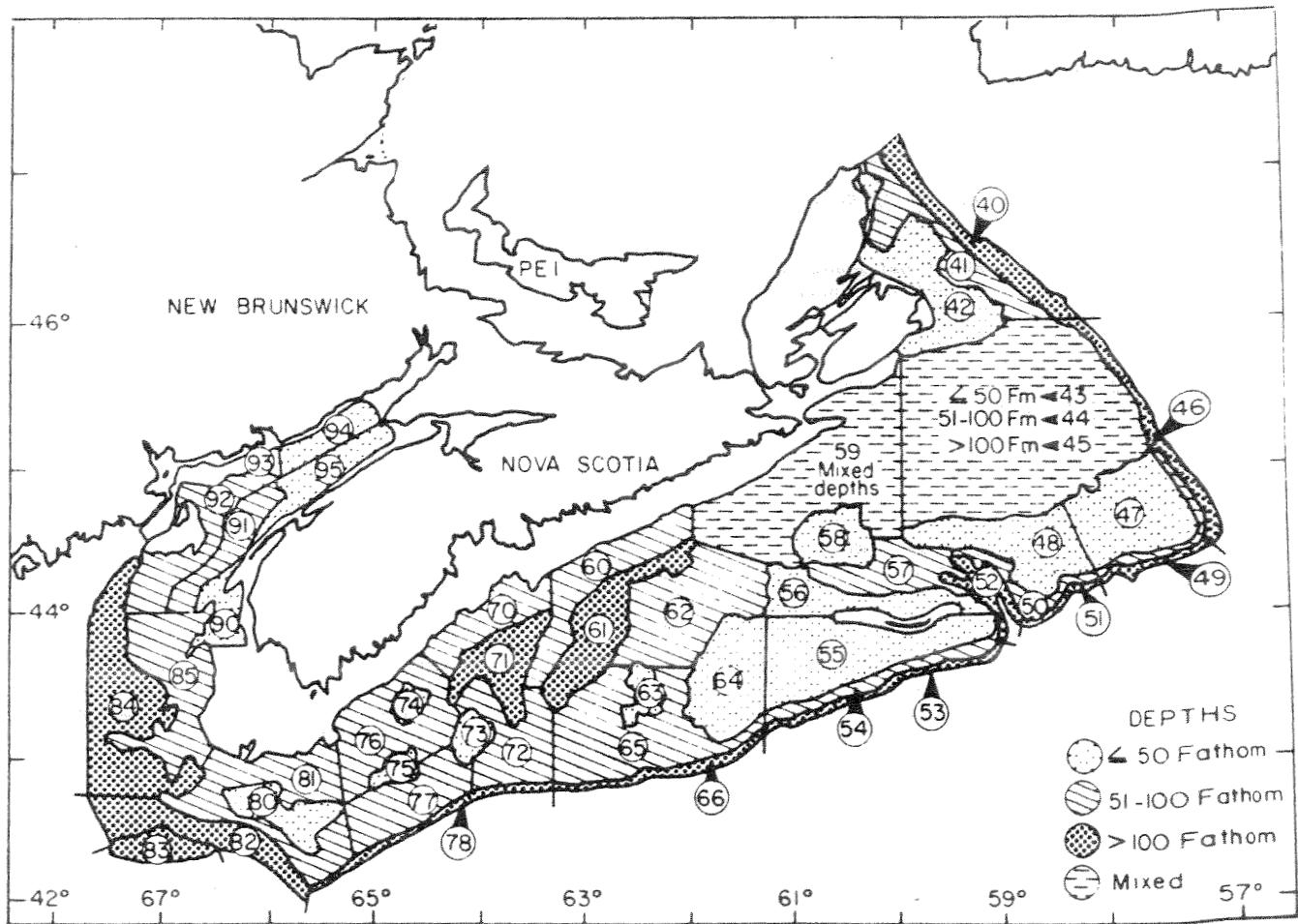


Fig. 2. Sampling strata on the Scotian Shelf and in the Bay of Fundy.

## OVERVIEW

The following is a stepwise overview of the analysis which can be considered in two parts: the first is the survey by survey analysis, the

second is an attempt to combine surveys and thus cut across time in a single analysis.

STEP	RESULT
DATA PREPARATION	
S1) species and site selection	
S2) transformation and standardization of species abundance data	R1) matching matrices of sites (trawl sets) times species and sites times environmental data
S3) estimation of missing values for environmental data	
ANALYSIS OF EACH SURVEY	
S4) estimation of intersite and interspecies (relative habitat preference) distances	R2) distance matrices
S5) clustering of species and sites, and ordination of these within the constraints imposed by cluster structure	R3) sites and species dendograms
S6) assignment of sites and species to groups on the basis of results 3 and 4	R4) two-way table of standardized species abundances at each site
S7) discrimination among sites groups on the basis of environmental variables	R5) site and species groups
S8) calculation of discriminant axis scores for each site	R6) discriminant space determined by the discriminant functions
S9) calculation of standardized values for each species and environmental variable at each site	R7) sites and site groups displayed in discriminant space
ANALYSIS ACROSS SURVEYS	
S10) summarization of species groups across all years	R8) gradients of environmental variables and species abundances in discriminant space
S11) summarization of spatial units (sampling strata) across all years	R9) overall species groups
S12-S17) repetition of steps 4 to 9 above using aggregated spatial units in each year as sites i.e. including all years in a single analysis	R10) stratum groups  R11-R17) same as results 2 to 8 above but showing inter-relationships of spatial units through time and their relationship to the physical environment

## DATA PREPARATION

### Fish Distribution

The data to be analysed are the catches taken on research vessel groundfish trawl surveys of the Scotian Shelf and Bay of Fundy (Table 1). A stratified random sampling design was used in these surveys, with stratification by depth and geographic location (Figure 2). Further details are given by Doubleday (1981) and by Halliday and Koeller (1981). For the summer surveys, A.T. Cameron, a Yankee 36 trawl was used, whereas for the spring and fall surveys, Lady Hammond, a Western IIA trawl was used.

The target duration (on bottom) and average speed for each tow were 30 minutes and 3.5 knots. This gives a 'standard tow' of 1.75 nautical miles. When duration or speed varied from the target values the catch of each species was adjusted to catch per 'standard tow' by the factor 1.75/actual distance towed.

### Selection of Sites and Species

Only trawl tows within the area comprising strata 40-95 (Figure 2), Scotian Shelf and Bay of Fundy, were used in this analysis. Tows which were less than 20 minutes in duration were excluded.

There were 91 demersal fish species (or groups of species) in the tows which were retained for analysis (Table 2). This excludes several invertebrates and pelagic fishes commonly taken in these surveys. Of the 94 demersal species, only 31 were considered to be sufficiently abundant to be included in the analysis. These were all species which contributed more than 0.1% to either total numbers or total weight, or more than 0.05% to both total numbers and total weight. These species are underlined in Table 2 which shows total numbers, total weight and total number of occurrences for each species over all surveys.

Table 1. Details of the surveys included in this analysis. There are two cruises per survey.

Cruise ID	Dates	# of Stations analysed
A175/A176	July 6-July 31 1970	67/73
A188/A189	June 29-July 22 1971	52/61
A200/A201	June 23-July 19 1972	66/84
A212/A213	July 9-August 3 1973	65/78
A225/A226	July 8-August 3 1974	80/80
A236/A237	July 15-August 6 1975	72/71
A250/A251	July 12-August 5 1976	64/77
A265/A266	July 9-July 30 1977	91/54
A279/A280	July 9-August 4 1978	79/63
A292/A293	July 6-July 27 1979	80/72
A306/A307	July 7-July 27 1980	63/85
A321/A322	July 4-July 25 1981	70/74
H013/H014	March 5-March 29 1979	47/73
H026/H027	Oct. 15-Nov. 8 1979	68/70
H033/H034	March 5-March 27 1980	49/58
H042/H043	Sept. 30-Oct. 22 1980	69/72
H048/H049	Feb. 23-March 19 1981	73/48
H064/H065	Sept. 30-Oct. 22 1981	64/65

A = A.T. Cameron, H = Lady Hammond

### Depth, Temperature, and Salinity

The average depth of each tow, as determined by echosounder, was used. Bottom temperature was determined by mechanical or expendable bathythermograph and by reversing thermometer. Salinity was determined by titration or with a conductivity salinometer.

### Sediment

In order to assign sediment characteristics to each station, we used a series of charts delimiting the areal extent of different sediment types on the Scotian Shelf (King 1971, Fader et al. 1982, Fader et al. 1977, King 1970, MacLean and King 1971, Maclean et al. 1977). The approximate amounts of gravel, sand, silt, and clay in each sediment type (King 1967) are shown in Table 3. Because of the apparent variability in and uncertainty about the percentage contribution of each size fraction to each sediment type, we ranked the sediment types within each size fraction occurring in each sediment type. For example (Table 3), Sable Island sand and gravel (75% gravel) contained the most gravel and received the highest rank for this size fraction, but contained no silt or clay, and thus received the lowest rank for these size fractions. We emphasize that percent composition was ranked across sediment types and within size fractions, and that a "rank" of zero was given to size fractions with a value of zero. In addition the size of the different fractions (gravel, sand, silt, clay) were expressed as consecutive integers (4,3,2,1). We felt that the uncertain nature of the data did not warrant more exact quantification.

Table 3. The percent contribution of each sediment fraction to each sediment type (above slash) and the rank of each sediment type within components (below slash).

Sediment type	Sediment fraction					Mean size	S.D.
	Gravel (4)	Sand (3)	Silt (2)	Clay (1)			
<i>Sable Island sand and gravel</i>							
( 50% gravel)	75/7	25/2	0/0	0/0	3.78	0.42	
(undet)	25/5	75/7	0/0	0/0	3.42	0.42	
( 50% gravel)	50/6	50/4	0/0	0/0	3.60	0.49	
<i>Sambro sand drift</i>	15/4	68/6	13/4	4/4	2.56	1.07	
<i>Scotian Shelf Laurentian silt</i>	3/3	64/5	17/5	16/5	2.33	1.05	
<i>Lahave clay</i>	0/0	30/3	47/7	23/6	1.81	0.73	

These data were then used to calculate the weighted mean and standard deviation of sediment size. The ranks within each sediment size fraction (Table 3) were used as the weights. Table 4 shows the correlations among the sediment variables.

Table 2. The total adjusted numbers and weight (kg) caught and the frequency of occurrence of groundfish species on the Scotian Shelf in the summer surveys 1970-1981 and the spring and fall surveys 1979-1981 (species names refer to the numbers column only, the weight and frequency columns are reorded.)

Species		Codes	Numbers	Codes	Weight	Codes	Frequency
Redfish	<i>Sebastes</i> spp.	23	169061	11	9103	10	1792
Haddock	<i>Melanogrammus aeglefinus</i>	11	130403	10	6870	201	1790
Silver Hake	<i>Merluccius bilinearis</i>	14	82184	23	5963	40	1766
American Plaice	<i>Hippoglossoides platessoides</i>	40	66028	220	2693	11	1401
Yellowtail Flounder	<i>Limanda ferruginea</i>	42	60126	16	2436	41	1105
Atlantic Cod	<i>Gadus morhua</i>	10	59259	40	2145	14	1085
Northern Sand Lance	<i>Ammodytes dubius</i>	610	24650	12	1803	12	1059
Thorny Skate	<i>Raja radiata</i>	201	18438	201	1796	23	974
White Hake	<i>Urophycis tenuis</i>	12	16498	42	1512	42	886
Longhorn Sculpin	<i>Myoxocephalus octodecemspinosus</i>	300	13882	14	1413	300	807
Spiny Dogfish	<i>Squalus acanthias</i>	220	12742	204	792	202	782
Witch Flounder	<i>Glyptocephalus cynoglossus</i>	41	12416	41	620	400	666
Atlantic Argentine	<i>Argentina silus</i>	160	9592	400	554	16	559
Pollock	<i>Pollachius virens</i>	16	8264	50	426	50	542
Longfin Hake	<i>Urophycis chesteri</i>	112	7989	15	358	320	513
Winter Skate	<i>Raja ocellata</i>	204	3867	30	333	30	504
Winter Flounder	<i>Pseudopleuronectes americanus</i>	43	3188	300	286	204	403
Red Hake	<i>Urophycis chuss</i>	13	2642	160	222	15	401
Smooth Skate	<i>Raja senta</i>	202	2611	320	219	220	381
Vahl's Eelpout	<i>Lycodes vahlii</i>	647	2394	43	198	160	375
Sea Raven	<i>Hemitripterus americanus</i>	320	1808	202	125	640	370
Maitled Sculpin	<i>Triglops murrayi</i>	304	1711	610	82	13	281
Atlantic Wolffish	<i>Anarhichas lupus</i>	50	1645	112	75	43	257
Angler	<i>Lophius americanus</i>	400	1528	640	73	112	255
Cusk	<i>Brosme brosme</i>	15	1197	13	71	304	228
Atlantic Halibut	<i>Hippoglossus hippoglossus</i>	30	1159	200	50	410	175
Ocean Pout	<i>Macrozoarces americanus</i>	640	1087	203	38	114	119
Common Grenadier	<i>Nezumia bairdi</i>	410	991	647	33	241	109
Eelpout	<i>Lycodes</i> spp.	642	966	501	31	647	97
Little Skate	<i>Raja erinacea</i>	203	496	19	30	306	92
Arctic Hookear Sculpin	<i>artediellus uncinatus</i>	306	478	642	20	203	91
Atlantic Hagfish	<i>Myxine glutinosa</i>	241	322	31	20	642	86
Offshore Hake	<i>Merluccius albidus</i>	19	316	221	11	31	83
Arctic Eelpout	<i>Lycodes reticulatus</i>	641	267	641	7	501	74
Fourbeard Rockling	<i>Enchelyopus cimbrius</i>	114	255	52	7	610	63
Blackbelly Rosefish	<i>Helicolenus dactylopterus</i>	123	249	143	5	641	61
Daubed Shanny	<i>Lumpenus maculatus</i>	623	208	51	5	19	51
Greenland Halibut	<i>Reinhardtius hippoglossoides</i>	31	204	410	3	340	47
Windowpane	<i>Scophthalmus aquosus</i>	143	187	150	1	123	47
Black Dogfish	<i>Centroscyllium fabricii</i>	221	167	122	1	143	40
Alligatorfish	unid. <i>Aspidophoroides</i> spp.	351	129	611	1	623	37
Barndoor Skate	<i>Raja laevis</i>	200	122	304	0	622	33
Gulf Stream Flounder	<i>Citharichthys arctifrons</i>	44	120	241	0	351	32
Alligatorfish	<i>Aspidophoroides monopterygius</i>	340	107	114	0	150	31
Lumpfish	<i>Cyclopterus lumpus</i>	501	90	306	0	200	26
Snakeblenny	<i>Lumpenus lumpretaeformis</i>	622	87	623	0	630	26
Atlantic Tomcod	<i>Microgadus tomcod</i>	17	47	340	0	701	15
Butterfish	<i>Peprilus triacanthus</i>	701	35	622	0	350	13
Shortnose Greeneye	<i>Chlorophthalmus agassizi</i>	156	35	44	0	414	13
Rock Grenadier	<i>Coryphaenoides rupestris</i>	414	34	630	0	742	11
Radiated Shanny	<i>Ulvaria subbifurcata</i>	625	34	350	0	156	10
Atlantic Poacher	<i>Agonus decagonus</i>	350	33	351	0	625	10
Wrymouth	<i>Cryptacanthodes maculatus</i>	630	32	701	0	51	9
Cunner	<i>Tautogolabrus adspersus</i>	122	31	502	0	122	7
Atlantic Batfish	<i>Dibranchus atlanticus</i>	742	22	603	0	221	7
Batfishes	<i>Ogcocephalidae</i>	694	19	63	0	603	7
Wolf Eelpout	<i>Lycenchelys verrillii</i>	603	13	240	0	52	7
Atlantic Spiny Lumpsucker	<i>Eumicrotremus spinosus</i>	502	12	414	0	502	6
Spotted Wolffish	<i>Anarchichas minor</i>	51	12	505	0	240	6
Shorthorn Sculpin	<i>Myoxocephalus scorpius</i>	301	12	742	0	301	5
Fourline Snakeblenny	<i>Eumesogrammus praecisus</i>	626	12	151	0	63	4
Northern Wolffish	<i>Anarhichas denticulatus</i>	52	9	155	0	505	4
Sea Lamprey	<i>Petromyzon marinus</i>	240	9	301	0	155	4
Polar Sculpin	<i>Cottunculus microps</i>	307	9	307	0	307	4
Longtooth Anglemouth	<i>Gonostoma elongatum</i>	155	6	115	0	694	4

Table 2. (Cont'd)

Species	Codes	Numbers	Codes	Weight	Codes	Frequency
Threebeard Rockling <u>Gaidropsarus ensis</u>	115	6	118	0	616	4
Müller's Pearlside <u>Maurolicus muelleri</u>	158	5	159	0	17	3
Northern Searobin <u>Prionotus carolinus</u>	330	5	625	0	118	3
Gelatinous Seasnail <u>Liparis koefoedi</u>	505	4	643	0	159	3
Boa Dragonfish <u>Stomias boa ferox</u>	159	4	694	0	330	3
Roughhead Grenadier <u>Macrourus berglax</u>	411	4	158	0	626	3
Fish Doctor <u>Gymnelis viridis</u>	616	4	617	0	643	2
Greenland Cod <u>Gadus ogac</u>	118	3	620	0	158	2
Esmarks Eelpout <u>Lycodes esmarki</u>	643	3	621	0	617	2
Common Wolf Eel <u>Lycenchelys paxillus</u>	617	2	142	0	744	2
Newfoundland Eelpout <u>Lycodes lavalaei</u>	620	2	180	0	727	2
Rock Gunnel <u>Pholis gunnellus</u>	621	2	205	0	741	2
Stout Beardfish <u>Polymixia nobilis</u>	744	2	330	0	142	1
White Barracudina <u>Notolepis rissoii</u>	727	2	331	0	180	1
Fourspot Flounder <u>Paralichthys oblongus</u>	142	1	411	0	205	1
Spinytail Skate <u>Raja spinicauda</u>	205	1	412	0	331	1
Armored Searobin <u>Peristedion miniatum</u>	331	1	413	0	411	1
Roughnose Grenadier <u>Trachyrhynchus murrayi</u>	412	1	504	0	412	1
Longnose Grenadier <u>Coelorhynchus carminatus</u>	413	1	507	0	413	1
Striped Seasnail <u>Liparis liparis</u>	504	1	616	0	504	1
Longfin Seasnail <u>Careproctus longipinnis</u>	507	1	626	0	507	1
Cardinal Fish <u>Epigonus denticlatus</u>	677	1	677	0	677	1
American John Dory <u>Zenopsis ocellata</u>	704	1	704	0	704	1
Short Barracudina <u>Paralepis atlantica</u>	711	1	711	0	711	1
Barrelfish <u>Hyperoglyphe perciformis</u>	743	1	712	0	743	1
Beardfish <u>Polymixia lowei</u>	771	1	727	0	771	1

Table 4. Correlations among the sediment variables.

	Clay	Silt	Sand	Gravel	Mean Size
Silt	0.98	1.00	-0.30	-0.93	-0.97
Sand	-0.35	-0.30	1.00	0.34	0.31
Gravel	-0.93	-0.93	0.34	1.00	0.97
Mean Size	-0.99	-0.97	0.31	0.97	1.00
S.D.	0.62	0.64	0.28	-0.38	-0.55

The high intercorrelations present (Table 4) can cause computational problems in some of the analyses, and can also make interpretation more difficult. We therefore transformed the sediment data to three new independent variables with principal components analysis (Cooley and Lohnes 1971). The scores on the first three axes were used as values for these new variables. The percent of variance in each axis is shown in Table 5.

Table 5. Percent variance of principal components.

PC	Eigenvalue	Percent of total
		variance
1	3.600	60.01
2	1.096	18.27
3	1.278	21.31

These axes can be interpreted by examining the correlations between the sediment variables and the principal component scores on each axis (Table 6). The first principal component is highly correlated with gravel and mean size and highly negatively correlated with clay and silt. Thus, samples with generally coarser sediment will have higher scores and those with finer sediment will have lower scores on principal component axis 1. We call this variable SEDSIZE.

Table 6. Correlations of the sediment variables with the first three principal components (PC).

	PC 1 SEDSIZE	PC 2 SEDSAND	PC 3 SEDSORT
1. Clay	-0.89	-0.22	-0.40
2. Silt	-0.89	-0.17	-0.41
3. Sand	+0.22	0.96	-0.15
4. Gravel	+0.99	0.13	+0.08
5. Mean Size	+0.94	0.15	+0.29
6. S.D.	-0.34	0.22	0.91

The scores on axis 2 are primarily correlated with the amount of sand, and we thus call this variable SEDSAND. The third principal component axis is chiefly negatively correlated with the standard deviation of the sediment size distribution. Sediments with high scores on this axis will be well sorted, and we thus call this variable SEDSORT.

The scores, or values, for each new sediment variable are shown in Table 7. In the subsequent analyses correlating sediment (and other variables) with the fish distributions, each station received the values in Table 7, which correspond to the type of sediment shown at the station's position on the charts of sediment types.

Table 7. Scores for each sediment type on the three composite sediment variables.

Sediment Type	Composite variable		
	SEDSIZE	SEDSAND	SEDSORT
Sable Island sand and gravel ( 50% gravel)	1.75	-0.15	0.93
( 50% gravel)	1.51	0.70	0.72
(undetermined)	1.57	0.21	0.74
Sambro Sand	-0.32	0.44	-0.68
Scotian Shelf drift	-0.83	0.17	-0.78
Laurentian silt	-1.77	-0.47	-0.55
Lahave clay	-1.91	-0.89	-0.39

#### ECOLOGICAL DISTANCE INDICES

The starting point for the calculation of the ecological distances used in the cluster analyses is a sites by species matrix of species importance values (abundance, frequency, biomass, etc.). From this, inter-sample or inter-species distance matrices are calculated.

In this study we use a new inter-sample distance measure, and a modification of a published inter-species distance measure. In this section we provide considerable computational details of these distance measures. Many readers may wish to ignore this detail and can do so by omitting those paragraphs with a solid line in the right hand margin.

#### Inter-Sample Distances

There are many distance indices for measuring the dissimilarity among sets of sample pairs (Clifford and Stephenson, 1975). In all of these, the underlying model is that the distance index measures biological change, and that the distance index between paired samples increases as the amount of biological change increases. Thus, two samples with very dissimilar species composition will theoretically have a larger dissimilarity value than two samples with similar species composition. In actuality, all distance measures reach a maximum value at a certain point and then either remain constant or decline, even as the amount of biological change continues to increase (Figure 3) (Beals, 1973; Swan, 1970). In addition, given a constant amount of biological change, the variance of the distance index can be large and varied.

These severe inaccuracies stem from fundamental differences between the underlying assumptions of distance indices and the realistic properties of ecological and community data. All distance indices are based upon the assumption that species importance values vary linearly as biological change takes place. In practice, this assumption is rarely met (Beals, 1973, Austin, 1980), since species importance values tend to change in a non-linear, non-monotonic fashion as overall biological change is taking place, usually along pertinent environmental gradients (Figure 4) (Austin, 1976; Beals, 1973; Swan, 1970). In addition, the values are truncated, i.e. species importance values reach a value of zero and remain zero as the environment become more

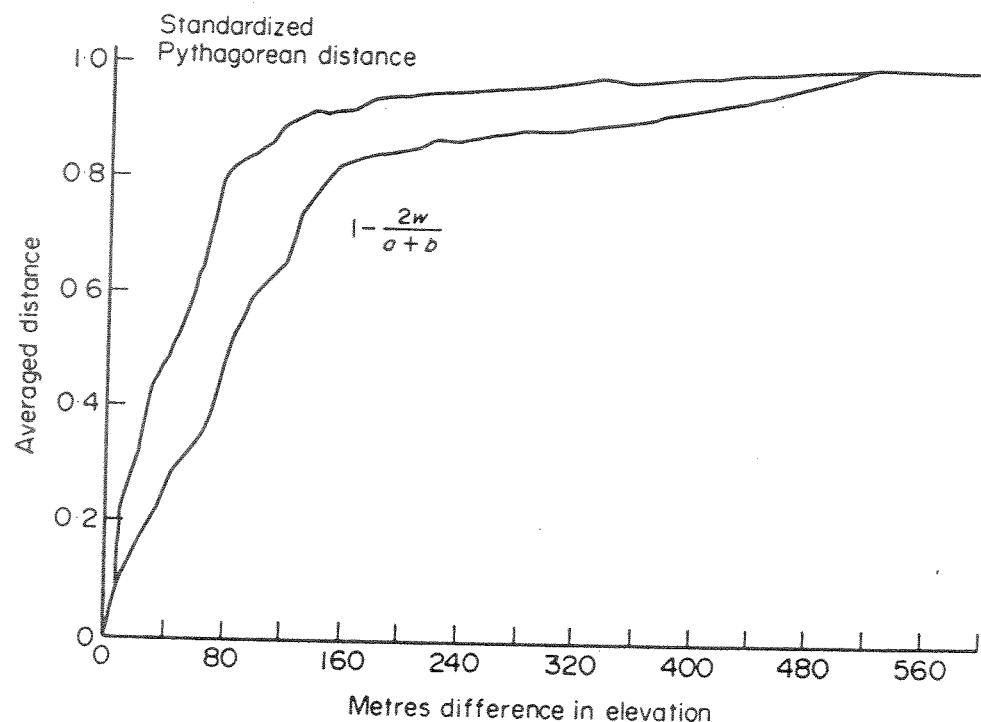


Fig. 3. Relation of two distance measures to an environmental gradient along which there is constant biological change with elevation. The distance measures are insensitive to the larger amounts of biological change. Distances were averaged for pairs of stands with 10, 20, 30, etc. meters difference in elevation. Data taken from the Rift Valley of Ethiopia, from 1000 to 1900 m, collected at 10 m intervals, ninety samples in all (from Beals, 1969).

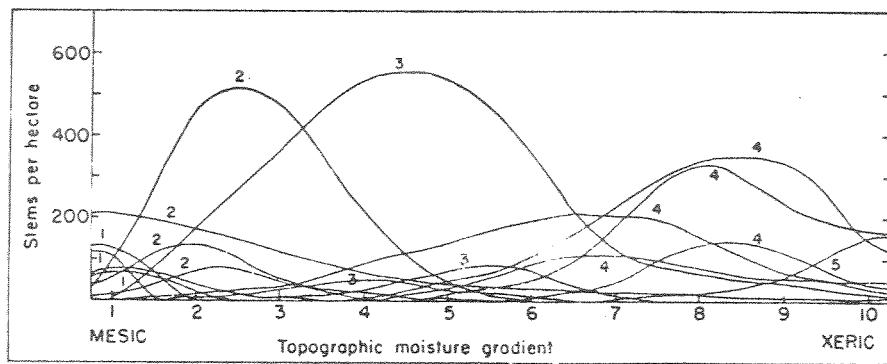


Fig. 4. Typical pattern of species distributions along an environmental gradient. Population distributions are shown for major tree species in the 1830-2140 m elevation belt in the Santa Catalina Mountains, southern Arizona, from mesic ravines (left) to xeric southwest slopes (right) (from Whittaker and Niering, 1965).

unfavourable to the species in question (Swan, 1970). This accounts for the leveling off illustrated in Figure 3. As a result, distance indices are insensitive to larger magnitudes of actual biological change. Another assumption in most if not all distance indices is that the importance values of each species change at the same rate as overall biological change takes place. This assumption is rarely met, because the slopes of species importance curves along environmental gradients can be radically different (Figure 4). This increases the variance of the distance measure.

#### The ZAD Index

A new distance index designed to cope with these ecological realities is described here. This measure, called the Zero Adjusted Distance (or ZAD) index, cannot be described by a simple formula, since it involves several steps. The total information contained in a set of species importance values is obtainable only by viewing the data from several different perspectives.

Figure 5 shows the relationship between a typical distance index (curve Q) and the ideal distance measure (curve I), which should increase linearly with increasing biological change between samples. The ZAD index calculates Q and Z (Figure 5) separately, and then sums them to arrive at I. Q (the quantitative component) is a distance estimate calculated directly from the species importance values. The calculations here attempt to compensate for the problems caused by non-linear, non-monotonic changes in species abundance, and by unequal rates of change in abundance among species. Z (the zero adjustment component) adjusts for the leveling off of curve Q by adding a steadily increasing amount to Q in order to reach the ideal distance, I. Z is calculated separately using the inter-species distances. It is designed to compensate for truncation of species importance values as increased overall biological change takes place. Thus, Q is most important for estimating the shorter distances, while Z increasingly contributes more as the distances become longer.

#### Calculation of Q

The quantitative component (Q) of the inter-sample distance is based on the quantitative species differences, and is calculated as:

$$Q_{ij} = \frac{\sum_{k=1}^s [W_{ijk} B_{ijk} |X_{ki} - X_{kj}|]}{\sum_{k=1}^s [W_{ijk} B_{ijk} \text{MAX}(X_{ki}, X_{kj})]}$$

where s is the number of species, and i and j are the samples being compared. The X's are species importance values transformed by a square root and standardized by the species maximum. The absolute value of the difference in abundance of species k at two sites i and j ( $|X_{ki} - X_{kj}|$ ) is termed the X difference.

The transformation makes changes in importance values more linear as overall biological change occurs (Smith, 1976), and reduces variability in the rates of change of different species. The standardization removes the irrelevant effect of scale on X differences, since these will otherwise tend to be larger in the more abundant species irrespective of the amount of overall biological change. As will be seen, it also creates a somewhat predictable relationship between the magnitude of the X difference and the 'breadth' of the species.

**Calculation of  $B_{ijk}$ :** As a constant amount of overall biological change takes place, rates of change in species importance values will vary unpredictably among species, depending on their abundance or breadth of distribution (Figure 6a). When the data are standardized by species maximum, however, species with wide breadths will tend to have lower rates of change than will species with narrower breadths (Figure 6b). As the example in Figure 7 shows, the predictable inverse relationship between breadth and rate of change in standardized importance values can be used to equalize the relative contributions of the widespread and narrow species. This is done by multiplying each X difference by the appropriate  $B_{ijk}$ , which is a measure of the relevant 'breadth' or range of habitats over which species k is distributed. Figure 7 presents a simplified example, in which the species distribution curve is symmetrical and both samples i and j are on the same side of the species peak. In practice, adjustments must be made for asymmetrical curves, for instances when i and j are on opposite sides of the peak, and for multidimensional species distributions.

The specific method for calculating B involves determining the range of the species in an ordination space computed from a component of the  $Z_{ij}$  values. These calculations are somewhat complex, since a species may have different 'breadths' on either side of its peak, or along different gradients of biological change. Because of this,  $B_{ijk}$  is calculated separately for each ij comparison (see Appendices A and B for a detailed discussion).

**Calculation of  $W_{ijk}$ :** As overall biological change takes place, non-monotonic changes in importance values can cause distortions in the X differences (Beals, 1973). The most reliable X differences will occur with species which have both values (in the two samples being compared) on the same side of their peak value (Smith, 1976). This is because their importance values will increase monotonically with the true amount of biological change. In contrast, when the samples being compared are on opposite sides of a species' peak, the X differences can be unrealistically small (Figure 8). The worst X differences will occur when both samples being compared are far from, and on the opposite sides of, the peak value for the species, since the actual amount of biological change will be large and the X difference small. The least distorted X differences (with samples on opposite sides of the peak) will occur when one of the samples being compared is relatively near the peak value for that species. These alternatives are

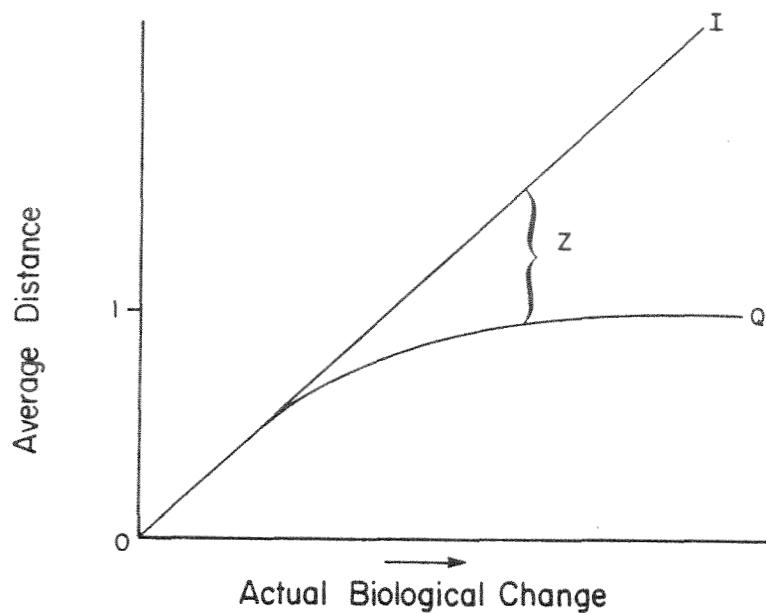


Fig. 5. Relationship between the two components of the ZAD distance index and the ideal distance curve, I. Q, the quantitative component, levels off at 1, while Z, the zero adjustment component, continues to increase with increasing biological change.

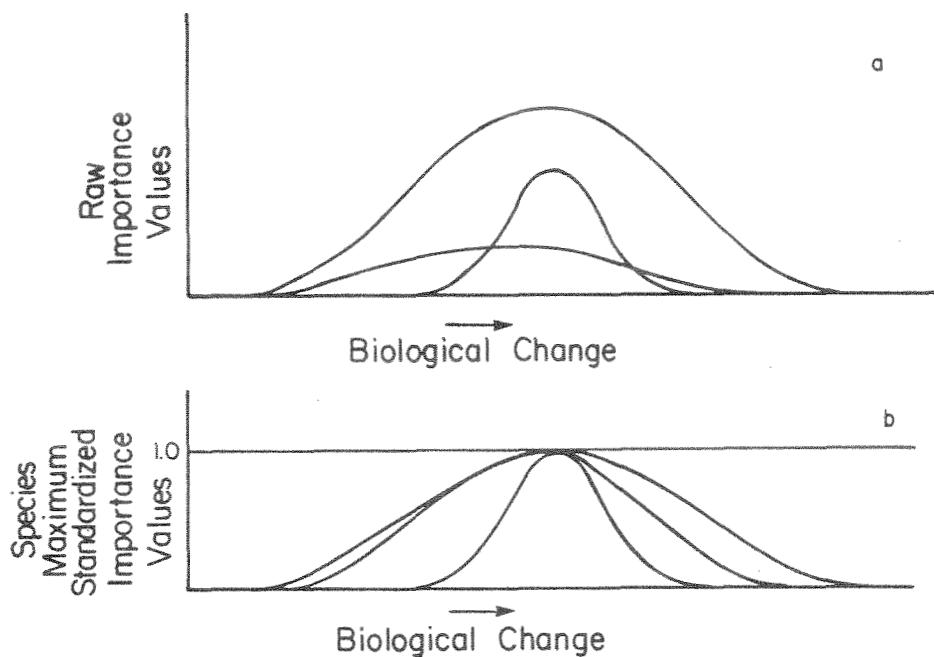


Fig. 6. a) Species distributions along a biological gradient. With raw data, and when comparing sites on the same side of the species peak, there is an unpredictable relationship between slope, or rate of change in a species importance value, and increasing biological change. b) Same data as a), standardized by species maximum. Slopes of species curves, on the same side of the peak, are now predictably, and inversely, related to species breadth along the gradient.

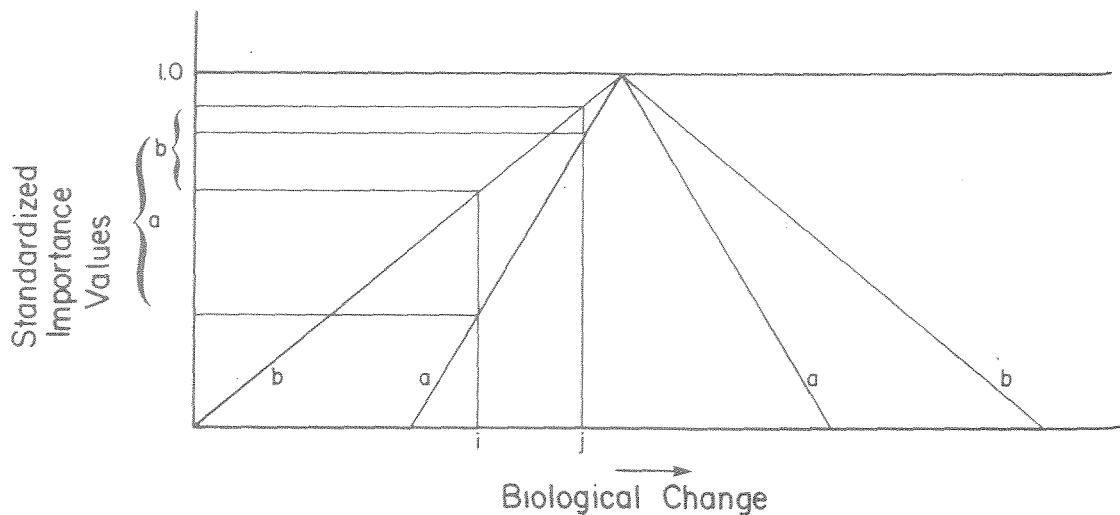


Fig. 7. Example of the use of  $B$  to equalize the contribution to  $Q$  of species with different breadths. Species a's breadth is half that of species b, and its slope is twice as high. The  $X$  difference for species a (shown in brackets on the  $yx$  axis) is therefore twice as great.  $X_{ja} - X_{ja} = 0.5$  and  $X_{jb} - X_{jb} = 0.25$ . Multiplying each of these  $X$  differences by a term ( $B$ ) proportional to each species breadth along the gradient equalizes the magnitude of the  $X$  differences, e.g.  $(0.5) 1 = 0.5$  and  $(0.25) 2 = 0.5$ . To facilitate making this point the species distribution curves are shown with straightlines. Such lines should represent the average of the range of curves (concave to convex) usually encountered.

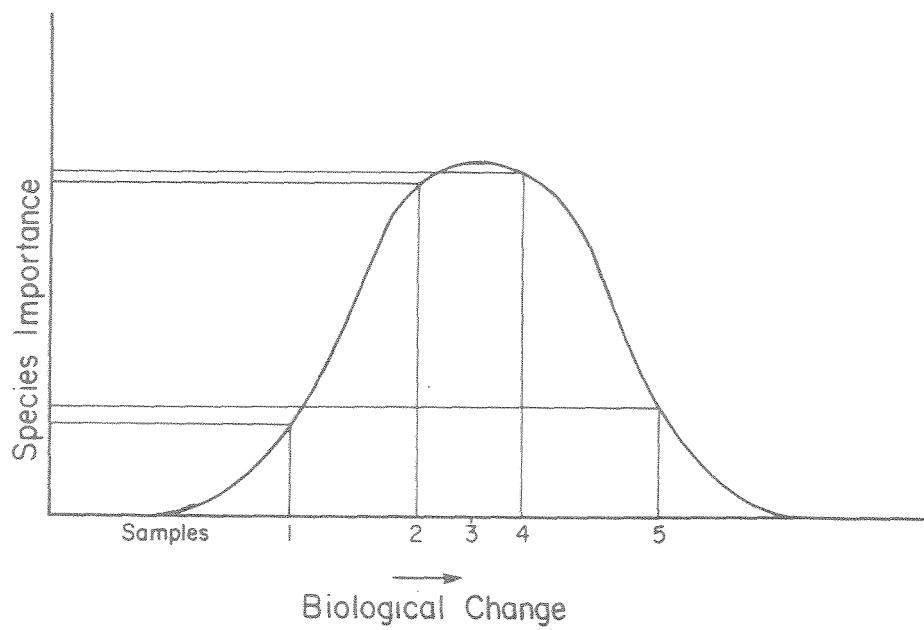


Fig. 8. The effect of sample position relative to the peak on the accuracy of inter-sample comparisons. The  $X$  difference between samples 1 and 2 or between samples 4 and 5 is a much more accurate measure of the true biological change between samples than is the  $X$  difference between samples 1 and 5 or between 2 and 4. Samples closer to the peak, however, (e.g. 2 and 4) furnish better comparisons than samples far from the peak (e.g. 1 and 5).

illustrated in Figure 8.

The  $W_{ijk}$  values are designed to correct for these distortions by giving more weight to those  $X$  differences that convey better information about the actual amount of biological change (see Appendices A and B for further detail).

**Denominator of Q:** The denominator for the  $Q_{ij}$  equation is the maximum possible value the numerator could obtain if there were no species in common in the two samples being compared. Division by this maximum value scales the  $Q$  values from 0-1. Such predictability in the scale of  $Q$  is important when subsequently adding  $Z$  to  $Q$ . In addition, it considerably improves the  $Q$  values, especially the longer ones, which would otherwise fluctuate widely and randomly around the asymptote of  $Q$ . This is because, once complete species turnover has occurred between two samples, the direction of change of the  $X$  difference is dependent solely on whether more species are increasing or decreasing in abundance along a particular part of the gradient.

#### The 'Zero-Adjustment' Component, $Z$

The calculation of this component requires two steps as follows.

a) For each zero value in the data matrix, an estimate of the degree to which the species in question is 'missing' is calculated. The method used is conceptually the same as that proposed by Swan (1970) to measure 'degree of absence' of species not occurring in a sample. We have tested Swan's procedure with simulated data and found it to be increasingly insensitive to biological change as a species becomes more 'missing'. A more sensitive technique is proposed here. The method calculates the 'degree of absence' for a species absent from a sample as:

$$M_{ki} = \frac{\sum X_{mi} D_{km}}{\sum X_{mi}},$$

where  $M_{kj}$  is the degree of absence of species  $k$  in sample  $i$ , and  $X_{mi}$  is the square-root transformed, species maximum standardized value of species  $m$  in sample  $i$ . Species  $m$  occurs in sample  $i$  and species  $k$  does not occur in sample  $i$ .  $D_{km}$  is the inter-species distance between species  $k$  and species  $m$ . The inter-species distance should measure relative habitat preferences. This is discussed below.  $M_{ki}$  is actually the weighted average distance from species  $k$  (which is absent from sample  $i$ ) to all species which actually do occur in sample  $i$ . If species  $k$  is very different in habitat preference compared to the other species in a sample, then it will have a relatively high  $M$  value for that sample (i.e., it has a high degree of absence). After all  $M$  values are calculated, they are rescaled so that the minimum  $M$  value is zero. This is because the

$M_{kj}$  values tend to be high by a constant amount.

b) The  $M$  values are used to calculate independent estimates of the between-sample distances. These estimates might be expressed as:

$$E_{ij} = \max_{k=1}^s (M_{ki}, M_{kj}).$$

Species which occur in one and only one of the two samples ( $i$  or  $j$ ) are considered when selecting the maximum. The rest of the  $M$  values are ignored. This is a reasonable estimate of distance since the "most missing species" occurring in only one of the samples should indicate how different the samples really are.

We have, however, selected a more conservative procedure which does not rely on a single maximum  $M$  value. This is calculated as:

$$E_{ij} = \frac{\sum_{k=1}^s M_{ki} M_{kj}}{\sum_{k=1}^s M_{ki} + \sum_{k=1}^s M_{kj}}.$$

As above, only those species occurring in one of the two samples are considered in the sums. This estimate is simply the weighted average of the  $M$  values, with each  $M$  weighted by its own value. This gives more weight to the larger  $M$  values. Only the largest 50% of the distance values are used in the weighted average.

The  $E_{ij}$  values are based on species absence in one of the two samples being compared. As the samples being compared are more similar, there will be fewer and fewer species which are absent from one sample and present in the other. This leads to two important properties of  $E_{ij}$ . 1) The shorter  $E_{ij}$  values will be the least reliable, because they are based on the least amount of information. 2) The shorter  $E_{ij}$  values will tend to be too short in relation to the actual amount of biological change. This is because they are insensitive to changes in species importance when a species is present in both samples. Such changes are very important when comparing biologically similar samples.

These properties are ideal for calculating  $Z_{ij}$ , because we wish the shorter distances to be based mostly on  $Q_{ij}$ . The  $E_{ij}$  values will not become large enough to add significantly to the final distance until larger amounts of biological change take place.

**Calculation of Z From E:** It can be seen (Figure 5) that the contribution of  $E$  must increase exponentially as  $Q$  levels off.  $E$ , however, will tend to vary linearly with the true amount of biological change, since it is an independent estimate of inter-sample distance. To make the contribution of  $E$  exponential, it must be multiplied by a factor dependent on the rate at which  $Q$  levels off. We calculate such a factor

as follows:  $F_{ij} = \text{MAX}(1, 3Q_{ij}^2)$ . Table 8 shows values of F as Q increases. Tests with simulated data show these values to be sufficient to compensate for the leveling off of Q. Therefore  $Z = F_{ij}E_{ij}$ , and the final ZAD distance will be:

$$D_{ij} = Q_{ij} + F_{ij}E_{ij}$$

Theoretically, D should approach the ideal distance line in Figure 5. Tests with simulated data show this to be the case. In addition, analyses with actual survey data have shown good results when subjectively compared with analyses using other distance indices.

Table 8. Values of F as the value of Q increases. The exponential increase in F as Q approaches one is required to compensate for the leveling off of Q (see Figure 5).

$Q_{ij}$	$F_{ij}$
-.58	1.00
.70	1.47
.80	1.92
.90	2.43
.95	2.71
1.00	3.00

Some may argue that much computation could be avoided by simply summing F and Q to obtain the final distance. This would have two major drawbacks. It would greatly magnify any error in Q as Q levels off, since F is derived from Q. With the ZAD distance, E is an independent estimate of the distance, and a large amount will be added to Q only if both Q and E are relatively large. Secondly, after Q reaches a value of one (its asymptote), F would become a constant value of three. Beyond this point, such an index would be incapable of measuring further biological change. The ZAD distance, however, continues to increase after Q levels off, since E continues to increase. It may also be argued that E could be used directly as a distance measure. Since E is based on species absences, it utilizes progressively less information as the samples being compared become more similar. We would thus not expect E to estimate the shorter distances as well as Q, which is based on increasing information as samples become more similar.

#### Inter-Species Distances

The inter-species distance matrix is used in the computation of the  $E_{ij}$  component of the inter-site distance index (ZAD). However, the inter-species distances are also useful in their own right (Austin and Belbin, 1982). As noted, these distances should measure the relative habitat preferences of the species. Most inter-species distance indices are related to inter-species overlap, which is unsuitable for our purposes. This is because overlap measures cease to change in value once two species are non-overlapping. We require a measure which continues to increase as the species in question are found in more dissimilar habitats. Without this characteristic in the

inter-species distance, E values become constant once all the species in the samples being compared are non-overlapping. The steps in the Calculation of the inter-species distances are as follows.

#### Data Transformation and Standardization

The species importance values are first transformed by a square root. This dampens the larger chance fluctuations which may occur in the more abundant species. Following the transformation, the data are standardized by the species maximum, which scales all species abundances from 0-1. Removing the effect of scale is necessary for the measurement of inter-species overlap in the second step below (Smith, 1976). If the data are not standardized, overlapping species with species importance values on different scales could still have large inter-species distances.

#### Calculation of Inter-Species Overlap

The Bray-Curtis distance index is used to measure the distributional overlap of the species. The distances are actually inversely proportional to the overlap. Bloom (1981) demonstrates the suitability of the Bray-Curtis index for this purpose. These overlap values may be distorted by uneven sampling of the different temporal and spatial habitats in the survey areas (Colwell and Futuyma, 1971). This can be corrected for somewhat by reusing each sample in the overlap calculations. The number of times a sample is reused is proportional to the calculated sample distinctness (Smith, 1976, Smith and Guggenheim, In prep.).

#### Calculation of Relative Habitat Preference

The 'overlap' distances are converted to distances which measure the relative habitat preference of the species. Such distance values are proportional to the dissimilarity of the habitats in which the species being compared are found.

To accomplish this, the inter-species distance matrix from the previous step is subjected to the TWO-STEP procedure described in Austin and Belbin (1982), and slightly modified here.

Our computations differ from those described in Austin and Belbin (1982) in two ways. First, we transform the species importance values by a square root and then standardize by the species maximum. Second, to calculate the distance matrix measuring relative habitat preference ( $T$ ), we use

$$T_{ij} = \frac{\sum_{k=1}^m |D_{ik} - D_{jk}|}{n},$$

where  $D_{ik}$  and  $D_{jk}$  are distances from rows i and j, respectively, of the asymmetric Bray-Curtis distance matrix, i and j are the species being compared, n is the number of times that  $D_{ik}$  and  $D_{jk}$  are not both equal to

1, and m is the number of species.

Austin and Belbin (1982) do not include a denominator in the calculations. We do so because we wish to put T on the same scale as D, i.e. 0-1. We could accomplish this by using the average of the  $|D_{ik} - D_{jk}|$  values. In this case the denominator would be m instead of n. However, n is more appropriate because it is the number of comparisons that actually contribute information to T. When  $D_{ik} = D_{jk} = 1$ , there is no information conveyed by species k about the relationship between species i and j. Species k has no relationship to either. This does not by any means indicate that species j and k are similar in their relative habitat preferences.

Without the division by n (or m), the range of T would be somewhat dependent on the number of species used in the calculations. It is important that the scale of T be predictable, since we are indirectly calculating Z from the inter-species distances. The final inter-sample distances are the sum of Q and Z, and the scale of Z cannot be affected by something as irrelevant as the number of species used in the calculations.

This technique should work well for species which are in similar or moderately similar habitats. The distances between species in the more dissimilar habitats will still tend to be too short. To correct for this, the STEP-ACROSS procedure originally conceived by Williamson (1978) and generalized by Smith (1981b) is used. Here the longer distances are recalculated from the shorter distances.

#### HIERARCHICAL CLASSIFICATION

Hierarchical classification displays the relationships between entities (the units being classified) with a two-dimensional, hierarchical structure called a dendrogram. Agglomerative classification successively fuses the most similar entities (or groups of entities) to form larger groups or clusters. This is in contrast to the divisive technique which successively divides larger groups into smaller groups or single entities (Williams, 1971).

The starting point for constructing the dendrogram is the distance matrix. The shortest distance in the matrix is chosen and the two corresponding entities are fused into a single group. The distance between the new group (representing the fused entities) and all other entities is then calculated and entered into a new distance matrix. The process of selecting the shortest distance and fusing the corresponding entities is repeated until all entities are joined in a single group.

Clustering strategies differ in the method of calculating the distance between new groups (entities). The strategy used here is the flexible clustering or sorting strategy. Associated with this method is the variable coefficient beta. As the beta value increases (i.e. approaches 1.0), the clustering becomes weaker and few distinct groups will result. The

dendograms suffer from excessive 'chaining', i.e. entities join groups one at a time rather than forming distinct clusters. The disadvantages of this type of result are that there are few groups to interpret, and the relationships among entities are poorly defined. This defeats the purpose of the analysis.

Very low values of beta (i.e. approaching -1.0) force all entities into one of a number of approximately equally-sized, tightly clustered groups. This makes interpretation very easy and clear-cut, but the results are forced into such a pattern even if it does not represent reality. The probability of misclassification is also higher.

Values of beta near zero produce results about halfway between these two extremes. In practice, many ecologists have found that an empirically selected beta value of -0.25 gives satisfactory results (Clifford and Stephenson, 1975). This beta value tends to give distinct, easily interpreted and realistic clusters.

#### TWO-WAY COINCIDENCE TABLES

The dendograms from the site and species classification analyses were used to construct two-way coincidence tables, which are simply the biological data matrix with the rows (species) and columns (sites) arranged in the same order as on the corresponding dendograms. The data values were standardized and converted to symbols for compactness and ease of interpretation. The symbols in this study were based on species mean (of values 0) standardized data.

Two-way tables are informative and valuable because similar sites and species are grouped, and appear in contiguous positions in the table. As a result, biological patterns can easily be seen and interpreted. In addition, reference to the table is very useful when choosing groups from the dendograms.

The specific order of entities along a dendrogram can be quite arbitrary, however, since any one node on the dendrogram can be rotated 180 degrees without changing any groupings. The clustering algorithm was therefore modified to create a maximally informative order of entities along the dendrogram. The main trend in the data was found by calculating scores for each entity along a polar ordination axis. The order of entities along the dendrogram was made to approach the order along the ordination axis by appropriate rotation of the nodes. As a result, the rows and columns of the two-way table are arranged in an order consistent with the major patterns of change found in the data.

#### MULTIPLE DISCRIMINANT ANALYSIS

Correlations between classification groups and environmental parameters were studied with multiple discriminant analysis (Cooley and Lohnes, 1971; Hope, 1969; as canonical analysis of discriminance). As in Smith (1976), Green and Vascatto (1978), and Bernstein et al.

(1978), classification techniques were used to generate the groups used in the analysis. Weighted discriminant analysis (Smith, 1978) was used to increase the sensitivity of the analysis to information from the classification analysis about the strength of group membership, group cohesiveness, and intergroup relationships.

The stations or strata (depending on the particular analysis) are represented as points in a multidimensional space defined by the environmental variables. These points are projected onto axes that minimize the within-group variation while maximizing the between-group variation. These axes are independent and are correlated with the variables potentially important in the group separation. The environmental variables correlated with the axes are indicated with standardized coefficients (Green, 1971) or with coefficients of separate determination (Hope, 1969). The latter were used here.

The conditions necessary for statistically testing the significance of the separation of groups along the various axes (Green, 1971) are rarely, if even, met. However, the success of classification of sites into their groups on the basis of their scores on the discriminant axes is indicative of the discreteness of the groups. The classification of sites was achieved by first calculating the centroid or mean position of each group in discriminant space. Each site was then assigned to the group to whose centroid it was closest. Success is measured by the percent correct classification for each group.

#### PRINCIPAL COORDINATES ANALYSIS

In principal coordinates analysis, each sample corresponds to a point in a multi-dimensional space. The distances between points in this space are proportional to the biological dissimilarity of the corresponding samples. This space is viewed through dimensions which give a maximal amount of information about the patterns of biological change. These dimensions are termed axes, and the coordinates of the points of each axis are called scores. The first few axes will usually represent the major independent trends of community change. Principal coordinates analysis is discussed more fully in Sneath and Sokal (1973).

#### RESULTS

##### TWO-WAY CLUSTERING AND DISCRIMINANT ANALYSIS OF INDIVIDUAL SURVEYS

The next 18 sections (1970 summer - 1981 fall) present detailed results of the analysis of each survey. The reader interested primarily in the overall picture may wish to read only the first of these (1970 summer) then proceed to the section entitled "Consistency of Species Groups Through Time".

##### 1970 Summer

We discuss the results of this first survey in detail to provide an example of how to

interpret the cluster and discriminant analyses for the other surveys. Results of subsequent survey will be summarized only. We present enough information, however, for readers to develop further interpretations and conclusions on their own.

The dendrogram resulting from cluster analysis of the sites (Figure 9), and the two-way table (Figure 11) permit an assessment of the relative differences among sites. There are two major breaks that divide the sites into three main groups (Figure 11). These major site groups are indicated with separate symbols on a map of the Scotian Shelf (Figure 12). The first group of sites (I) includes those at greater depths, along the edge of the shelf and in basins. The second major site group (II) is made up of stations on the eastern part of the shelf, while the third (III) occurs on the western shelf and in the Bay of Fundy.

The two-way table (Figure 11) shows that these major site groups also have distinct assemblages of fishes. In general, silver hake, angler, white hake, smooth skate, witch, redfish, grenadier, and longfin hake are relatively common and abundant at the deep sites of major site group I. Other species, except for thorny skate, are relatively scarce. In major site group II, on the eastern shelf, sea raven, yellowtail, longhorn, cod, plaice, and thorny skate are relatively abundant. All other species are relatively scarce. Finally, site group III is characterized by relatively abundant haddock, but only scattered occurrences of other species.

The site dendrogram also displays relative differences among sites within the three major groups (Figure 9). This, along with information from the two-way table (Figure 11) was used to further divide the sites into 24 smaller site groups. Each of these smaller site groups is also characterized by a distinct species assemblage. For example, site group 2 has relatively abundant grenadier and longfin hake, typical of major site group I (Figure 11). It has, however, very few of the other species common in this major group (i.e. thorny skate, white hake, smooth skate, and witch).

The species clustering (Figure 10) permits an identification of species groups and species with similar habitat preferences. There are two extremes of a continuum of species, those like barndoor skate, lance, and mailed sculpin, that were not consistently found with other species, and those like smooth skate, witch, and redfish, whose distributions match (Figure 10). The tendency of species to form consistent groups from year to year is the focus of a separate analysis below.

The two-way table (Figure 11) is a means of illustrating the association of species with areas, and then inferring the habitat requirements or preferences of these species. The discriminant analysis described below, however, provides a more powerful method of inferring the influence of environmental variables on species distributions.

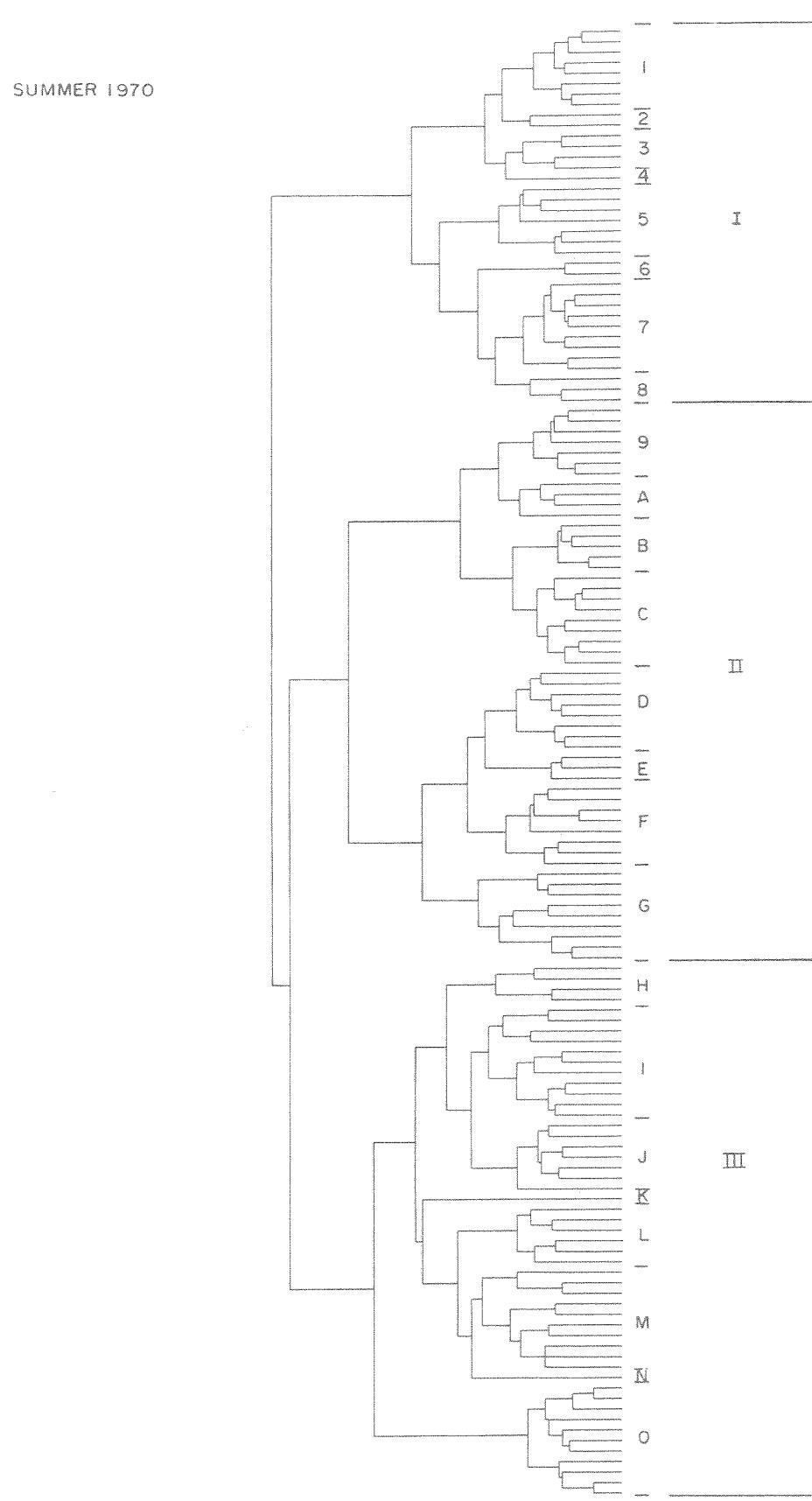


Fig. 9. The site dendrogram, summer 1970. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 11.

SUMMER 1970

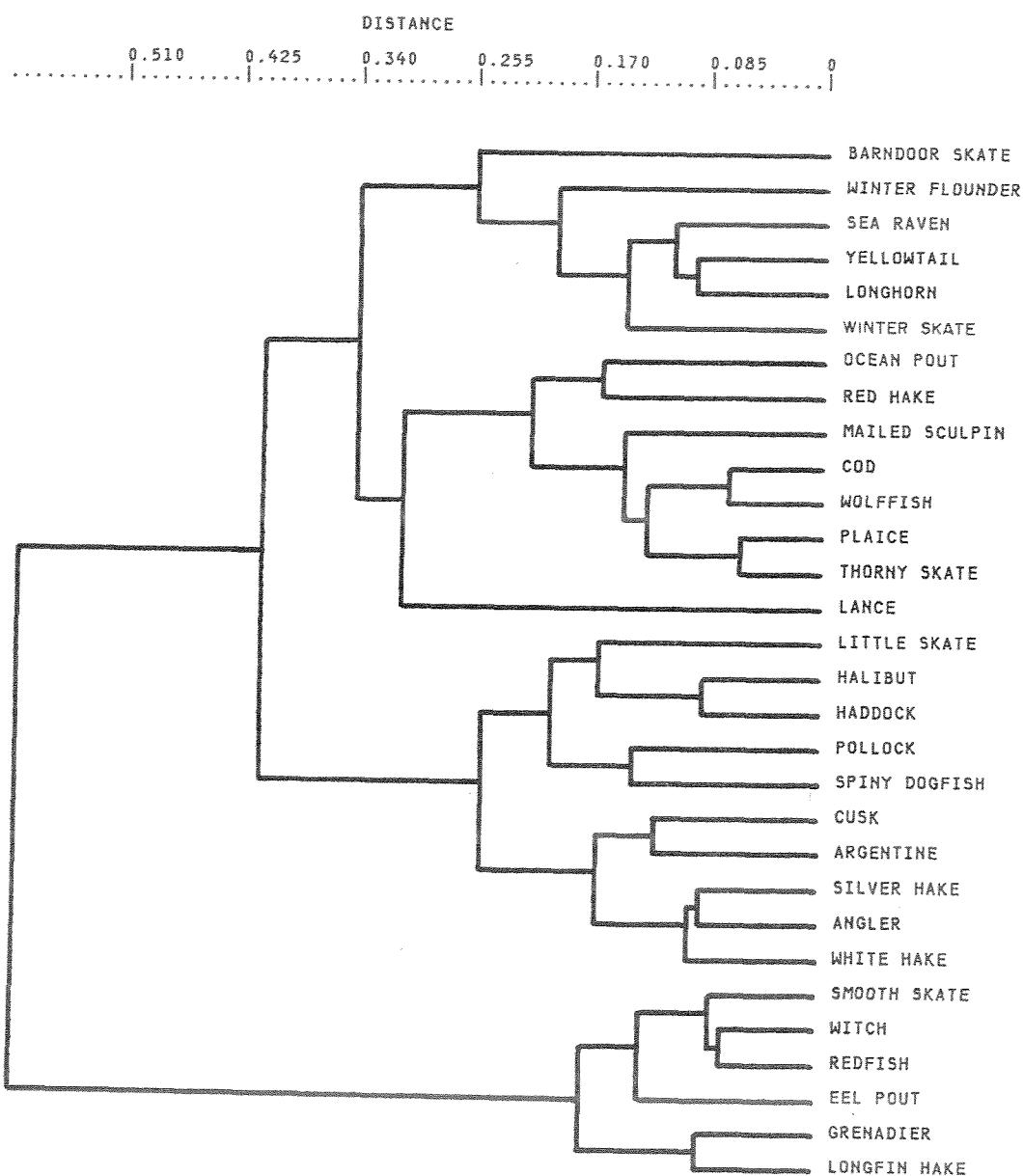


Fig. 10. The species dendrogram, summer 1970.

Fig. 11. The sites times species two-way table, summer 1970. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; - = 0.5-1.0; ++ = 1-2; \* = greater than 2.

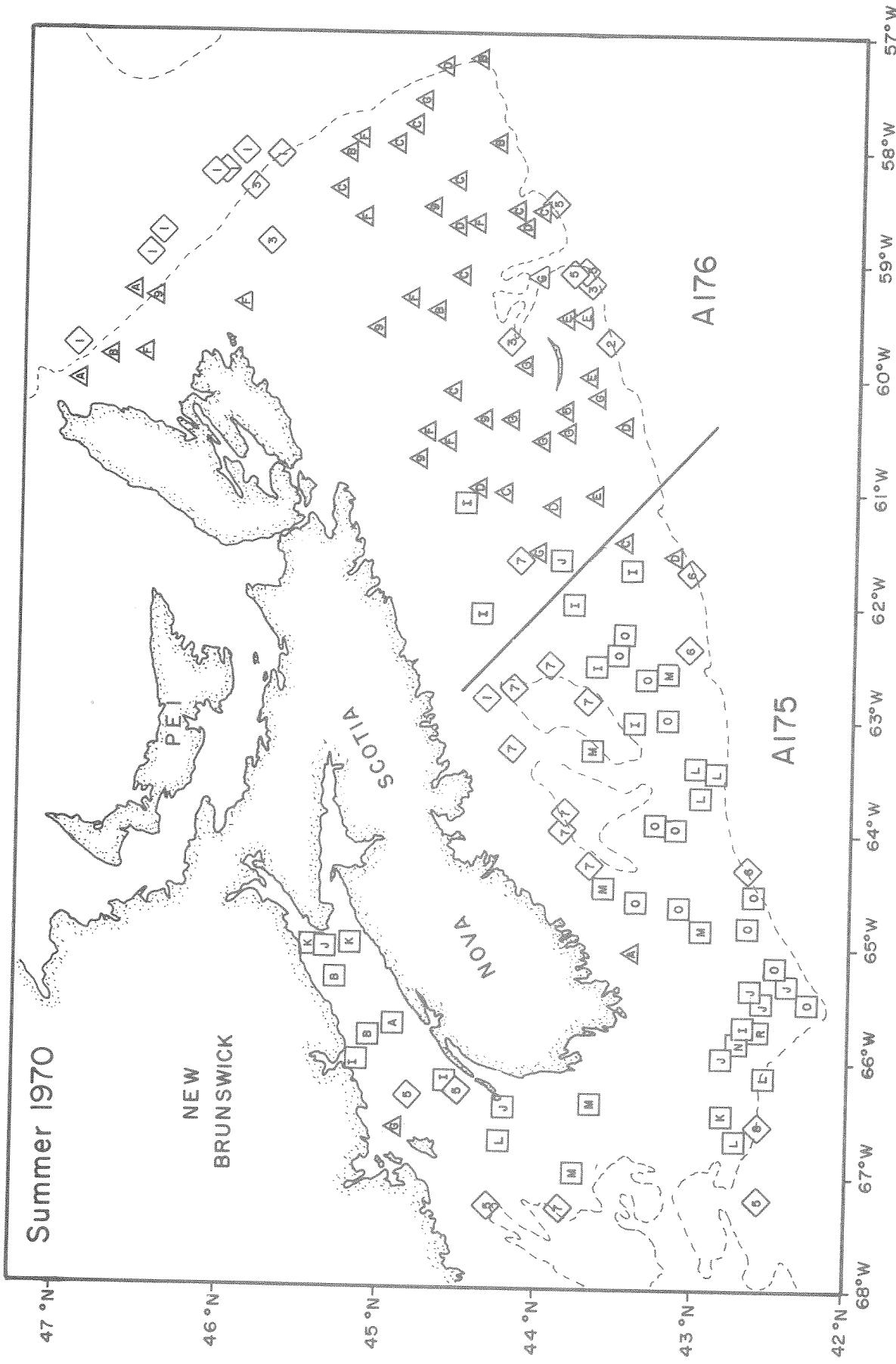


Fig. 12. The areal distribution of site groups, summer 1970. The symbols correspond to those in Figure 11.

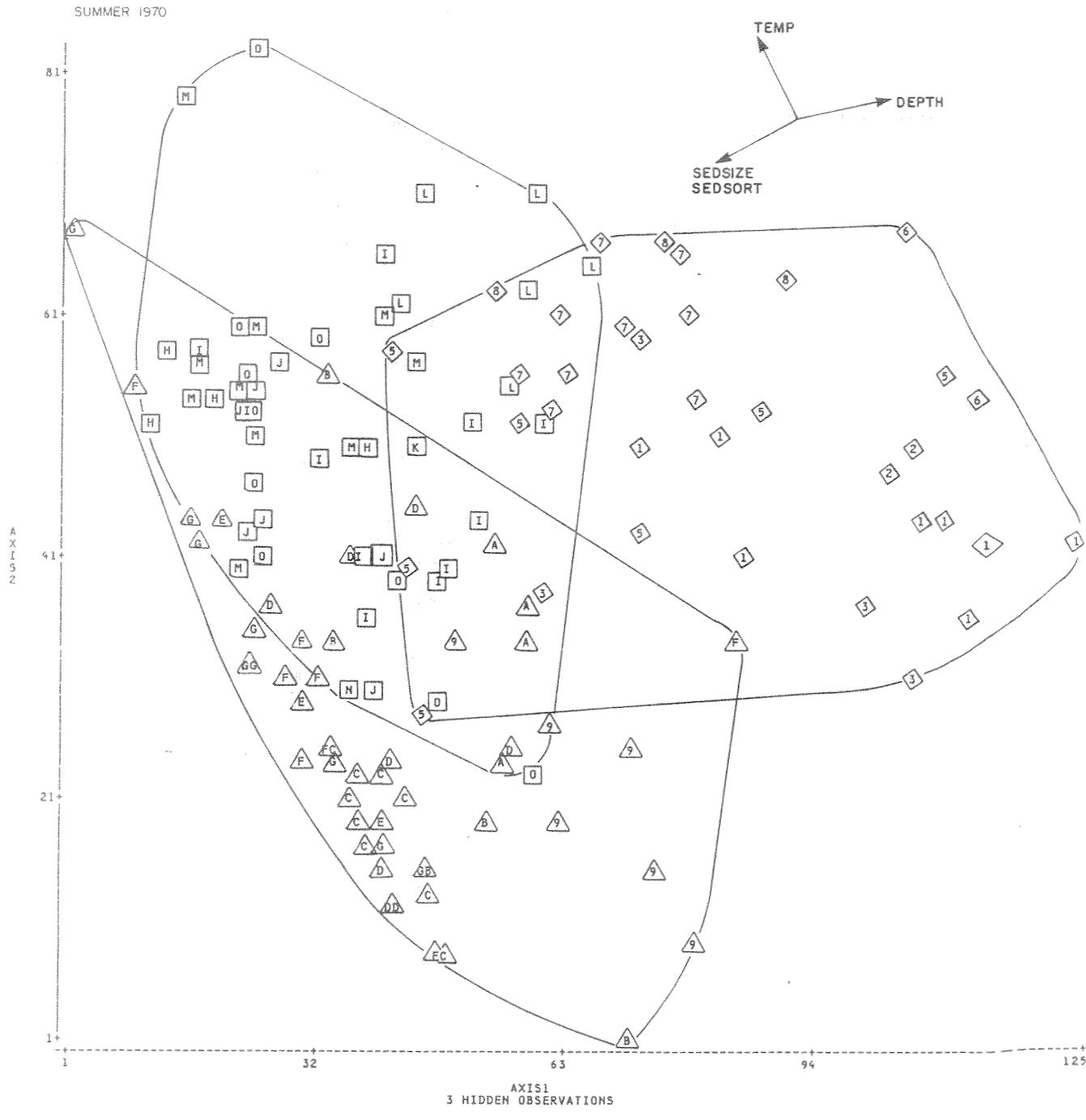


Fig. 13. The distribution of site groups in discriminant space, summer 1970. The symbols and numbers/letter codes correspond to those in Figure 11. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

Each site is plotted in the space formed by the first and second discriminant axes (Figure 13). Since the first two axes accounted for 95.1% of the group separation (Table 9), we considered it unnecessary to treat any subsequent axes. In addition, subsequent axes provided no further separation among the major site groups. Depth, sediment size factor, and sediment sorting factor contributed most to axis 1, while temperature, sediment size factor, and sediment sorting factor contributed most to axis 2 (Table 9).

Table 9. Coefficients of separate determination (Summer 1970). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	32.6	0.1	1.7	11.6
2. Temp	0.8	24.1	27.6	3.2
3. Salinity	3.3	9.0	9.3	18.2
4. SEDSIZE	37.3	30.4	29.7	35.5
5. SEDSAND	8.6	15.9	17.0	7.8
6. SEDSORT	17.4	20.6	14.7	23.7
Eigenvalues	8.2	2.4	0.3	0.1
Percent of Group Separation	73.7	21.5	3.1	1.2

The standardized values for each environmental variable at each station are plotted in the space defined by the first two discriminant axes (Figure 14) in order to show their interrelationships. Values range from 1-9 for each variable. For example, the 1's in Figure 14 indicate stations with relatively low temperature, and the 9's stations with relatively high temperature. The plots of standardized environmental variables are summarized on Figure 13 by arrows that illustrate the gradient of each important variable in the discriminant space.

The major site groups are shown in the discriminant space created by the first two axes (Figure 13). Separation of the groups is a function of the values of the environmental variables that characterize each site group. One of the primary values of this analysis is that it permits the development of explicit hypotheses about the influence of a suite of environmental variables on the structure of the species assemblages. This is because the species assemblages, as illustrated in the two way table (Figure 11), were used to define the site groups.

Site group I (along the shelf edge and in basins) is concentrated in the upper right portion of the space, an area with the greatest depth, intermediate temperatures, and small, poorly sorted sediment particles. Since the two-way table (Figure 11) shows that silver hake, angler, white hake, smooth skate, witch, redfish, grenadier, and longfin hake are relatively abundant in site group I, this suggests that these species are found predominantly in environments characterized by the just-described suite of environmental variables. The eastern shelf sites (major site group II) are grouped in the lower left of the

space, characterized by shallow depth, low temperature, and large, well sorted sediment particles. The western shelf sites (major site group III) occupy the upper left part of the space. Sites in this area had shallow depth, and variable (intermediate to warm) temperature, with a wide range of sediment size and sediment sorting.

There is some overlap between major site groups in the discriminant space. In some cases this can be related to aspects of species distributions illustrated in the two-way table (Figure 11). For example, three sites from site group 5 are far to the left of the rest of the sites in their major site group (I). These three sites are shallower, and have larger, better sorted sediments than other sites in group I. The two-way table (Figure 11) shows that site group 5 also has much fewer witch and redfish than other sites in group I.

#### 1971 Summer

There are four major breaks in the site dendrogram (Figure 15) and the two-way table (Figure 17) that divide the sites into five major spatial groups (Figure 18). The breaks were based on the dendrogram and on the distribution of species assemblages illustrated in the two-way table (Figure 17). The first group of stations (major site group I) includes stations along the edge of the shelf and in basins, and is characterized by relatively abundant longfin hake, grenadier, silver hake, angler, redfish, white hake, and witch. Other species are rare or absent. The second group of stations (II) is along the edge of the shelf, and on parts of Emerald and Banquereau Banks. Relatively abundant cod, plaice, thorny skate, and mailed sculpin characterize these sites. Major site group III includes stations on Sable Island Bank and parts of Banquereau Bank, with relatively abundant plaice, sea raven, winter flounder, longhorn, yellowtail, and winter skate. Major site group IV is made up of a few stations characterized mainly by an absence of most species. Major site group V is in the Bay of Fundy and on parts of Browns, Lahave, and Western Banks, with relatively abundant haddock, cod, and wolffish.

The sites are further subdivided into 22 subgroups, each with distinct species assemblages. For example, site group I has fewer haddock and more sea raven than other site groups in major site group V. Site group 6 has the relatively abundant plaice and thorny skate typical of major site group III, but lacks the species common in other site groups in major group III.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 16) and the two-way table (Figure 17). Some species, such as barndoor skate, eel pouts, ocean pout, and red hake are relatively rare and their distributions do not consistently correspond with those of any other species. A comparison of the two-way table (Figure 17) with the map of the site groups on the Scotian Shelf (Figure 18) reveals the spatial distribution of the species groups. For

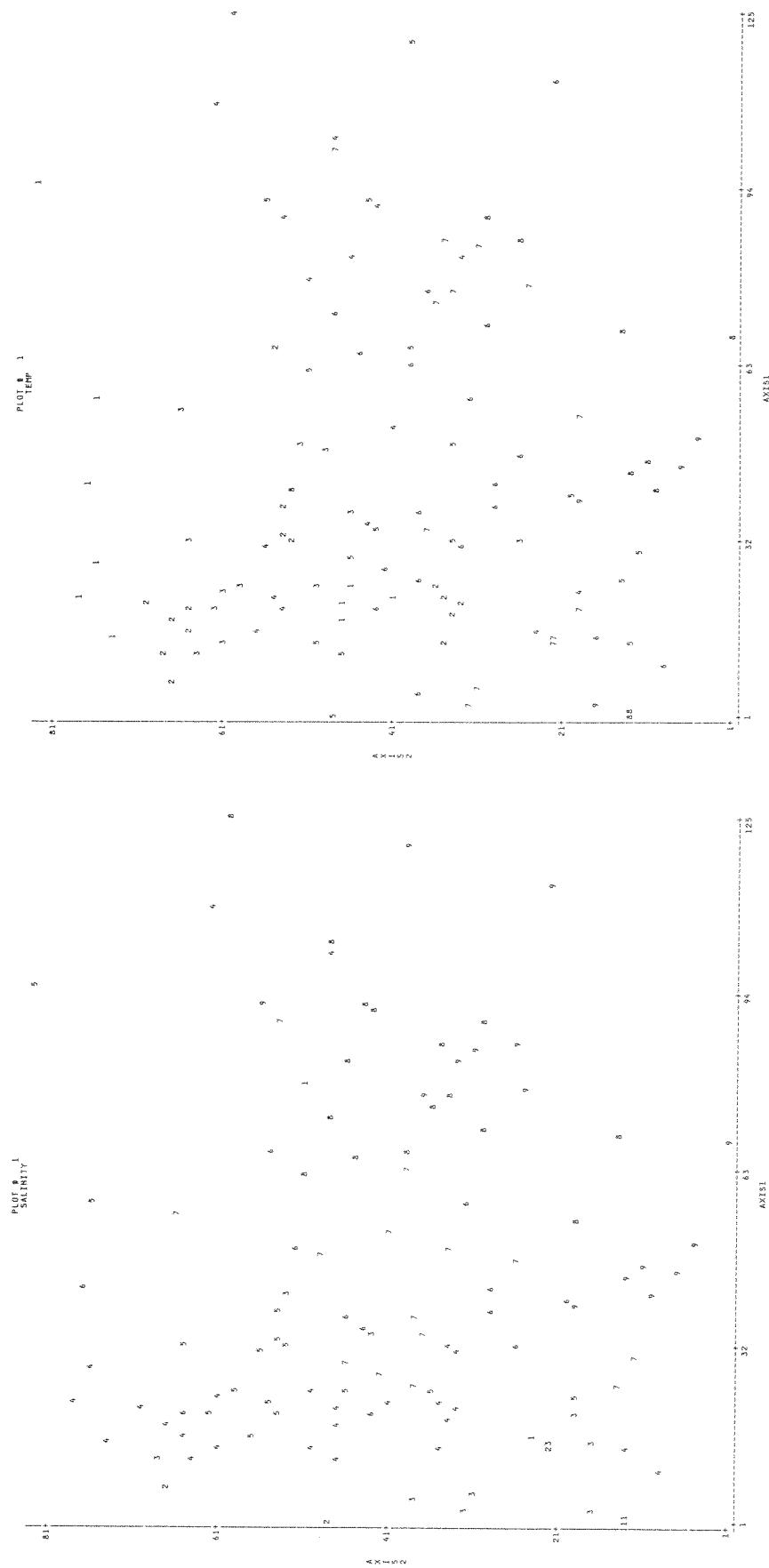


Fig. 14. The gradients of the environmental variables in discriminant space, summer 1970.

Fig. 14. (Continued)

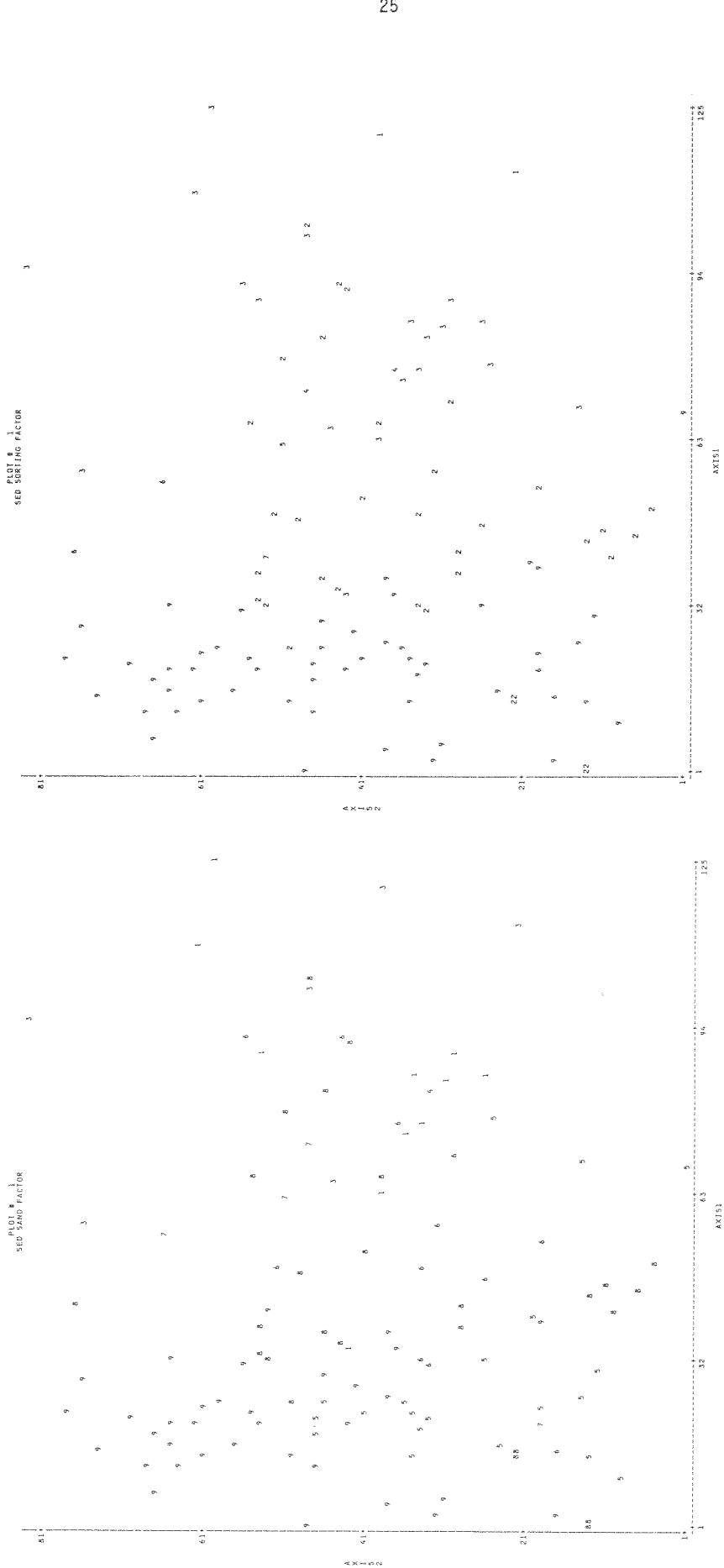


Fig. 14 (Continued)

SUMMER 1971

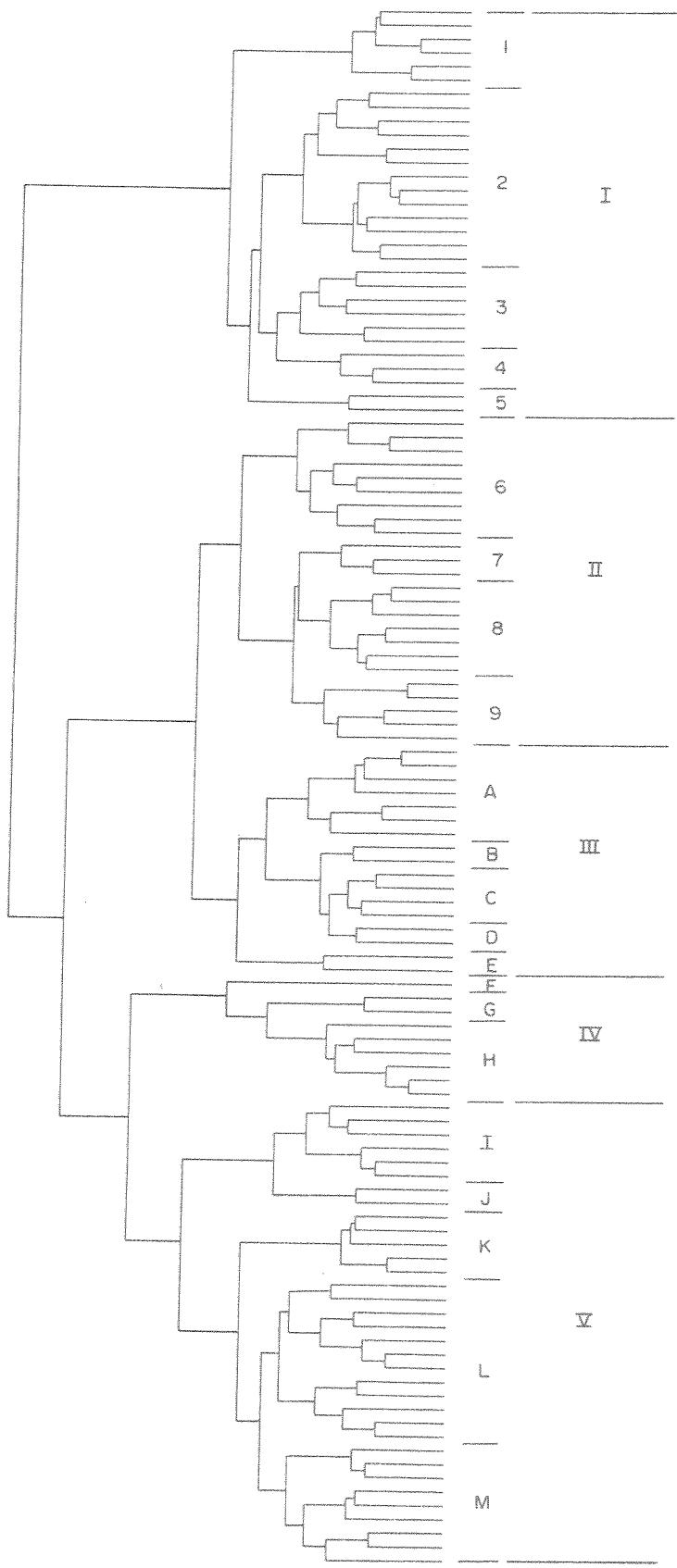


Fig. 15. The site dendrogram, summer 1971. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 17.

SUMMER 1971

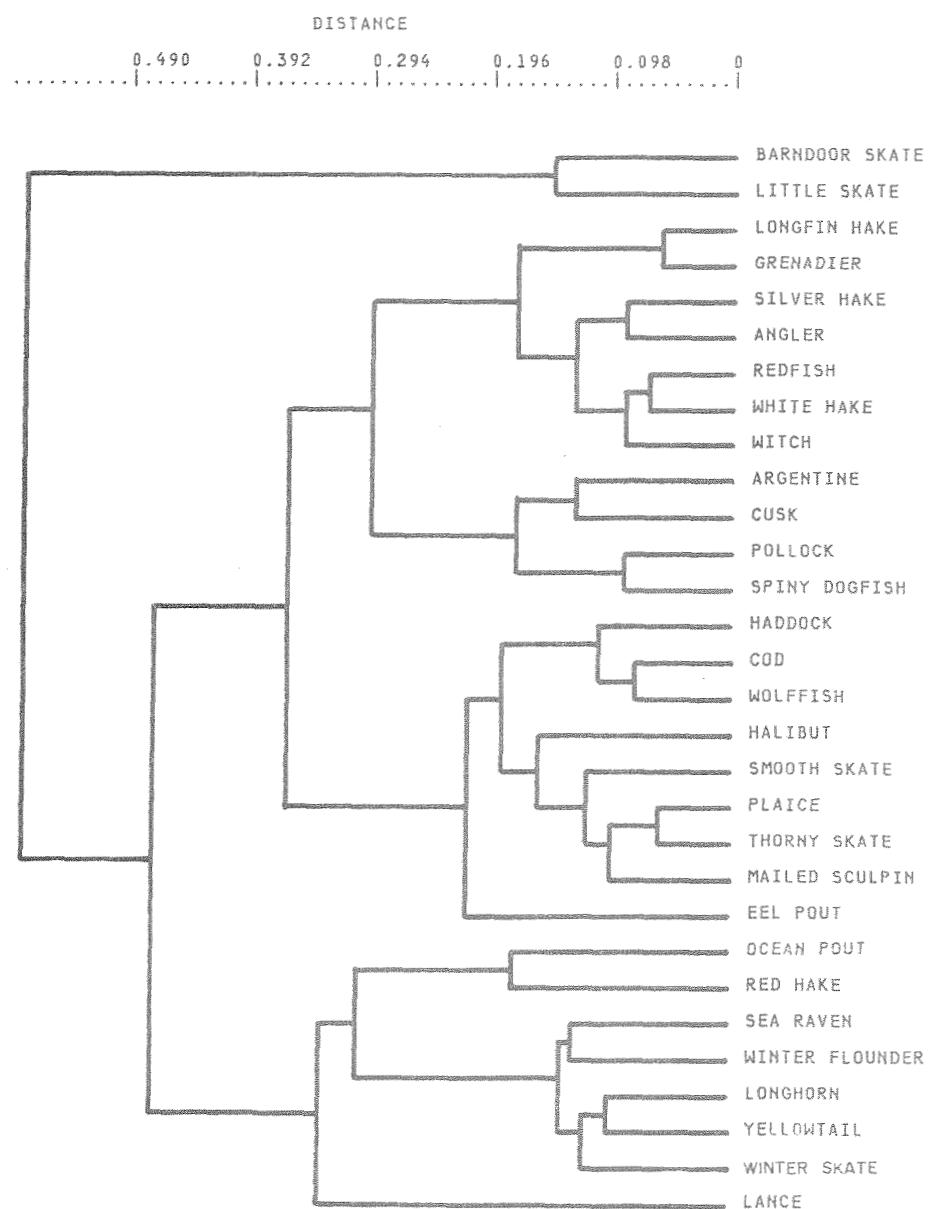


Fig. 16. The species dendrogram, summer 1971.

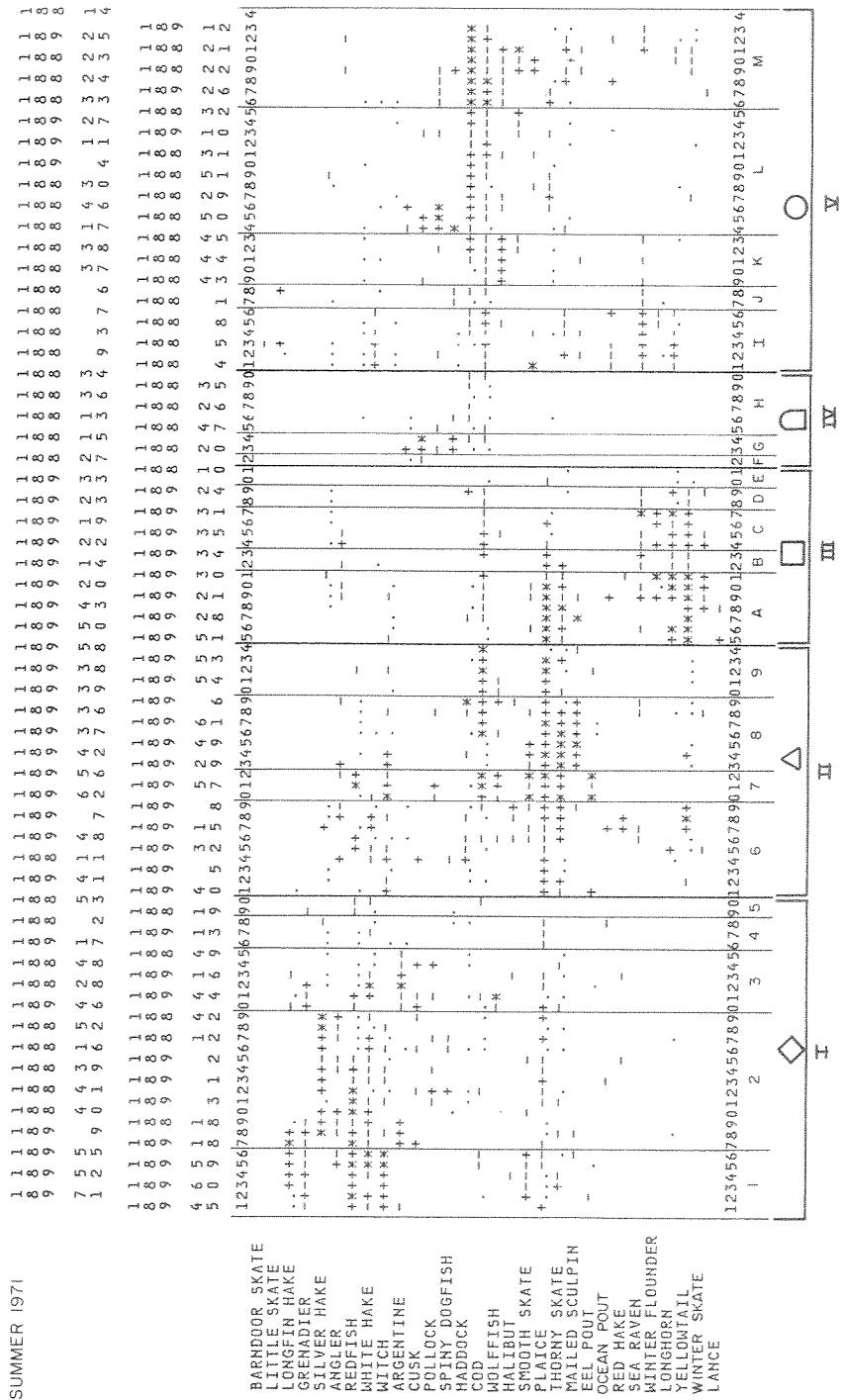
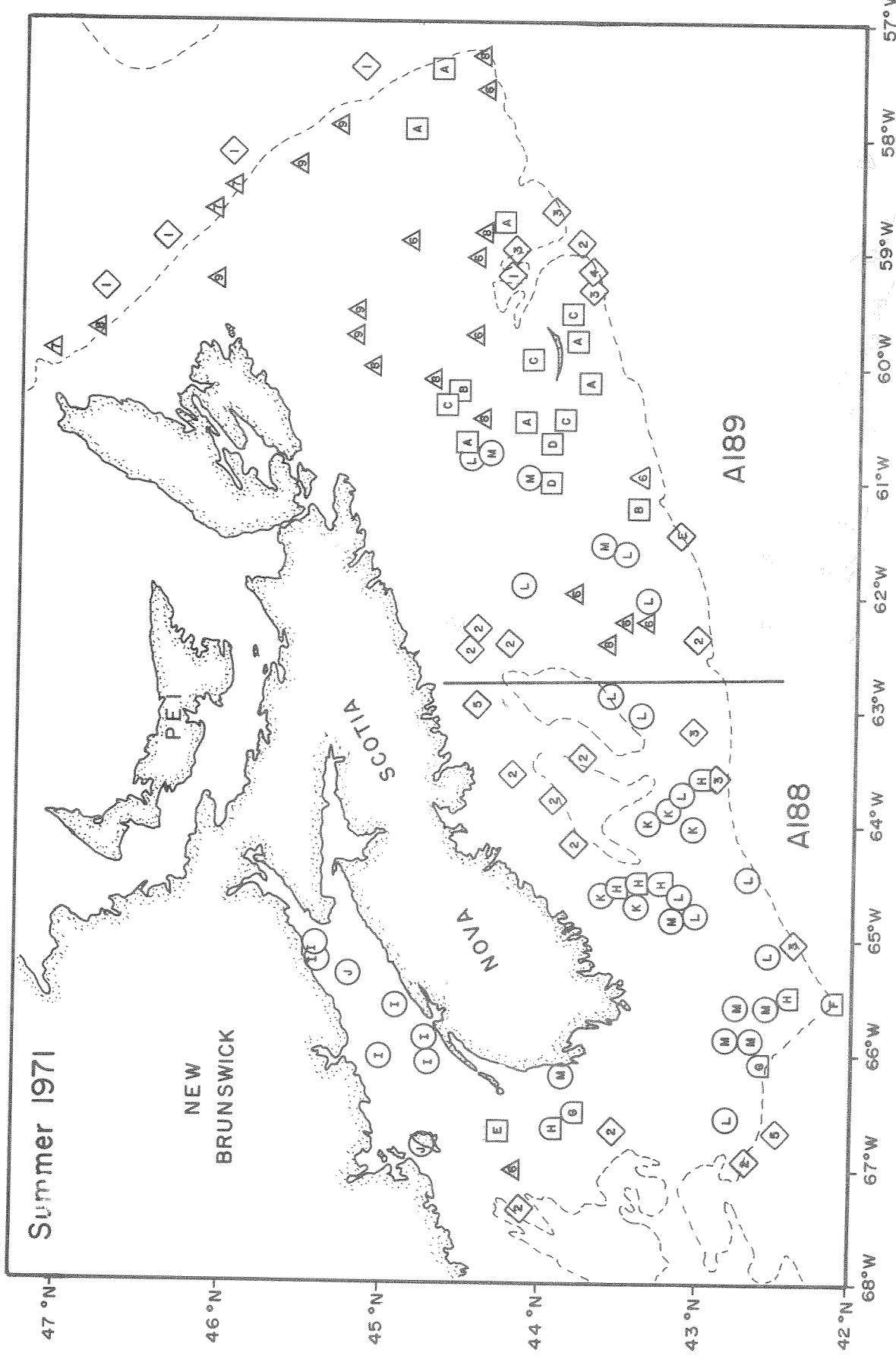


Fig. 17. The sites times species two-way table, summer 1971. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; + = 0.5-1.0; + = 1-2; \* = greater than 2.



**Fig. 18.** The areal distribution of site groups, summer 1971. The symbols correspond to those in Figure 17.

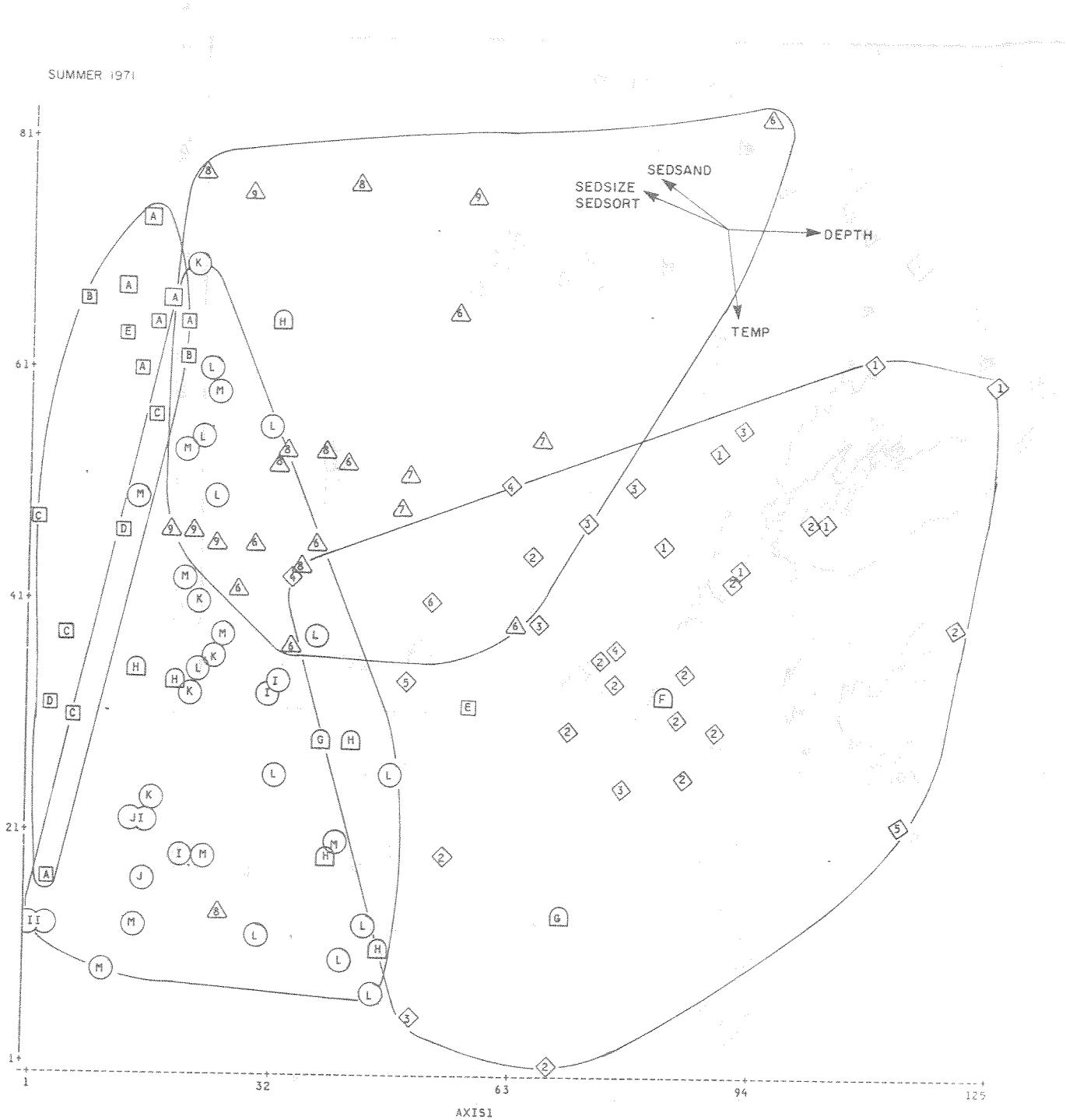


Fig. 19. The distribution of site groups in discriminant space, summer 1971. The symbols and number/letter codes correspond to those in Figure 17. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

example, sea raven, winter flounder, longhorn, yellowtail, and winter skate are only found consistently in major site group III, on Sable Island Bank and part of Banquereau Bank.

The major site groups are well separated in discriminant space (Table 10, Figure 19). Subsequent axes provide no further separation. Major site group I occupies the lower right segment of the space, with the greatest depth, intermediate to warm temperature, and smaller grained, poorly sorted sediments, with variable amounts of sand. Group I is completely separated from group V, which covers an area of the discriminant space characterized by shallow depth, intermediate temperature, and large grained, well sorted sediments, with intermediate to high amounts of sand. Major site group III is at the far left of the space. These stations have the shallowest depth, low to intermediate temperature, and the largest grained, best sorted sediments, with the highest amount of sand. One station in this group is far to the right in the discriminant space, in the area occupied by major site group I. The two-way table (Figure 17) shows that this station (188-10) has very low abundances of the species characteristic of site group III. Major site group II occupies the top centre part of the space, and overlaps groups I and V. These stations are at shallow to intermediate depths, and variable (low to intermediate) temperature, with intermediately sized and sorted to large and well sorted sediments, relatively high in sand content. The stations in major site group IV are scattered throughout the space. Since these stations generally have relatively low abundances of a very few species, it is difficult to interpret this pattern.

Table 10. Coefficients of separate determination (Summer 1971). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant Axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	48.7	0.2	0.2	5.7
2. Temp	0.5	44.4	19.6	5.6
3. Salinity	8.0	1.3	18.8	41.9
4. SEDSIZE	27.0	13.6	40.5	9.7
5. SEDSAND	1.1	20.0	1.4	20.4
6. SEDSORT	14.6	20.6	19.5	16.8
Eigenvalue	6.4	1.2	0.6	1.3
Percent of Group Separation	76.7	13.8	7.0	1.6

#### 1972 Summer

There are three major breaks in the site dendrogram (Figure 20) and the two-way table (Figure 22) that divide the sites into four major spatial groups (Figure 23). The first major group (I) includes stations in the Bay of Fundy and on Sable Island, Middle and Banquereau Banks on the eastern shelf. These stations had relatively abundant winter flounder, sea raven, longhorn, and yellowtail, as well as cod, plaice, and thorny skate. The second group of stations (II) is concentrated on the western shelf, including Brown's and Lahave Banks. This group has relatively abundant haddock, wolffish,

and cod, and only scattered occurrences of other species. Major site group III includes stations along the edge of the shelf and scattered across the western shelf. Relatively abundant cusk and argentine, and scattered occurrences of other species, characterize these sites. The last major site group (IV) is stations in basins and along the edge of the shelf. The dendrogram and two-way table (Figures 20, 22) indicate the further subdivisions into smaller site groups.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 21) and the two-way table (Figure 22). A comparison of the two-way table with the map of the site groups on the Scotian Shelf (Figure 23) indicates the spatial distribution of the species groups.

Only some of the major site groups are well separated in discriminant space (Table 11, Figure 24). Major site group I is separated from major site groups III and IV along axis 1. Site group I is characterized by shallow depth and low to intermediate salinity, with large grained sediments. Groups III and IV have variable (intermediate to great) depth, and high salinity, with small grained sediments. In addition, group I stations have lower temperature than group III and IV stations. Group II is also separated from groups III and IV on axis 1, but is almost completely overlapped by group I. Similarly, group III is almost completely overlapped by group IV. These overlapping groups were not separated by any subsequent discriminant axes. As their positions in discriminant space indicate (Figure 24), groups I and IV occupy a broad range of environmental parameters. The two-way table (Figure 22) shows that groups I and IV contain a correspondingly wide range of species.

Table 11. Coefficients of separate determination (Summer 1972). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	39.2	7.7	6.4	2.1
2. Temp	4.5	64.1	11.3	2.1
3. Salinity	38.5	1.2	27.8	6.6
4. SEDSIZE	8.7	16.6	32.7	25.3
5. SEDSAND	6.6	6.0	9.2	27.0
6. SEDSORT	2.3	4.4	12.6	36.9
Eigenvalues	5.2	1.0	0.3	0.1
Percent of Group Separation	76.7	15.4	4.3	1.9

#### 1973 Summer

There are six major breaks in the site dendrogram (Figure 25) and the two-way table (Figure 27) that divide the sites into spatial groups (Figure 28). Two of the resultant major site groups (III and IV) include a total of only five stations where almost no fish occur. Another (group V) has only scattered occurrences of several species. Of the remaining four major site groups, group I includes stations in the Bay of Fundy, on Sable Island, and Western Banks, and on eastern Banquereau Bank. This

SUMMER 1972

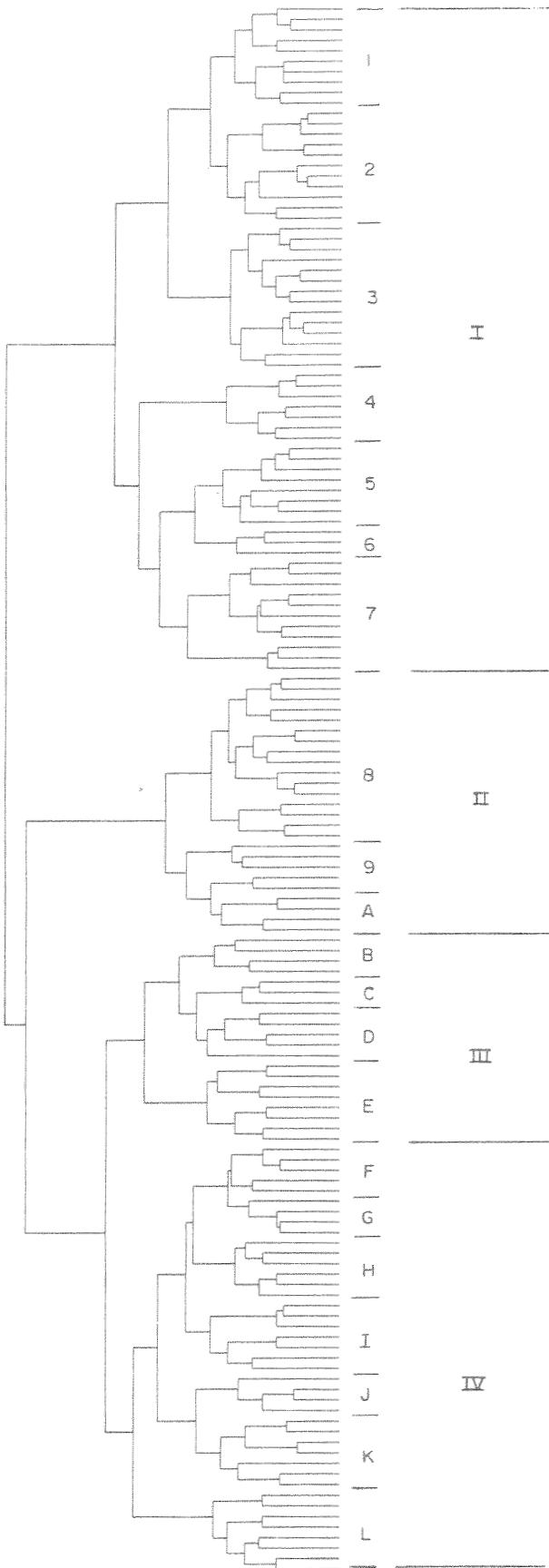


Fig. 20. The site dendrogram, summer 1972. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 22.

SUMMER 1972

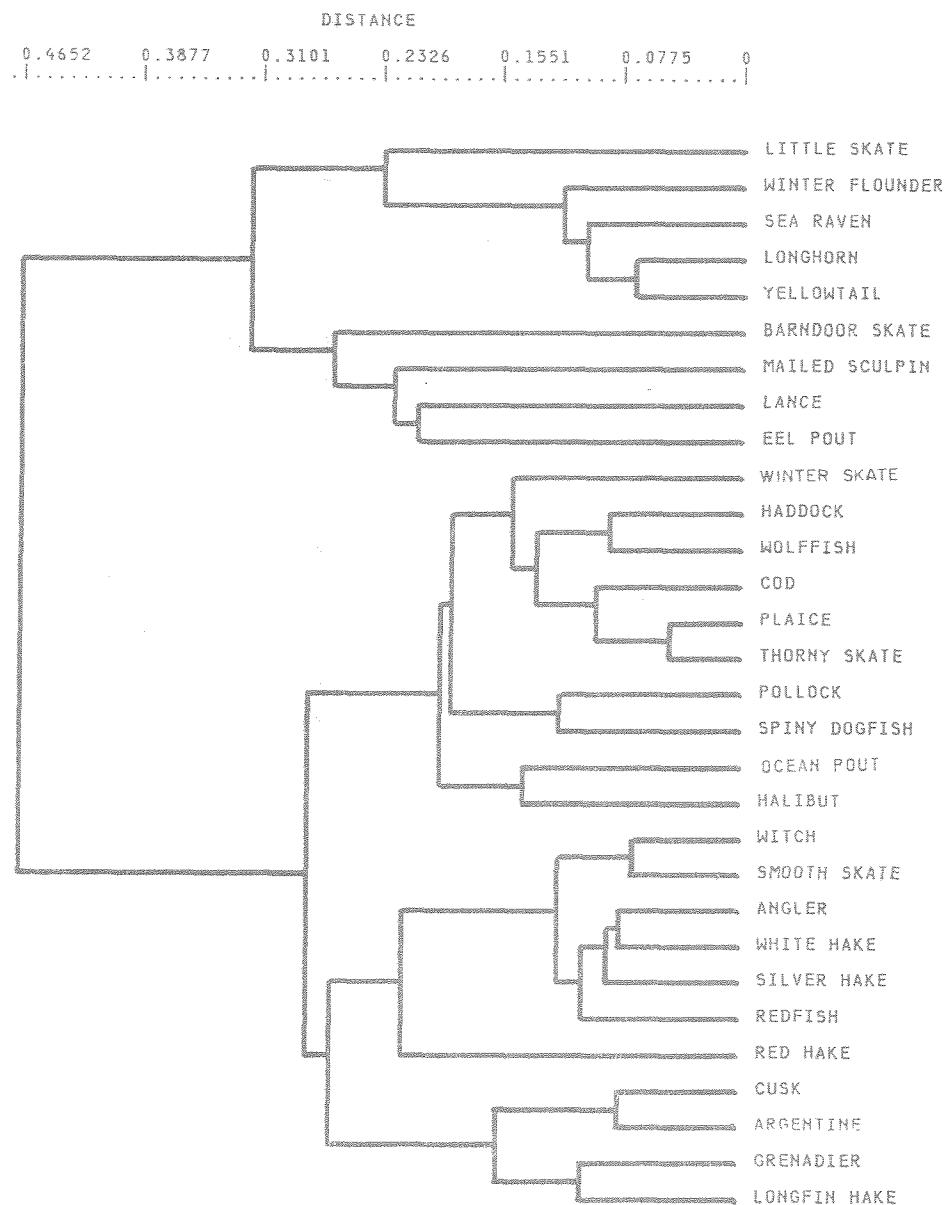


Fig. 21. The species dendrogram, summer 1972.

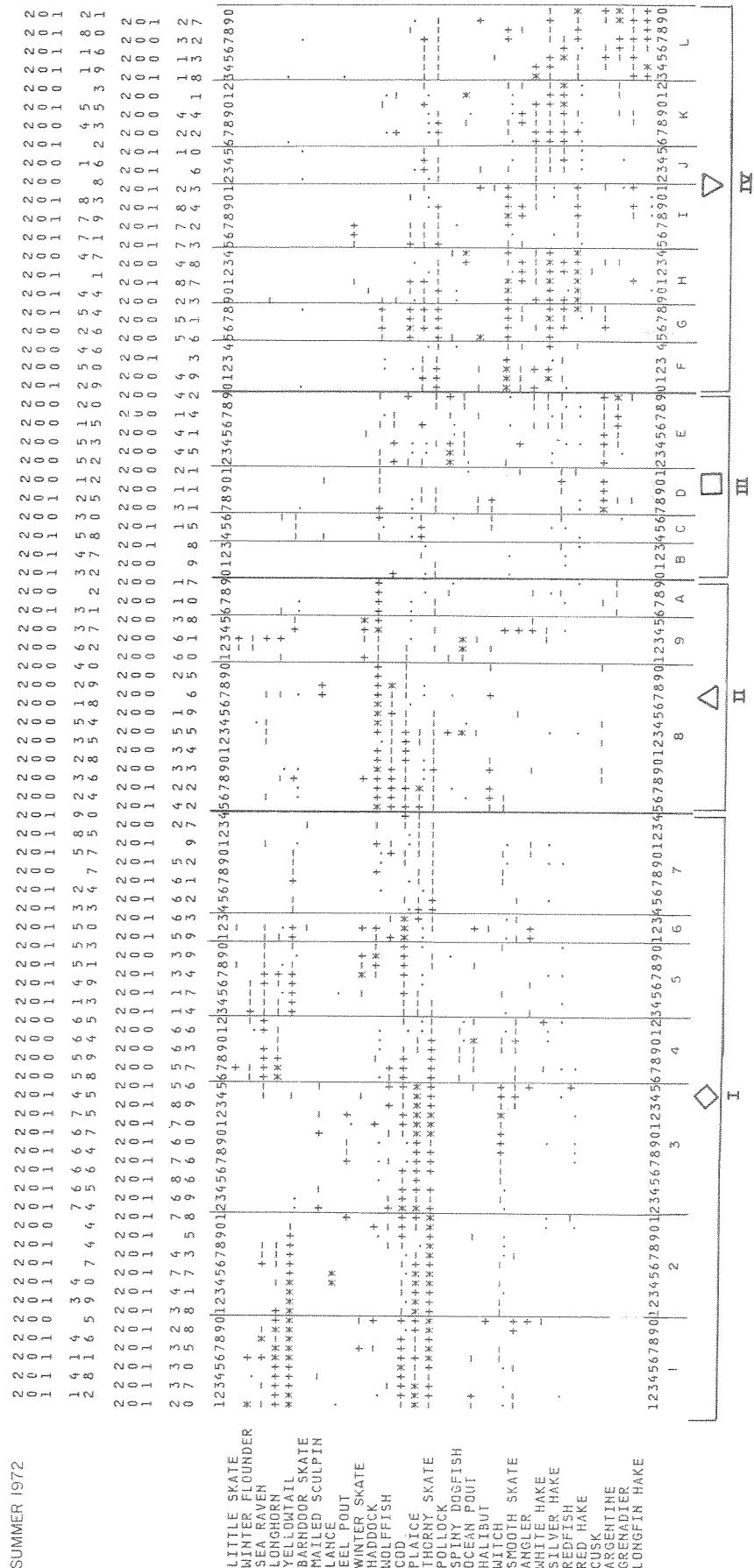


Fig. 22. The sites times species two-way table, summer 1972. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; + = 0.5-1.0; + = 1-2; \* = greater than 2.

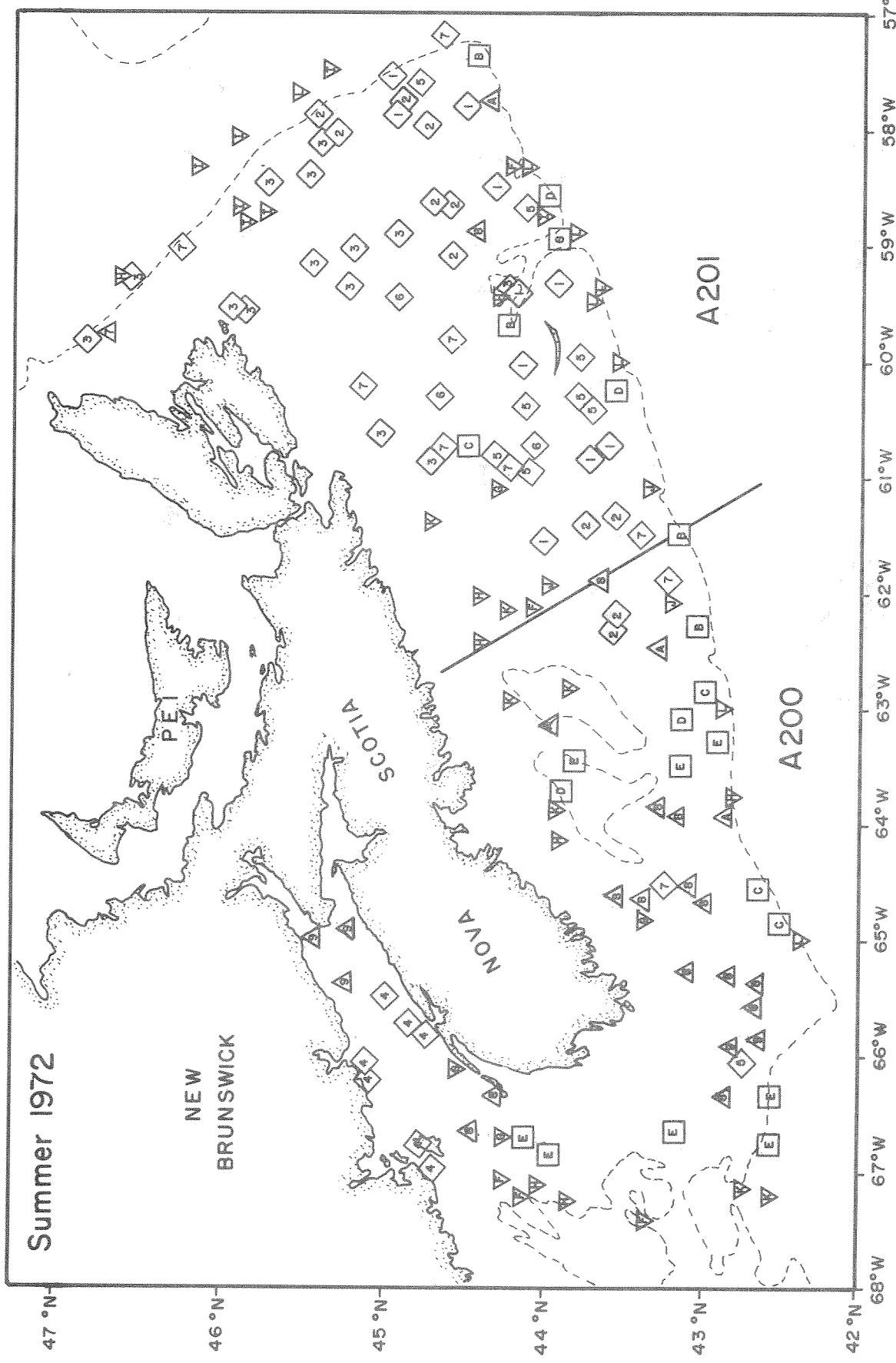


Fig. 23. The areal distribution of site groups, summer 1972. The symbols correspond to those in Figure 22.

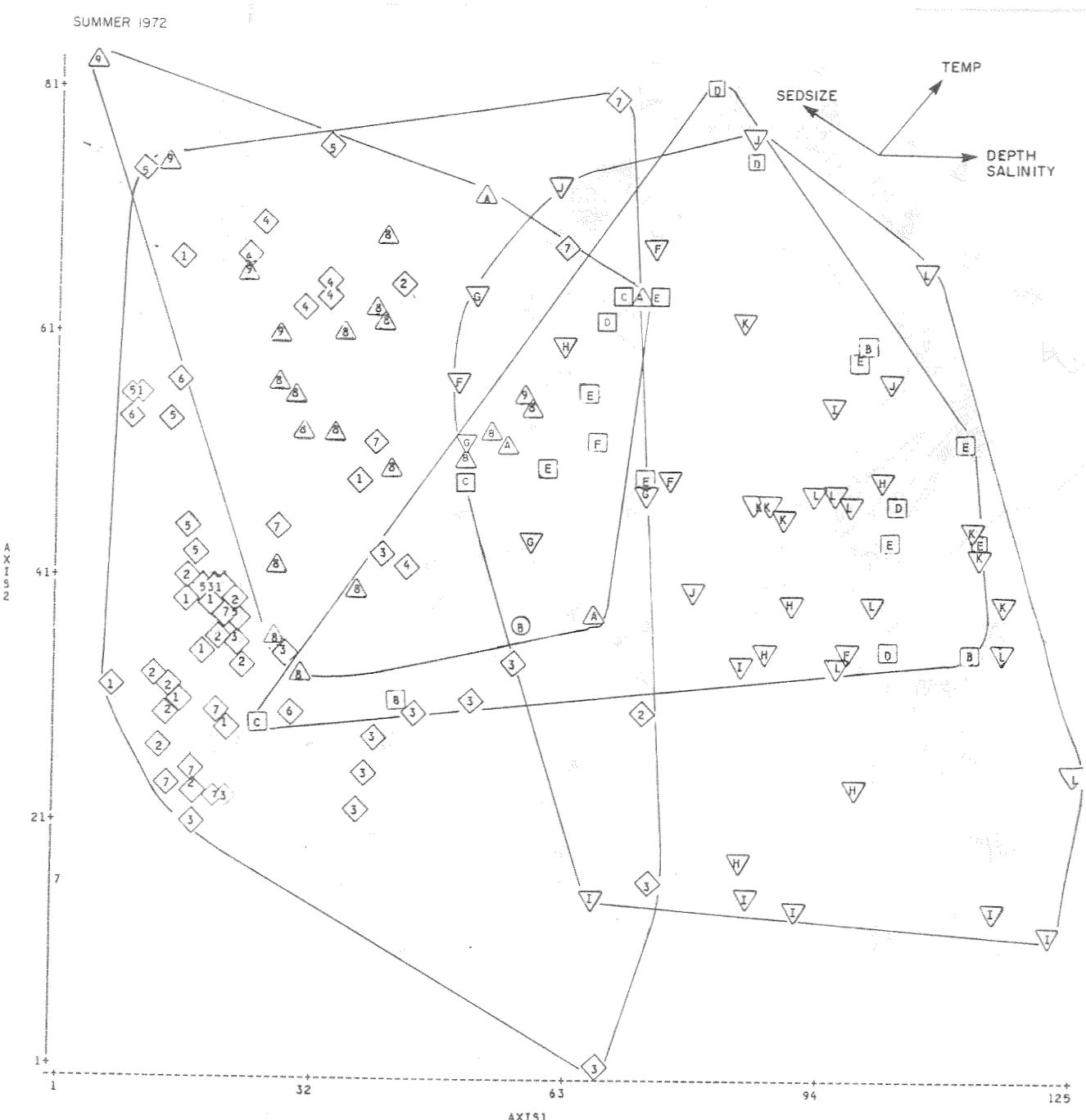


Fig. 24. The distribution of site groups in discriminant space, summer 1972. The symbols and number/letter codes correspond to those in Figure 22. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

SUMMER 1973

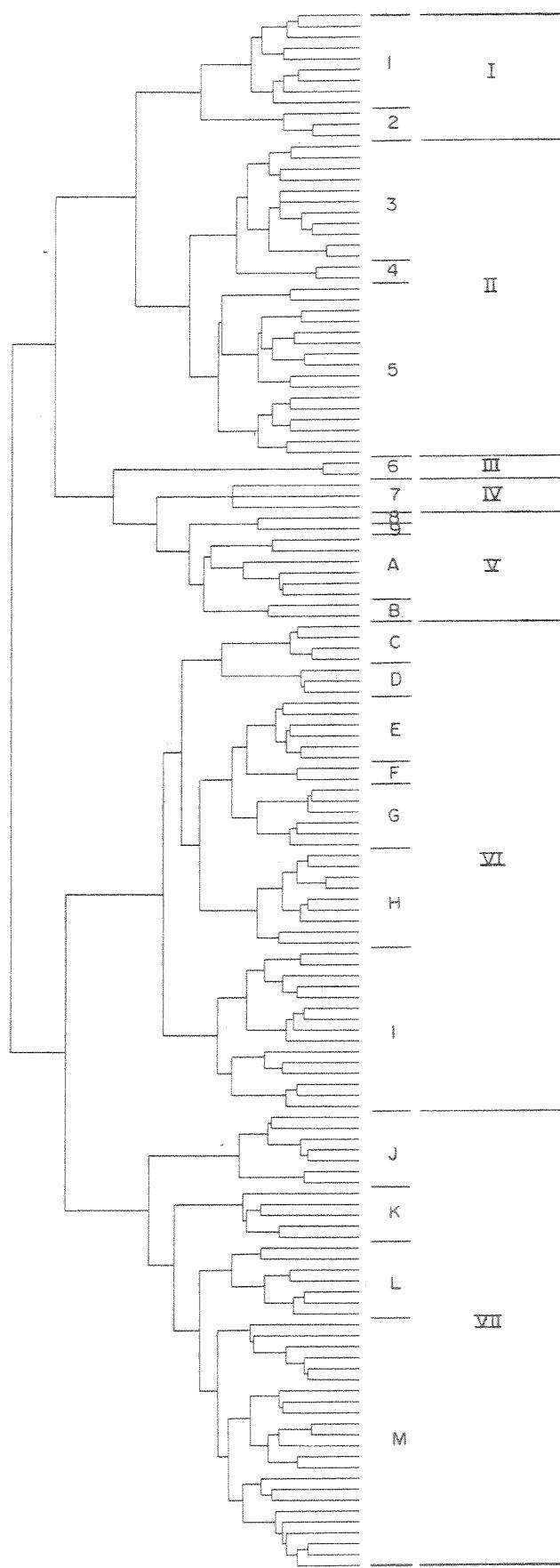


Fig. 25. The site dendrogram, summer 1973. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 27.

SUMMER 1973

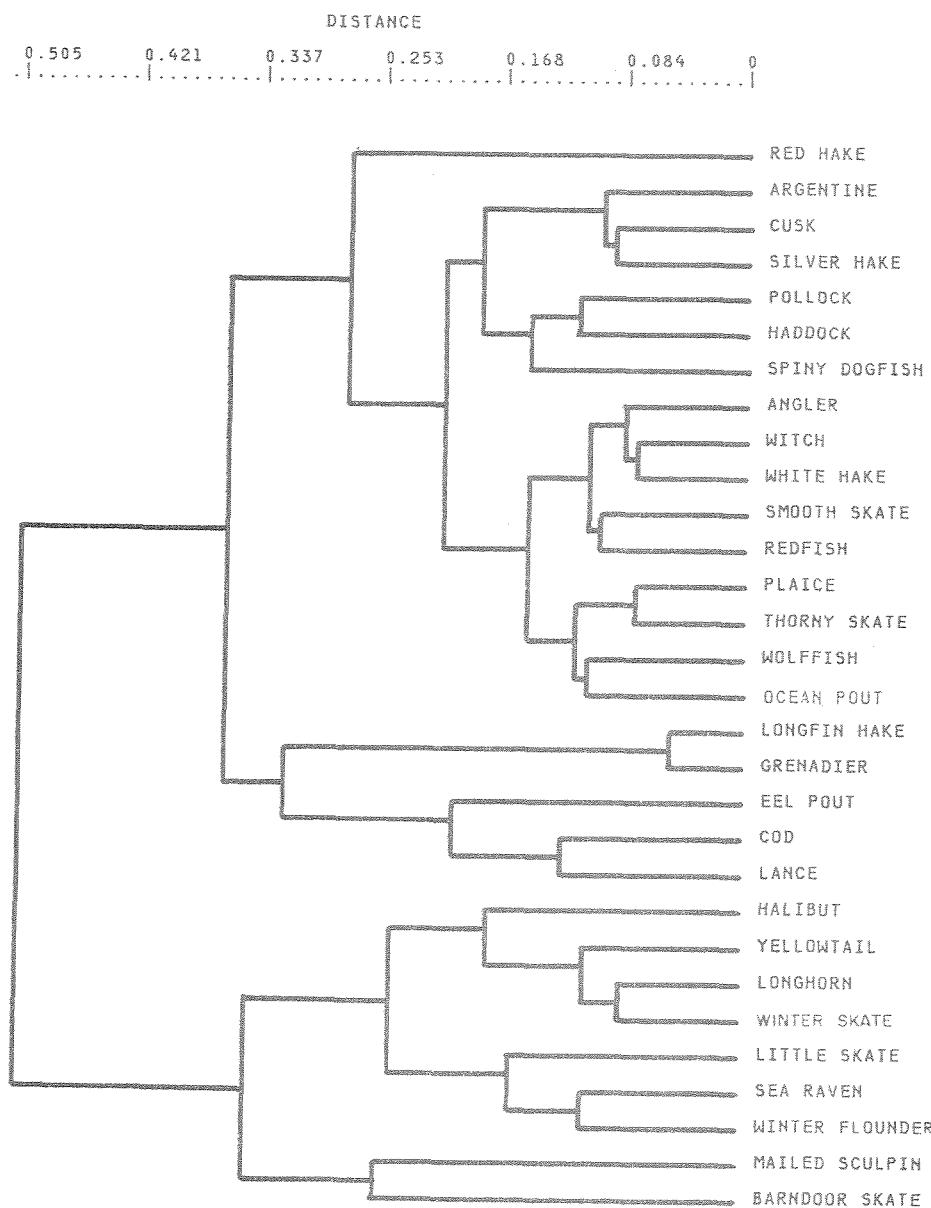


Fig. 26. The species dendrogram, summer 1973.

Fig. 27. The sites times species two-way table, summer 1973. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; - = 0-0.5; - = 0.5-1.0; + = 1-2; \* = greater than 2.

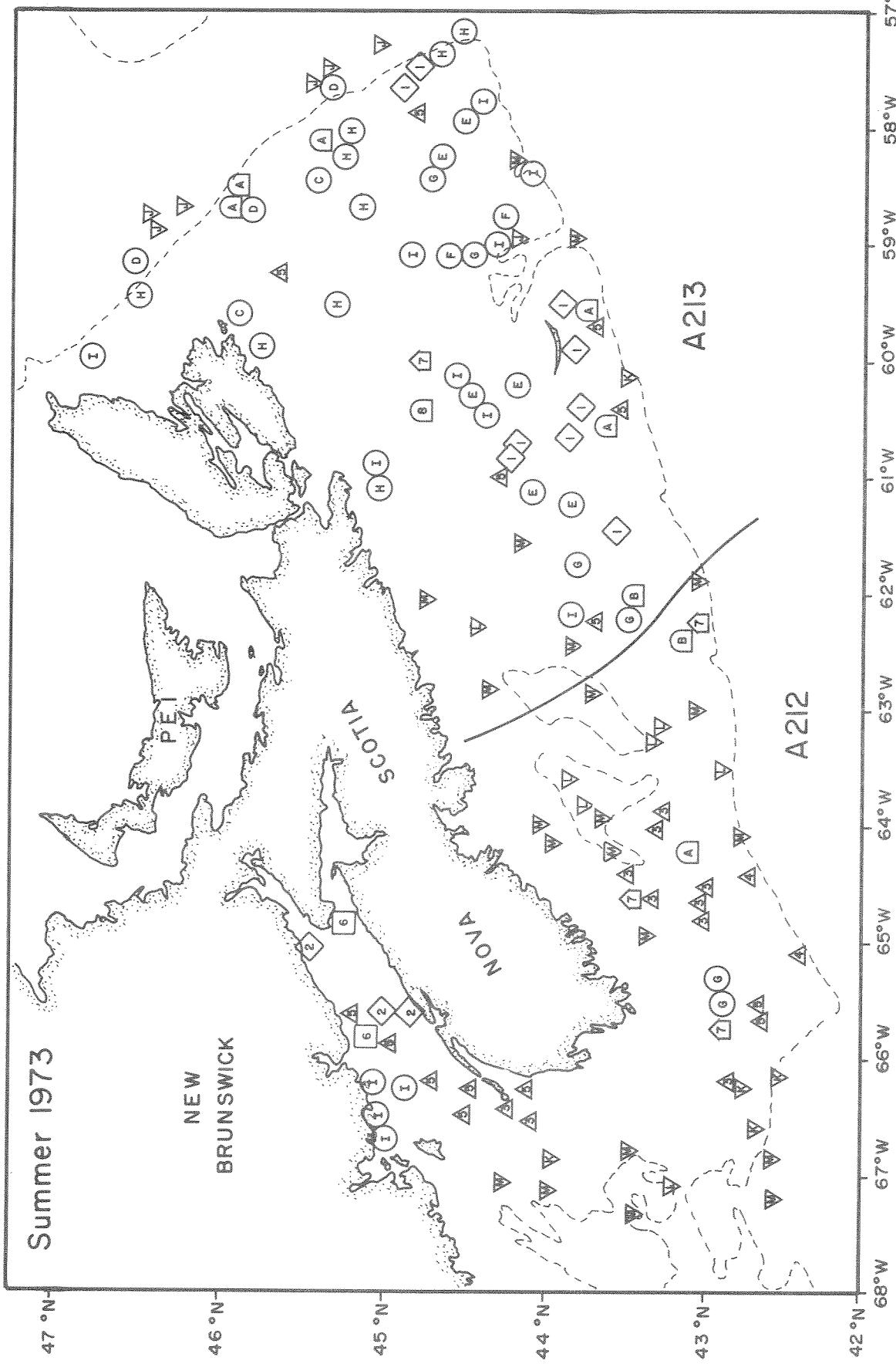


Fig. 28. The areal distribution of site groups, summer 1973. The symbols correspond to those in Figure 27.

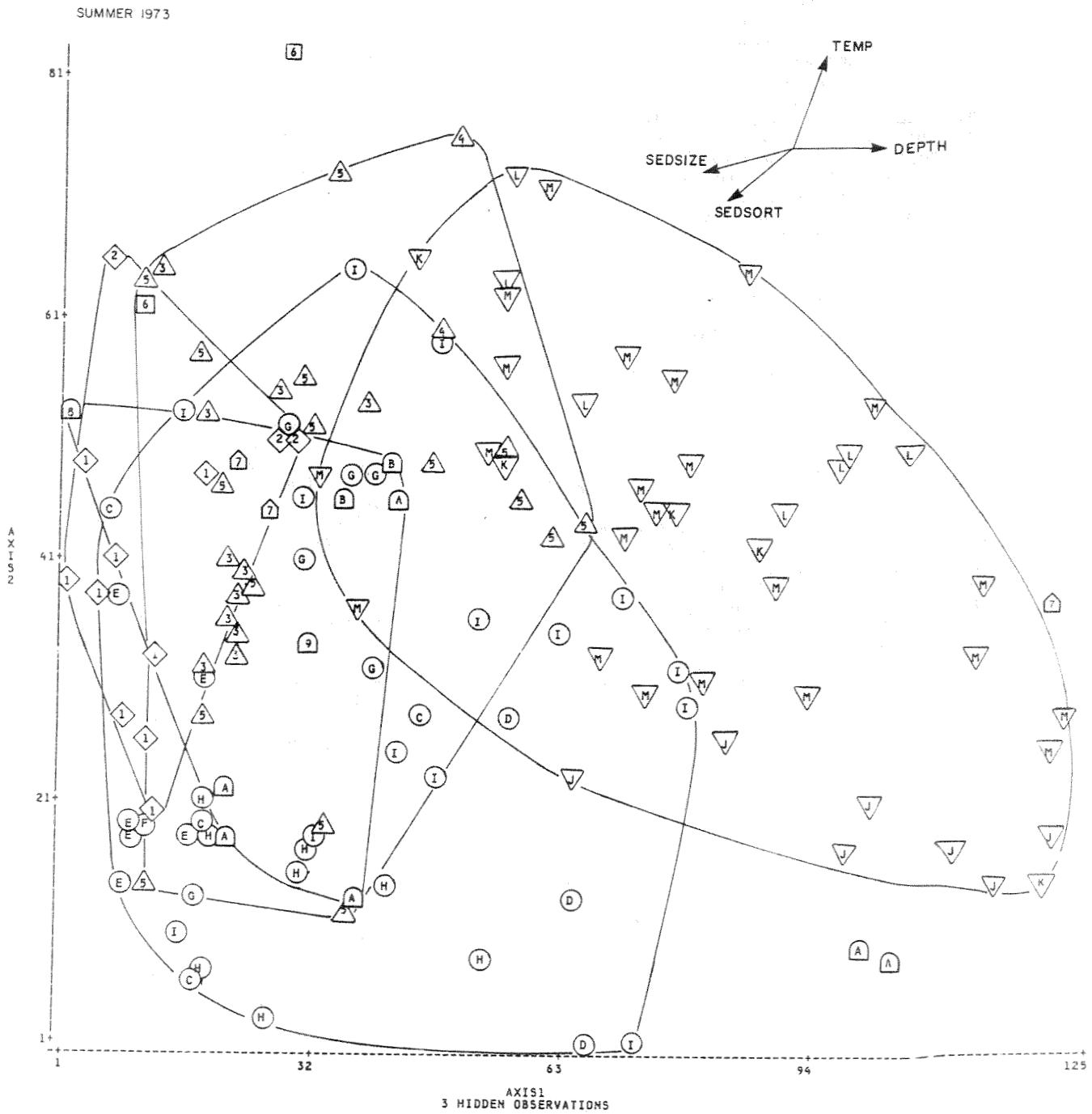


Fig. 29. The distribution of site groups in discriminant space, summer 1973. The symbols  $\diamond$  and number/letter codes correspond to those in Figure 11. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

group of stations had relatively abundant cod, yellowtail, longhorn, winter skate, and sea raven. Major site group II is concentrated in the Bay of Fundy and on the western shelf banks, with scattered stations on the eastern shelf. Relatively abundant haddock with scattered occurrences of many other species, characterize this group of stations. Major site group VI is stations in the Bay of Fundy and on the eastern shelf banks, with relatively abundant plaice, thorny skate, and cod. The last major group of stations (VII) is along the edge of the shelf and in basins, and is characterized by relatively abundant silver hake, and frequent occurrences of angler, witch, white hake, and redfish.

Groups of species with similar distributions across stations are shown on the species dendrogram (Figure 26) and the two-way table (Figure 27). The spatial distribution of these species groups can be estimated by comparing the two-way table to the map of the site groups on the Scotian Shelf (Figure 28).

Some of the major site groups are well separated along axis 1 in the discriminant space (Table 11, Figure 29). All major site groups show considerable overlap along axis 2, which is dominated by temperature (Table 12). Major site group I is characterized by the shallowest depth, and intermediate temperature, with generally large grained, well sorted sediments. The two stations in this group that are positioned farthest to the right along axis 1 (212-10,11), and that overlap group II, are at shallow depth but have a typically small grained sediments. The two-way table (Figure 27) also shows that these stations contain no yellowtail, which are usually relatively abundant at other stations in this major site group. Major site group II occupies an intermediate position along axis 1. These stations are at shallow depth, with intermediate to large grained sediments that are either very poorly sorted or very small sorted. Major site group VII is farthest to the right along axis 1, at intermediate to great depth, with generally small grained, poorly sorted sediments. Major site group VI overlaps group II almost completely, and is not separated from this or any of the other groups by subsequent axes. The small groups (III, IV, V) are scattered through the discriminant space.

Table 12. Coefficients of separate determination (Summer 1973). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	53.7	3.1	3.4	6.0
2. Temp	0.6	65.7	3.3	0.4
3. Salinity	12.2	1.7	51.9	9.1
4. SEDSIZE	21.4	12.6	36.6	41.1
5. SEDSAND	0.3	3.2	2.7	41.4
6. SEDSORT	11.8	13.8	2.2	2.0
Eigenvalue	4.0	0.8	0.3	0.2
Percent of Group Separation	75.2	14.8	5.5	3.0

#### 1974 Summer

There are five major breaks in the site dendrogram (Figure 30) and the two-way table (Figure 32) that divide the sites into spatial groups (Figure 33). One of the resulting major site groups (V) contains no species, and another (IV) contains only five stations with scattered occurrences of a few species. Of the remaining four major site groups, group I includes stations along the eastern edge of the shelf and on the eastern shelf. These stations have relatively abundant thorny skate, plaice, and cod, and few other species. Major site group II is concentrated on Bonquereau, Sable Island, and Western Banks, and contains relatively abundant thorny skate, plaice, and cod, as well as yellowtail, longhorn, sea raven, and winter skate. Stations in major site group III are in the Bay of Fundy, and on the western half of the shelf. Species relatively abundant in these stations include cod and haddock. Frequent occurrences of several other species such as ocean pout, pollock, smooth skate, white hake, thorny skate, wolffish, longhorn, and sea raven also characterize these stations. The last major site group (VI) is concentrated along the edge of the shelf and in basins, and include a few stations on the western shelf. Argentine, cusk, silver hake, spiny dogfish, redfish, angler, smooth skate, white hake, and witch are relatively frequent and abundant.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 31) and the two-way table (Figure 32). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 33).

The major site groups occupy distinct areas in the discriminant space (Table 13, Figure 34), although there is some overlap. Groups are separated on both axes 1 and 2, and subsequent axes provided no further separation. Major site group I is characterized by very low to intermediate temperature, and a wide range of sediment size and sediment sorting, from the smallest grained, most poorly sorted sediments, to the largest grained, best sorted ones. Stations in this group also span a range from shallow to intermediate depth. The two outliers in this group (stations 225-7,8 furthest up on axis 2) are the only stations in site group I to lack cod (typical of site group II) and contain ocean pout (typical of site groups III and VI). Major site group II is separated from group I along axis 2. It is characterized by intermediate temperature, the largest, most well sorted sediments, and very shallow depth. Major site group III occupies an intermediate position on both axes. These stations are at shallow depth with intermediate temperature, and sediments that are either large grained and well sorted, or of intermediate size and poorly sorted. Major site group VI is to the right along axis 1, with intermediate to warm temperature, and generally small grained, poorly sorted sediments. These stations are at intermediate depth. The smaller groups (IV and V) are scattered throughout the discriminant space.

SUMMER 1974

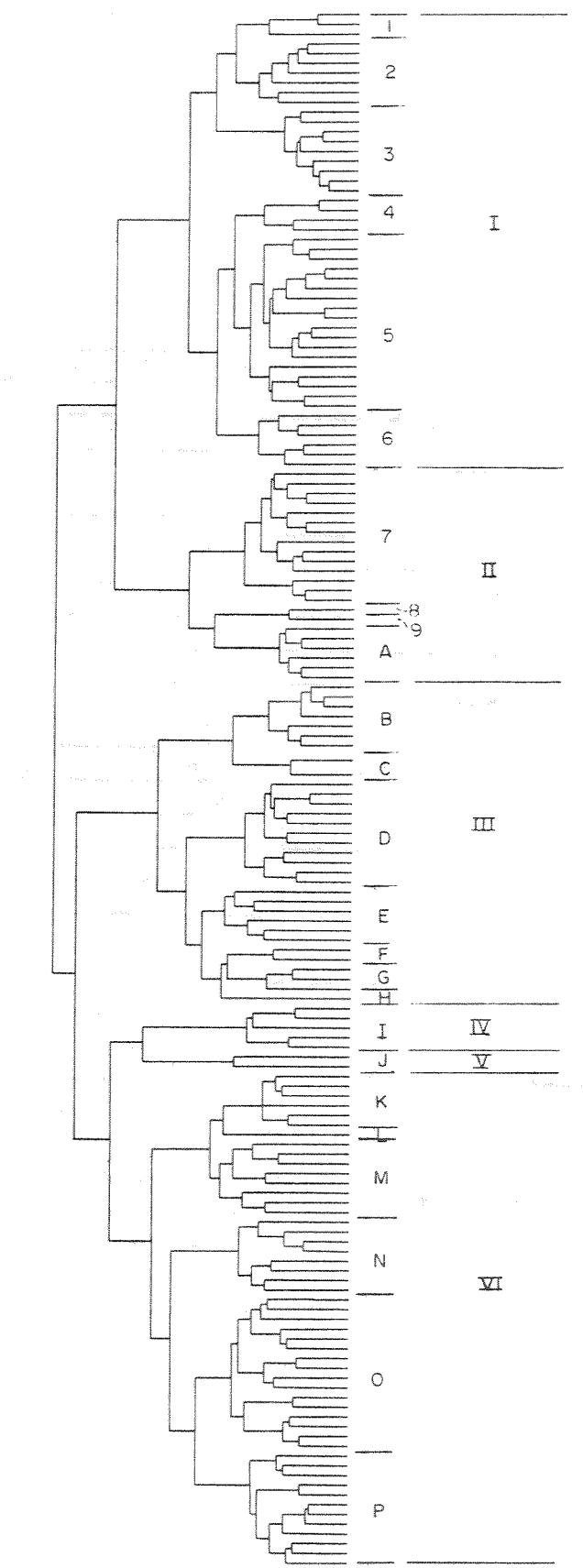


Fig. 30. The site dendrogram, summer 1974. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 32.

SUMMER 1974

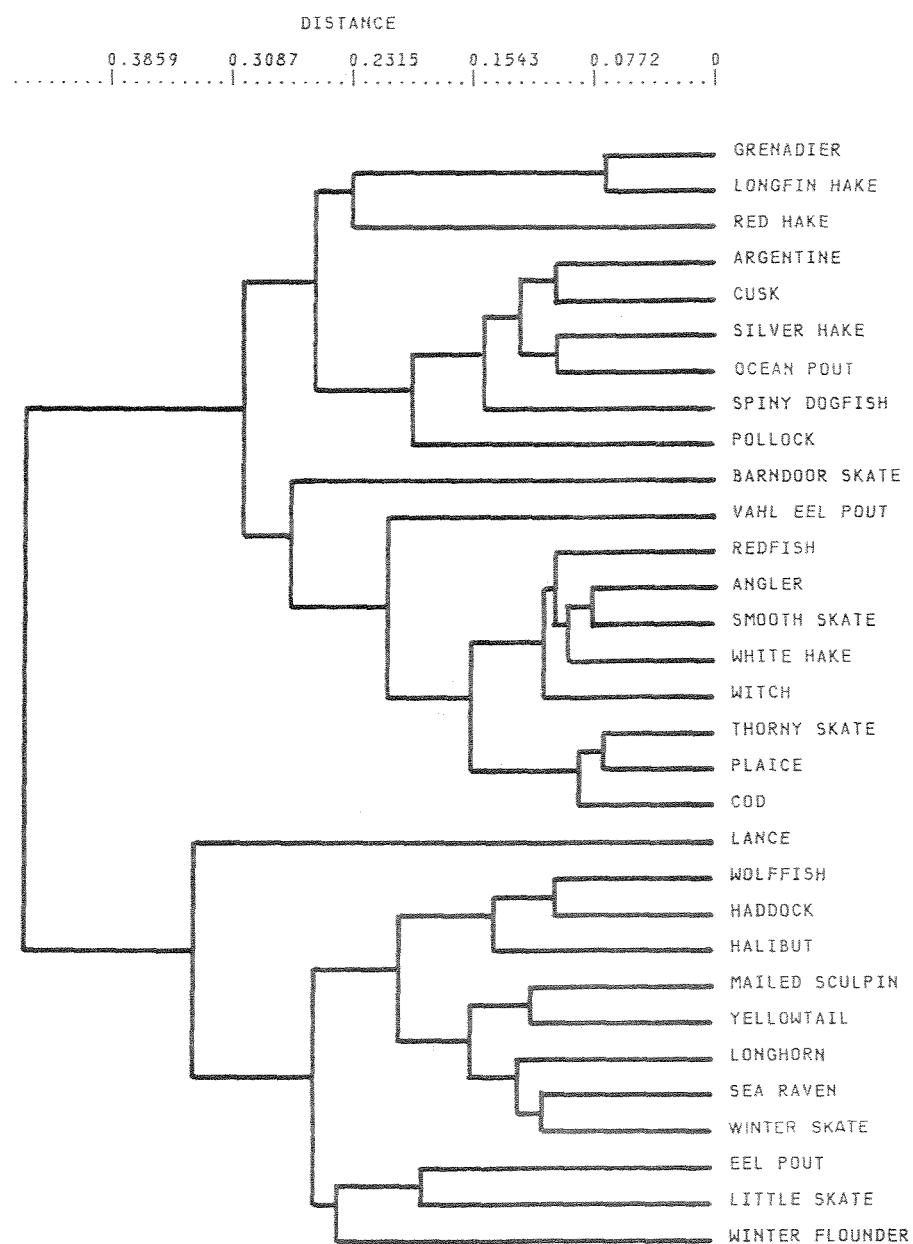


Fig. 31. The species dendrogram, summer 1974.

Fig. 32. The sites times species two-way table, summer 1974. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; - = 0.5-1.0; + = 1-2; x = greater than 2.

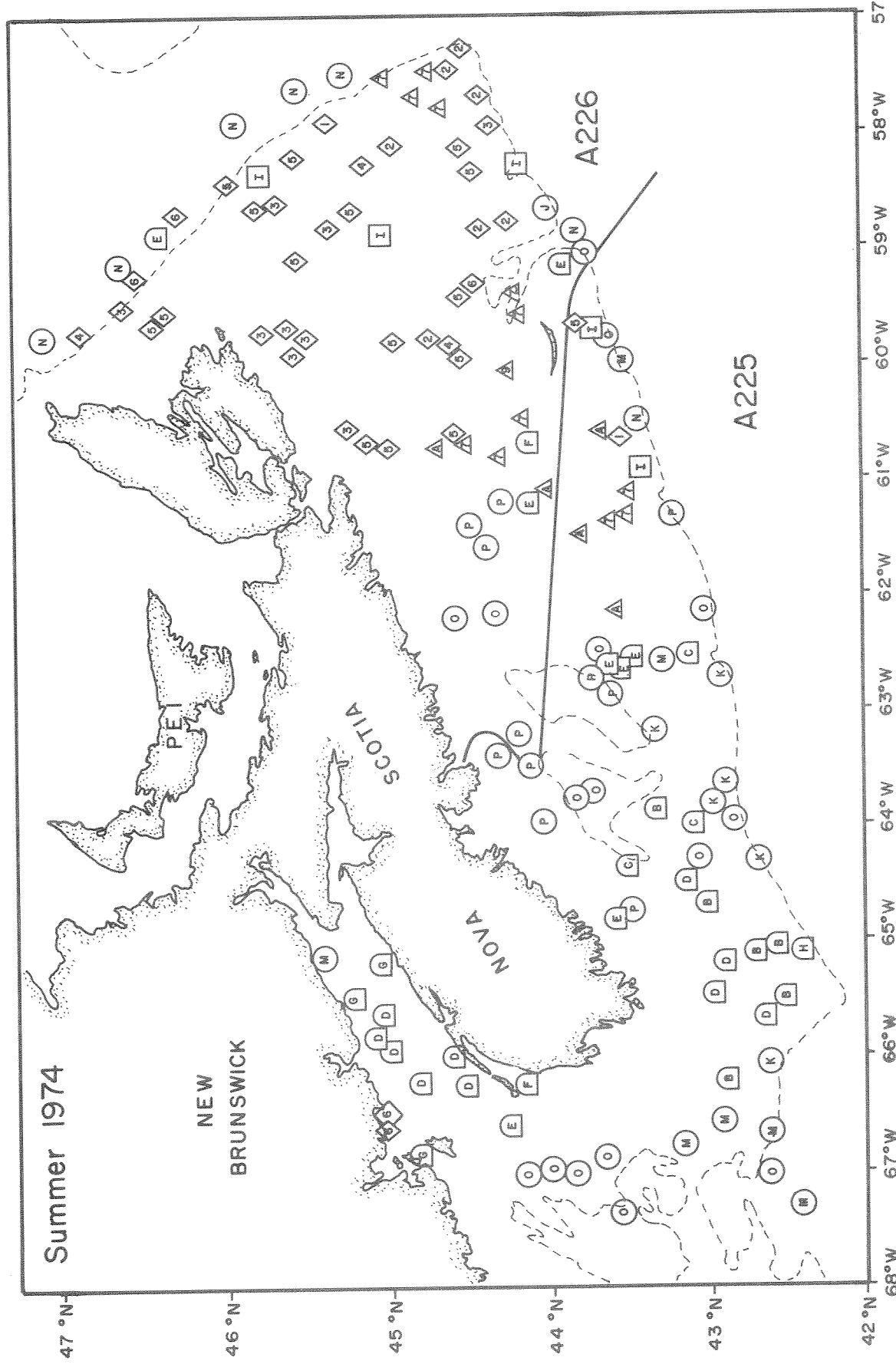


Fig. 33. The areal distribution of site groups, summer 1974. The symbols correspond to those in Figure 32.

SUMMER 1974

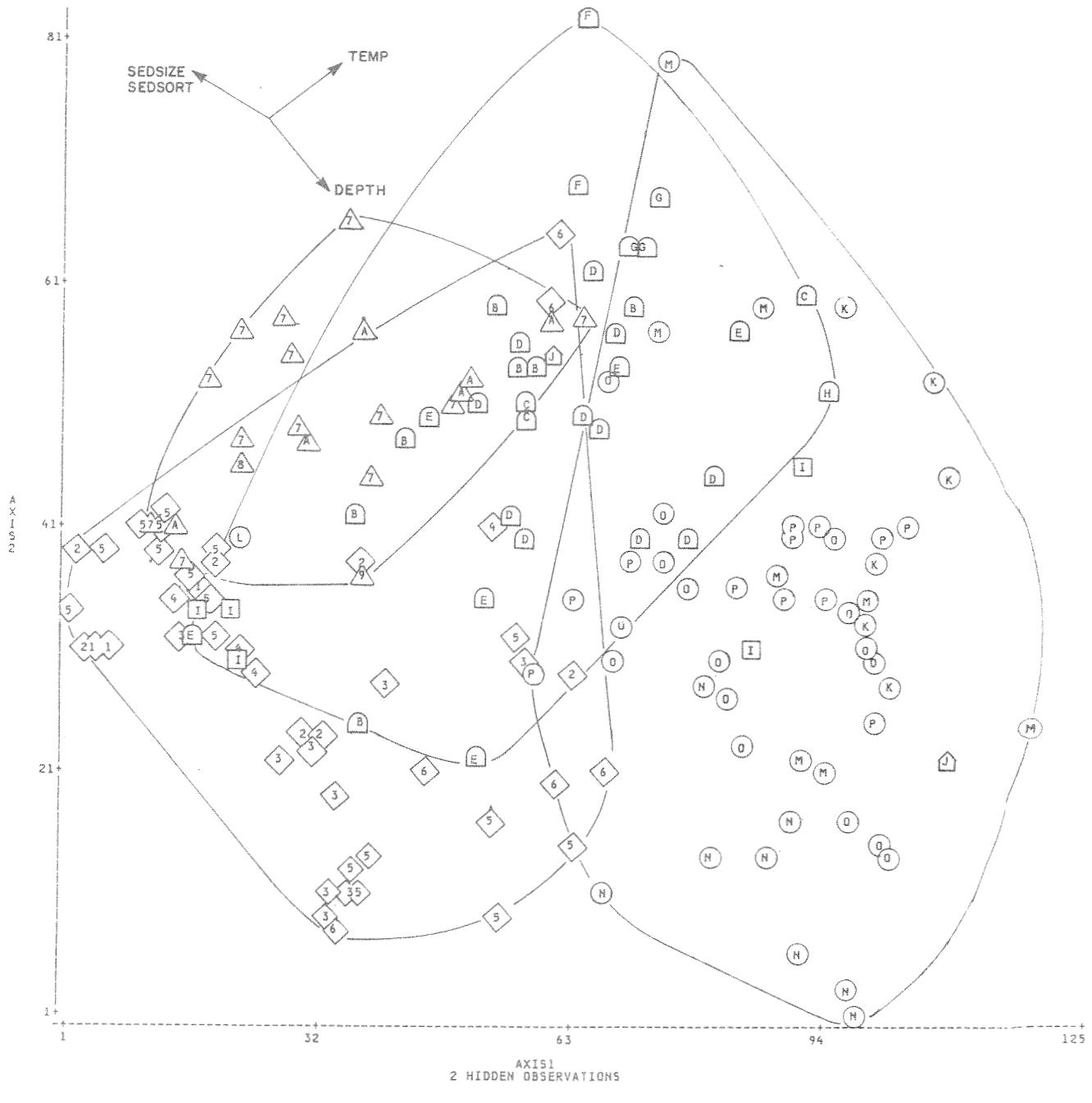


Fig. 34. The distribution of site groups in discriminant space, summer 1974. The symbols and number/letter codes correspond to those in Figure 32. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

Table 13. Coefficients of separate determination (Summer 1974). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	14.9	21.1	1.8	0.6
2. temp	37.3	31.5	2.0	0.2
3. Salinity	0.3	12.0	12.1	10.3
4. SEDSIZE	20.9	26.1	45.5	27.9
5. SEDSAND	6.3	3.7	12.2	13.0
6. SEDSORT	20.4	5.7	26.5	47.9
Eigenvalue	3.7	1.6	0.3	0.2
Percent of Group Separation	62.8	27.3	4.9	3.4

#### 1975 Summer

There are four major breaks in the site dendrogram (Figure 35) and the two-way table (Figure 37) that divide the stations into spatial areas (Figure 38). One of the resultant major site groups (II) contains only eight stations with scattered occurrences of a few species. Of the remaining four large major site groups, group I includes stations along the edge of the shelf and in the basins, as well as a few stations in the mouth of the Bay of Fundy. These stations have relatively abundant angler, silver hake, white hake, and redfish, as well as frequent occurrences of cusk, witch, thorny skate, plaice, and smooth skate. Major site group III is concentrated on the eastern shelf, including some stations along the eastern edge of the shelf. Relatively abundant witch, thorny skate, and plaice, and almost no occurrences of any other species, characterize these stations. Stations in major site group IV are in the Bay of Fundy and on the eastern shelf banks. Species relatively common and abundant in these stations are thorny skate, plaice, smooth skate, ocean pout, cod, longhorn, yellowtail, sea raven, and winter flounder. The last major site group (V) is made up of stations on the western shelf with relatively abundant wolffish and haddock.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 36) and the two-way table (Figure 37). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of station groups on the Scotian Shelf (Figure 38).

The major site groups occupy different, but somewhat overlapping, areas in the discriminant space (Table 14, Figure 39). Groups are separated along both axes 1 and 2, with no further separation provided by any subsequent axes. Major site group I is to the right of axis 1 and is characterized by intermediate to great depth and salinity, intermediate to warm temperature, and small grained sediments. Major site group III is positioned at the centre of axis 1 and near the top of axis 2. These stations are at shallow depth, with intermediate salinity, very low temperature, and either intermediate or large grained sediments. The one station in this group that is farthest down along axis 2 (237-43) is biologically, as well

as environmentally, similar to group I (see two-way table, Figure 37). It has anomalously high temperature and salinity, and is the only station in group III to have relatively low abundances of both skate and plaice. In addition, it has three of the species more characteristic of group I (silver hake, white hake, and redfish). Site group V is characterised by shallow to intermediate depth, with intermediate temperature and salinity, and intermediate to large grained sediments. Group IV overlaps groups III and V, but also includes stations with the lowest salinity, highest temperature, and shallowest depth, with the largest grained sediments.

Table 14. Coefficients of separate determination (Summer 1975). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	21.3	1.9	1.7	13.3
2. Temp		3.0	67.4	3.3
3. Salinity			30.4	4.7
4. SEDSIZE				25.0
5. SEDSAND			28.1	11.2
6. SEDSORT				44.5
Eigenvalues			2.4	9.1
Percent of Group Separation			14.9	51.5
	5.2	1.2	0.3	0.8
	74.7	17.8	3.9	1.8

#### 1976 Summer

There are three major divisions in the site dendrogram (Figure 40) and the two-way table (Figure 42) that divide the sites into spatial areas (Figure 43). Major site group I is made up of stations along the edge of the shelf and in the basins. The relatively abundant species in this group are angler, redfish, witch, white hake, silver hake, smooth skate, and pollock. Plaice and thorny skate were also occasionally present. The second major site group (II) is concentrated in the Bay of Fundy, where a variety of species were relatively common, including white hake, thorny skate, cod, longhorn, and sea raven. Major site group III is concentrated exclusively on the western shelf. It is characterized primarily by relatively abundant halibut and haddock. Major site group IV occurs only on the eastern shelf. Plaice, wolffish, thorny skate, cod, yellowtail, and longhorn were relatively abundant in this area.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 41) and the two-way table (Figure 42). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 43).

The major site groups are well separated along axes 1 and 2 of the discriminant space (Table 15, Figure 44). Subsequent axes provided no further separation. Major site group I is to the right along axis 1 and near the centre of axis 2. These stations are at intermediate depth, with intermediate to warm temperature and

SUMMER 1975

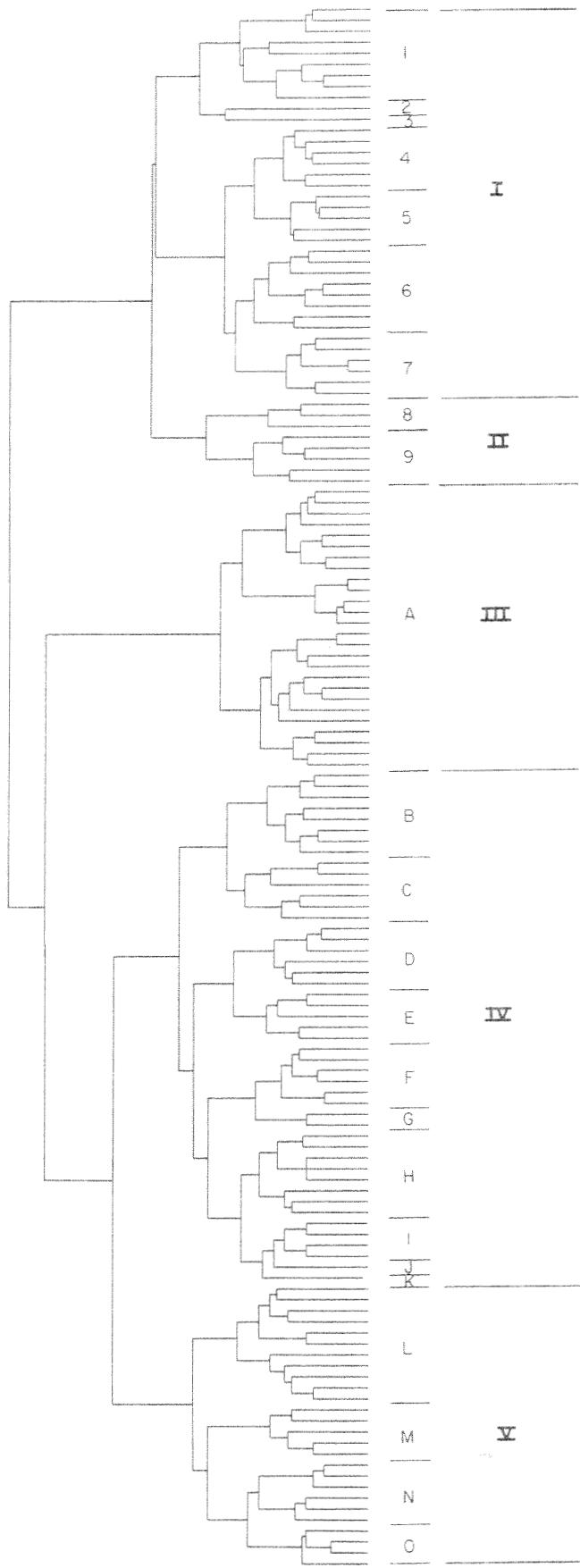


Fig. 35. The site dendrogram, summer 1975. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 37.

SUMMER 1975

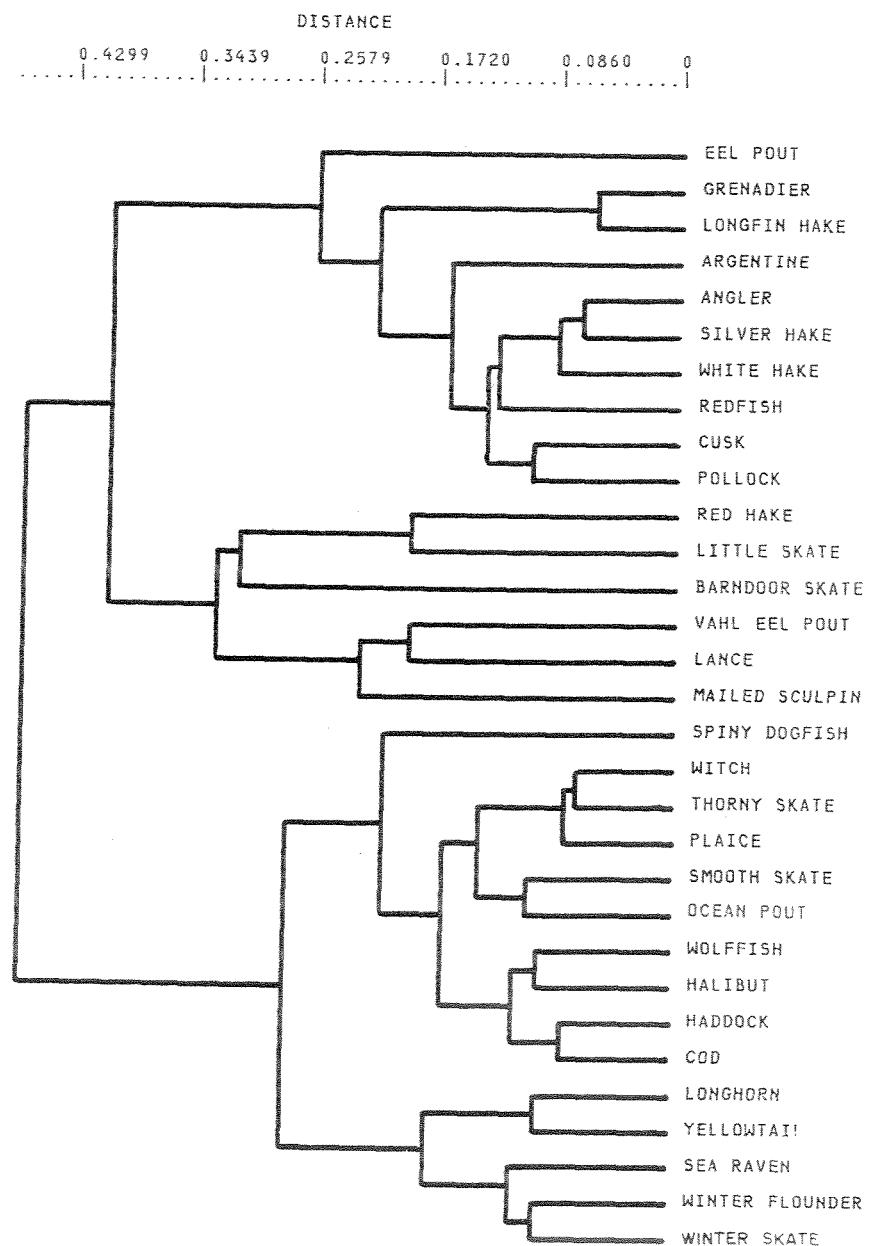


Fig. 36. The species dendrogram, summer 1975.

Fig. 37. The sites times species two-way table, summer 1975. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0.5-1.0; + = 1-2; \* = greater than 2.

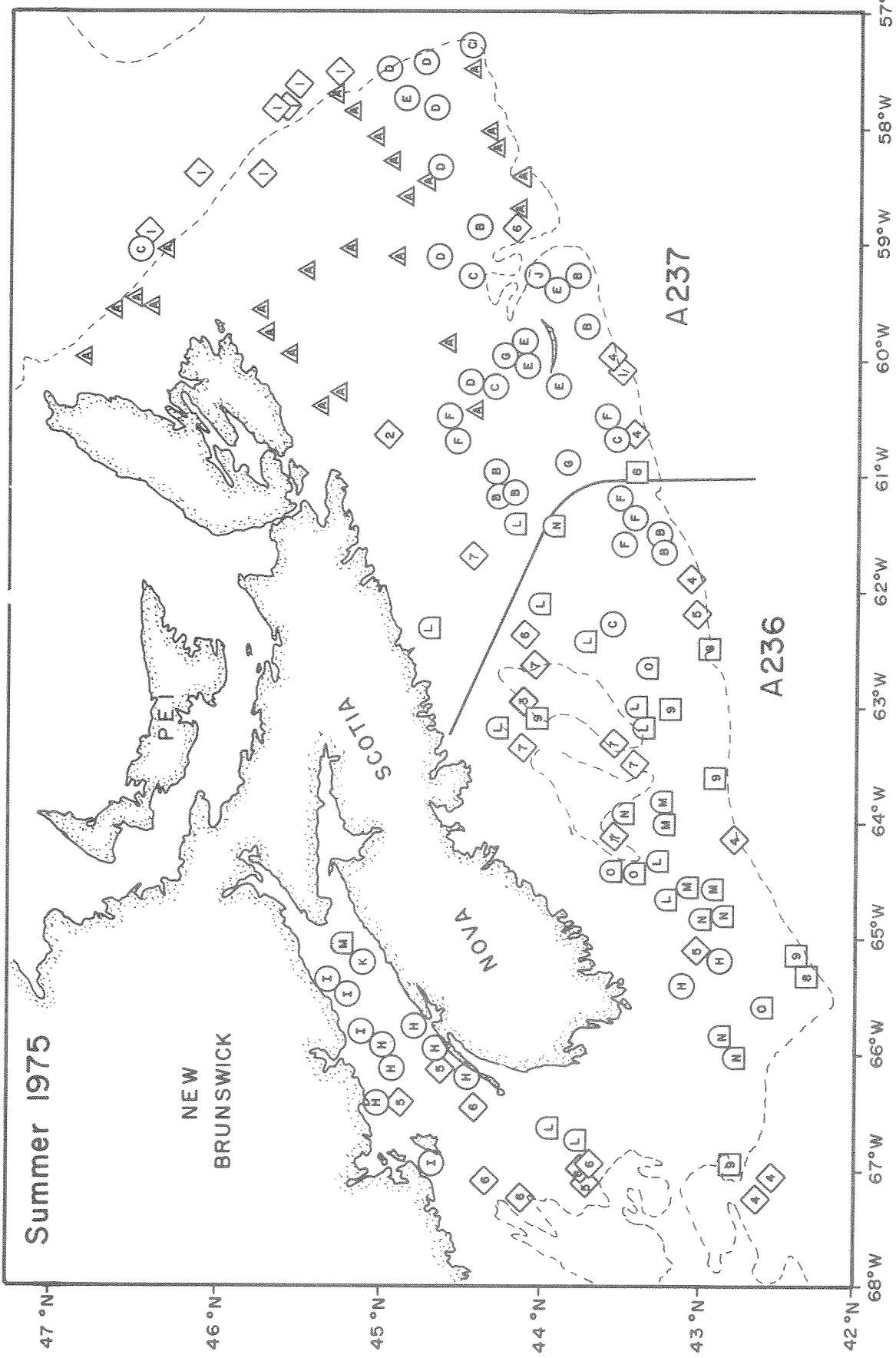


Fig. 38. The areal distribution of site groups, summer 1975. The symbols correspond to those in Figure 37.

SUMMER 1975

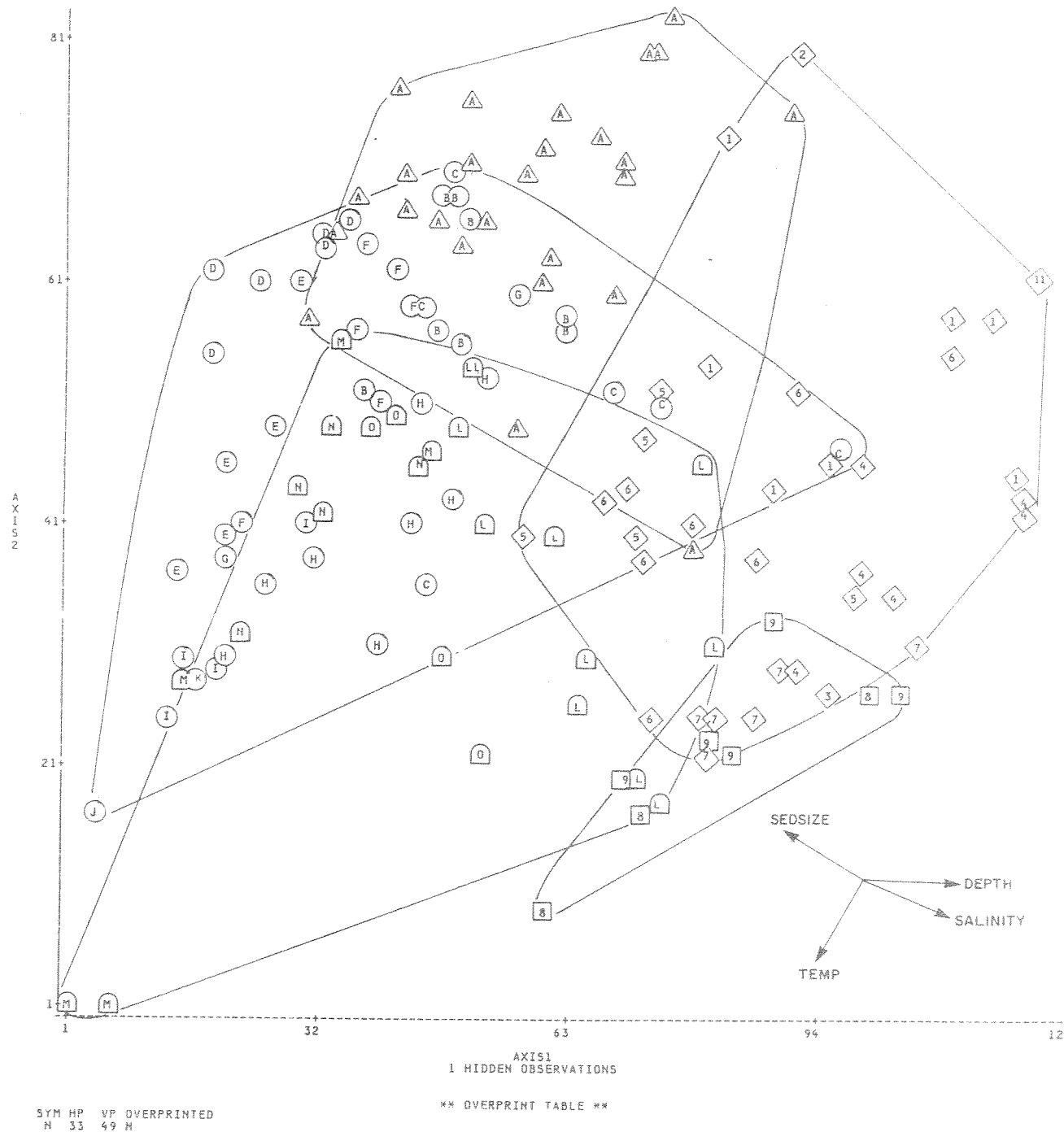


Fig. 39. The distribution of site groups in discriminant space, summer 1975. The symbols and number/letter codes correspond to those in Figure 37. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

SUMMER 1976

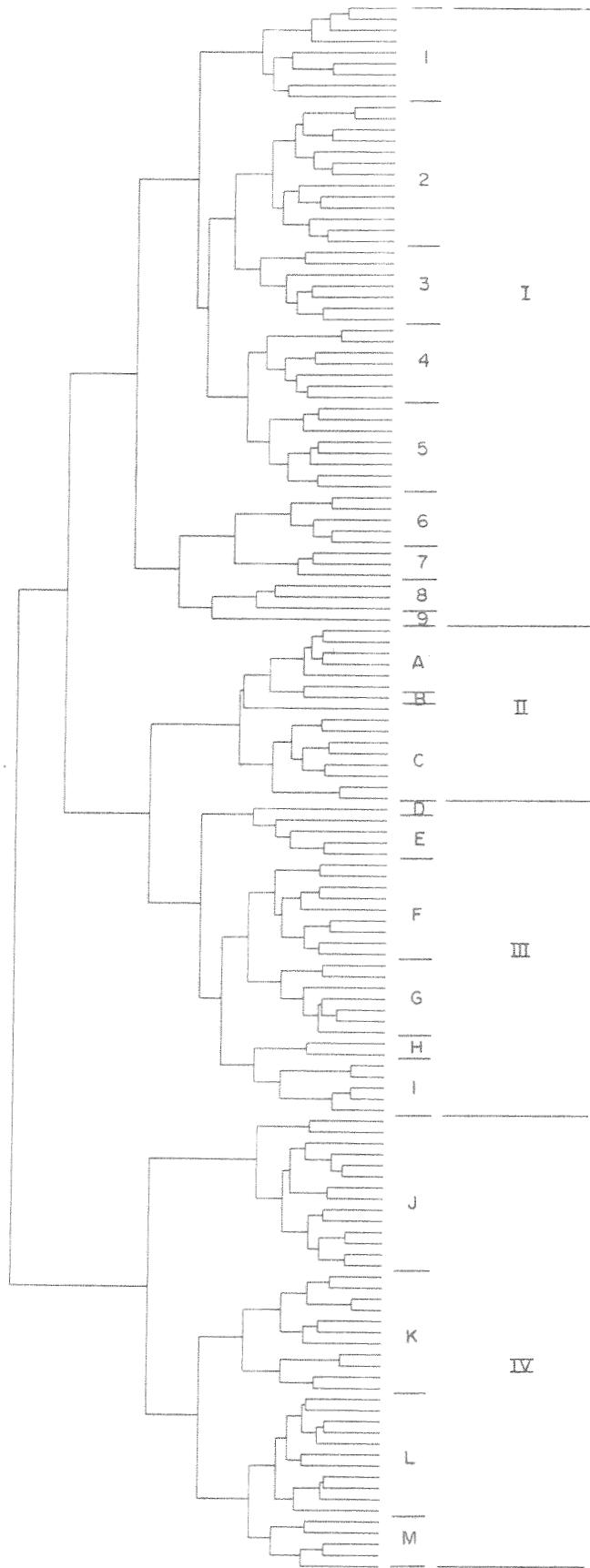


Fig. 40. The site dendrogram, summer 1976. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 42.

SUMMER 1976

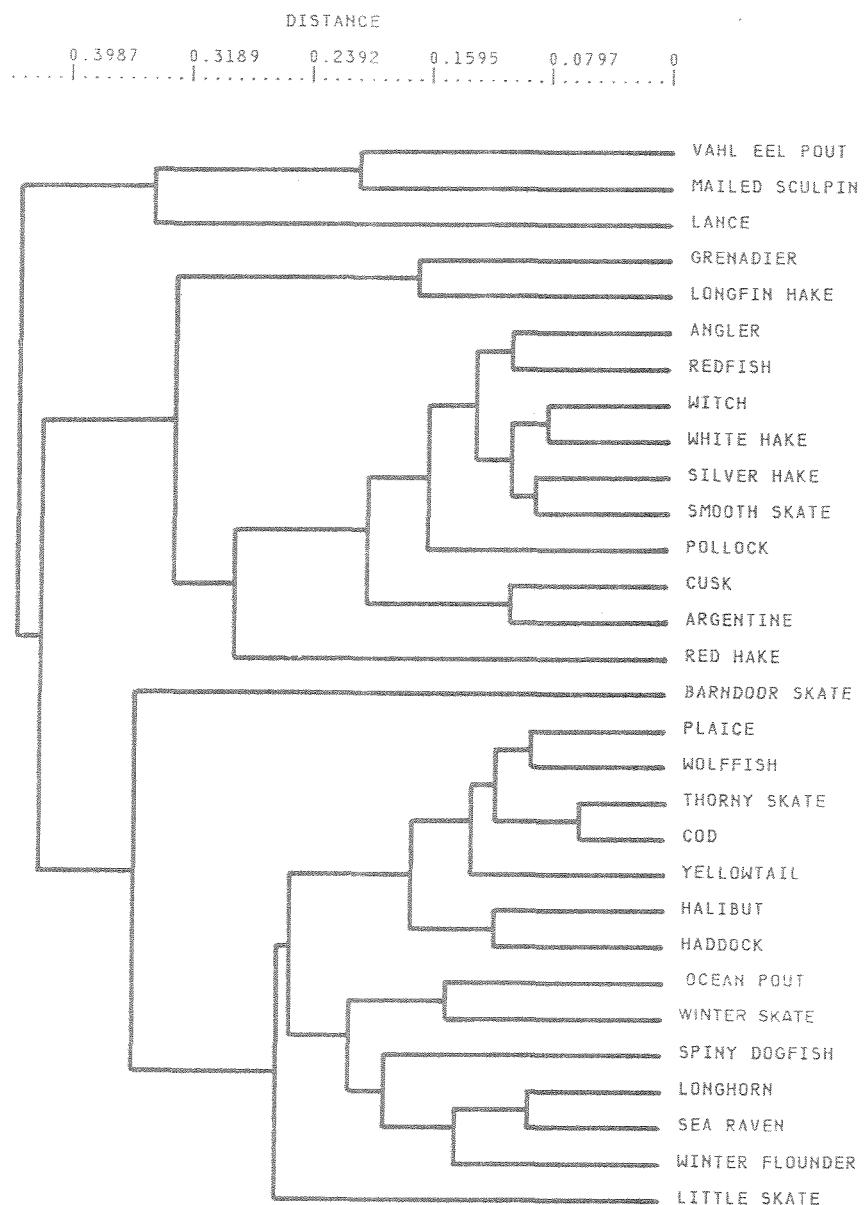


Fig. 41. The species dendrogram, summer 1976.

Fig. 42. The sites times species two-way table, summer 1976. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; . = 0-0.5; - = 0.5-1.0; + = 1-2; \* = greater than 2.

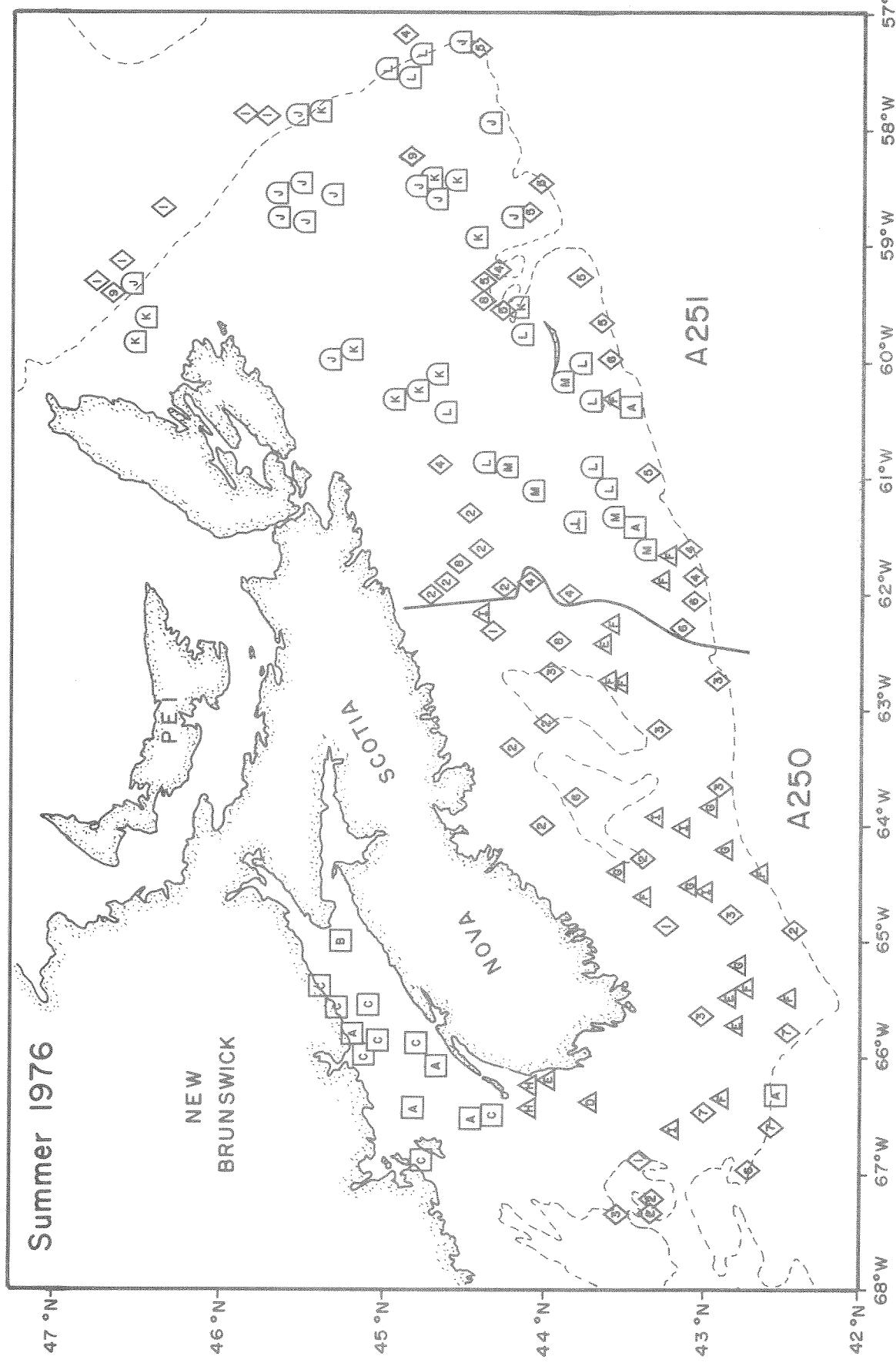


Fig. 43. The areal distribution of site groups, summer 1976. The symbols correspond to those in Figure 42.

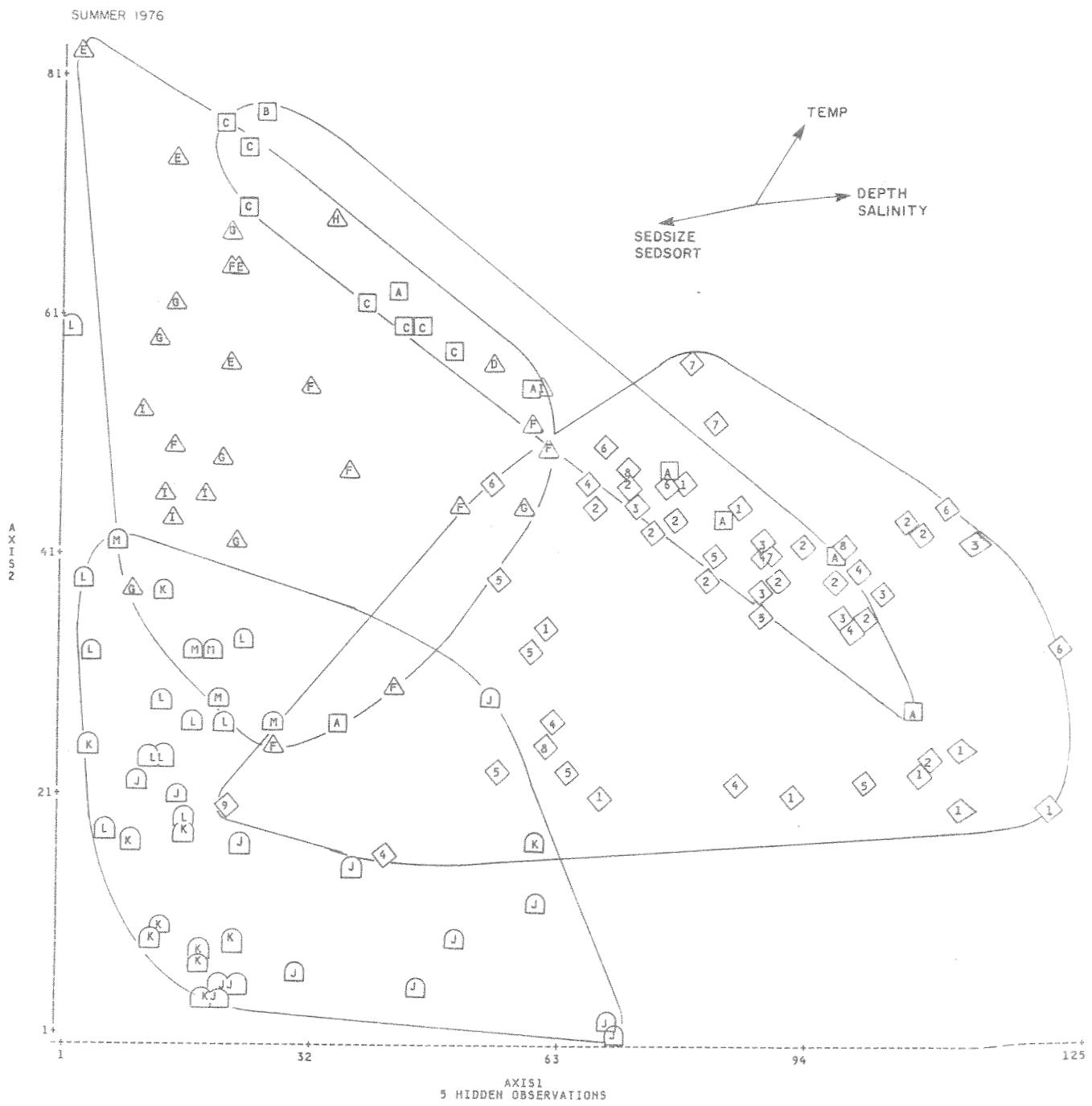


Fig. 44. The distribution of site groups in discriminant space, summer 1976. The symbols and numbers ~~r~~ <sup>1</sup> ~~d~~ correspond to those in Figure 42. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

high salinity. Sediments are generally small grained and well sorted. The two outliers (stations 251-21, 74), furthest to the left along axis 1 in the space occupied by site group IV, are unique in that one contains no species, and other is the only station in group I to contain all the species characteristic of site group IV (plaice, wolffish, thorny skate, cod, and yellowtail). Site group IV occupies the lower left portion of the discriminant space, characterized by shallow depth, the lowest temperature and salinity, and the largest, most well sorted sediments. Major site group III is concentrated in the upper left quadrant of the space. The stations are at shallow depth, with intermediate to warm temperature, intermediate salinity, and predominantly large grained, well sorted sediments. The stations in site group II stretch in a narrow band across the space occupied by site groups I and III. These stations are at shallow to intermediate depth, with warm temperature, intermediate to high salinity, and intermediate sized, poorly sorted sediments.

Table 15. Coefficients of separate determination (Summer 1976). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	17.0	0.2	1.3	0.1
2. Temp	0.1	76.9	0.9	2.7
3. Salinity	16.0	5.2	20.6	3.4
4. SEDSIZE	43.8	4.7	39.0	30.8
5. SEDSAND	6.0	6.4	14.8	13.8
6. SEDSORT	17.1	6.5	23.4	49.2
Eigenvalue	4.3	2.3	0.5	0.1
Percent of Group Separation	58.2	31.6	7.4	1.7

#### 1977 Summer

There are five major divisions in the site dendrogram (Figure 45) and the two-way table (Figure 47) that divide the sites into spatial areas (Figure 48). One of the resultant major site groups (II) contains no species. Of the remaining five major groups, group I includes stations in the Bay of Fundy, along the edge of the shelf, and on banks on both the eastern and western shelf. Species most common in this group are smooth skate, witch, thorny skate, and plaice. Stations in major site group III are along the edge of shelf, in basins, and on banks on the western shelf. These stations include scattered occurrences of many species. Major site group IV includes only a few stations concentrated on the eastern shelf. Thorny skate, plaice, and cod characterize this site group. Major site group V is concentrated on the eastern shelf, and longhorn, yellowtail, thorny skate, plaice, and cod are relatively abundant in this group. The stations in major site groups VI occur in the Bay of Fundy, on the western shelf, and along the western part of Sable Island Bank. These stations include relatively abundant ocean pout, sea raven, winter flounder, haddock, wolffish, cod, and halibut.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 46) and the two-way table (Figure 47). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 48).

There is considerable overlap among the five major site groups in the discriminant space created by axes 1 and 2 (Table 16, Figure 49). Subsequent axes provided no further separation among the groups. Major site group I is characterized by a wide range of depth and temperature, intermediate to high salinity, and a wide range of sediment size and sediment sorting. Group III is almost completely contained within the boundaries of group I, and, like group I, has wide ranges of all environmental variables. Site group IV is positioned centrally on axis 1, and near the top of axis 2. These stations are at shallow to intermediate depth, with lower temperature, intermediate salinity, and sediments that are either extremely large grained and well sorted, or small grained and poorly sorted. Major site group V is to the left of axis 1, at shallow depth, with low to intermediate temperature, intermediate salinity, and predominantly large, well sorted sediments. The last site group (VI) is characterized by shallow depth, intermediate temperature, and low to intermediate salinity, with intermediate sized, poorly sorted to large grained, well sorted sediments.

Table 16. Coefficients of separate determination (Summer 1977). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	15.7	0.1	2.2	2.3
2. temp	0.0	42.7	6.1	12.3
3. Salinity	15.1	3.9	42.4	4.3
4. SEDSIZE	40.3	17.6	34.4	16.1
5. SEDSAND	6.6	15.9	5.1	29.5
6. SEDSORT	22.2	19.8	9.8	35.7
Eigenvalues	2.2	0.7	0.2	0.1
Percent of Group Separation	67.5	21.7	7.3	1.8

#### 1978 Summer

There are three major breaks in the site dendrogram (Figure 50) and the two-way table (Figure 52) that divide the sites into spatial areas (Figure 53). The first major site group (I) occurs primarily along the edge of the shelf and in basins. It is characterized by relatively abundant redfish, witch, silver hake, angler, and longfin hake. Major site group II also includes stations along the shelf edge, as well as in basins on the eastern shelf. These stations contain almost no species, except for relatively low abundances of plaice and smooth skate. The stations in major site group III occur in the Bay of Fundy, on the western shelf banks, and on Sable Island Bank. They are characterized by relatively frequent occurrences of many species, including longhorn, sea raven, thorny skate, cod, haddock, and silver hake.

SUMMER 1977

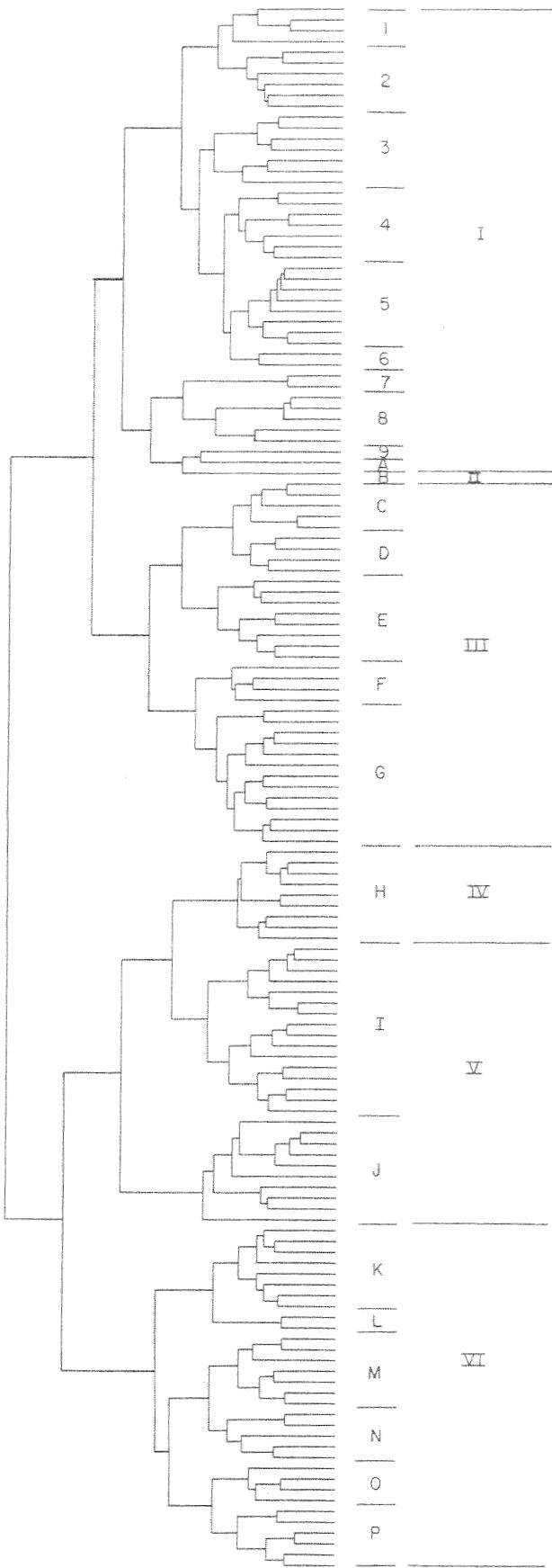


Fig. 45. The site dendrogram, summer 1977. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 47.

SUMMER 1977

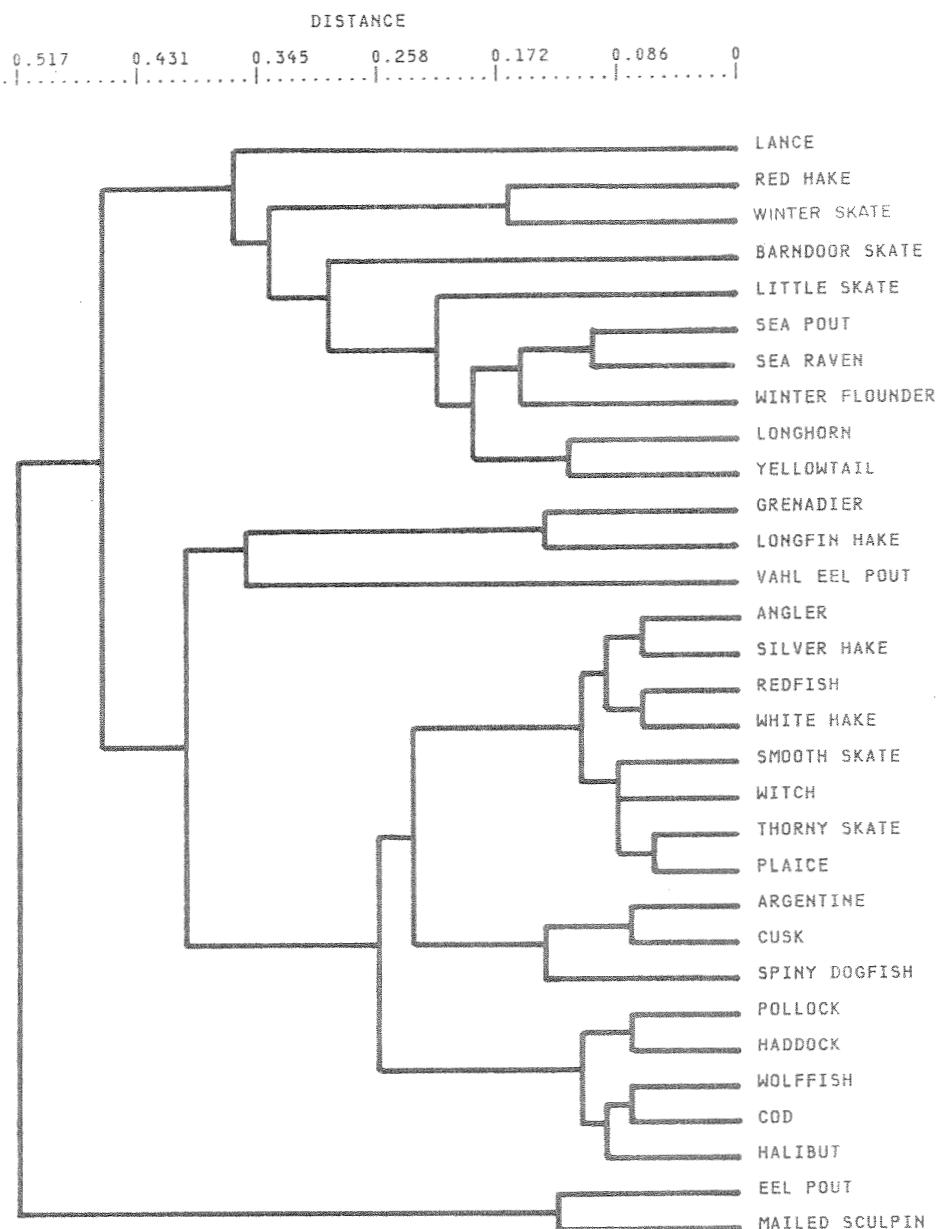


Fig. 46. The species dendrogram, summer 1977.

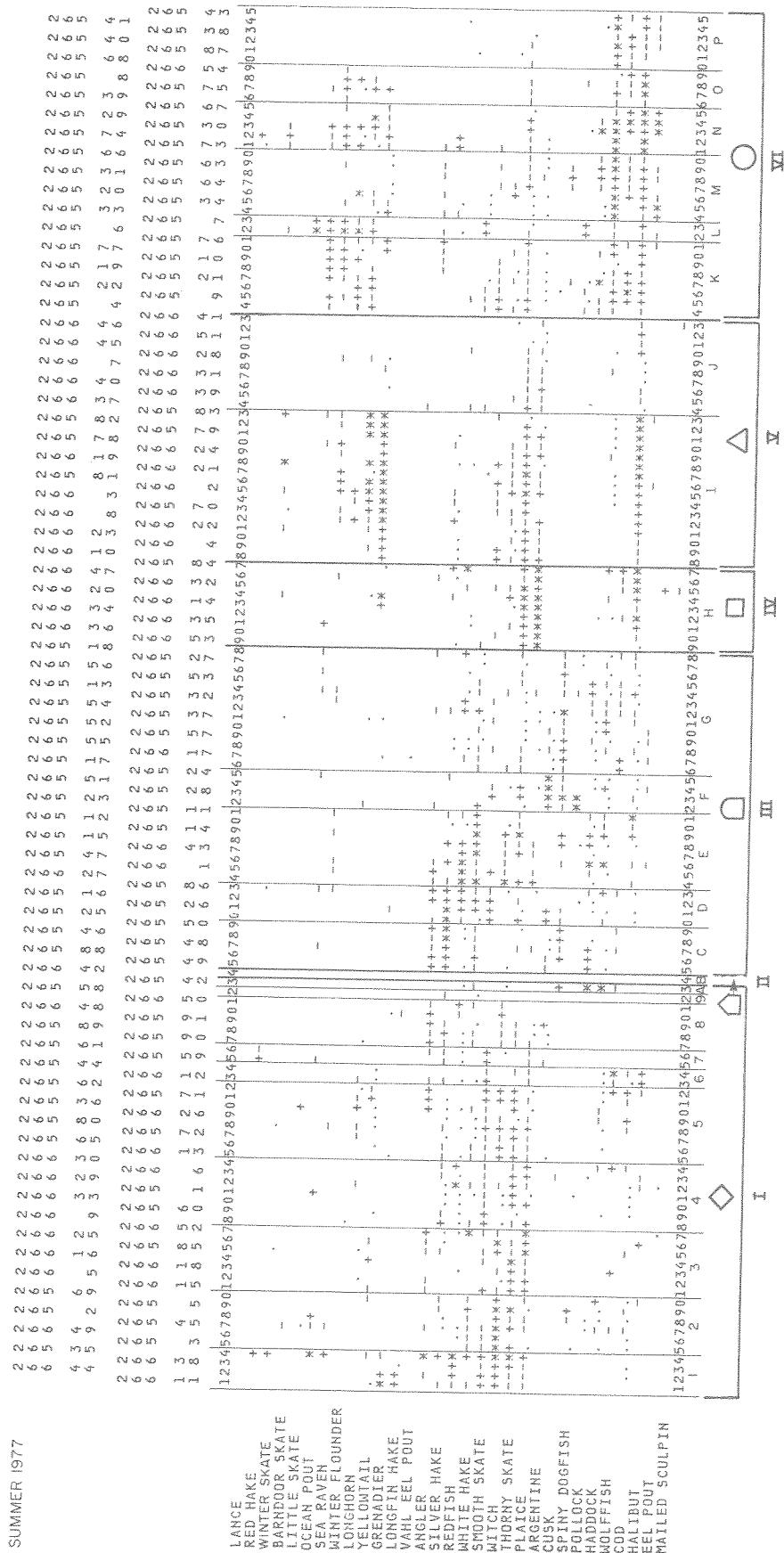


Fig. 4.7. The sites times species two-way table, summer 1977. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; - = 0.5-1.0; + = 1-2; \*\* = greater than 2.

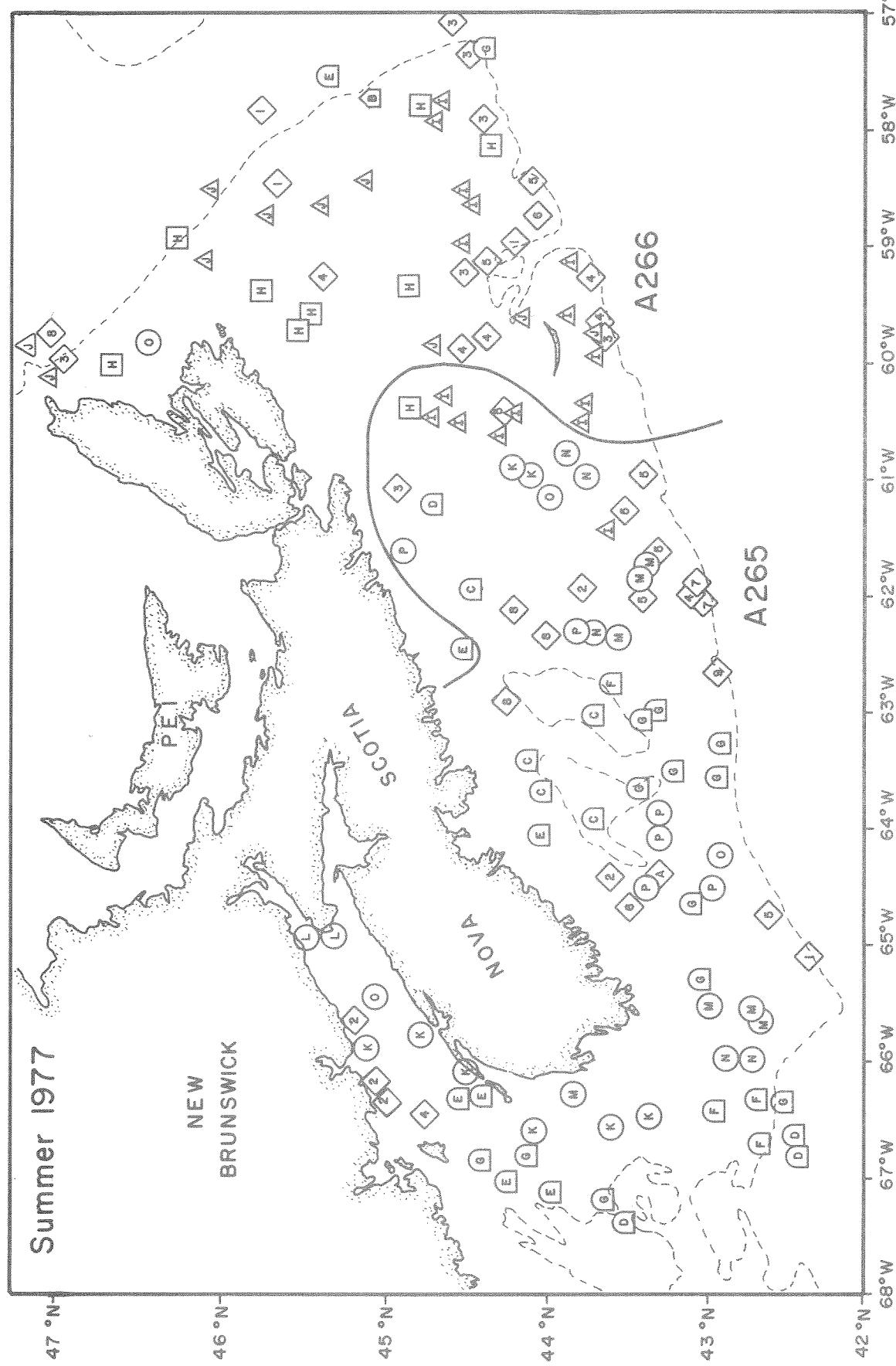


Fig. 48. The areal distribution of site groups, summer 1977. The symbols correspond to those in Figure 47.

SUMMER 1977

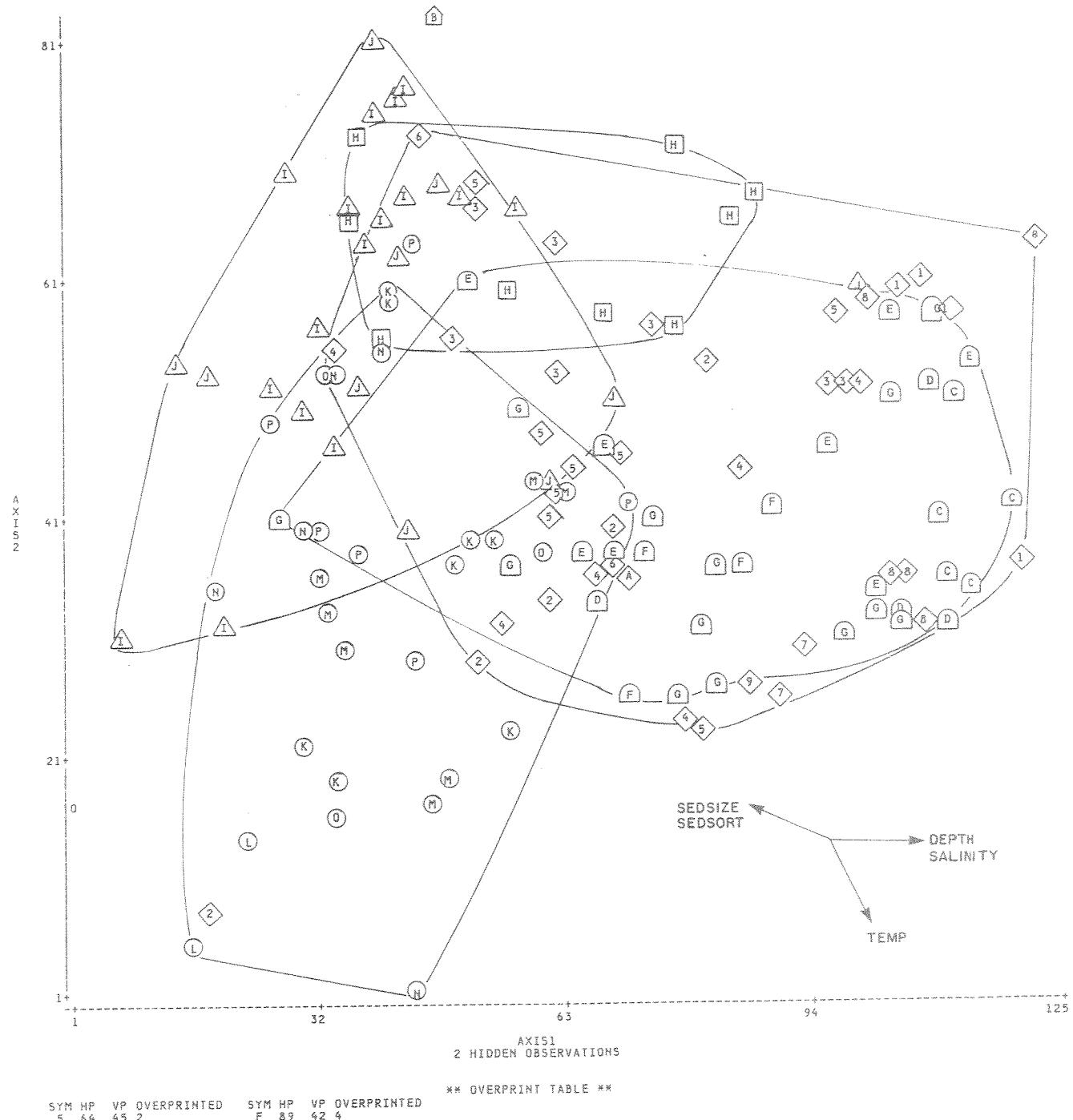


Fig. 49. The distribution of site groups in discriminant space, summer 1977. The symbols and number/letter codes correspond to those in Figure 47. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

SUMMER 1978

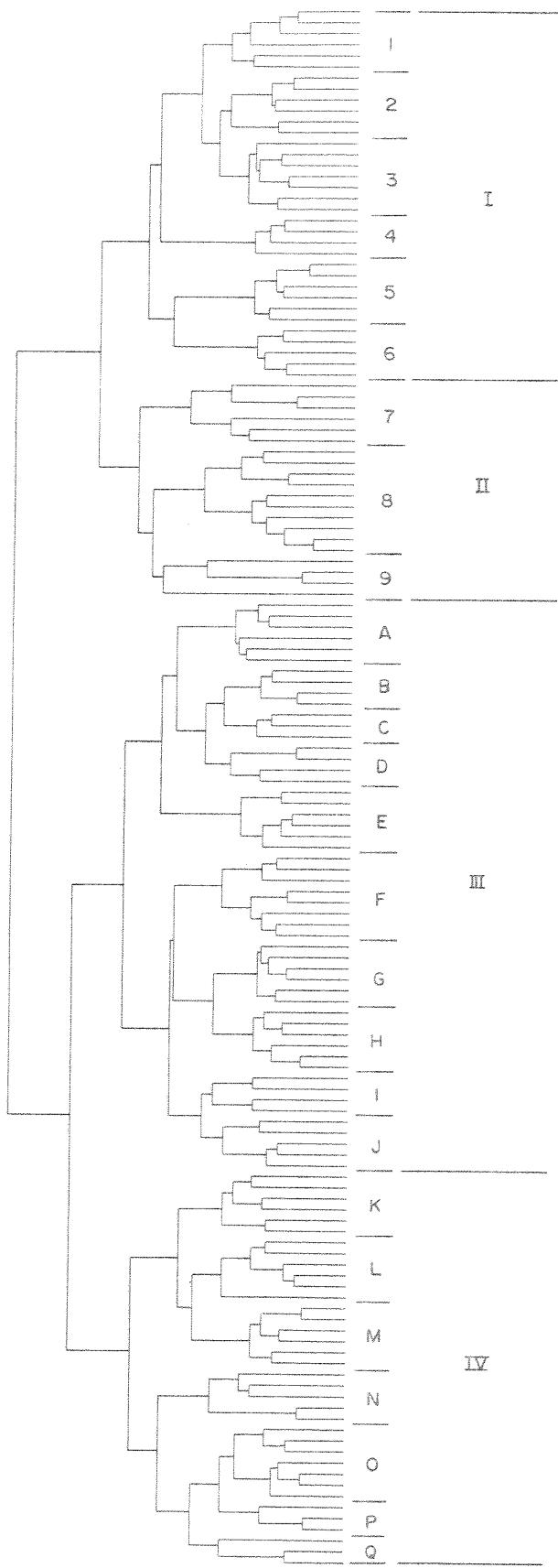


Fig. 50. The site dendrogram, summer 1978. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 52.

SUMMER 1978

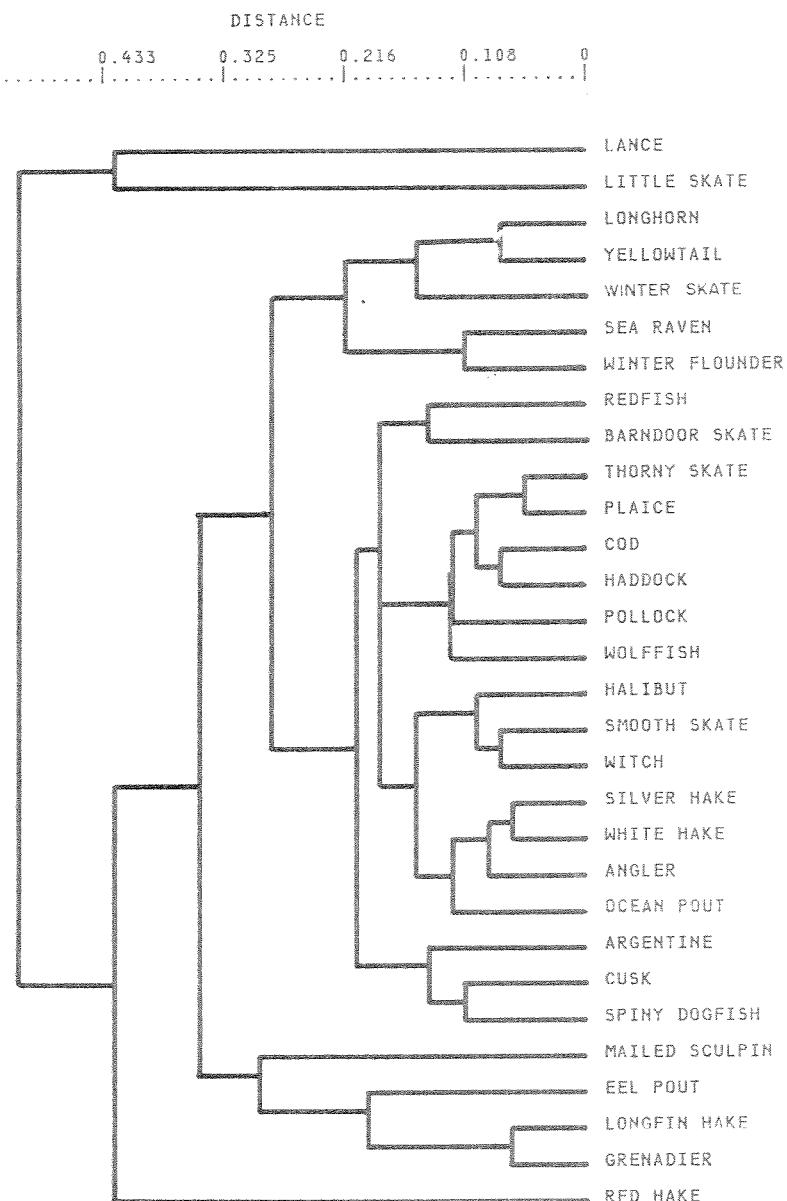


Fig. 51. The species dendrogram, summer 1978.

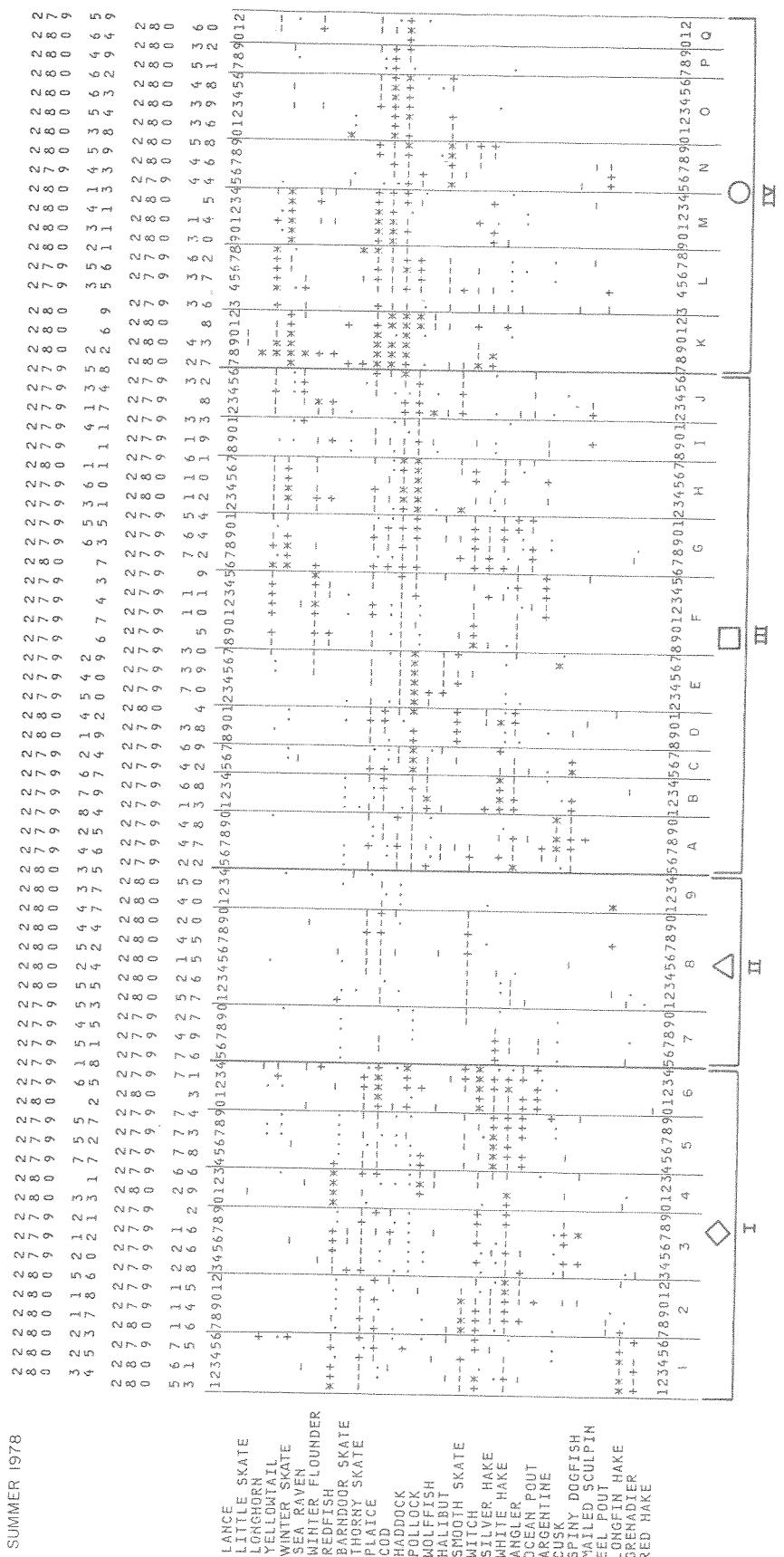


Fig. 52. The sites times species two-way table, summer 1978. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These cores correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; + = 0-0.5; \* = 0.5-1.0; + = 1-2; \* = greater than 2.

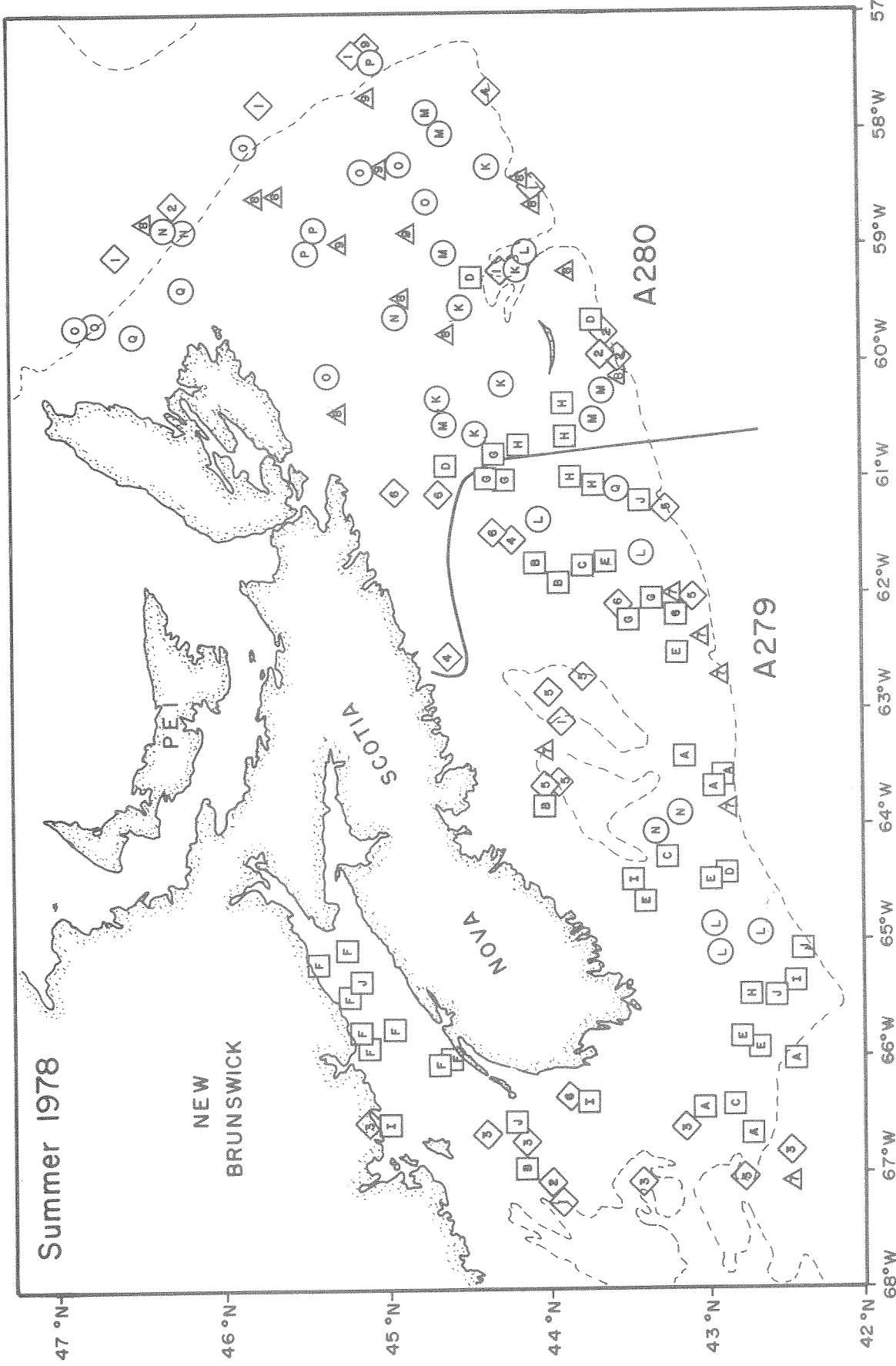


Fig. 53. The areal distribution of site groups, summer 1978. The symbols correspond to those in Figure 52.

SUMMER 1978

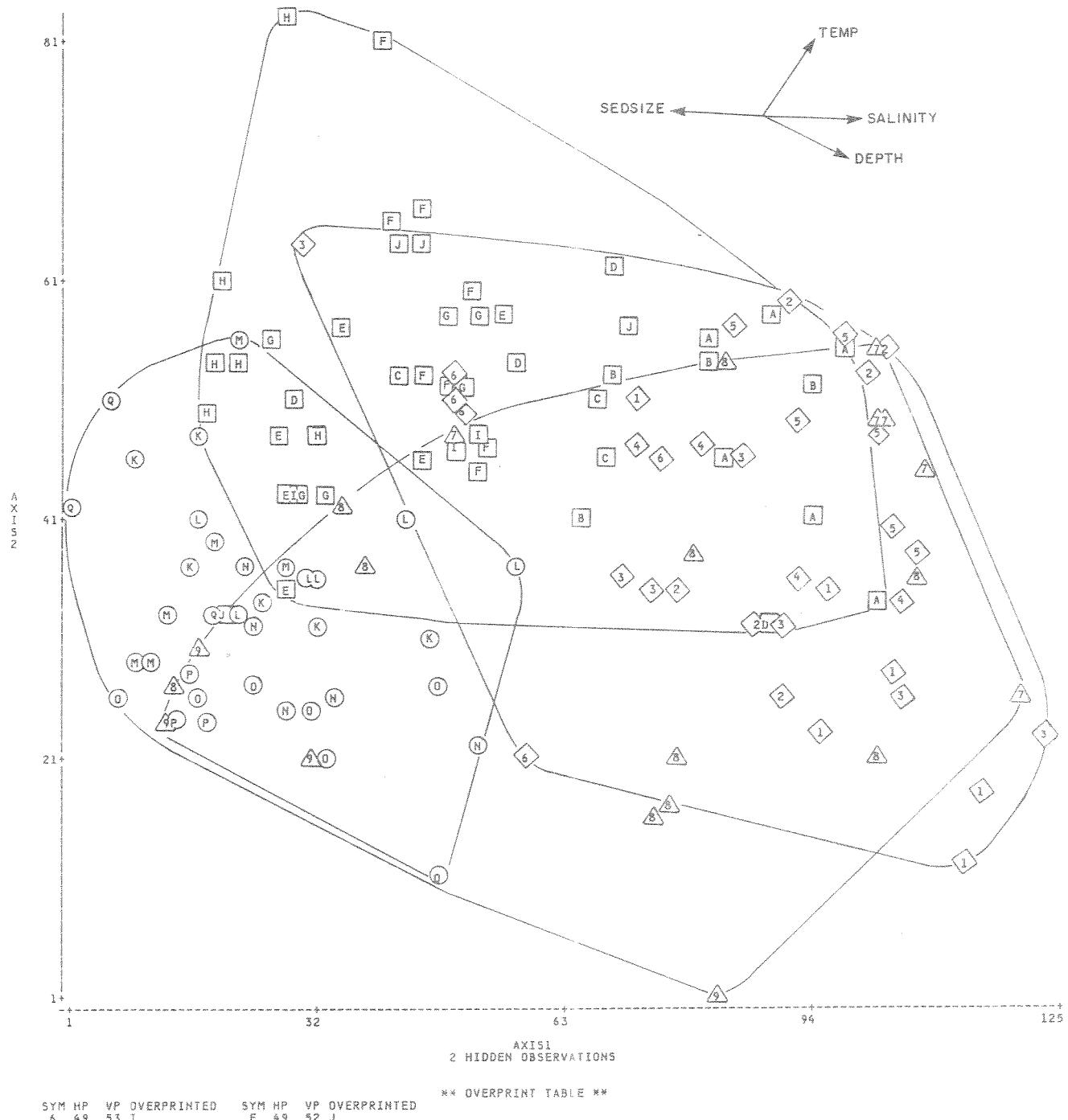


Fig. 54. The distribution of site groups in discriminant space, summer 1978. The symbols and number-letter codes correspond to those in Figure 52. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

Major site group IV is scattered along the eastern edge of the shelf, as well as on banks on both the eastern and western parts of the shelf. Longhorn, yellowtail, thorny skate, plaice, and cod are relatively abundant in this site group.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 51) and the two-way table (Figure 52). The spatial distribution of the species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 53).

The major site groups occupy distinct segments of the discriminant space (Table 17, Figure 54), although there is some overlap, particularly among groups I, II, and III. Group I is characterized by an extreme range of depths, warm temperature, intermediate to high salinity, and mostly small to intermediate sized sediments. Group II also covers an extreme range of depths, as well as an extreme range of temperatures, with intermediate to high salinity, and an extreme range of sediment sizes. Stations in site group III were at shallow to intermediate depth, intermediate to high temperature and salinity, with intermediate to large grained sediments. Group IV is concentrated to the left of axis 1, and is characterized by shallow depth, low temperature, intermediate salinity, and extremely large grained sediments.

Table 17. Coefficients of separate determination (Summer 1978). These show the relative importance of each variable on each axis. The Eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	42.1	19.2	6.4	8.8
2. Temp	18.4	76.2	2.2	0.9
3. Salinity	20.4	0.6	27.6	25.0
4. SEDSIZE	14.4	2.3	15.1	12.4
5. SEDSAND	0.4	1.7	35.1	16.0
6. SEDSORT	4.3	0.0	13.6	36.9
Eigenvalues	4.1	1.0	0.2	0.2
Percent of Group Separation	73.1	18.0	4.1	2.9

#### 1979 Summer

There are five major breaks in the site dendrogram (Figure 55) and the two-way table (Figure 57) that divide the sites into spatial areas (Figure 58). One of the resultant major site groups (III) contains no species. Major site group I is primarily along the eastern edge of the shelf and is characterized by relatively abundant grenadier, longfin hake, redfish, white hake, witch, and Vahl's eel pout. Very few other species occur here. Site group II included stations in the mouth of the Bay of Fundy, in basins, along the edge of the shelf, and scattered on the eastern shelf. Many species are relatively common in this site group and white hake, cusk, pollock, spiny dogfish, and silver hake are particularly abundant. Stations in major site group IV are at the head of the Bay of Fundy and on the western shelf.

Only haddock is relatively abundant. Stations in site group V are primarily on Sable Island Bank, with some on Banquereau and Browns Bank. Thorny skate, haddock, cod, yellowtail, and longhorn are relatively common and abundant. Major site group VI is concentrated on the eastern shelf, and is characterized by thorny skate and plaice, with few occurrences of other species.

Groups of species with similar distributions across sites are shown on the species dendrogram (Figure 56) and the two-way table (Figure 57). The spatial distribution of the species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 58).

The first two discriminant axes account for most of the variability among sites (Table 18, Figure 59). Subsequent axes provided no further separation among site groups. Major site group I is to the right along axis 1 and toward the bottom of axis 2. These stations are at intermediate to great depth, with intermediate temperature, and mostly small grained, poorly sorted sediments. Site group II occupies a large area of the discriminant space, and is characterized by an extremely wide range of all environmental variables. Major site group IV is located to the left along axis 1, and has predominantly shallow depth, intermediate to warm temperatures, and intermediate sizes, poorly sorted to large grained, well sorted sediments. Site group V overlaps group IV to a large extent, but differs in having the shallowest depth, low to intermediate temperatures, and predominantly very large grained, well sorted sediments. Stations in major site group VI occupy the lower left corner of the discriminant space. These stations are characterized by shallow to intermediate depth, low temperature, and sediments that were either large and well sorted or small grained and poorly sorted. The two-way table (Figure 57) shows that major site groups that occupy a small part of the discriminant space (i.e. I and VI) also have limited and distinct species assemblages. In contrast, groups that fill a large part of the space (i.e. II and IV) contain either frequent occurrences of many species (II) or almost no species at all (IV).

Table 18. Coefficients of separate determination (Summer 1979). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	52.0	17.4	1.2	7.1
2. Temp	13.0	56.9	12.2	2.0
3. Salinity	9.2	0.0	13.9	47.6
4. SEDSIZE	7.4	13.8	16.5	0.2
5. SEDSAND	4.0	8.2	12.1	38.5
6. SEDSORT	14.4	3.7	44.1	4.6
Eigenvalue	4.1	1.0	0.1	0.6
Percent of Group Separation	77.3	19.0	1.9	1.2

SUMMER 1979

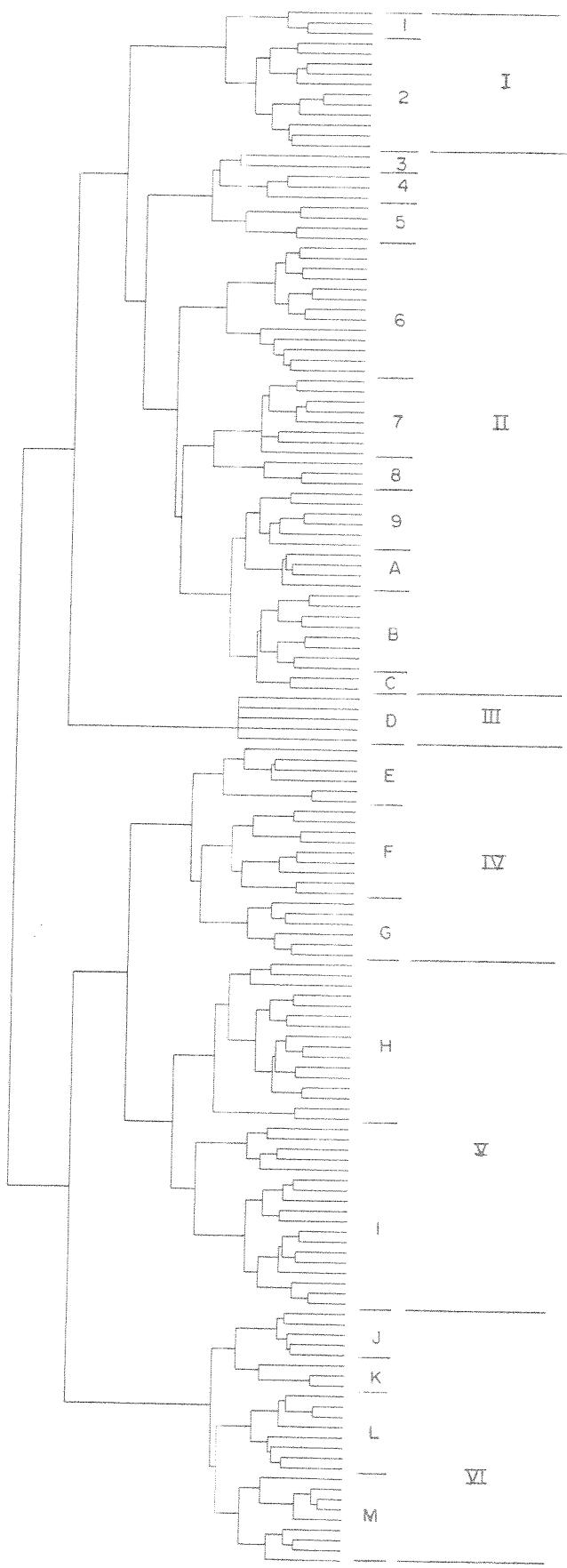


Fig. 55. The site dendrogram, summer 1979. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 57.

SUMMER 1979

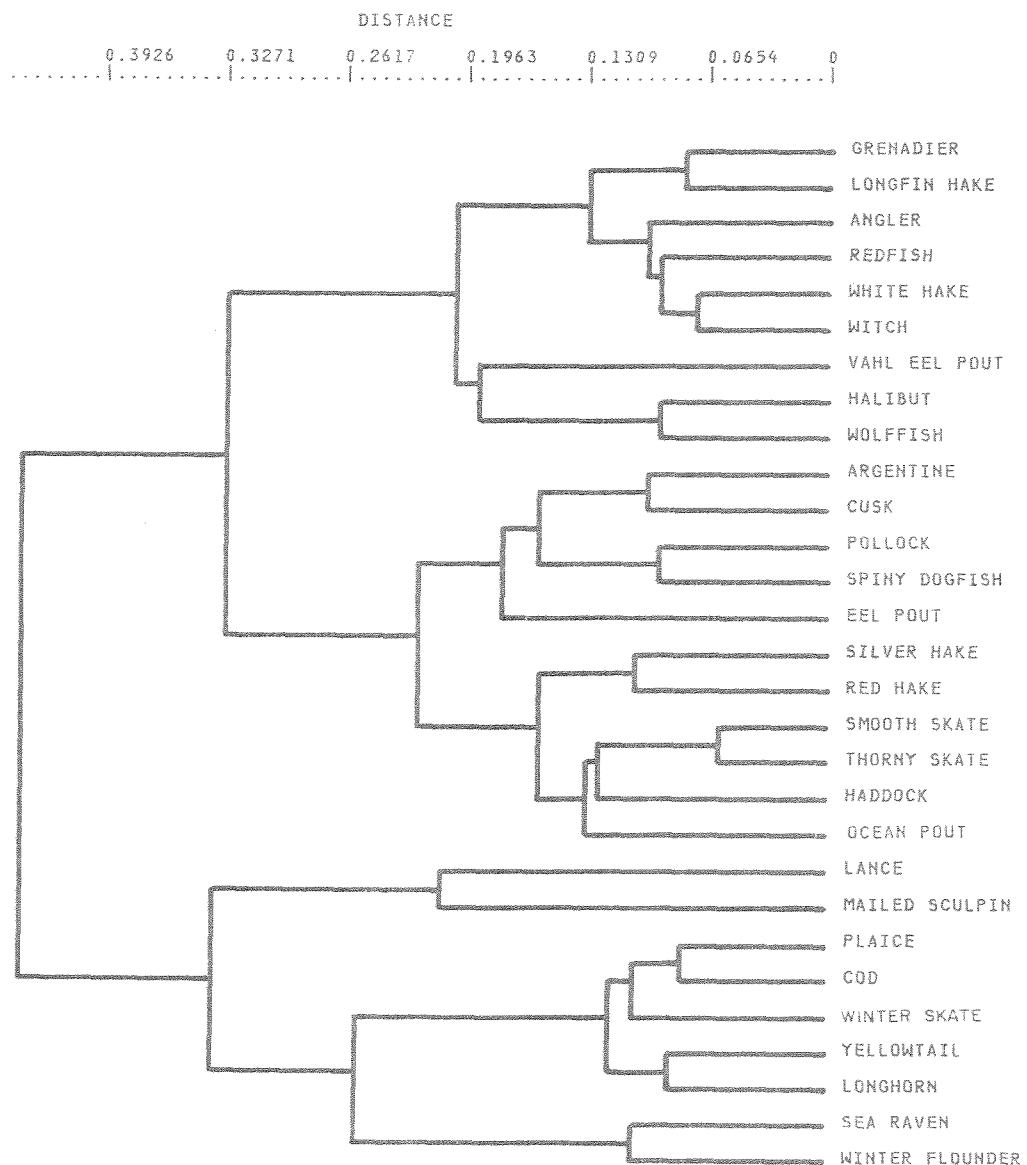


Fig. 56. The species dendrogram, summer 1979.

Fig. 57. The sites times species two-way table, summer 1979. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; + = 0.5-1.0; ++ = 1-2; \* = greater than 2.

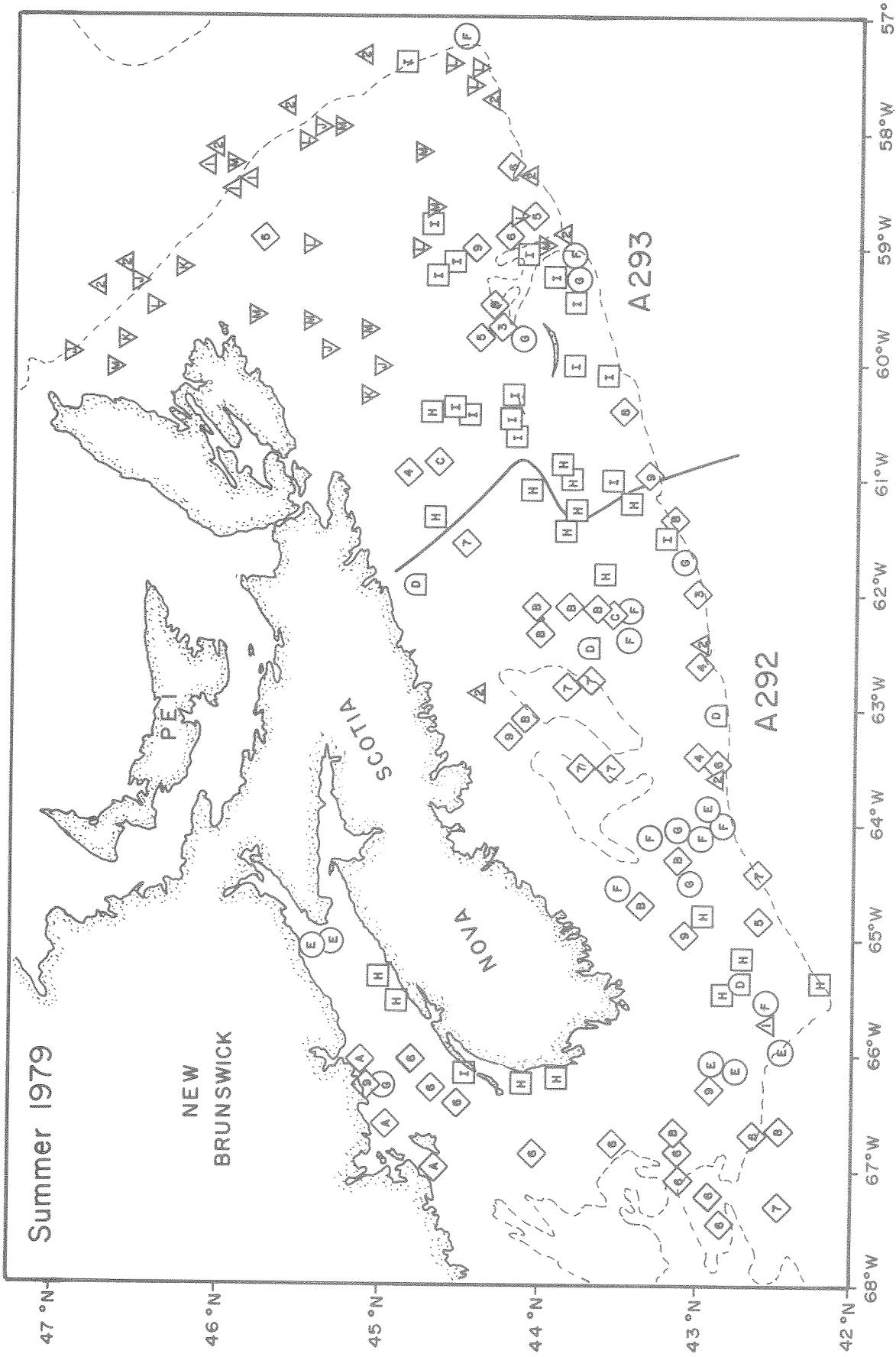


Fig. 58. The areal distribution of site groups, summer 1979. The symbols correspond to those in Figure 57.

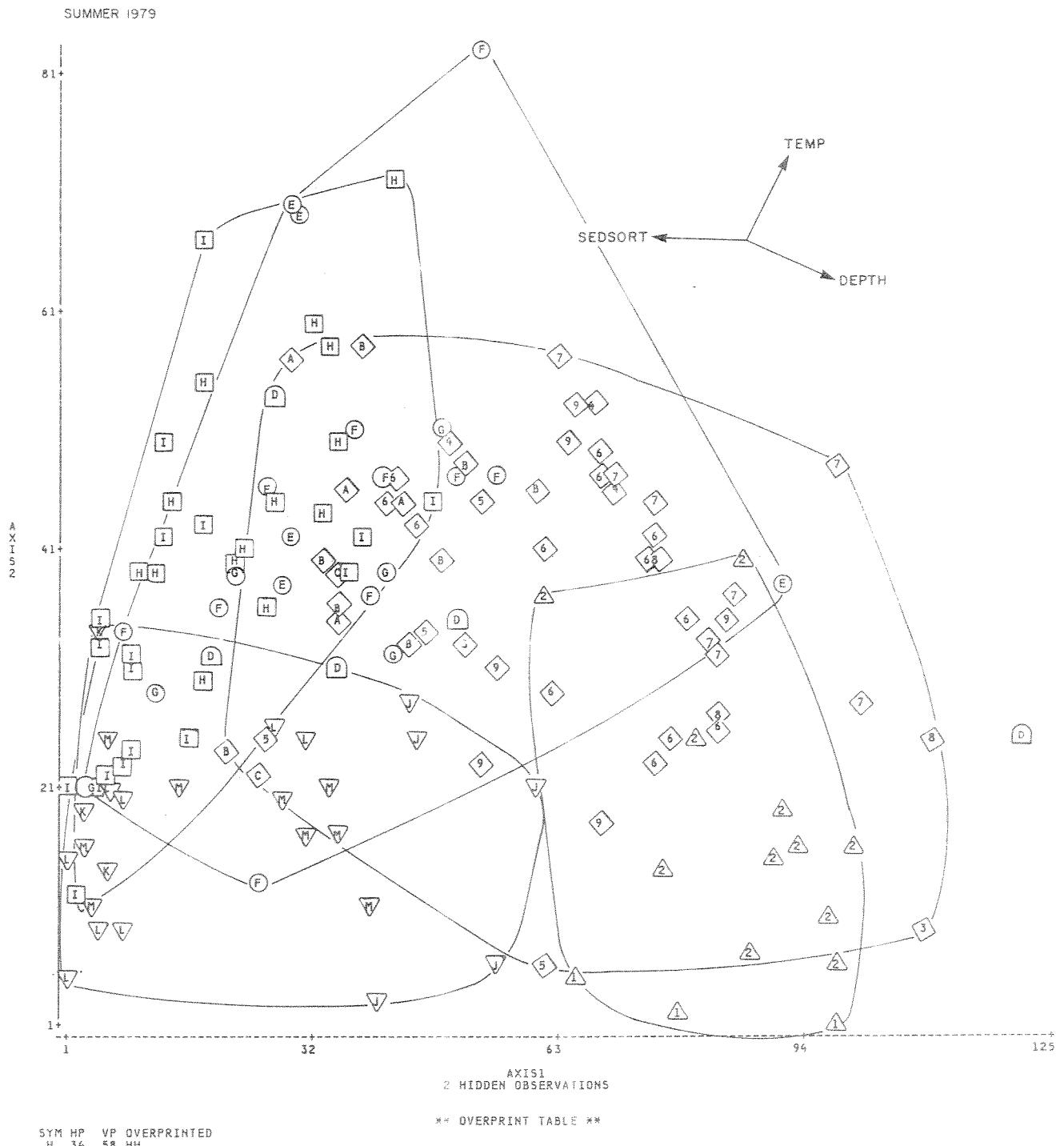


Fig. 59. The distribution of site groups in discriminant space, summer 1979. The symbols and number/letter codes correspond to those in Figure 57. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

## 1980 Summer

There are three major breaks in the site dendrogram (Figure 60) and the two-way table (Figure 62) that divide the sites into spatial areas (Figure 63). One of the resultant groups (II) is small and contains no species. Of the remaining groups, the first (I) is widely spread and includes stations in the Bay of Fundy, as well as on the eastern and western shelf. This group is characterized by relatively abundant haddock and cod, with lesser occurrences of thorny skate, plaice, yellowtail, and longhorn. Major site group III is concentrated on the eastern shelf and contains relatively abundant thorny skate, plaice, cod, and yellowtail, with very few occurrences of other species. The stations in site group IV are also widely spread, in the Bay of Fundy, along the edge of the shelf, and in basins. This is the only site group in which grenadier, redfish, cusk, argentine, white hake, witch, angler, silver hake, and red hake are relatively abundant.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 61) and the two-way table (Figure 62). The spatial distribution of the species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 63).

The first two discriminant axes account for most of the variability among sites (Table 19, Figure 64), and subsequent axes provide no further separation. Major site group I is located to the left along axis 1, at predominantly shallow depths, with an extreme range of temperatures, intermediate salinity, and extremely large grained sediments. Site group III occupies a subset of the space occupied by site group I. Group III is characterized by very shallow depth, a wide range of temperatures, intermediate salinity, and predominantly large grained sediments. Group IV is widely spread on both axes, and incorporates wide ranges of depth and temperature, intermediate to high salinity, and small to intermediate sized sediments.

Table 19. Coefficients of separate determination (Summer 1980). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	39.1	8.3	0.5	40.4
2. Temp	2.6	74.9	9.5	2.6
3. Salinity	18.1	3.4	52.5	2.7
4. SEDSIZE	28.1	8.7	30.9	53.2
5. SEDSAND	1.6	2.0	0.3	0.3
6. SEDSORT	10.4	2.7	6.4	1.0
Eigenvalue	3.6	0.7	0.3	0.2
Percent of Group Separation	72.9	14.7	6.3	3.8

## 1981 Summer

There are three major breaks in the site dendrogram (Figure 65) and the two-way table (Figure 67) that divide the sites into spatial areas (Figure 68). One of the resultant major site groups (III) includes only three stations

with a single occurrence of one species. Of the remaining groups, the first (I) includes stations in the Bay of Fundy and on the eastern Scotian Shelf. Yellowtail, thorny skate, cod, and plaice are relatively abundant in this site group. Major site group II includes the Bay of Fundy, the western shelf, and Sable Island Bank. This is the only site group with relatively abundant winter flounder, longhorn, sea raven, and ocean pout. Haddock and cod are also relatively abundant. Stations in major site group IV are concentrated along the edge of the shelf and in basins. Several species occur relatively frequently, including red hake, silver hake, angler, white hake, argentine, cusk, and redfish.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 66) and the two-way table (Figure 67) to the maps of site groups on the Scotian Shelf (Figure 68).

The three major site groups occupy distinct, but partly overlapping, areas in the discriminant space created by the first two axes (Table 20, Figure 69). Subsequent axes provided no further separation. All three groups covered extensive areas of the space. Site group I is characterized by shallow to intermediate depth, low to intermediate temperatures, intermediate to high salinity, and a wide range of sediment size and sediment sorting. Major site group II extends further up axis 2, and includes stations at predominantly very shallow depth, with an extreme range of temperature, intermediate to high salinity, and mostly large grained, well sorted sediments. Stations in site group IV are characterized by intermediate to great depth, intermediate to warm temperature, very high salinity, and predominantly small grained, poorly sorted sediments. A few stations in this group, furthest to the left on axis 1, had extremely large grained, poorly sorted sediments.

Table 20. Coefficients of separate determination (Summer 1981). These show the relative importance of each variable on each axis. The eigenvalue show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	19.9	14.4	0.2	0.3
2. Temp	12.4	51.4	1.3	0.5
3. Salinity	17.2	0.0	22.8	0.0
4. SEDSIZE	21.3	20.1	20.3	51.8
5. SEDSAND	10.5	6.6	7.8	20.4
6. SEDSORT	18.8	7.5	47.7	26.9
Eigenvalue	3.9	0.7	0.2	0.2
Percent of Group Separation	76.2	14.3	4.7	3.3

## 1979 Spring

There are four major breaks in the site dendrogram (Figure 70) and the two-way table (Figure 72) that divide the sites into spatial areas (Figure 73). One of the resultant major groups (II) contains no species, and another (III) only scattered occurrences of a few species. Of the remaining site groups, group I

SUMMER 1980

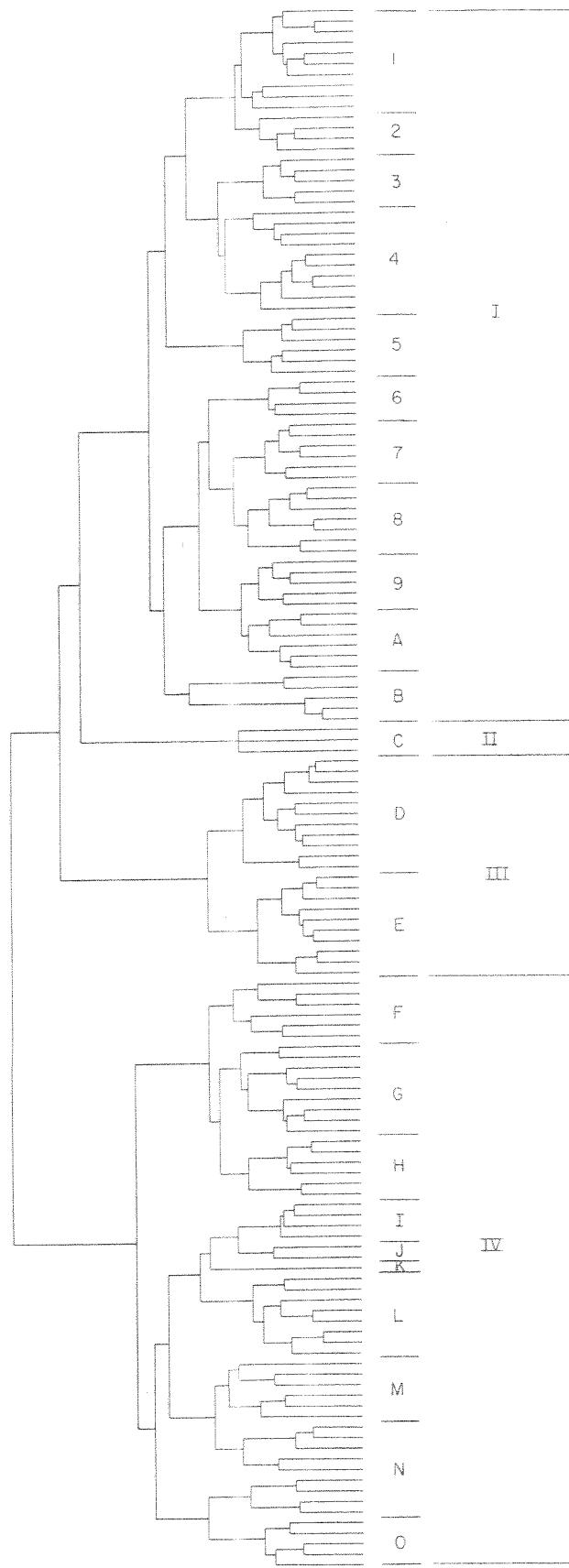


Fig. 60. The site dendrogram, summer 1980. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 62.

SUMMER 1980

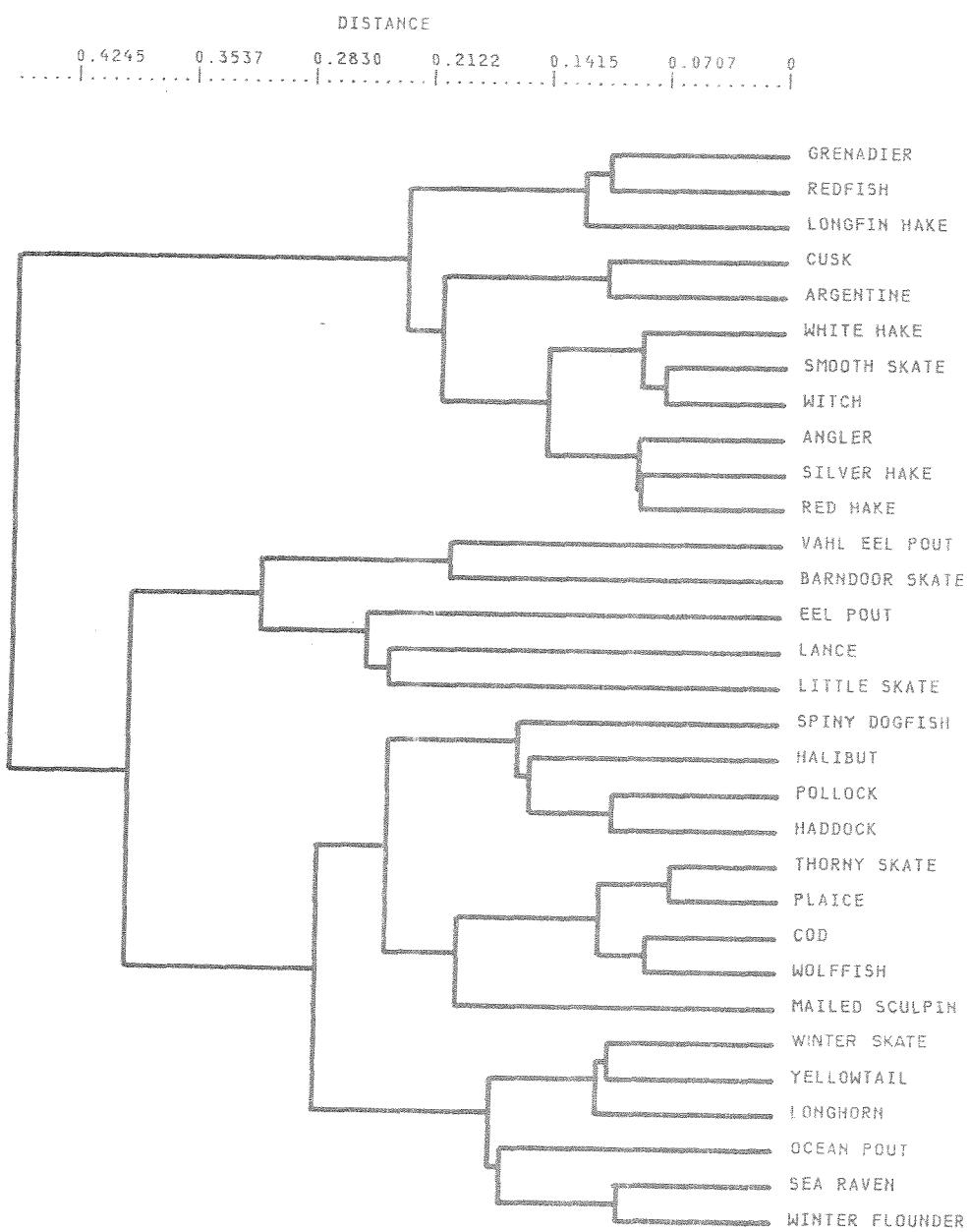
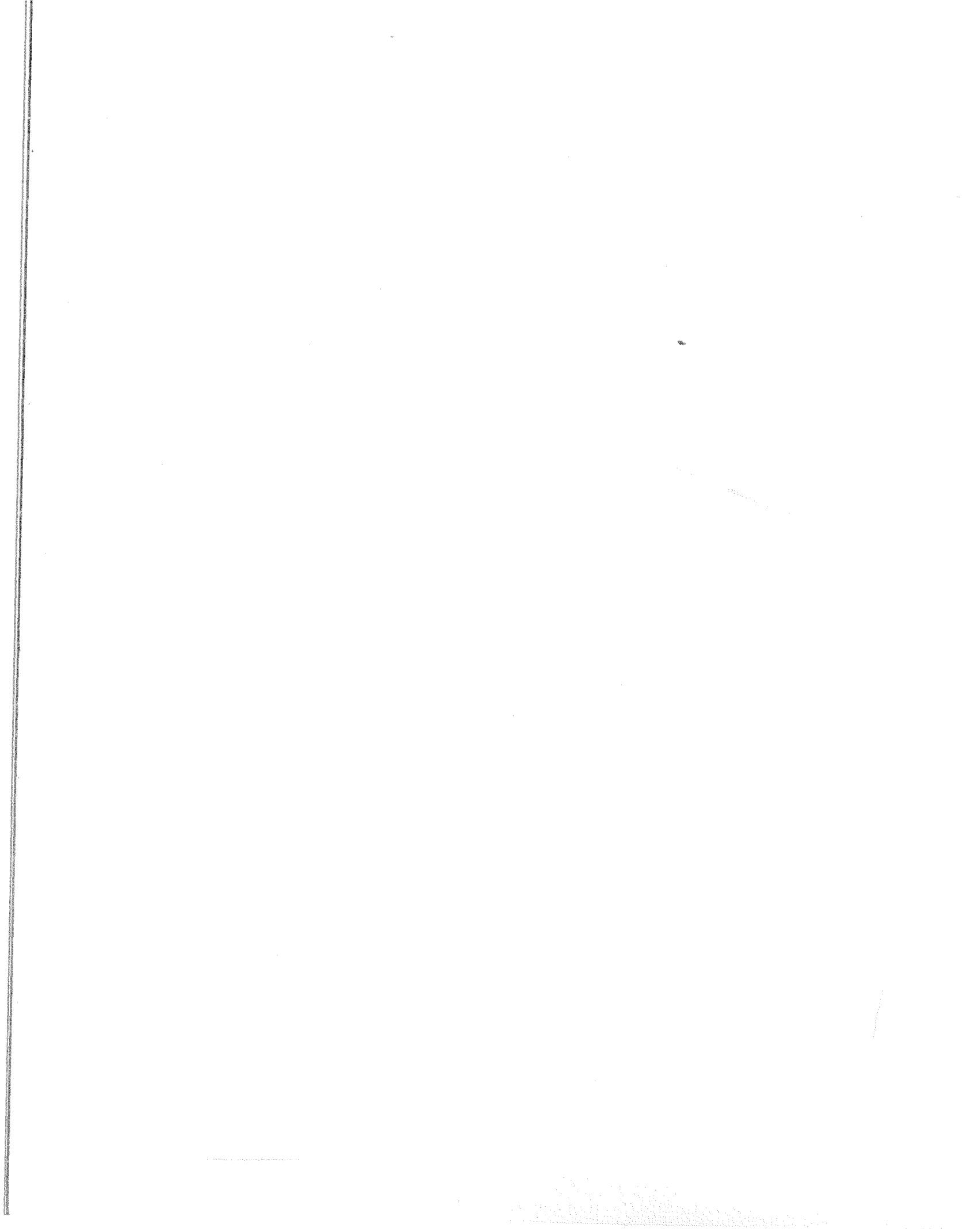


Fig. 61. The species dendrogram, summer 1980.



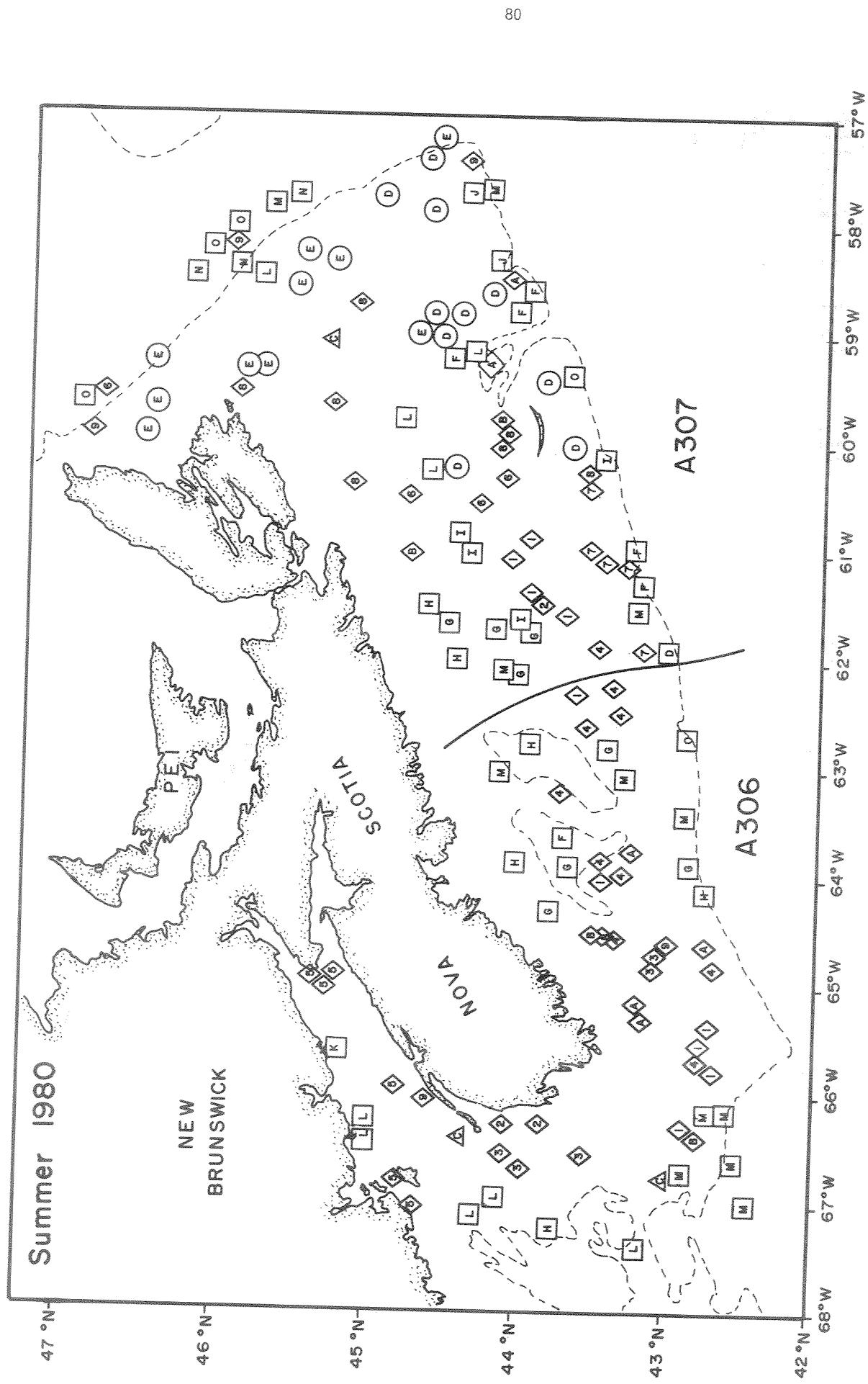


Fig. 63. The areal distribution of site groups, summer 1980. The symbols correspond to those in Figure 62.

SUMMER 1980

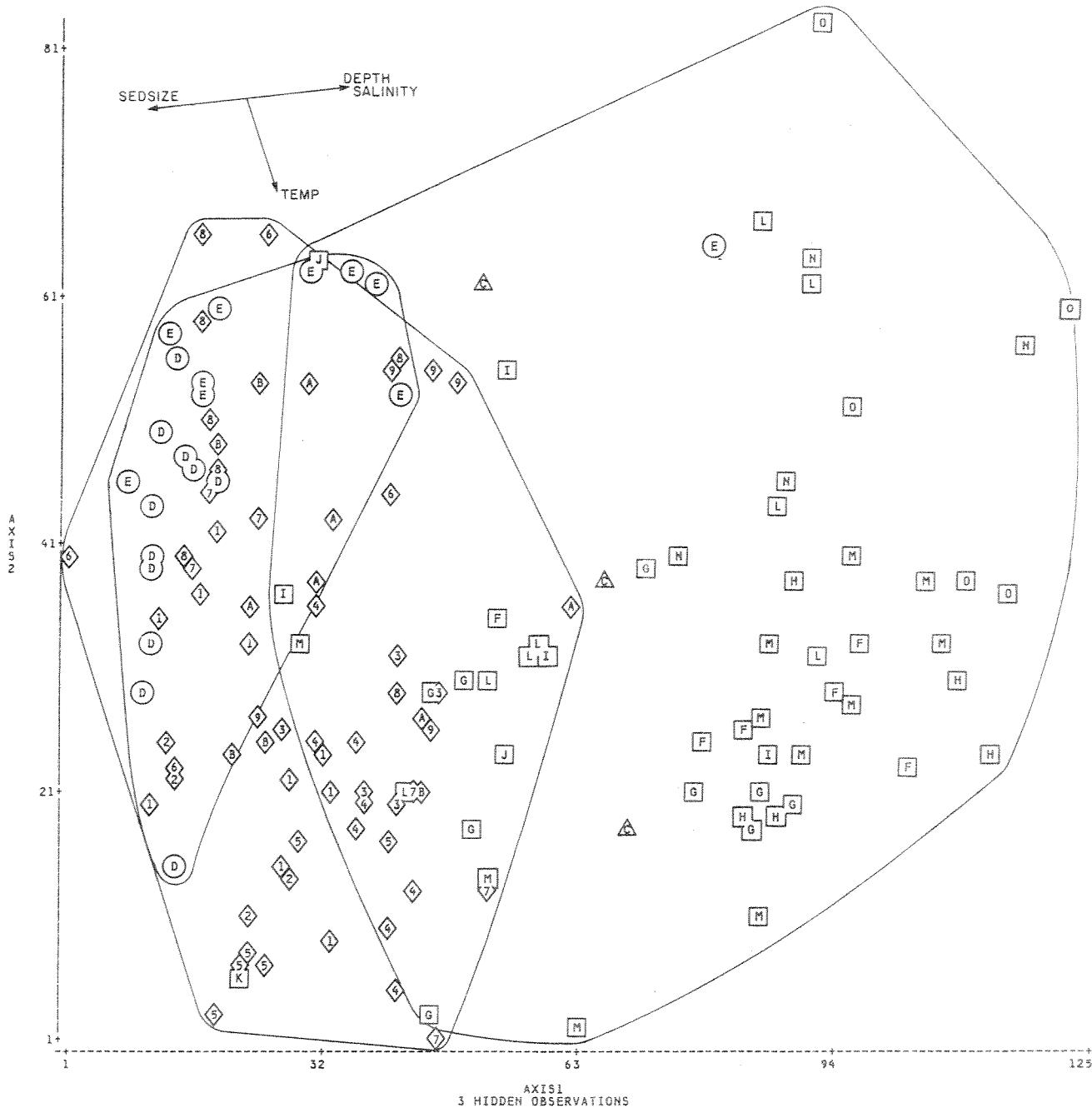


Fig. 64. The distribution of site groups in discriminant space, summer 1980. The symbols and number-letter codes correspond to those in Figure 62. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

SUMMER 1981

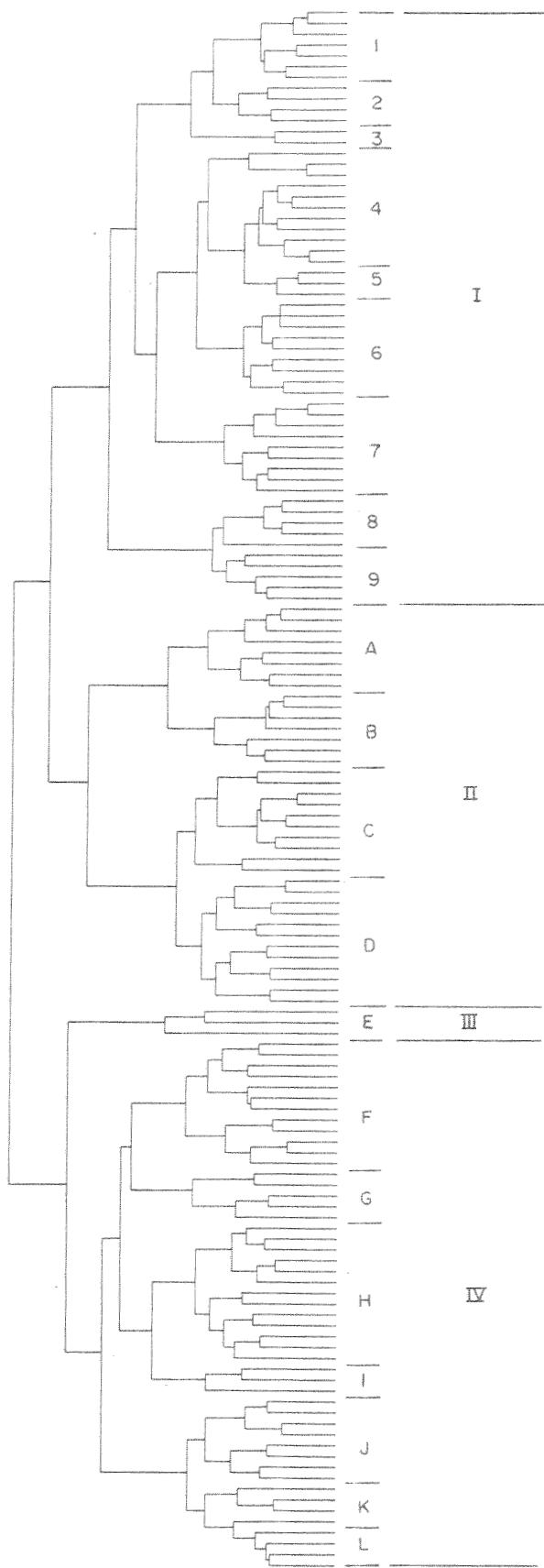


Fig. 65. The site dendrogram, summer 1981. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 67.

SUMMER 1981

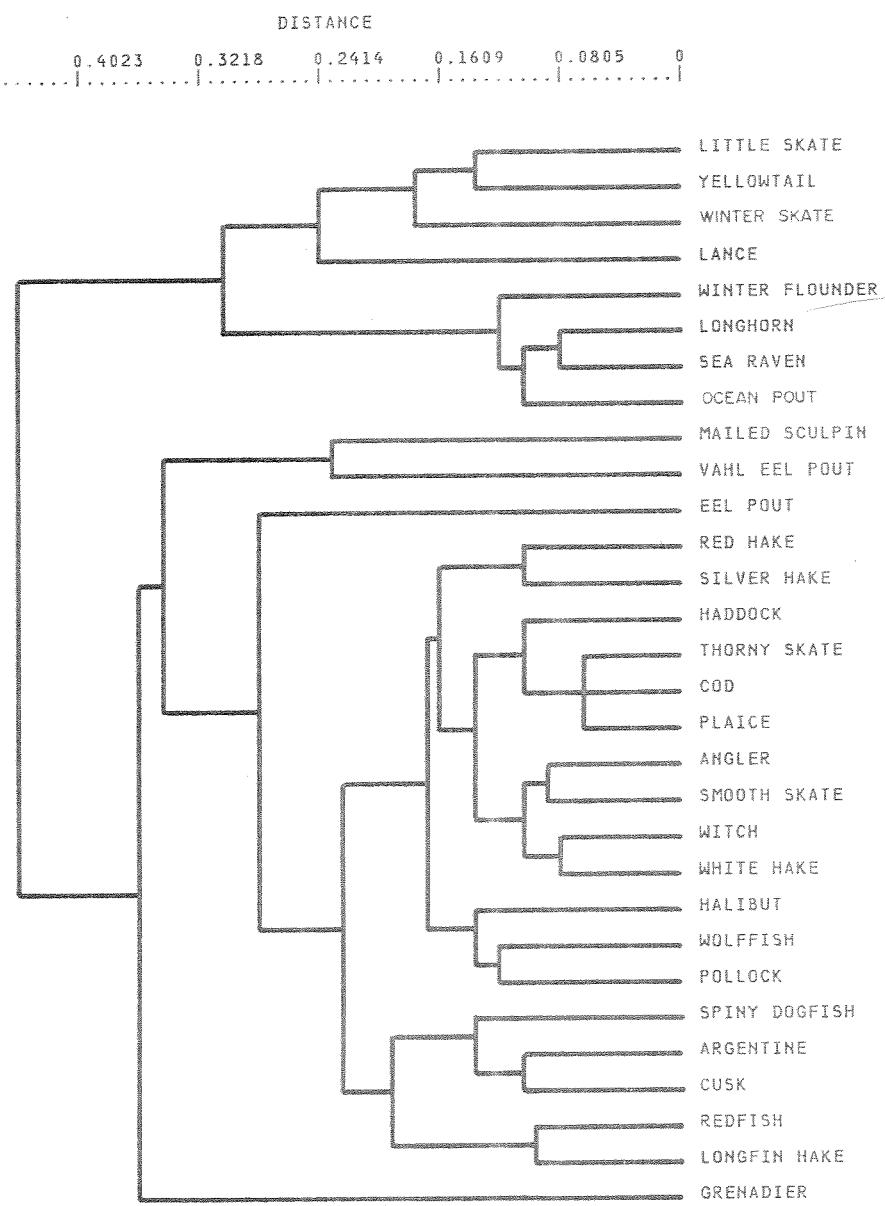


Fig. 66. The species dendrogram, summer 1981.

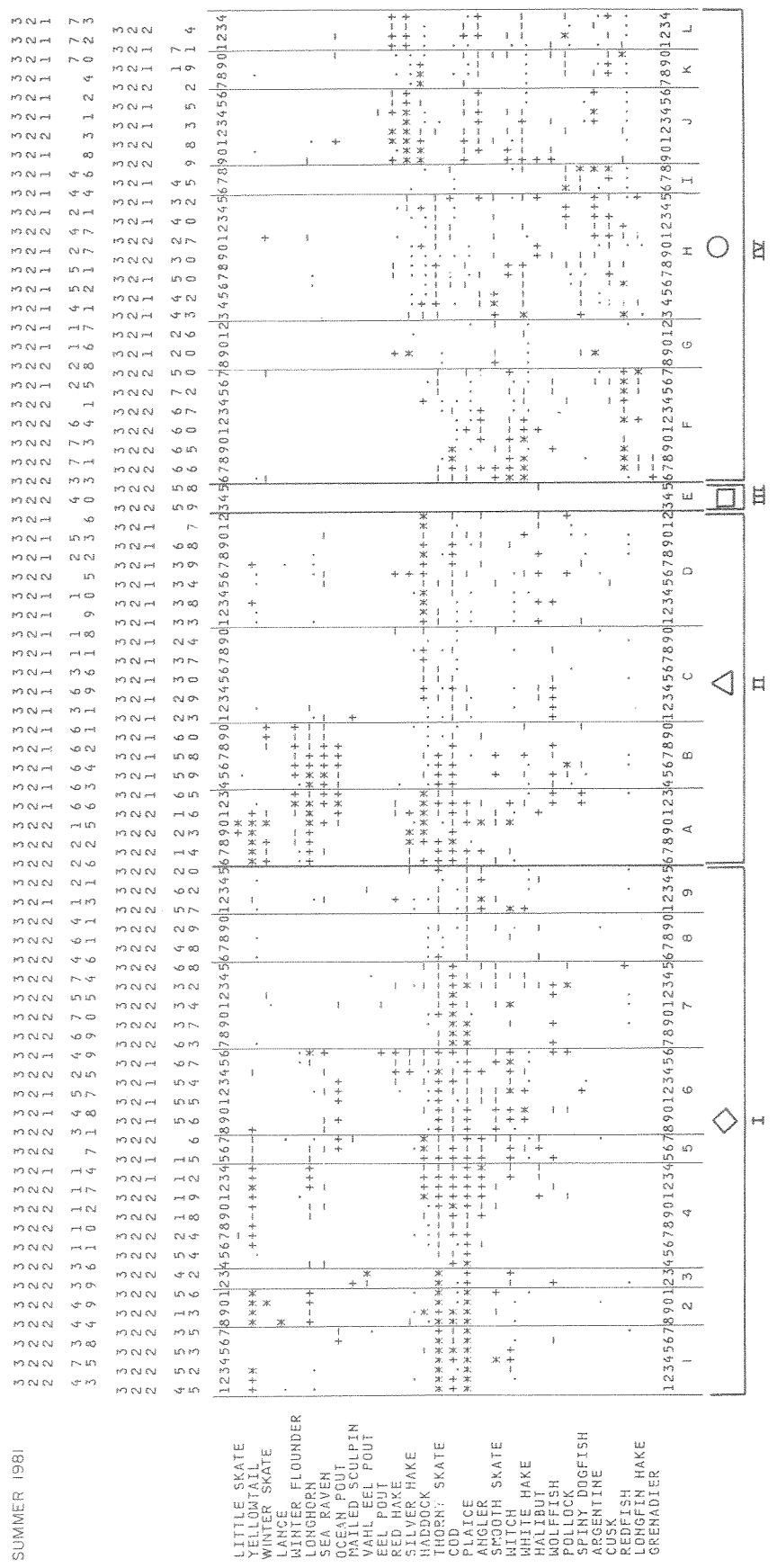


Fig. 67. The sites times species two-way table, summer 1981. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0.5-1.0; + = 1-2; x = greater than 2.

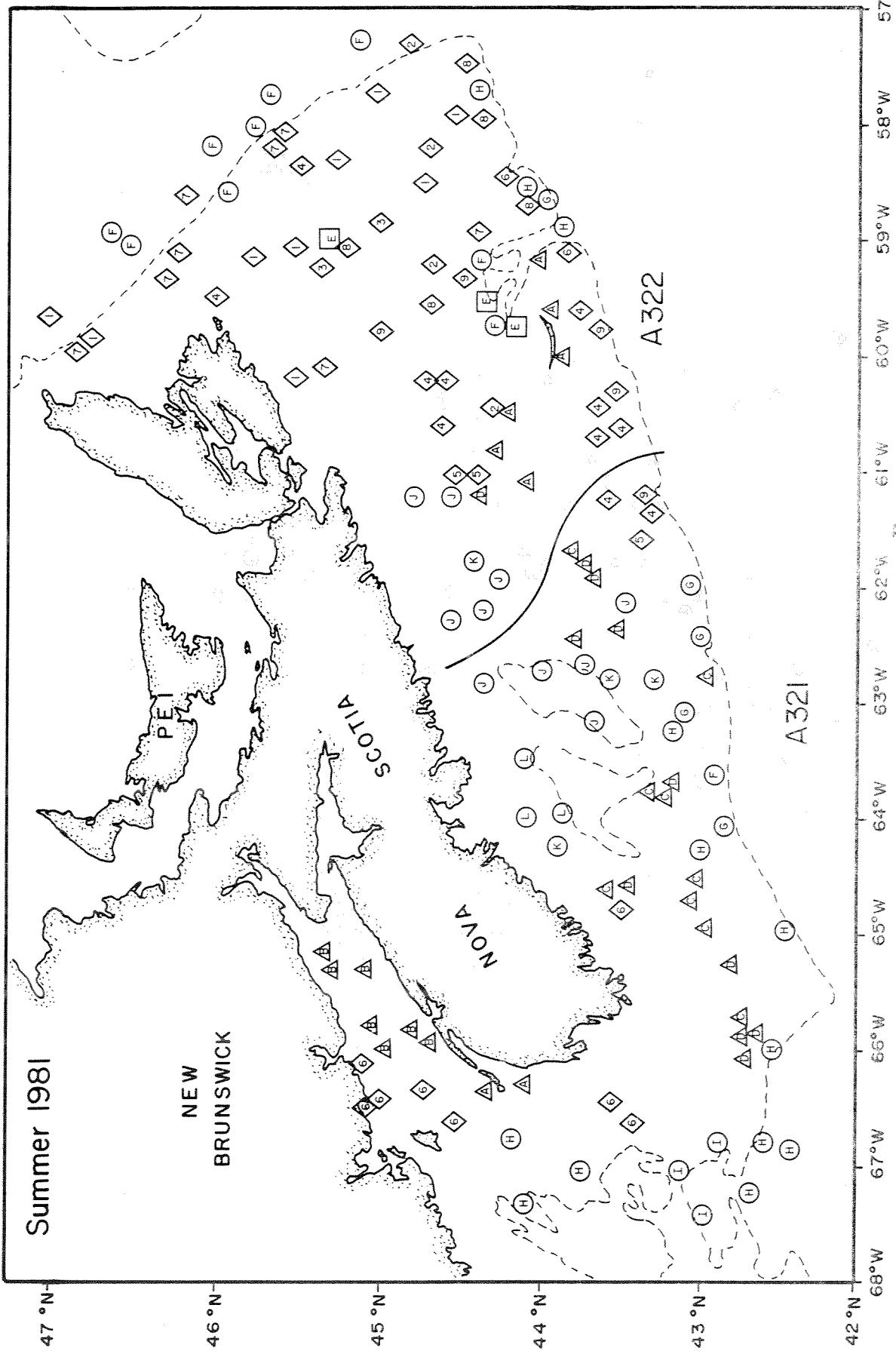


Fig. 68. The areal distribution of site groups, summer 1981. The symbols correspond to those in figure 67.

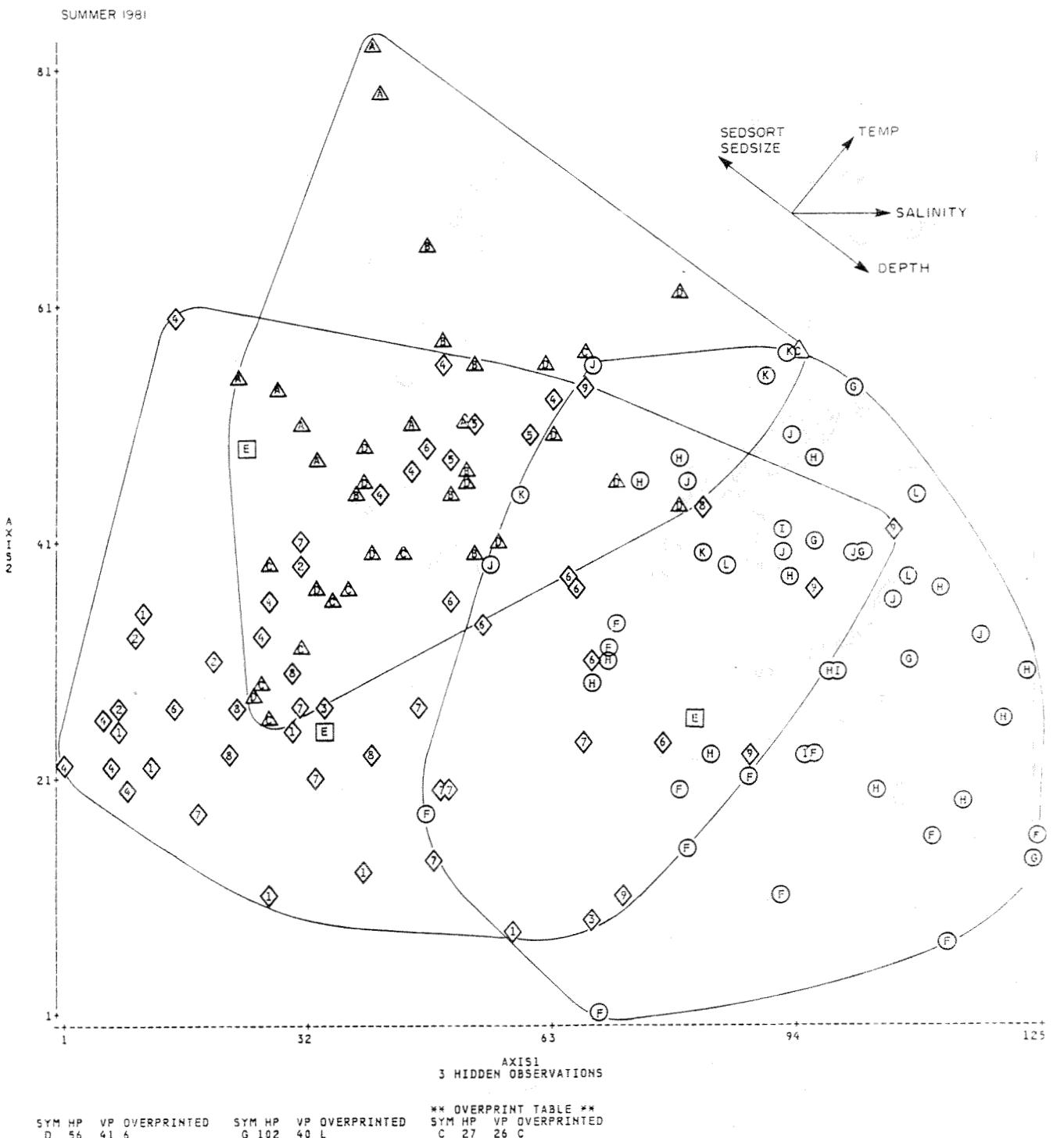


Fig. 69. The distribution of site groups in discriminant space, summer 1981. The symbols and number/letter codes correspond to those in Figure 67. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

is concentrated along the shelf edge and in the basins, and is characterized by relatively frequent occurrences of many species. Major site group IV includes stations along the shelf edge, and on Sable Island and Browns Banks, wolffish, cod, halibut, and haddock are relatively frequent and abundant in this site group. Stations in major site group V are in the Bay of Fundy and on the eastern shelf. Several species are relatively abundant at these stations, including longhorn, yellowtail, winter skate, sea raven, plaice, thorny skate, and cod.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 71) and the two-way table (Figure 72). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 73).

The major site groups are fairly well separated in the space formed by the first two discriminant axes (Table 21, Figure 74). Subsequent axes provided no additional separation. Major site group I is located to the right along axis 1. These stations are at intermediate to great depth and temperature, with relatively high salinity, and very small grained to intermediate sized sediments. Site group IV is characterized by shallow to intermediate depth and intermediate to high temperature, with a wide range of salinity, and intermediate to large grained sediments. Major site group V occurs in an area of the space characterized by very shallow to intermediate depth and very low temperature. These stations also have very low salinity and a range of sediment sizes, from very small to very large.

Table 21. Coefficients of separate determination (Spring 1979). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variables	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	9.8	28.9	0.3	18.5
2. Temp	40.5	13.7	0.3	4.8
3. Salinity	32.2	0.3	5.8	0.6
4. SEDSIZE	4.9	30.7	28.0	55.1
5. SEDSAND	11.5	13.3	3.7	12.0
6. SEDSORT	1.0	13.0	61.8	8.9
Eigenvalue	5.1	0.4	0.2	0.1
Percent of Group Separation	87.6	7.4	3.3	1.0

#### 1980 Spring

There were four major breaks in the site dendrogram (Figure 75) and the two-way table (Figure 77). One of the resultant groups (II) contains only one station with no species. Major site group I occurs along the edge of the shelf and in the basins (Figure 78). Several species are relatively common and abundant in this group. Major site group III occurs on the western shelf, and is characterized primarily by relatively abundant haddock, frequent occurrences of cod, and few occurrences of any other species. Stations in site group IV are in

the Bay of Fundy and the eastern shelf. Plaice and cod occur frequently, and there are scattered stations with relatively high abundances of longhorn, ocean pout, mailed sculpin, sea raven, and winter flounder. Major site group V is concentrated primarily on the eastern shelf, and is characterized by relatively frequent and abundant occurrences of plaice, winter skate, thorny skate, yellowtail, and longhorn.

Species with similar distributions across sites are shown in the species dendrogram (Figure 76) and the two-way table (Figure 77). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 78).

The major site groups show considerable overlap in discriminant space (Table 22, Figure 79), and axes other than 1 and 2 provided no further separation. The two-way table (Figure 77) shows that there is also considerable overlap in species assemblages among groups. Major site group I is characterized by intermediate to great depth, predominantly intermediate temperature and high salinity, and small grained sediments that were intermediately well sorted. The stations in site group III are characterized by shallow to intermediate depth, a wide range of temperature and salinity, and mostly large grained, well sorted sediments. The two stations in this group farthest to the right along axis 1 (34-40,41) have anomalously small grained sediments for this group. They are also the only stations in this major site group from which haddock are completely absent. Major site group IV is positioned to the left along axis 1, and is characterized by shallow to intermediate depth, low temperature, and intermediate salinity, with sediments that range from very large and well sorted to very small grained and poorly sorted. Major site group V is also located toward the left along axis 1. These stations are at very shallow depth, with very low temperature and salinity, and large grained, well sorted sediments. The only exceptions to this pattern are several stations in site group P, which were deeper, warmer, and more saline, with smaller, more poorly sorted sediments. The two-way table (Figure 77) shows that site group P also differs from other site groups in major group V by having much lower abundances of plaice, winter skate, thorny skate, yellowtail, and longhorn.

Table 22. Coefficients of separate determination (Spring 1980). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	22.7	3.7	23.6	1.9
2. Temp	13.2	8.7	16.9	4.0
3. Salinity	14.1	6.6	1.2	19.9
4. SEDSIZE	37.3	42.6	6.2	19.9
5. SEDSAND	3.5	13.4	9.1	22.8
6. SEDSORT	9.3	24.9	43.0	31.6
Eigenvalues	4.0	1.0	0.2	0.1
Percent of Group Separation	73.3	19.2	4.5	1.7

SPRING 1979

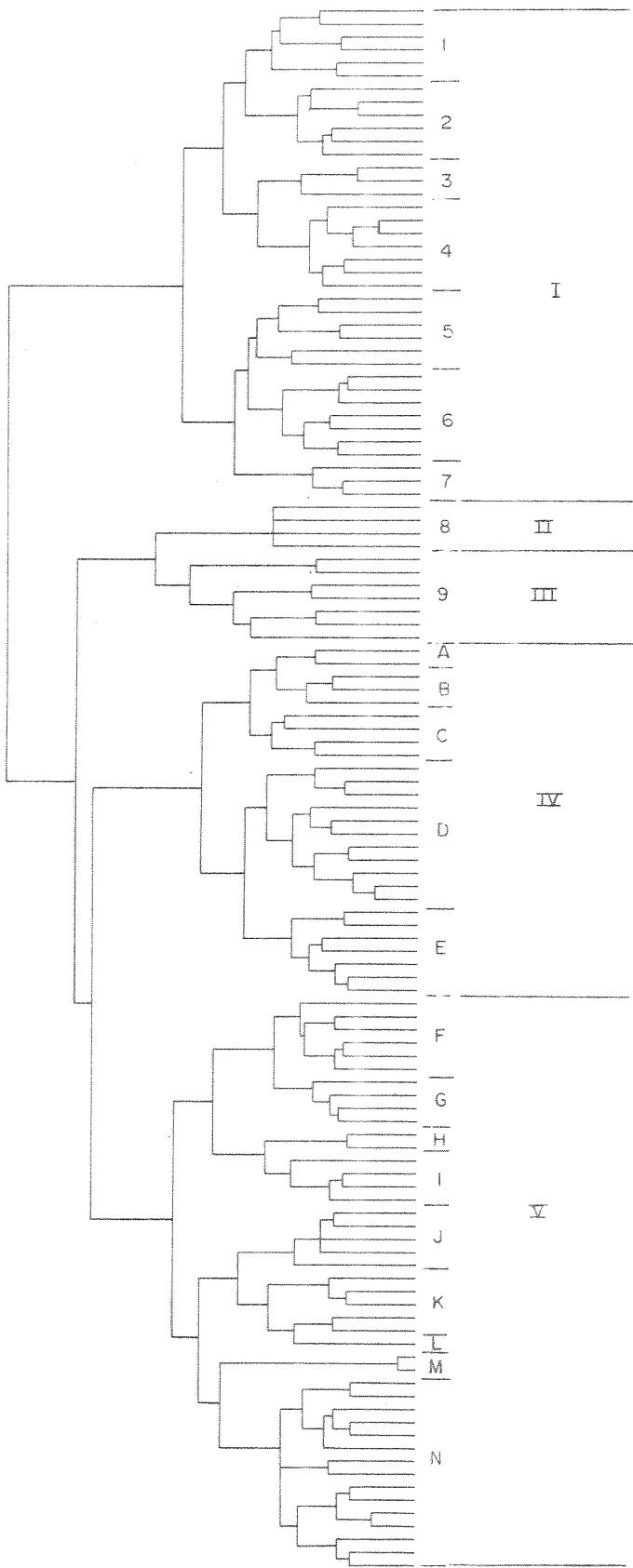


Fig. 70. The site dendrogram, spring 1979. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 72.

SPRING 1979

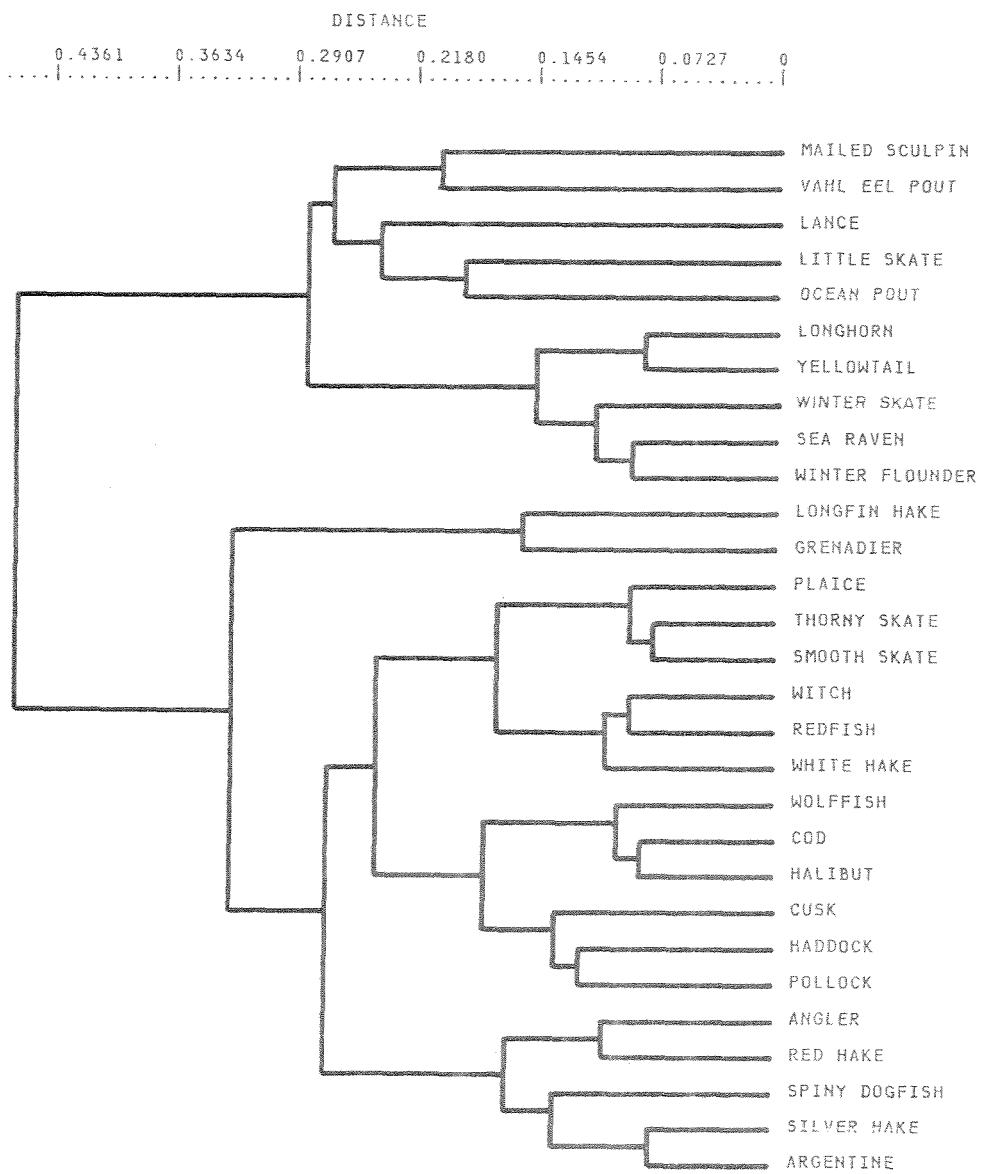


Fig. 71. The species dendrogram, spring 1979.

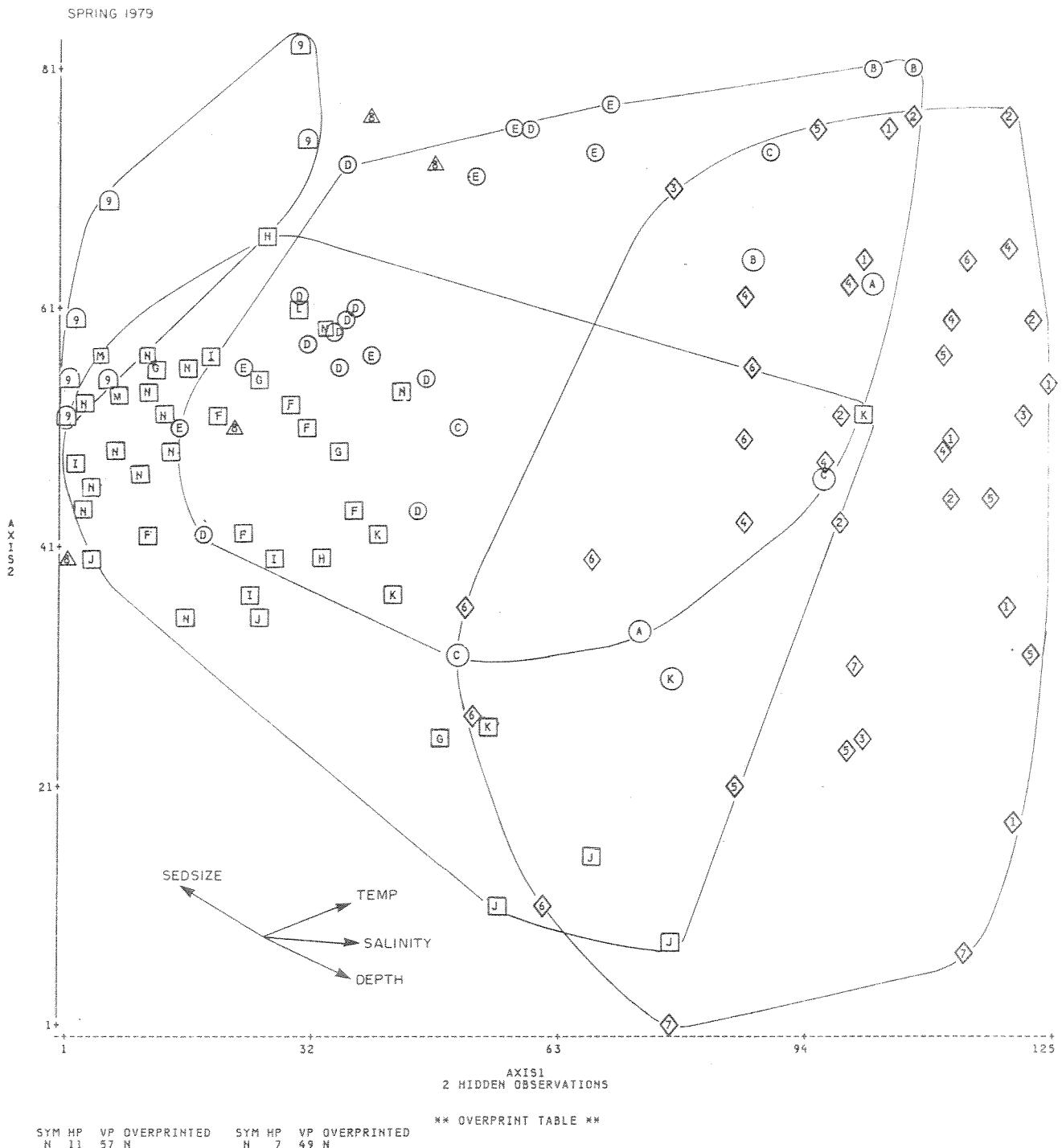


Fig. 74. The distribution of site groups in discriminant space, spring 1979. The symbols and number/letter codes correspond to those in Figure 72. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

SPRING 1980

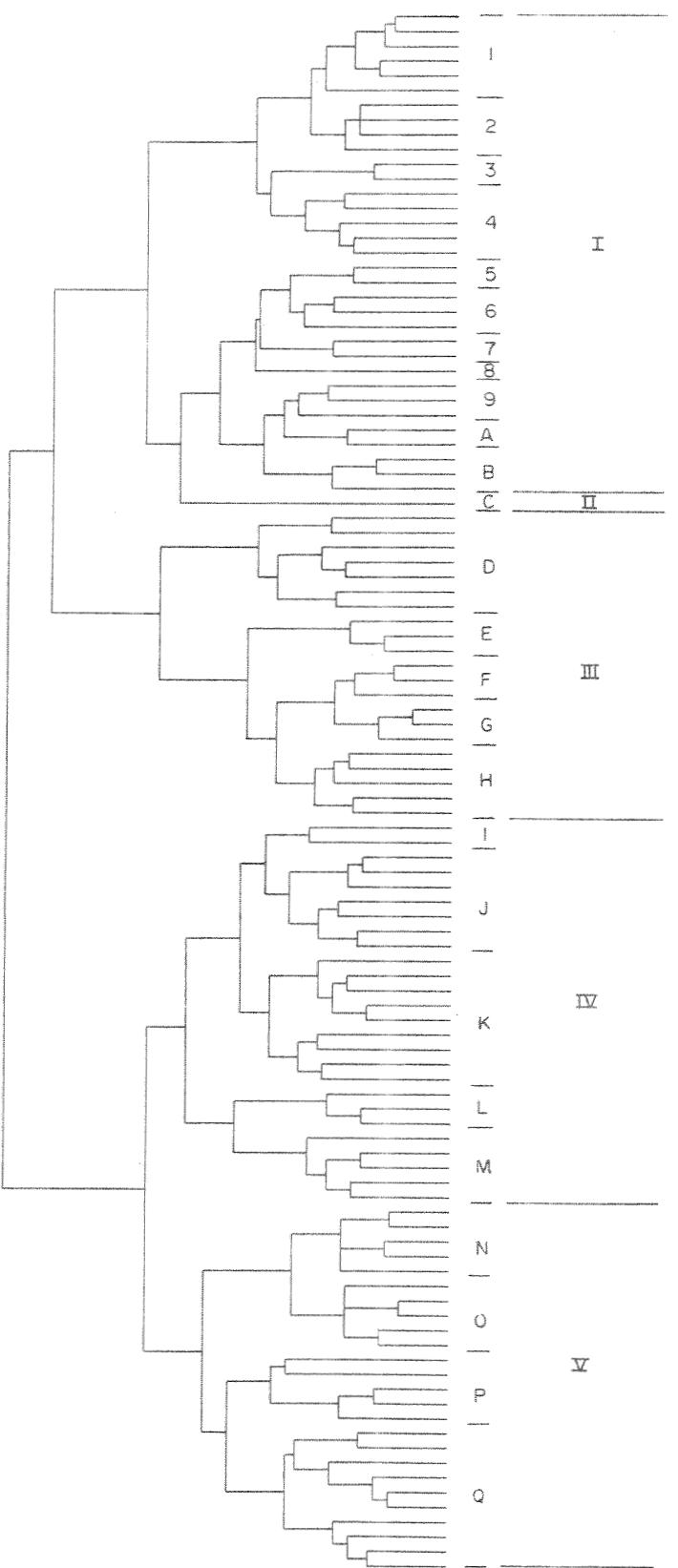


Fig. 75. The site dendrogram, spring 1980. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 77.

SPRING 1980

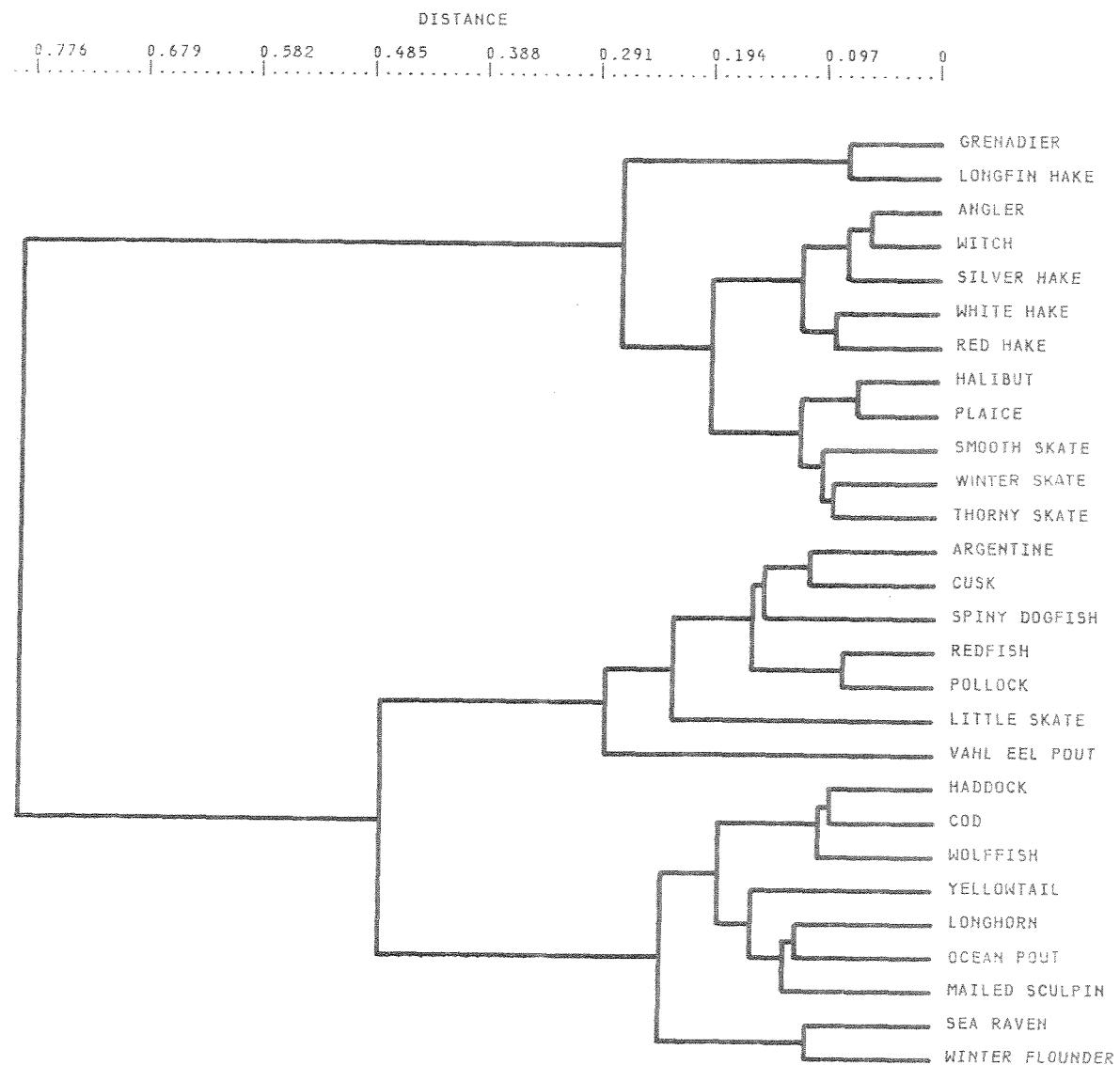
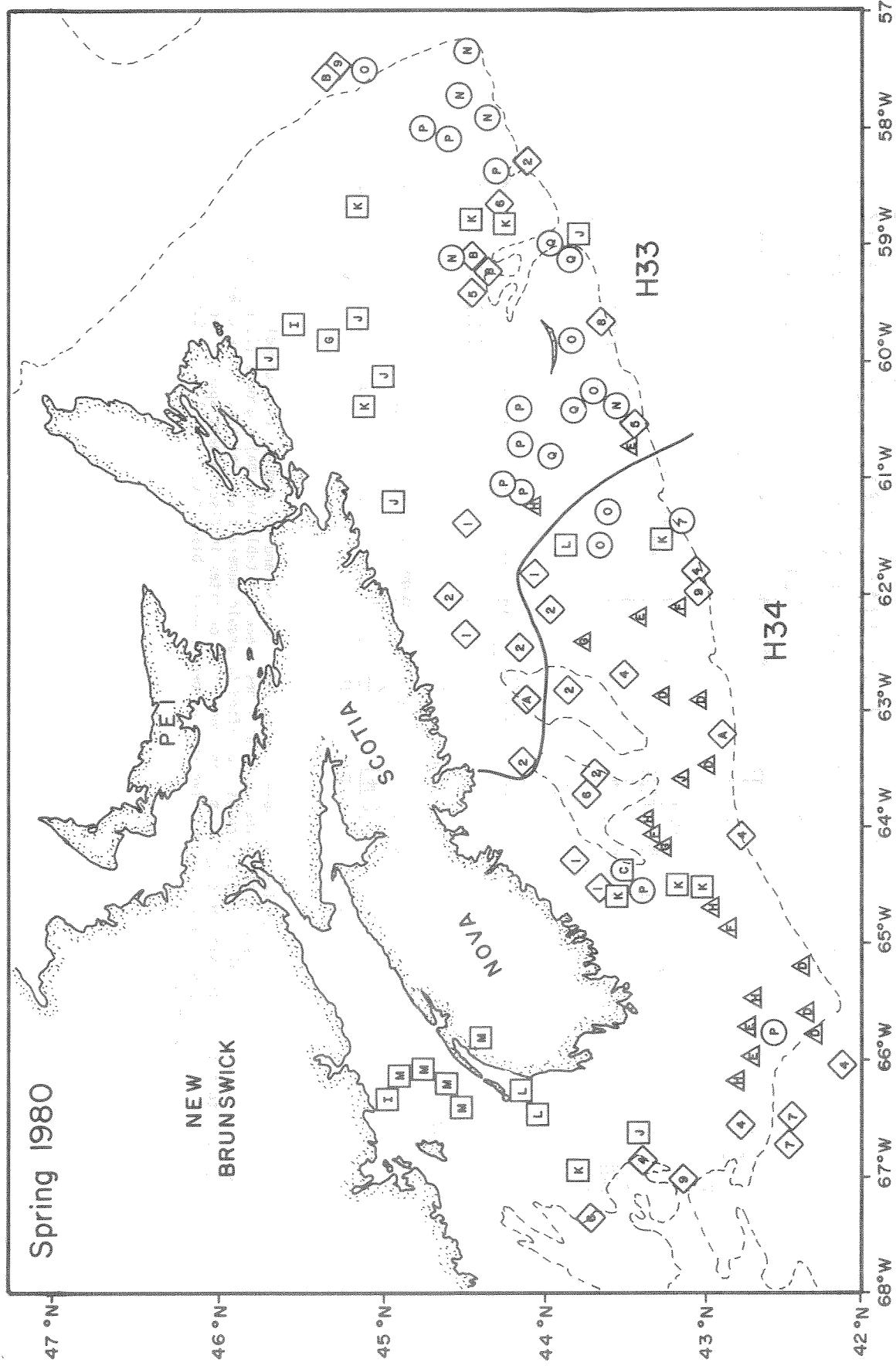


Fig. 76. The species dendrogram, spring 1980.

Fig. 77. The sites times species two-way table, spring 1980. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0-0.5; - = 0.5-1.0; + = 1-2; \*\* = greater than 2.



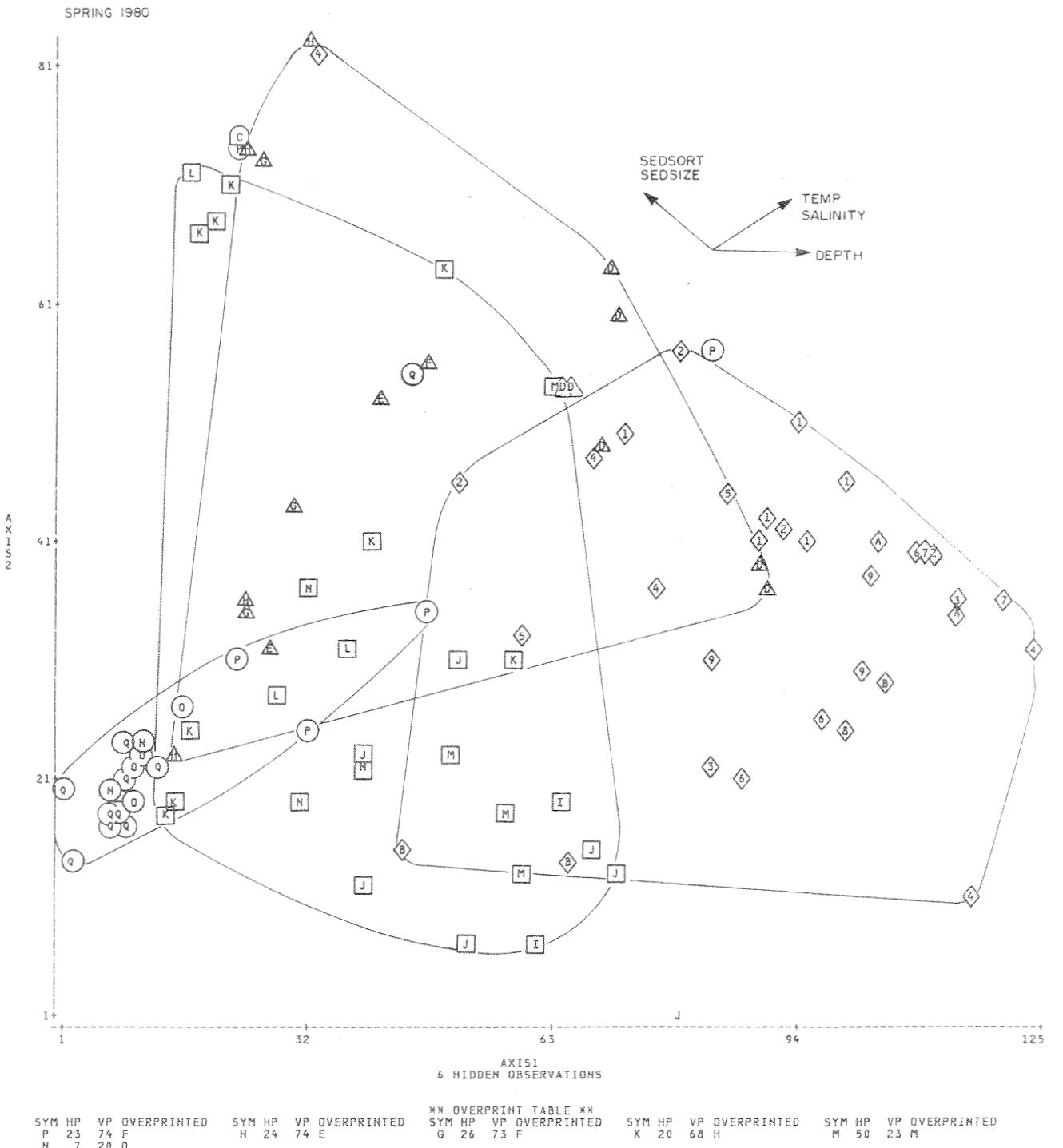


Fig. 79. The distribution of site groups in discriminant space, spring 1980. The symbols and number/letter codes correspond to those in Figure 77. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

## 1981 Spring

There are five major breaks in the site dendrogram (Figure 80) and the two-way table (Figure 82) that divide the sites into spatial areas (Figure 83). One of the resultant major site groups (V) contains only four stations with no species. Of the other major site groups, group I is located on Sable Island and Banquereau Banks, where only yellowtail, and, to a lesser extent, cod are relatively abundant. Site group II is located in the same areas, but also includes thorny skate, smooth skate, winter skate, and longhorn, as well as yellowtail. Stations in site group III are predominantly on the western shelf. Several species occur in these stations, but only haddock is relatively abundant. Major site group IV includes stations along the eastern edge of the shelf, in basins, and scattered on the western shelf. Witch, plaice, thorny skate, smooth skate, and cod are relatively abundant in these stations. Stations in major site group VI are along the edge of the shelf and in basins. These stations are characterized by relatively abundant argentine, silver hake, angler, red hake, and redfish.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 81) and the two-way table (Figure 82). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 83).

The major site groups are fairly well separated in the discriminant space formed by the first two axes (Table 23, Figure 84), except for group IV, which overlaps all the other groups. Subsequent axes provided no further separation. Site group I is at the shallowest depths, with low to intermediate temperature, and the largest, most well sorted sediments. Site group II occupies a small area to the left of axis 1. These stations are at the shallowest depths, with low temperature, and the largest, most well sorted sediments. The two-way table (Figure 82) shows that the wider temperature range in site group I is associated with a decrease in the relative abundance of plaice, thorny skate, winter skate, yellowtail, and longhorn. In all other respects, these two groups are environmentally similar. The stations in major site group IV are characterized by shallow to intermediate depth, and low to intermediate temperature, with a range of sediments, from large and well sorted to small and poorly sorted. Major site group VI occurs to the right of axis 1, and is characterized by intermediate to great depth, warm temperature, and small to intermediate sized, relatively poorly sorted sediments.

Table 23. Coefficients of separate determination (Spring 1981). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	28.4	13.6	2.9	0.5
2. Temp	27.0	43.0	6.2	20.6
3. Salinity	8.5	5.3	0.6	59.1
4. SEDSIZE	15.0	21.1	13.5	2.9
5. SEDSAND	5.4	4.5	69.8	0.8
6. SEDSORT	15.7	12.5	6.9	16.1
Eigenvalue	3.0	1.1	0.2	0.1
Percent of Group Separation	67.3	24.7	5.0	1.4

## 1979 Fall

There are five major breaks in the site dendrogram (Figure 85) and the two-way table (Figure 87) that divide the sites into spatial areas (Figure 88). One of the resultant site groups (I) contains no species. Major site group II is located along the shelf edge, and in basins, with a few stations scattered on the western shelf. Only pollock and cod are relatively abundant, and there are some occurrences of spiny dogfish, white hake, and cusk. Major site group III occurs at several locations on the eastern and western shelf and is characterized primarily by relatively abundant haddock, cod, and yellowtail. There are only a few occurrences of other species. The stations in major site group IV occur along the edge of the shelf, in the basins, and in the Bay of Fundy. They are characterized by relatively abundant white hake, angler, and silver hake, and lesser abundances of witch and plaice. Site group V is small and includes only stations along the edge of the shelf. Longfin hake and redfish are relatively abundant here, with lesser abundances of witch and thorny skate. Major site group VI is concentrated primarily on the eastern shelf, with a few stations in the Bay of Fundy and on the western shelf. These stations have relatively abundant thorny skate and plaice.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 86) and the two-way table (Figure 87). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 88).

The major site groups overlap completely on axis 2 in the discriminant space (Table 24, Figure 89), but some of them are well separated by axis 1. Subsequent axes provided no further separation. Major site group IV occupies a central position on both axes, characterized by intermediate depth and temperature, relatively high salinity, and an extreme range of sediment sizes. The one outlier far to the right along axis 1 (station 27-57) is anomalous in having very low abundances of only two species (Figure 87). These environmental parameters are almost identical to those of site group II, but the two-way table (Figure 87) shows that the species assemblages are quite distinct. Except for one

SPRING 1981

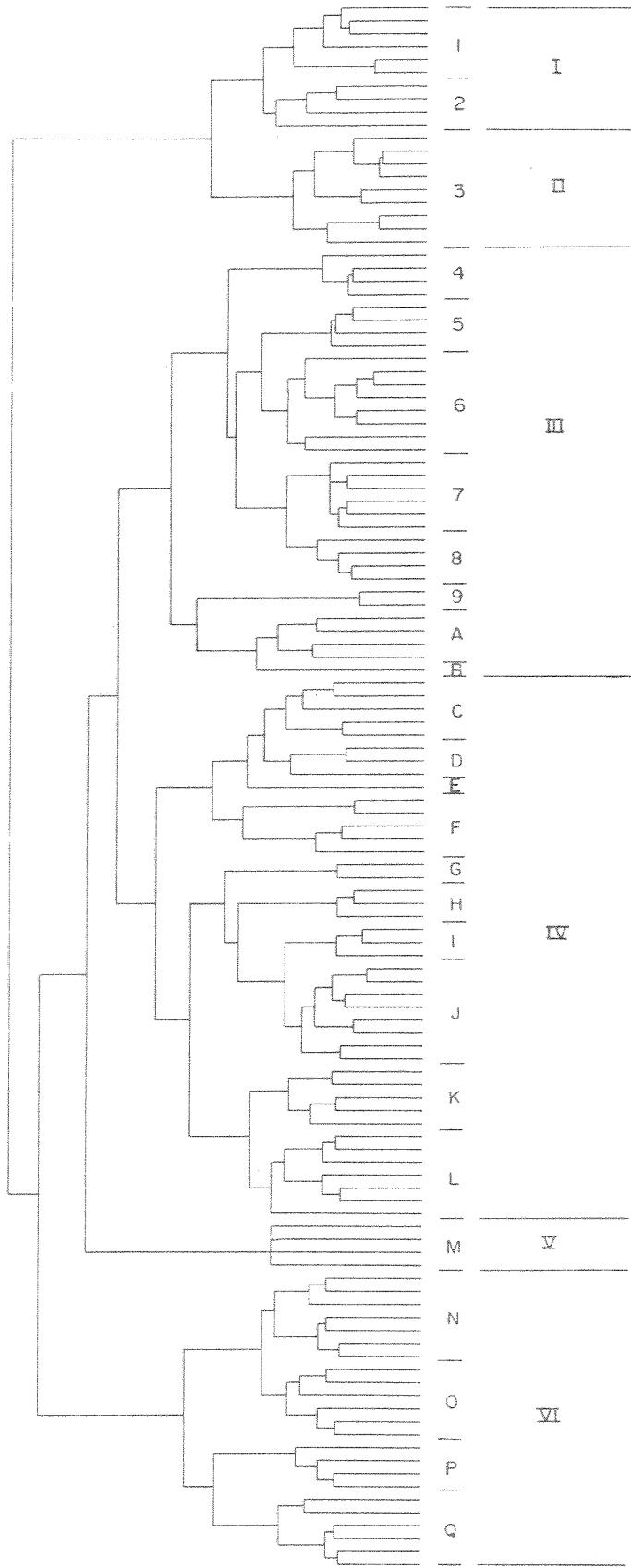


Fig. 80. The site dendrogram, spring 1981. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 82.

SPRING 1981

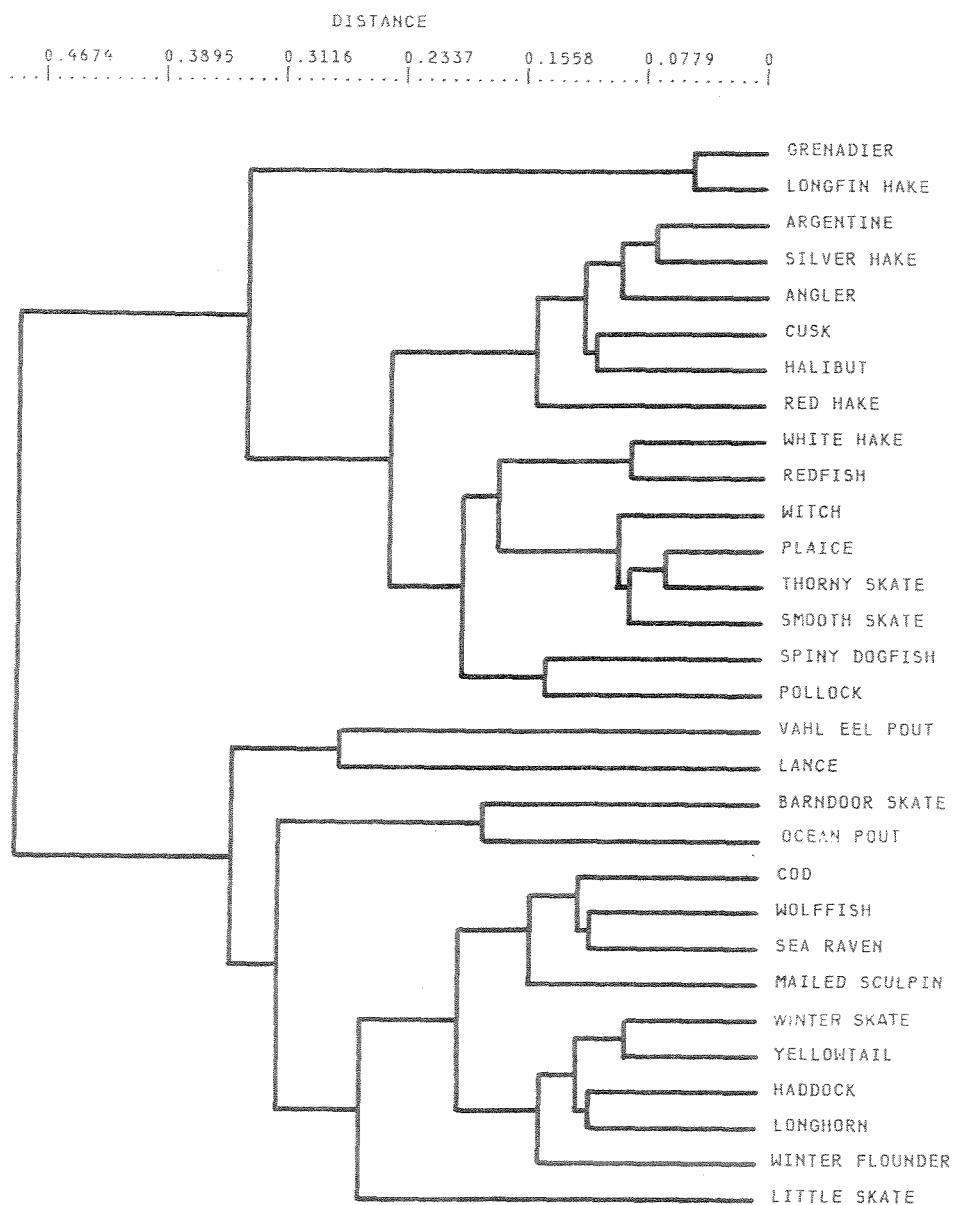


Fig. 81. The species dendrogram, spring 1981.

Fig. 82. The sites times species two-way table, spring 1981. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; + = 0-0.5; \* = 0.5-1.0; + = 1-2; \* = greater than 2.

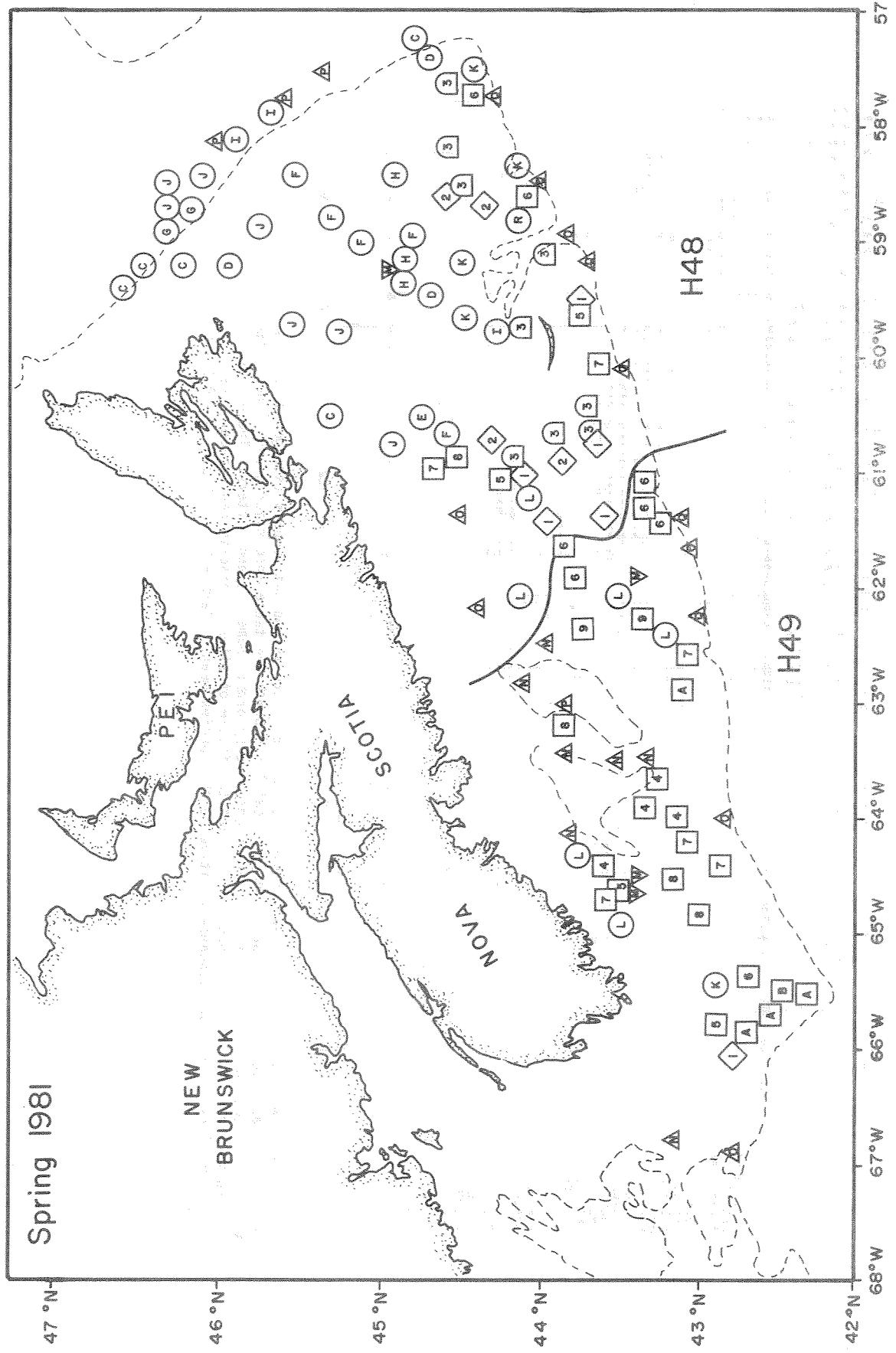


Fig. 83. The areal distribution of site groups, spring 1981. The symbols correspond to those in Figure 82.

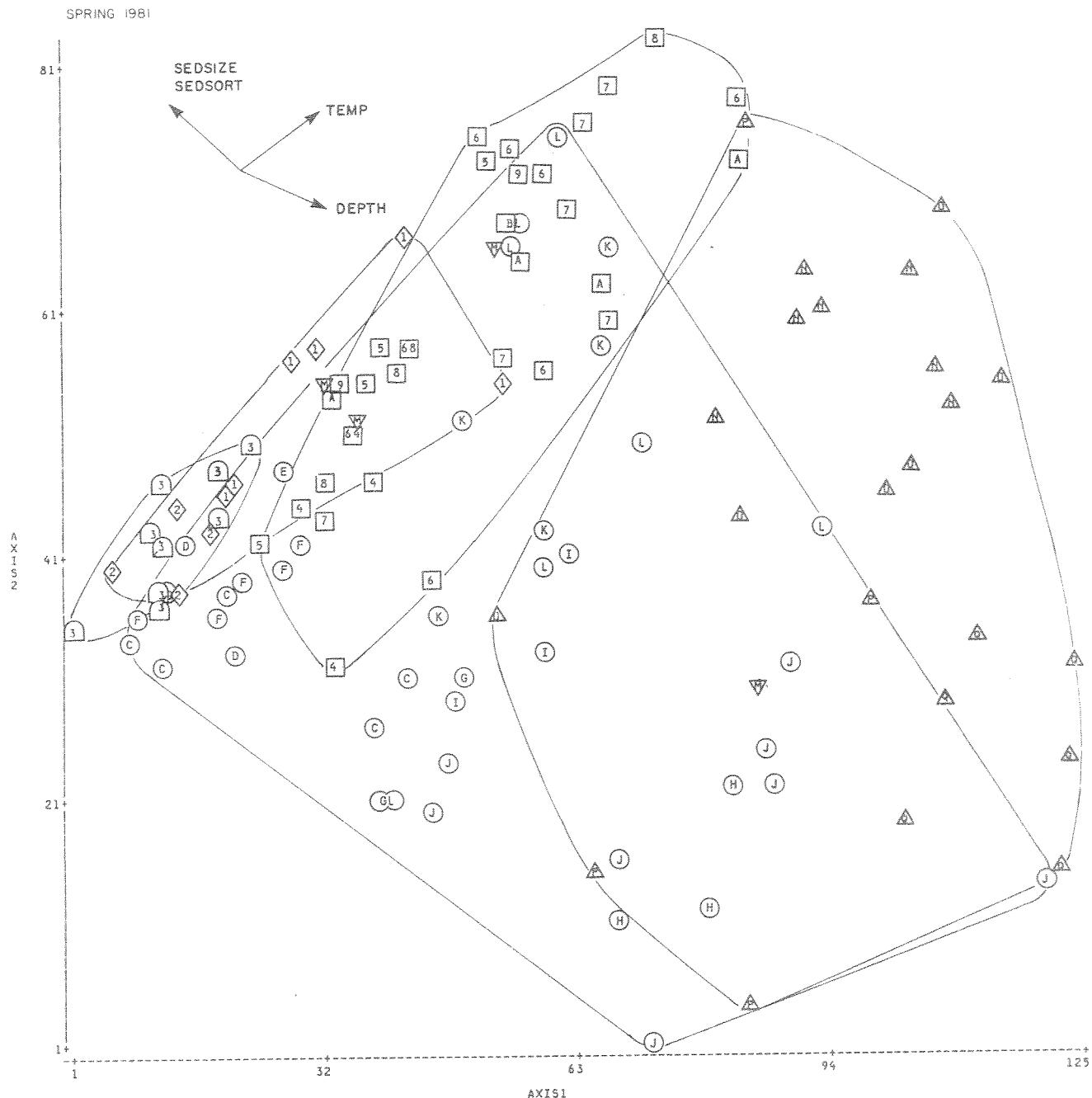


Fig. 84. The distribution of site groups in discriminant space, spring 1981. The symbols and number/letter codes correspond to those in Figure 82. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

FALL 1979

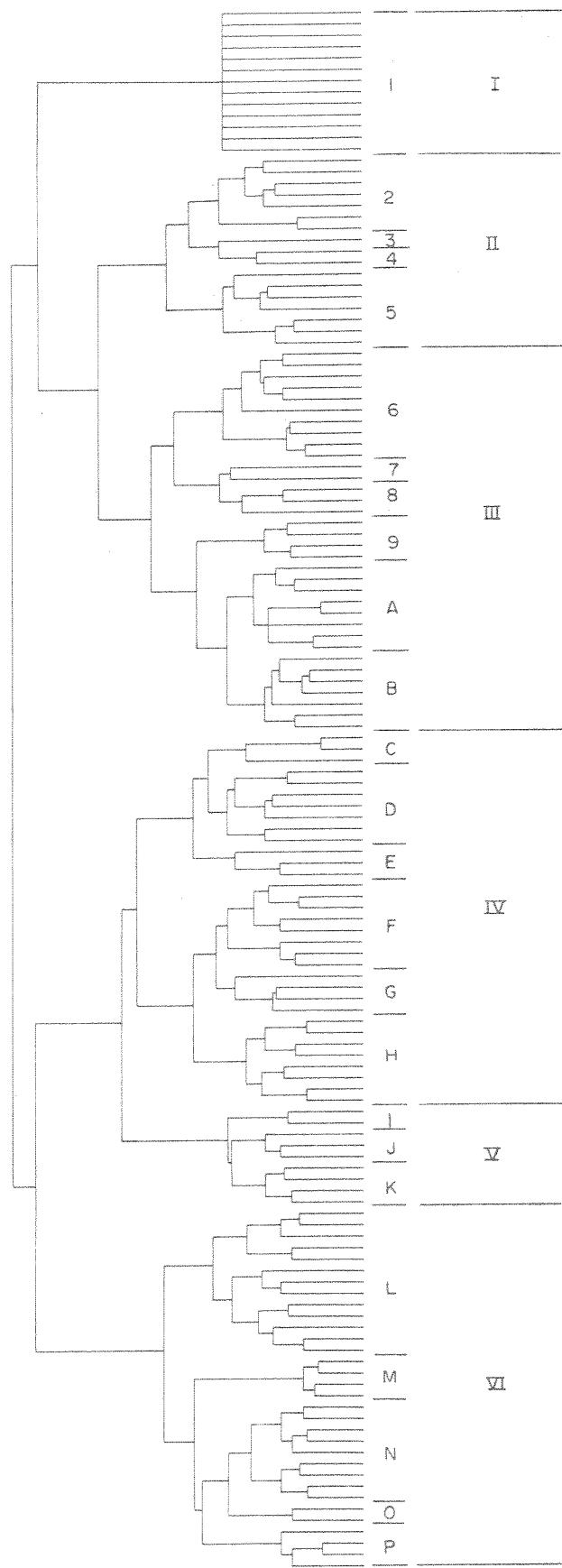


Fig. 85. The site dendrogram, fall 1979. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 87.

FALL 1979

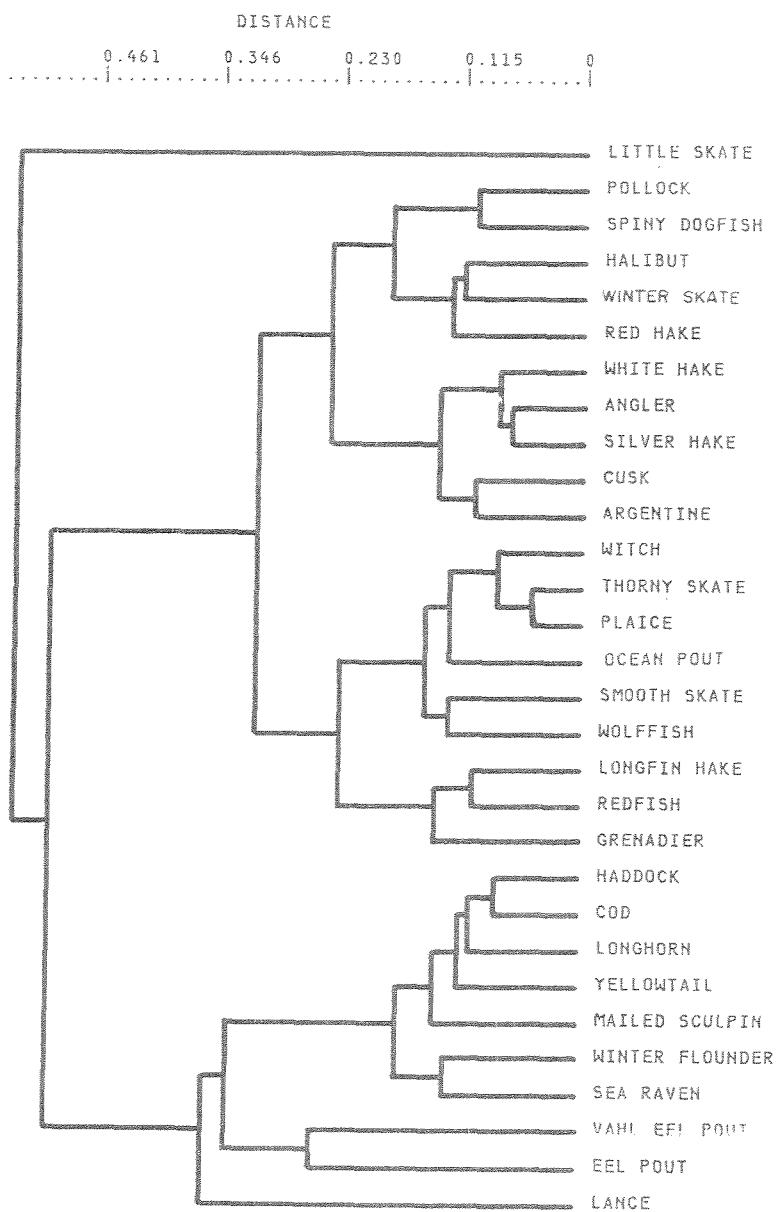


Fig. 86. The species dendrogram, fall 1979.

Fig. 87. The sites times species two-way table, fall 1979. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; + = 0-0.5; ~ = 0.5-1.0; + = 1-2; \* = greater than 2.

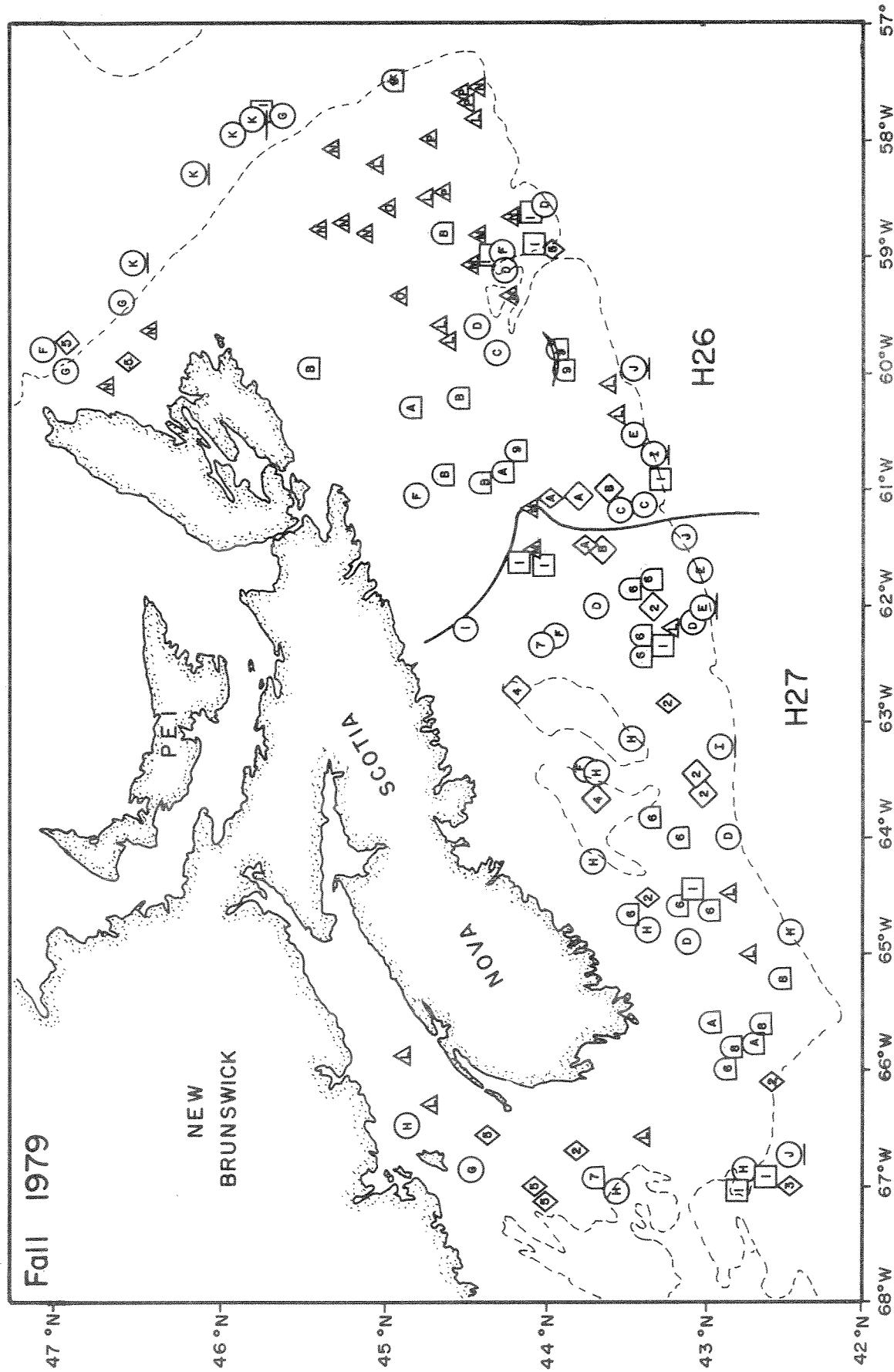


Fig. 88. The areal distribution of site groups, fall 1979. The symbols correspond to those in Figure 87.

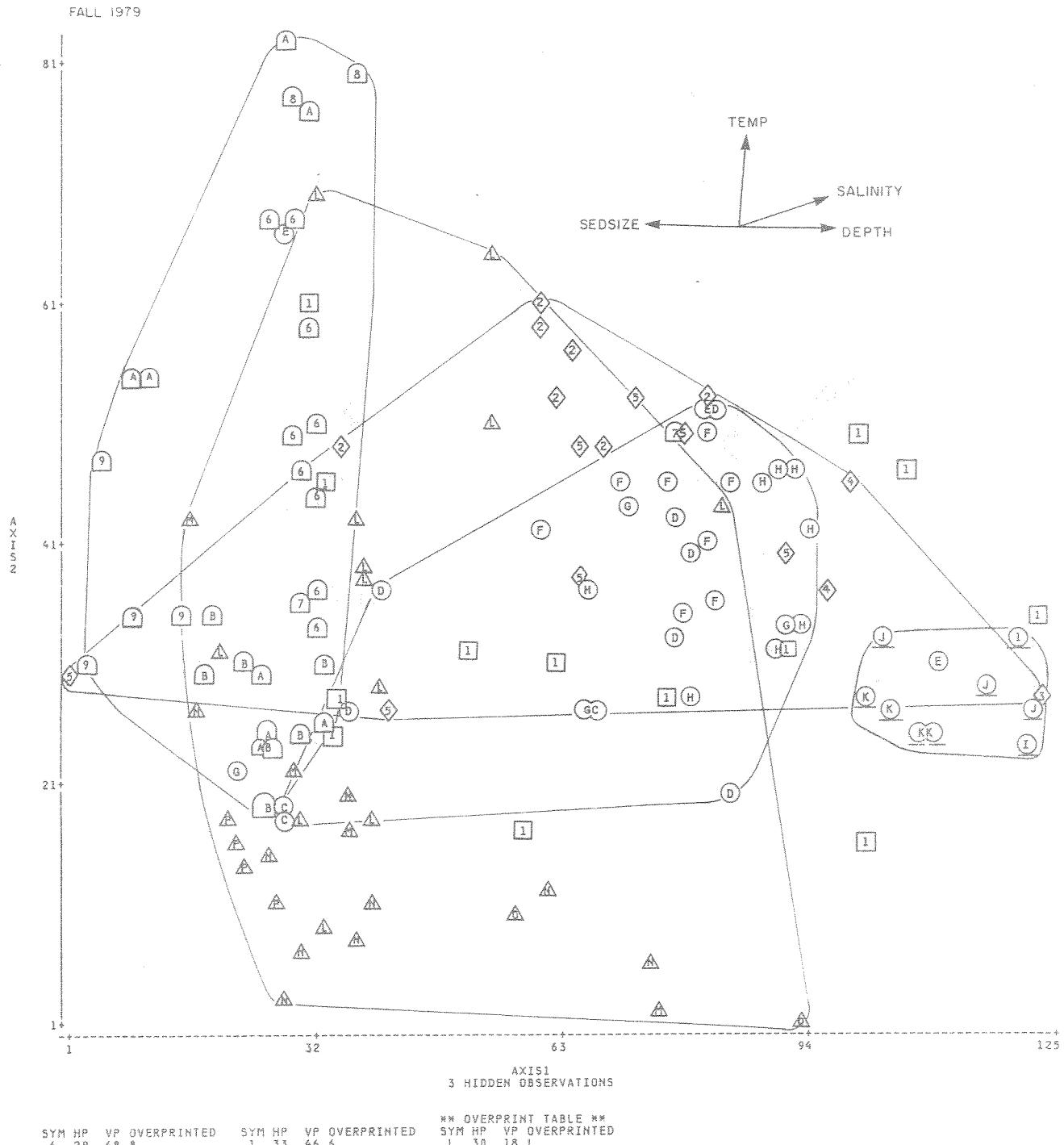


Fig. 89. The distribution of site groups in discriminant space, fall 1979. The symbols and number/letter codes correspond to those in Figure 87. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

station far to the left along axis 1, site group II is completely separated from site group III on axis 1. Group III is characterized by very shallow depth, intermediate to warm temperatures, intermediate salinity, and extremely large grained sediments. Site group V is far to the right along axis 1, and is characterized by great depth, intermediate temperature, high salinity, and small to intermediate sized sediments. Major site group VI overlaps all other site groups except V. Stations in this site group are at predominantly shallow depth, with a wide range of temperature, intermediate salinity, and intermediate to large grained sediments.

Table 24. Coefficients of separate determination (Fall 1979). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	36.8	1.2	39.3	8.4
2. Temp	0.5	64.1	2.0	27.4
3. Salinity	14.4	23.3	0.1	29.7
4. SEDSIZE	43.0	3.5	53.0	13.6
5. SEDSAND	0.0	4.8	3.0	12.6
6. SEDSORT	5.2	3.1	2.6	8.4
Eigenvalues	4.8	1.8	0.2	0.1
Percent of Group Separation	67.4	25.8	3.5	1.6

#### 1980 Fall

There are five major breaks in the site dendrogram (Figure 90) and the two-way table (Figure 92) that divide the sites into spatial areas (Figure 93). One of the resultant major site groups (IV) contains only four stations in which no species occur. Major site group I occurs along the edge of the shelf and in basins, with a few stations on the western shelf. Several species are relatively abundant in this group, including longfin hake, grenadier, white hake, silver hake, angler, redfish, and red hake. Site group II is also along the edge of the shelf, as well as on the eastern shelf. These stations are characterized by relatively abundant plaice and cod. Stations in major site group III occur in the Bay of Fundy, on Sable Island Bank, and elsewhere on the eastern shelf. These stations contain relatively frequent and abundant occurrences of many species, especially plaice, thorny skate, haddock, winter skate, yellowtail, longhorn, winter flounder, and sea raven. Site group V is concentrated primarily at the head of the Bay of Fundy, and no species are consistently relatively abundant here. Major site group VI is spread over the western shelf. Haddock is relatively abundant at these stations.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 91) and the two-way table (Figure 92). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 93).

The major site groups occupy distinct areas

in the discriminant space created by the first two axes (Table 25, Figure 94). Subsequent axes provided no further separation. Major site group I is characterized by intermediate to great depth, low to intermediate temperature, intermediate to high salinity, and small to intermediate sized sediments. Major site group II is characterized by shallow to intermediate depth, low temperature, intermediate salinity, and intermediate to large grained sediments. Stations in site group III are at shallow to intermediate depth, intermediate temperature, and a wide range of salinity, with intermediate to large grained sediments. Site group VI occupies a subset of the space occupied by group III. Group VI is characterized by shallow depth, intermediate temperature and salinity, and large grained sediments. Site group V occupies a still smaller subset of the same space, characterized by the shallowest depth, intermediate temperature and salinity, and intermediate to large grained sediments. The two-way table (Figure 92) shows that, just as groups III, VI, and V occupy successively smaller portions of the discriminant space, they contain successively smaller species assemblages.

Table 25. Coefficients of separate determination (Fall 1980). These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	45.8	4.7	0.1	8.7
2. Temp	0.4	78.8	1.7	1.1
3. Salinity	9.2	11.4	14.1	0.9
4. SEDSIZE	31.4	2.2	52.0	25.3
5. SEDSAND	5.9	1.5	8.6	15.5
6. SEDSORT	7.2	1.4	23.6	48.5
Eigenvalues	2.4	1.2	0.3	0.1
Percent of Group Separation	60.3	29.6	6.8	2.2

#### 1981 Fall

There are five major breaks in the site dendrogram (Figure 95) and the two-way table (Figure 97) that divide the sites into spatial areas (Figure 98). One of the resultant major site groups (III) contains no species. Major site group I occurs along the edge of the shelf, in basins, and in the Bay of Fundy. Plaice, red hake, silver hake, angler, and witch are relatively abundant in this group. Major site group II is predominantly along the edge of the shelf and in the Bay of Fundy. A wide range of species occur in this site group. Stations in major site group IV are concentrated on the eastern shelf, where cod, plaice, and thorny skate are relatively abundant. There are almost no occurrences of any other species. Stations in major site group V occur primarily on the western shelf and on Sable Island Bank. Only haddock is relatively abundant in these stations. Site group VI is concentrated in the Bay of Fundy and on Sable Island Bank, and is characterized by relatively abundant yellowtail, winter skate, longhorn, winter flounder, sea raven, ocean pout, thorny skate, and white hake.

FALL 1980

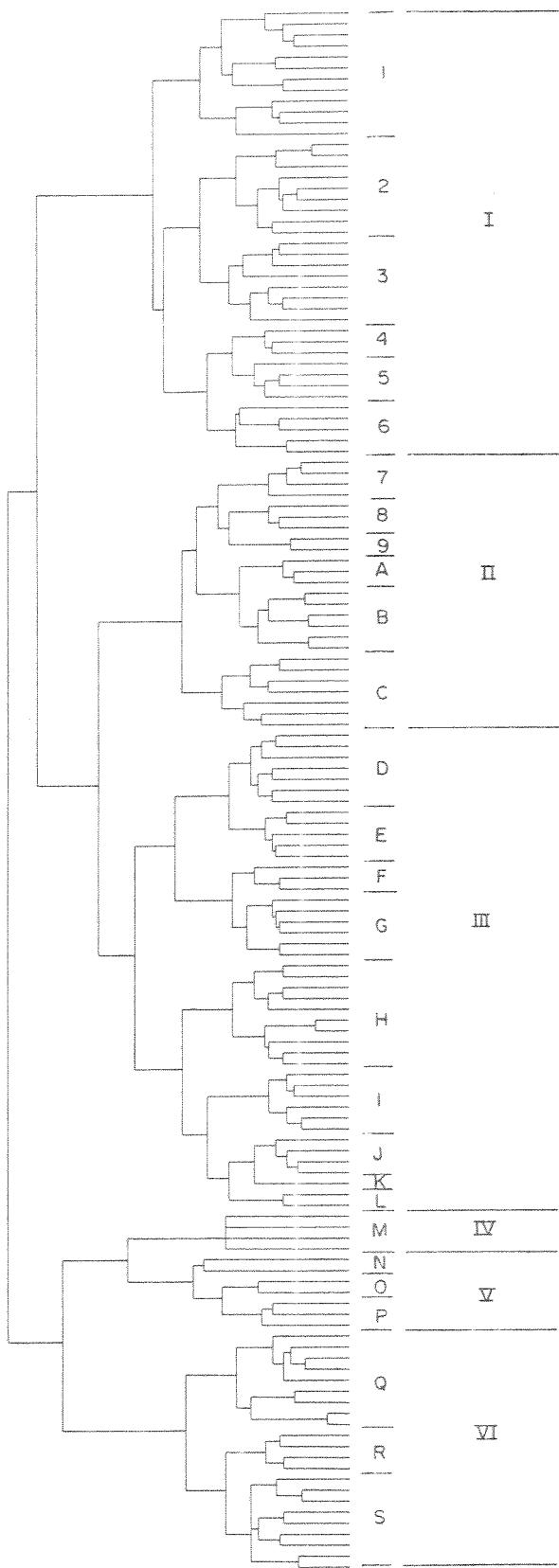


Fig. 90. The site dendrogram, fall 1980. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 92.

FALL 1980

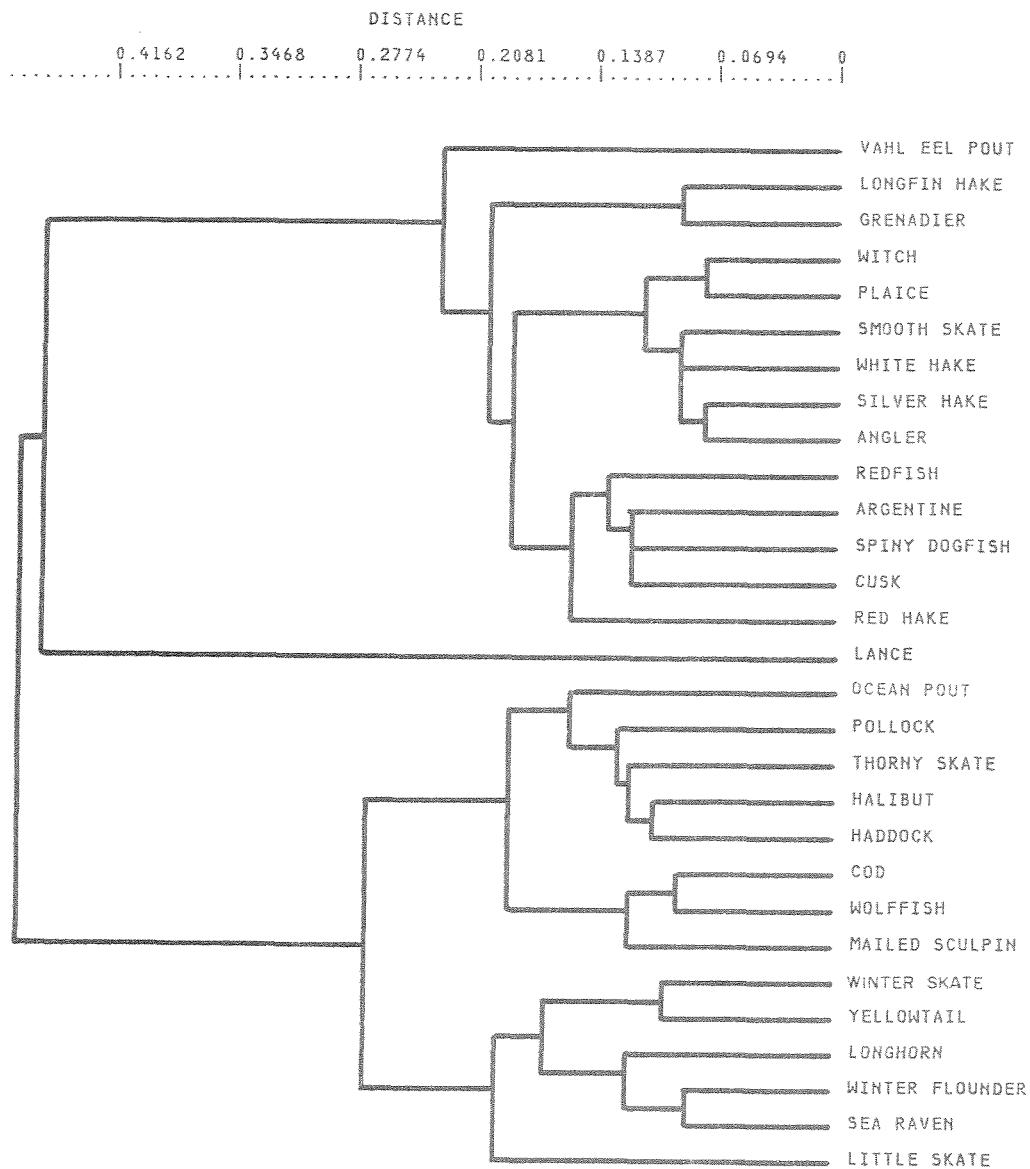


Fig. 91. The species dendrogram, fall 1980.

Fig. 92. The sites times species two-way table, fall 1980. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; \* = 0.5-1.0; + = 1-2; \*\* = greater than 2.

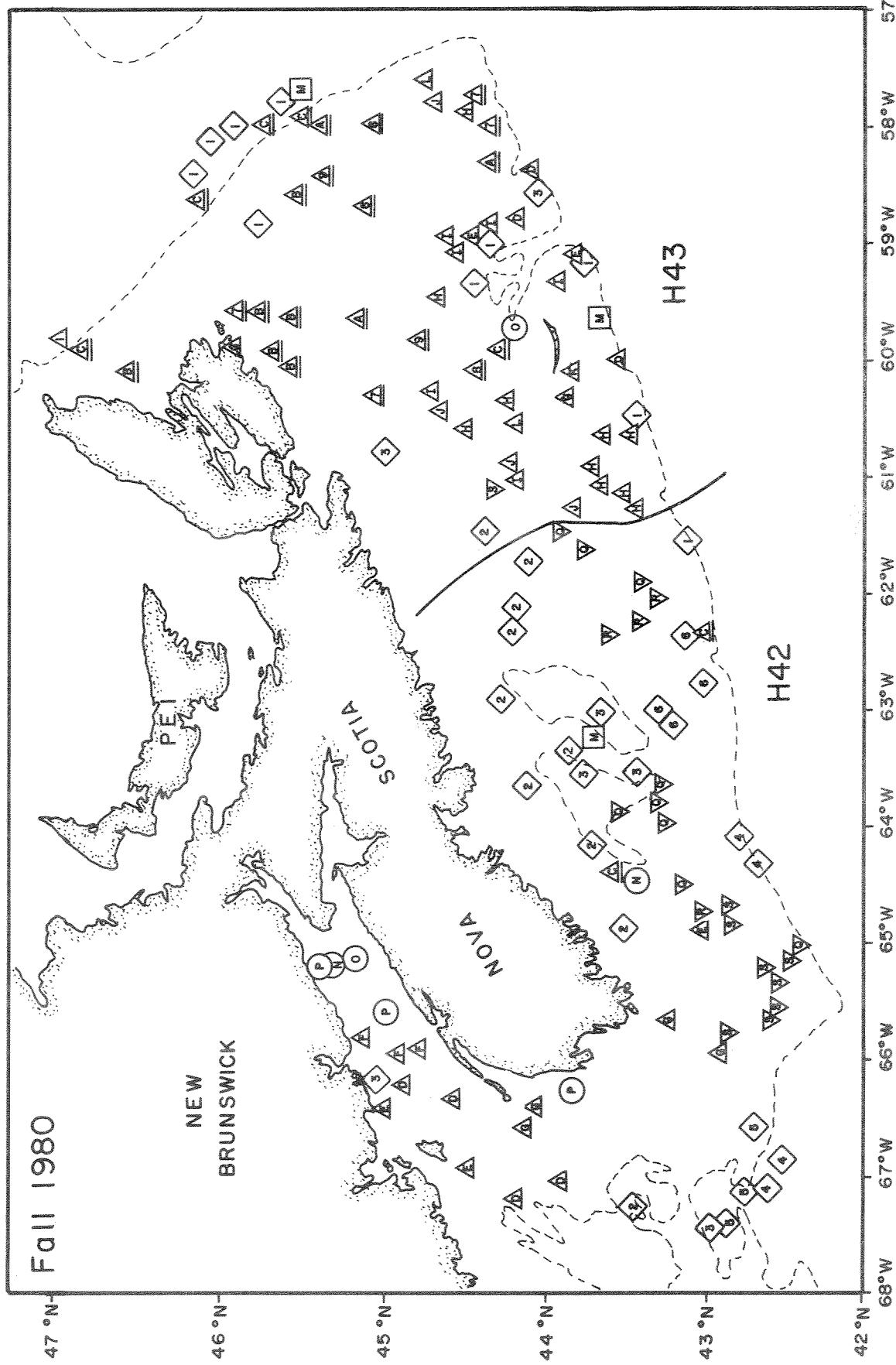


Fig. 93. The areal distribution of site groups, fall 1980. The symbols correspond to those in Figure 92.

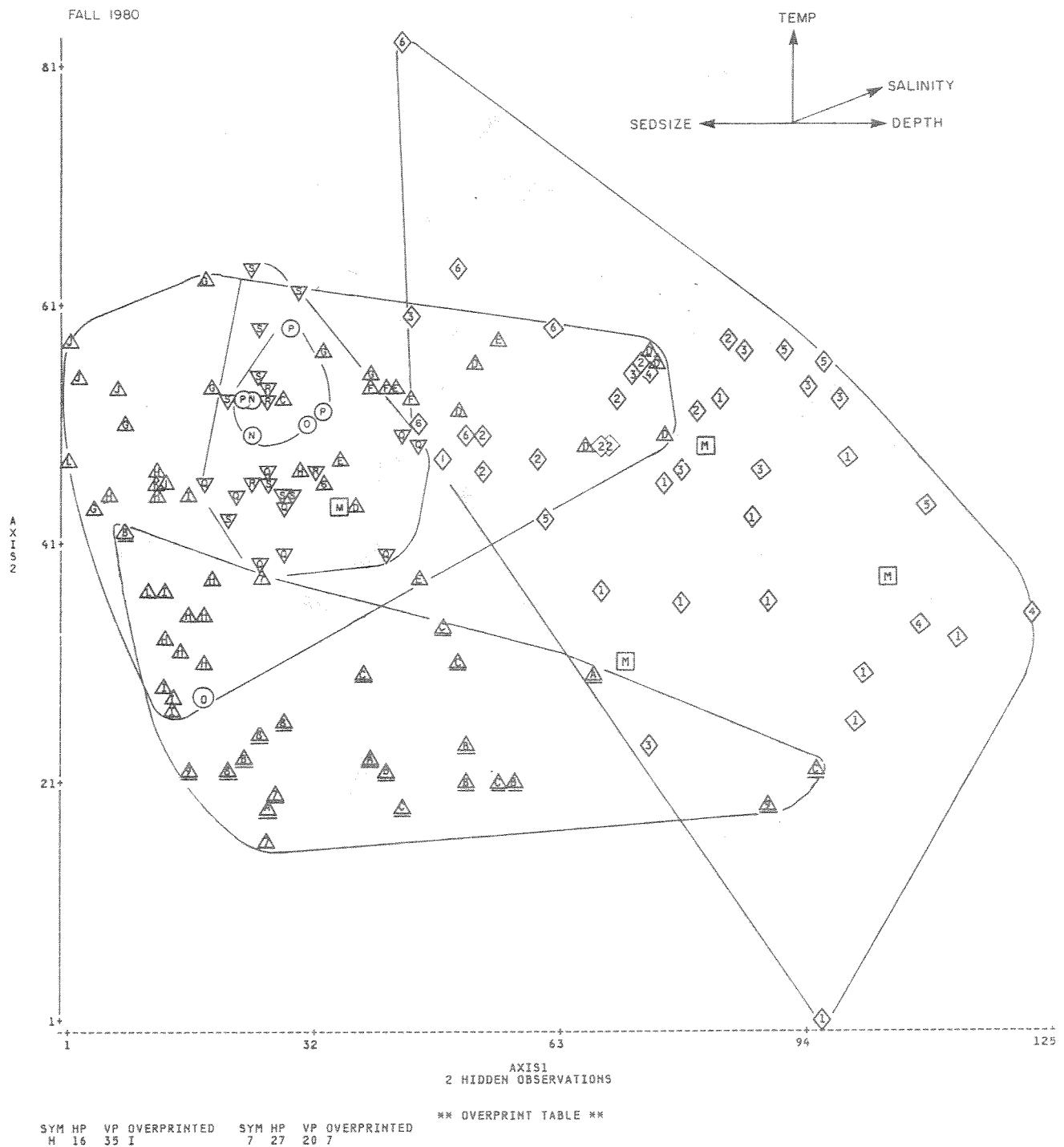


Fig. 94. The distribution of site groups in discriminant space, fall 1980. The symbols and number/letter codes correspond to those in Figure 92. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

FALL 1981

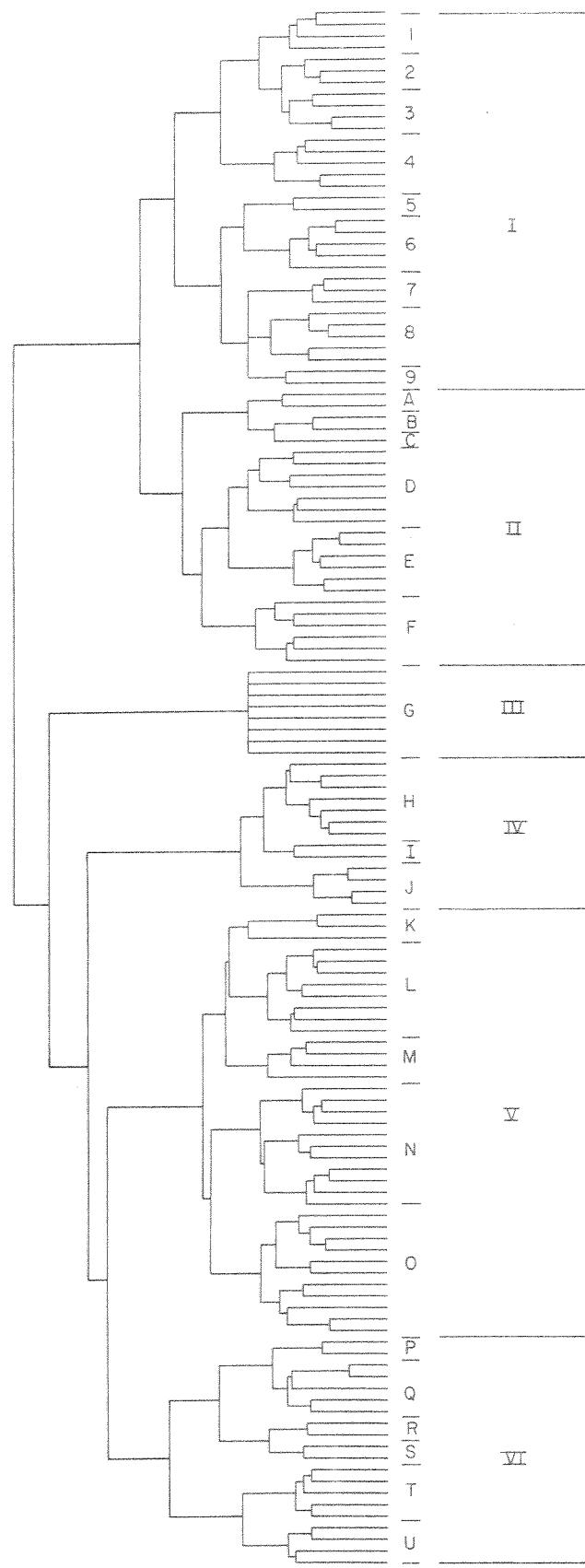


Fig. 95. The site dendrogram, fall 1981. The sequence of sites (top to bottom) in the dendrogram is the same as from left to right in Figure 97.

FALL 1981

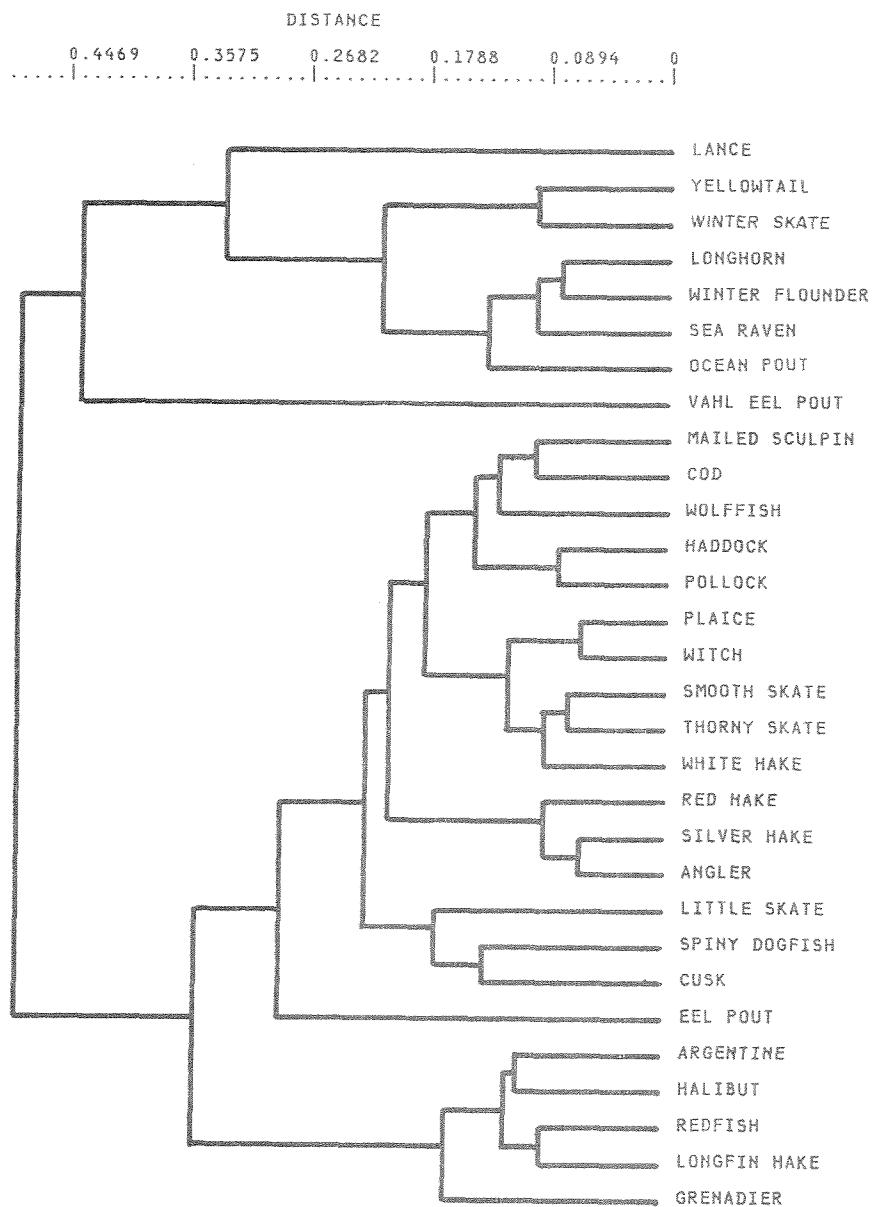


Fig. 96. The species dendrogram, fall 1981.

Fig. 97. The sites times species two-way table, fall 1981. Cruise and set numbers (staggered) across the top of the table identify each set. The vertical lines break the table into major groups (identified by symbols and roman numerals) and site groups identified by arabic numerals and letters. These codes correspond to those on the site dendrogram, map and the figure of sites in discriminant space. The symbols within the table show abundance relative to the species mean: blank = 0; . = 0-0.5; .. = 0.5-1.0; + = 1-2; \* = greater than 2.

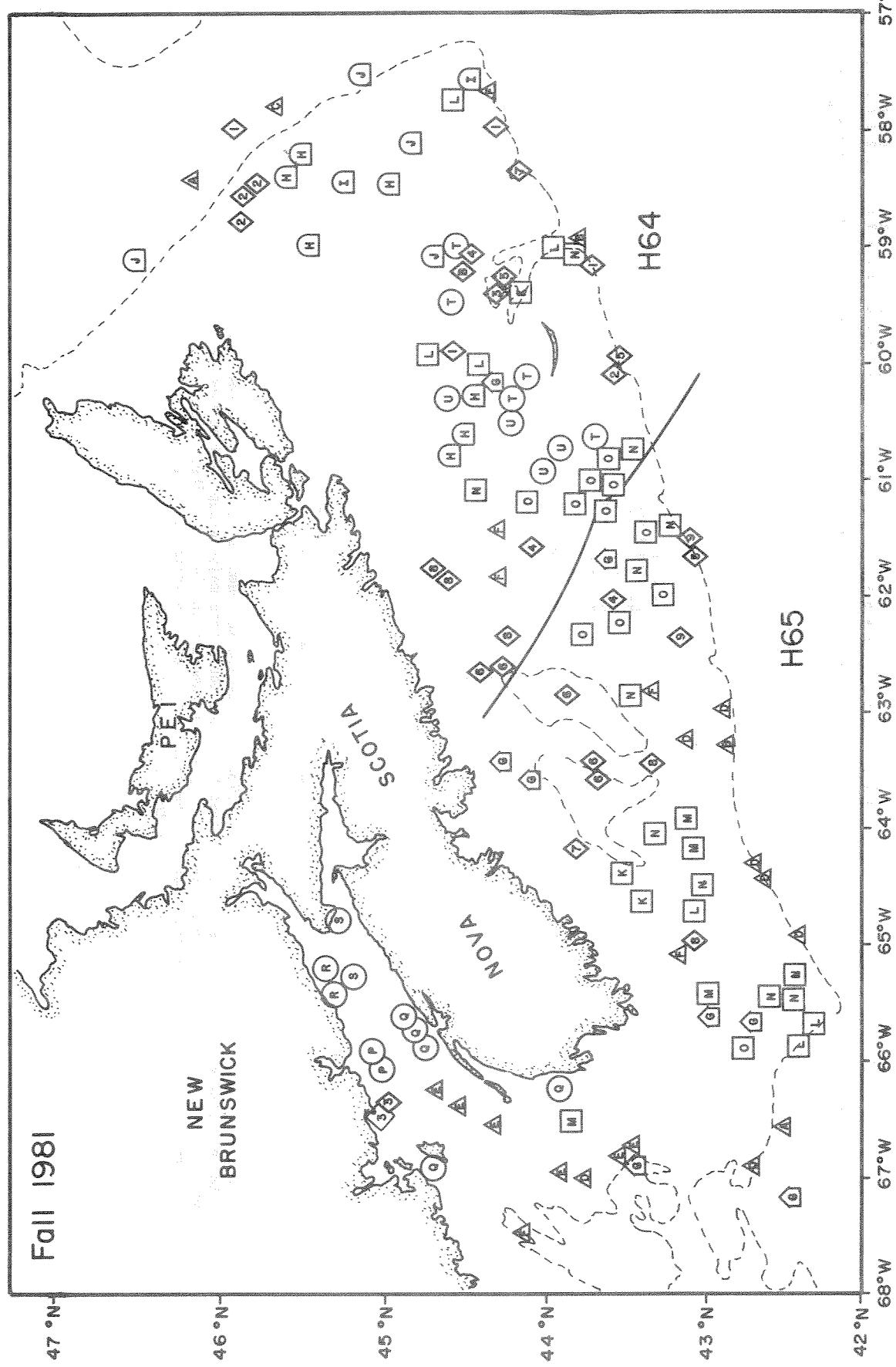


Fig. 98. The areal distribution of site groups, fall 1981. The symbols correspond to those in Figure 97.

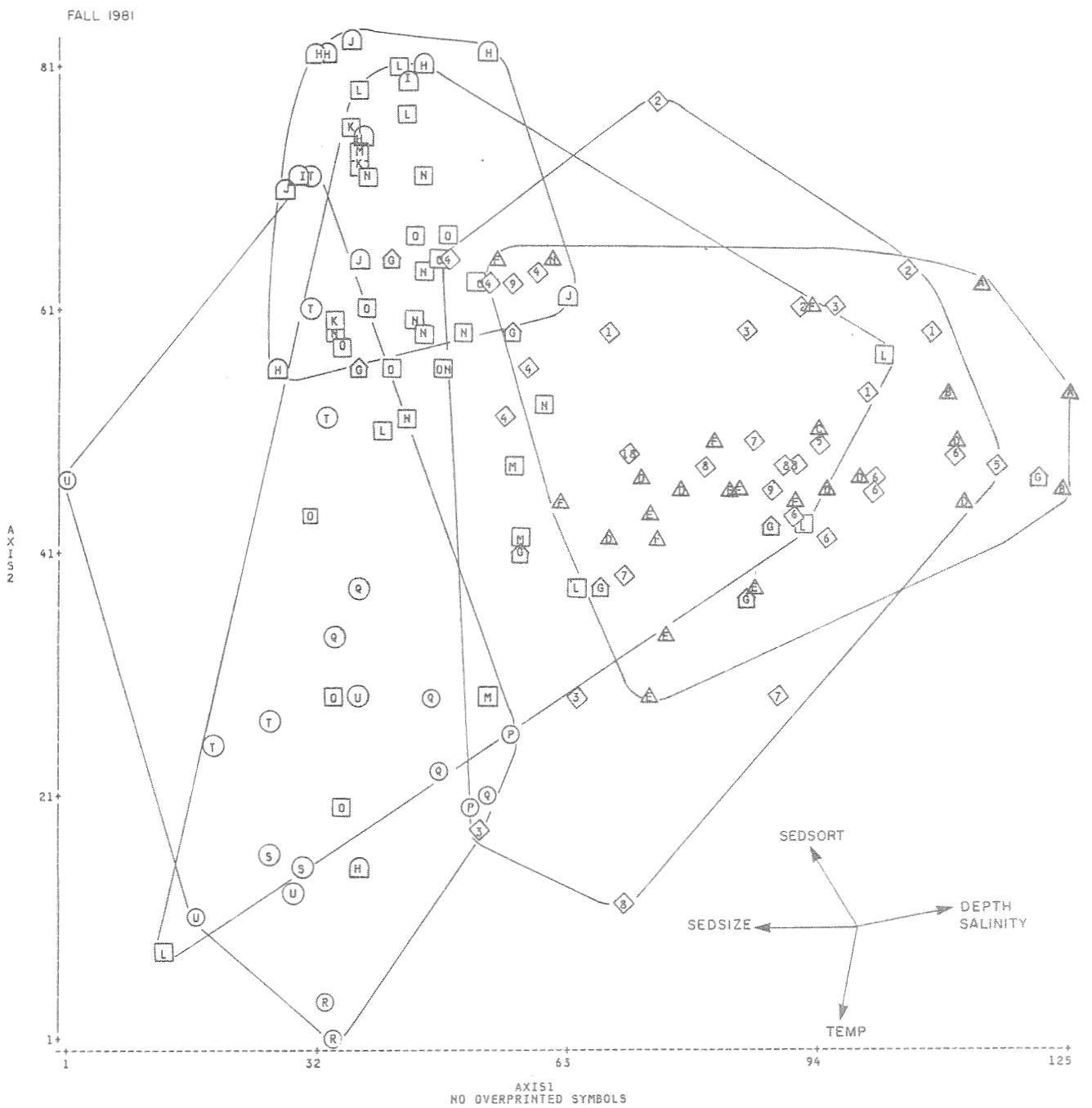


Fig. 99. The distribution of site groups in discriminant space, fall 1981. The symbols and number/letter codes correspond to those in Figure 97. The overprint table gives the coordinates (HP, VP) and identity of hidden (= overprinted) sites. The vector diagram summarizes the configuration of the environmental variables relative to the first two discriminant axes.

Groups of species with similar distributions across sites are shown in the species dendrogram (Figure 96) and the two-way table (Figure 97). The spatial distribution of species groups can be estimated by comparing the two-way table to the map of site groups on the Scotian Shelf (Figure 98).

The major site groups occupy distinct areas of the discriminant space (Table 26, Figure 99), although there is some overlap between groups. The first two discriminant axes account for most of the variability, and subsequent axes provide no further separation. Major site group I occupies the right half of the discriminant space, characterized by intermediate to great depth, predominantly intermediate temperature and high salinity, and sediments that are small to intermediate sized, but consistently poorly sorted. Major site group II is also to the right along axis 1, but is not as widely spread along axis 2 as is group I. These stations are characterized by intermediate to great depth, intermediate temperature, and high salinity, and the same type of sediment as group I. The stations in site group IV are typically at shallow depth, with very low temperature, intermediate salinity, and sediments that are extremely large grained and well sorted. Site group V overlaps groups I, II, and IV. It is characterized by predominantly shallow depth, an extreme range of temperature, intermediate salinity, and very large grained, well sorted sediments. Stations in site group VI are at the shallowest depth, with intermediate to high temperature, intermediate salinity, and intermediate sized, poorly sorted, or large grained, well sorted sediments.

Table 26. Coefficients of separate determination (Fall 1981). These show the relative importance of each variable on each axis. The Eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	34.0	0.1	17.7	6.4
2. Temp	0.0	61.0	11.3	5.1
3. Salinity	21.2	10.1	37.4	0.5
4. SEDSIZE	33.5	2.7	11.3	64.2
5. SEDSAND	2.5	0.3	0.8	10.8
6. SEDSORT	8.7	25.8	21.5	13.0
Eigenvalues	3.2	0.9	0.5	0.2
Percent of Group Separation	66.9	18.4	9.3	3.3

#### CLASSIFICATION OF SITES INTO SITE GROUPS

The distinctness of major sites groups in each survey is indicated by the percent of sites correctly classified (Table 27). It is clear that over all surveys the deepwater site group was most discrete, with classification success being commonly greater than 80%. The eastern shelf site groups, including the Sable Island Bank area, were next most discrete. Classificatory success was most variable for the Western Shelf and Bay of Fundy.

#### CONSISTENCY OF SPECIES GROUPS THROUGH TIME

The dendograms showing species groups in each summer survey indicate considerable consistency in group composition through time. However, since group structure does change from year to year we used the following procedure to arrive at composite or average species groups over all summer surveys. For each year the species dendrogram was subjectively split into groups of one or more species. A distance measure between each pair of species was calculated as 1 minus the proportion of years in which the species occurred in the same group (Tables 28, 29). This distance matrix was clustered using the Flexible sorting strategy ( $\beta = -0.25$ ) (Figure 100).

Definition of species groups in Figure 100 is again subjective. Eight of the species were judged as being in a group of their own. There were five pairs, of which halibut-haddock and spiny dogfish-pollock were the least strongly associated. The remaining 13 species comprised three groups.

There were too few surveys in either spring or fall for this approach to describing overall groups to be applicable.

#### SPECIES AND SPECIES GROUPS IN DISCRIMINANT SPACE

The objective of the following analysis is to display the relative positions of the species, and the species groups, derived in the previous section, in the environmental spaces defined by the discriminant analyses. Since the weighted discriminant space is constructed from the environmental variables, the relative abundances of species at stations in the discriminant space give a representation of their respective ranges of environmental tolerances or preferences. The standardized abundance of each species at each site can be displayed, just as with the standardized values of the environmental variables (Figure 14). Comparison of the relative placement of species' peak abundances from year to year will thus indicate temporal shifts in environmental preference.

The standarized abundances of the most important individual species and species groups in 1970 are shown in Figures 101 and 102. The placement of each site in the discriminant space corresponds exactly to that in the analysis of site groups from the summer of 1970 (Figure 13). Cod, plaice, and haddock occur at sites with a much wider range of environmental variables than do silver hake, yellowtail, and pollock (Figure 101). Cod, plaice, and haddock also appear relatively more tolerant to variation in temperature than to variation in depth or sediment characteristics. Their zones of maximum abundance in the discriminant space are elongated along the temperature gradient, but are much narrower along the gradients of depth and sediment characteristics. Similar inferences can be developed about the environmental ranges of the species groups shown in Figure 102. Each species group occupies a discrete portion of the discriminant space, characterized by particular

Table 27. The percent success in classifying sites into major site groups in each survey. Percent correct classification is above the /, number of sites in the group is below the /. Letter codes for group types or geographic areas are as follows: D = deep, E = eastern shelf, F = Bay of Fundy, L = low catch, N = no catch, S = Sable Island area, and W = western shelf.

Survey	MAJOR SITE GROUP							Overall
	I	II	III	IV	V	VI	VII	
Summer 1970	86/36 D	50/53 E	88/51 W-F					74
Summer 1971	83/30 D	50/24 E	65/17 S	22/9 L	59/34 W-F			61
Summer 1972	77/64 E-F	50/26 W-F	5/20 D	80/41 D				64
Summer 1973	42/12 S	31/29 W-F	100/2 L	0/3 N	40/10 ??	62/45 E	69/42 D	54
Summer 1974	70/47 E	64/22 S	40/33 W-F	0/5 L	0/2 N	78/51 D		63
Summer 1975	83/36 D	63/8 W	50/26 E	77/47 F-S	54/26 W			69
Summer 1976	80/56 D	63/16 F	86/28 W	78/41 E				79
Summer 1977	63/43 D	100/1 N	47/34 D	0/9 E-F	46/26 E	63/32 W-F		52
Summer 1978	50/34 D	20/20 F	77/52 W-F-S	86/36 E				65
Summer 1979	57/14 D	72/53 D	20/5 N	14/21 W-F	41/34 W-F	56/25 E		51
Summer 1980	80/68 W-F-S	0/3 N	57/21 E	88/56 D				78
Summer 1981	82/55 E-F	57/37 W-F	0/3 N	82/49 D				74
Spring 1979	53/49 D	0/4 N	14/7 L	67/27 W-E	84/44 E-F			68
Spring 1980	63/33 D	100/1 N	38/21 W	42/26 E-F	80/25 E-S			58
Spring 1981	40/10 S	33/9 S	75/32 W-S	67/42 E	0/4 N	87/23 D		65
Fall 1979	0/13 N	47/17 F-W	94/34 W-S	55/33 D	78/9 D	50/32 E		52
Fall 1980	70/41 D	80/25 E	66/44 E-F	25/4 E	43/7 W-F	59/22 W		66
Fall 1981	51/33 D	47/32 D	0/8 N	62/13 E	60/37 E-S	90/20 F-S		66

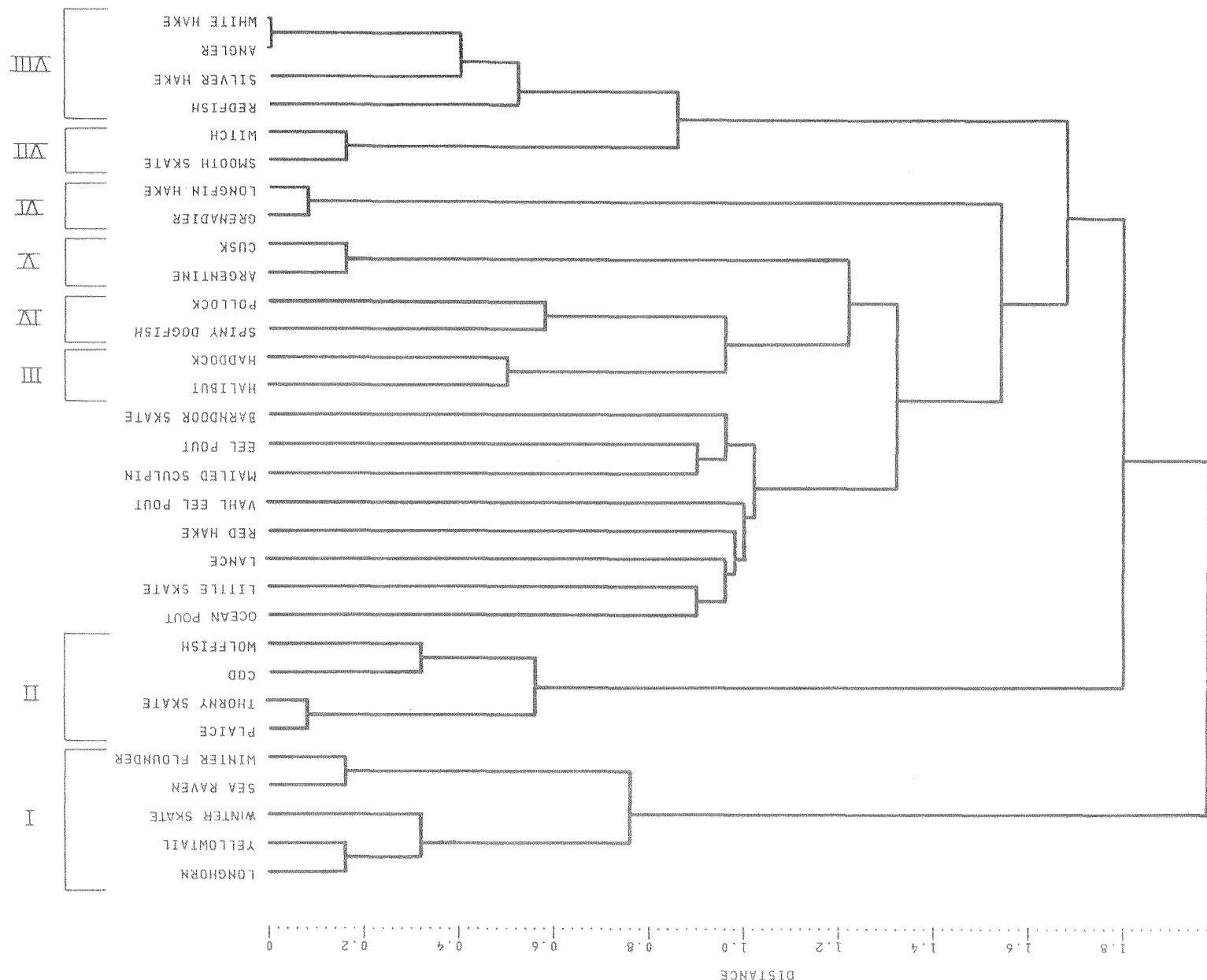
Table 28. The species group ID number assigned to each species in each summer survey after inspection of the species dendrogram. These group ID numbers are meaningful within surveys only.

Species	Year											
	70	71	72	73	74	75	76	77	78	79	80	81
cod	7	7	8	9	8	12	9	11	7	7	9	8
thorny skate	7	9	8	6	8	11	9	9	7	4	9	8
plaice	7	9	8	6	8	11	9	9	7	7	9	8
haddock	10	7	8	3	10	12	10	11	7	4	8	8
witch	14	4	12	5	7	11	5	9	8	1	2	13
white hake	13	4	13	5	7	3	5	8	9	1	2	13
silver hake	13	4	13	2	3	3	5	8	9	4	2	7
redfish	14	4	13	5	7	3	5	8	5	1	1	11
yellowtail	3	13	2	12	11	13	9	5	3	7	11	1
longhorn	3	13	2	12	11	13	13	5	3	7	11	3
smooth skate	14	9	12	5	7	11	5	9	8	4	2	13
wolffish	7	7	8	6	10	12	9	11	7	2	9	9
angler	13	4	13	5	7	3	5	8	9	1	2	13
pollock	11	6	9	3	4	3	5	11	7	3	8	9
sea raven	3	13	2	14	11	13	13	5	4	8	11	3
halibut	10	8	11	11	10	12	10	11	8	2	8	9
cusk	12	5	15	2	3	3	6	10	12	3	12	10
spiny dogfish	11	6	9	4	3	10	13	10	12	3	8	10
ocean pout	4	11	10	6	3	11	12	5	10	4	11	3
argentine	12	5	15	2	3	14	6	10	11	3	12	10
winter skate	3	13	7	12	11	13	12	2	3	7	11	1
winter flounder	2	13	2	14	14	13	13	5	4	8	11	3
longfin hake	15	3	16	7	1	2	4	6	15	1	1	11
grenadier	15	3	16	7	1	2	4	6	15	1	1	12
mailed sculpin	6	9	4	15	11	9	2	12	13	6	10	4
red hake	5	12	14	1	2	4	7	2	16	4	2	7
eel pout	16	10	6	8	12	1	14	12	14	3	5	6
lance	8	14	5	10	9	8	3	1	1	5	6	1
Vahl's eel pout	17	15	17	17	6	7	1	7	17	2	3	5
barndoor skate	1	1	3	16	5	6	8	3	6	9	4	4
little skate	9	2	1	13	13	5	12	4	2	9	7	1

Table 29. Distances between pairs of species based on the proportion of years in which they occurred in the same species group.

species occurred in the same group.

Fig. 100. Composite species dendrogram for summer 1970-1981. Based on the proportion of years in which



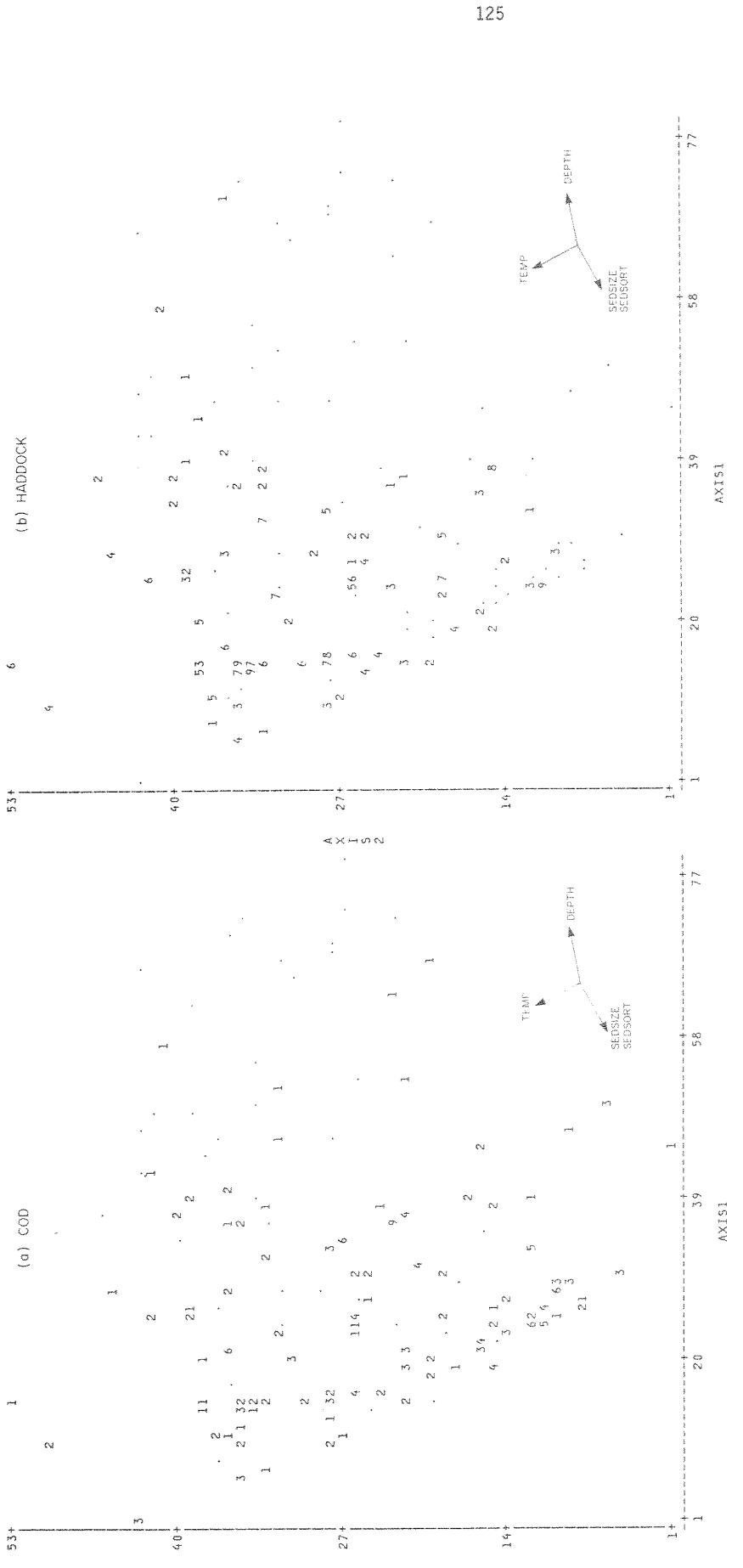
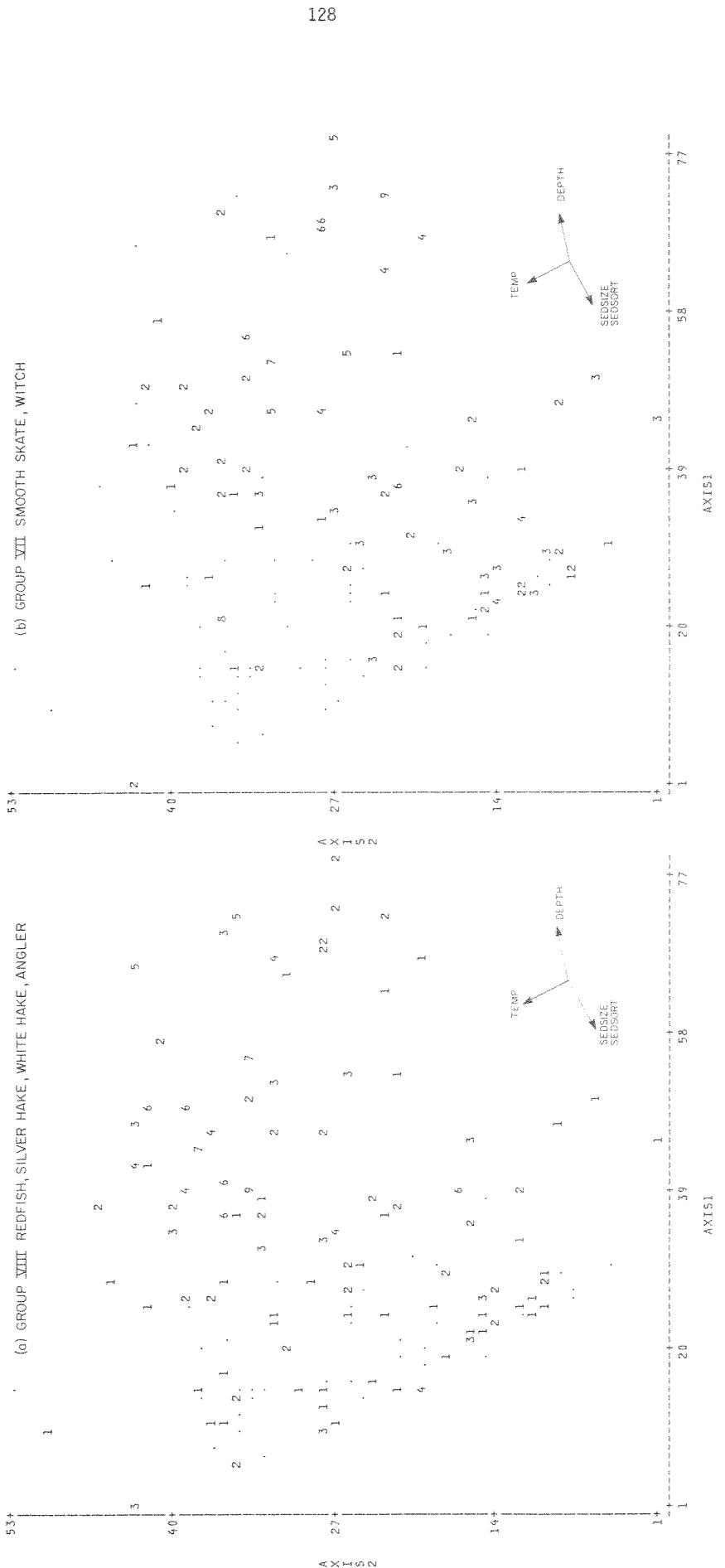


Fig. 101. The standardized abundances of major species in discriminant space (Summer 1970). Nine species were absent at sites indicated by a "•".

Fig. 102. The standardized abundances of species groups in discriminant space (Summer 1970).



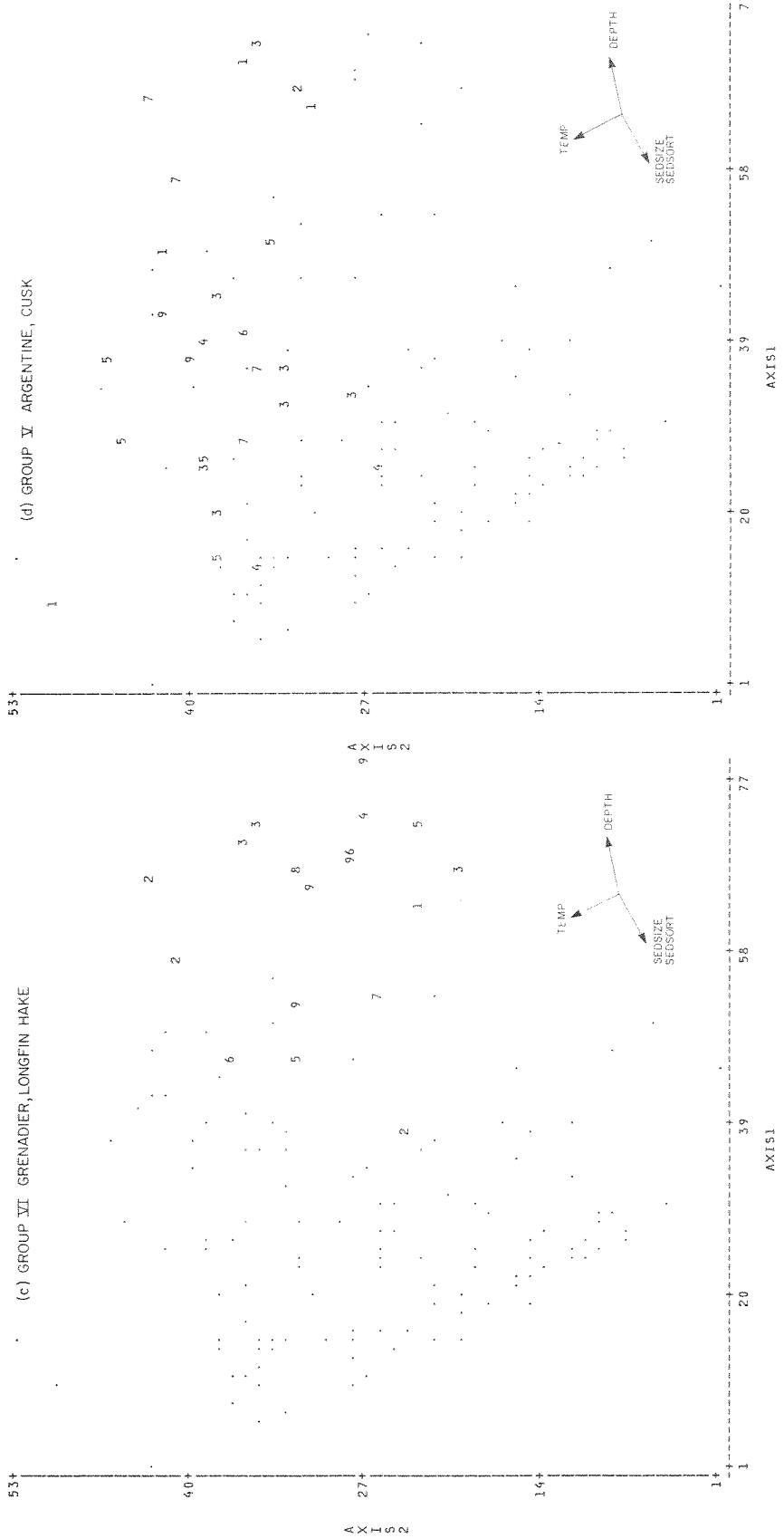


Fig. 102. (Continued)

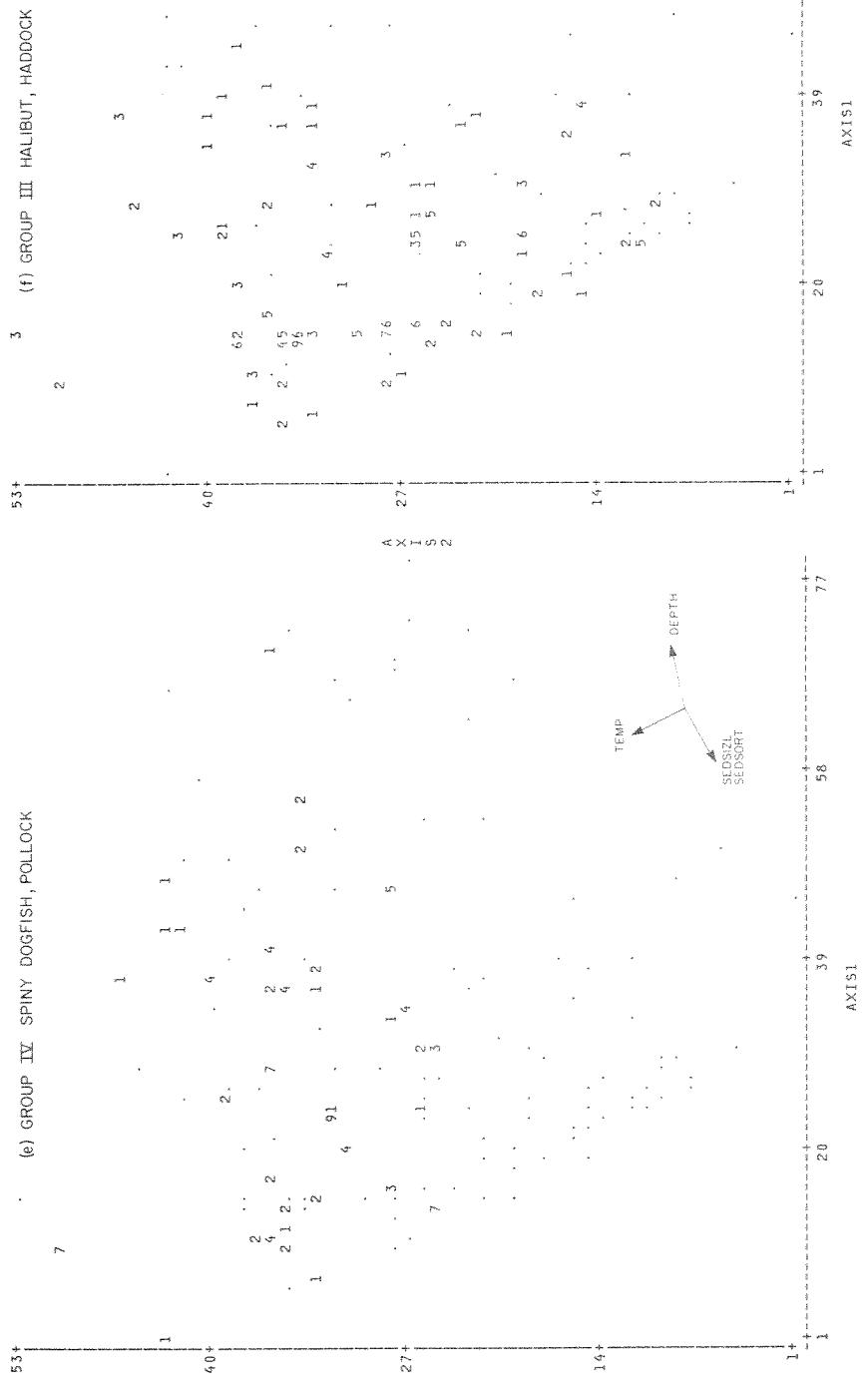


Fig. 102. (Continued)

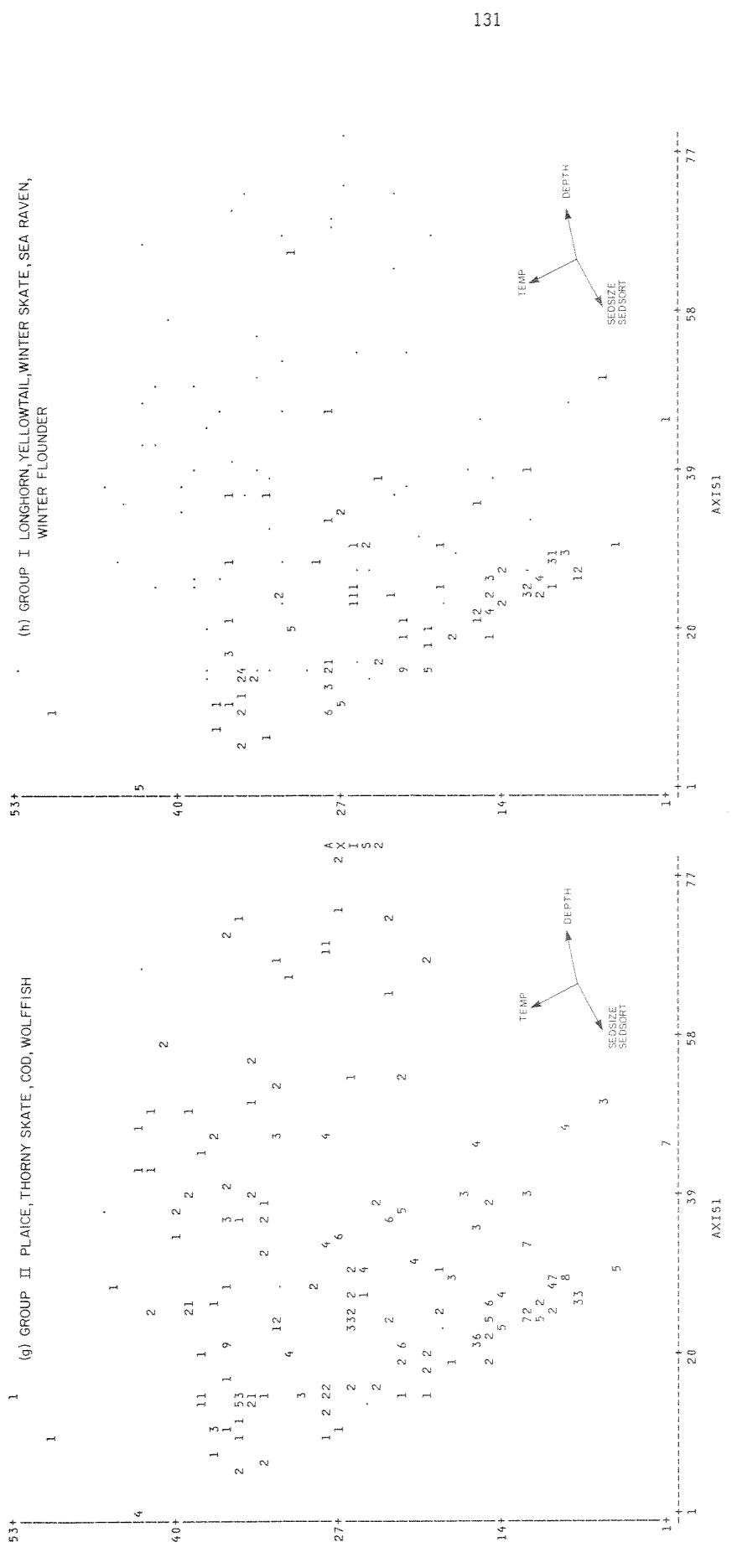


Fig. 102. (Continued)

sediment characteristics. Their zones of maximum abundance in the discriminant space are elongated along the temperature gradient, but are much narrower along the gradients of depth and sediment characteristics. Similar inferences can be developed about the environmental ranges of the species groups shown in Figure 102. Each species group occupies a discrete portion of the discriminant space, characterized by particular values of temperature, depth, sediment size, and sediment sorting. The value of this approach is that it displays in detail species', and species groups', responses to gradients in a multivariate suite of environmental variables.

In order to more easily compare the relationships among species' environmental preferences from year to year we calculated each species' and species group's mean position in discriminant space. The mean position for a species was calculated as the weighted average score of the sites in which the species occurs. The weights are the square-root transformed abundances of the species. This weighted average score should represent the average habitat of the species. Figures 103-105 show that species in the same species group are consistently close to each other in the discriminant space. This is not surprising, since species were assigned to groups on the basis of similar distributions, and these necessarily imply similar suites of environmental variables.

What is of most interest in this analysis is the comparison of species' and species groups' relative positions in the discriminant space from year to year (Figure 103). It must be remembered that the discriminant space is recalculated for each year's data. This is reflected in the slightly different selection and orientation of environmental variables in each year. In spite of this, the space is strikingly similar over time. The temperature gradient is usually oriented vertically in the space, with gradients of depth and sediment characteristics at right angles to temperature. If allowance is made for the slightly different orientation of these major gradients in each year, it can be seen that the relative positions of the major species and species groups are consistent over the whole period of the study. For example, the species group consisting of longhorn sculpin, yellowtail, winter skate, sea raven, and winter flounder is typically most abundant at the shallowest depths, with the largest, most well sorted sediments. In contrast, the grenadier-longfin hake group is always most abundant in an area of the space characterized by the greatest depth and smaller sediment size. Figures 103-105 should be inspected more closely if it is desired to identify such relationships in more detail.

## CONSISTENCY OF THE SPATIAL DISTRIBUTION OF SPECIES THROUGH TIME

### Definition of Stratum Groups

The maps showing the areal distribution of major site groups in each summer reveal noticeable consistency in the structure of site groups from year to year. There was year to year variability, however, and a procedure analogous to that used for species was used to derive composite site groups over all summer surveys. The areal units over which the sites were aggregated before being input to the grouping procedure were the strata on which the survey sampling design was based (Figure 2). Each stratum in each year was assigned a favorite major site group (Table 30). This was the major site group to which the majority of sites in that stratum belonged. Ties were broken by selecting the site group of the first set in that stratum in that survey. A distance measure between each pair of strata was calculated as 1 minus the proportion of years in which these strata had the same favorite major site group (Table 31). This distance matrix was then clustered using the group average sorting strategy. The resultant dendrogram (Figure 106) groups together strata which are similar in regard to how often they shared the same major site group.

The groupings of strata in Figure 106 were somewhat rearranged to bring strata which were geographically close into the same groups. This was done only when reference to the inter-stratum distance matrix (Table 31) indicated that it was reasonable to do so. In several cases the initial allocation of a stratum to a group of geographically distant strata rather than to a group of neighbouring strata was based on small differences in inter-stratum distance.

Thirteen stratum groups were defined (Figure 107). Each stratum group was characterised by a distinct species assemblage (Table 32). There were too few surveys in either spring or fall for this approach to deriving composite groups to be applicable.

### Clustering of Stratum Groups into Stratum/Year Groups

The species and the stratum groups for all summer surveys were clustered (Figures 108, 109). Stratum groups were consistently highly similar through time, as evidenced by the fact that the same stratum groups in successive years were usually grouped on the dendrogram (Figure 108). This is especially true of the East Banks, NE Mixed, West Banks, South Fundy, West Fundy, Basins, Shelf Slope, and Cabot Slope stratum groups. The groups of species which

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Fig. 103. The species' weighted mean positions in discriminant space during summers 1970-1981. The codes are as follows: An = Angler; Ar = argentine; Bn = barndoor skate; Co = Cod; Cu = cusk; Ep = eelpouts; Gr = grenadier; Ha = haddock; Hl = halibut; Lf = longfin hake; Lh = longhorn sculpin; Lt = little skate; Ms = mailed sculpin; Op = ocean pout; Pl = plaice; Po = pollock; Rf = redfish; Rh = red hake; Rv = sea raven; Sd = spiny dogfish; Sh = silver hake; Sl = sandlance; Sm = smooth skate; Th = thorny skate; Ve = Vahl's eelpout; Wf = wolffish; Wi = winter flounder; Wh = white hake; Ws = winter skate; Wt = witch; and Yt = yellowtail.

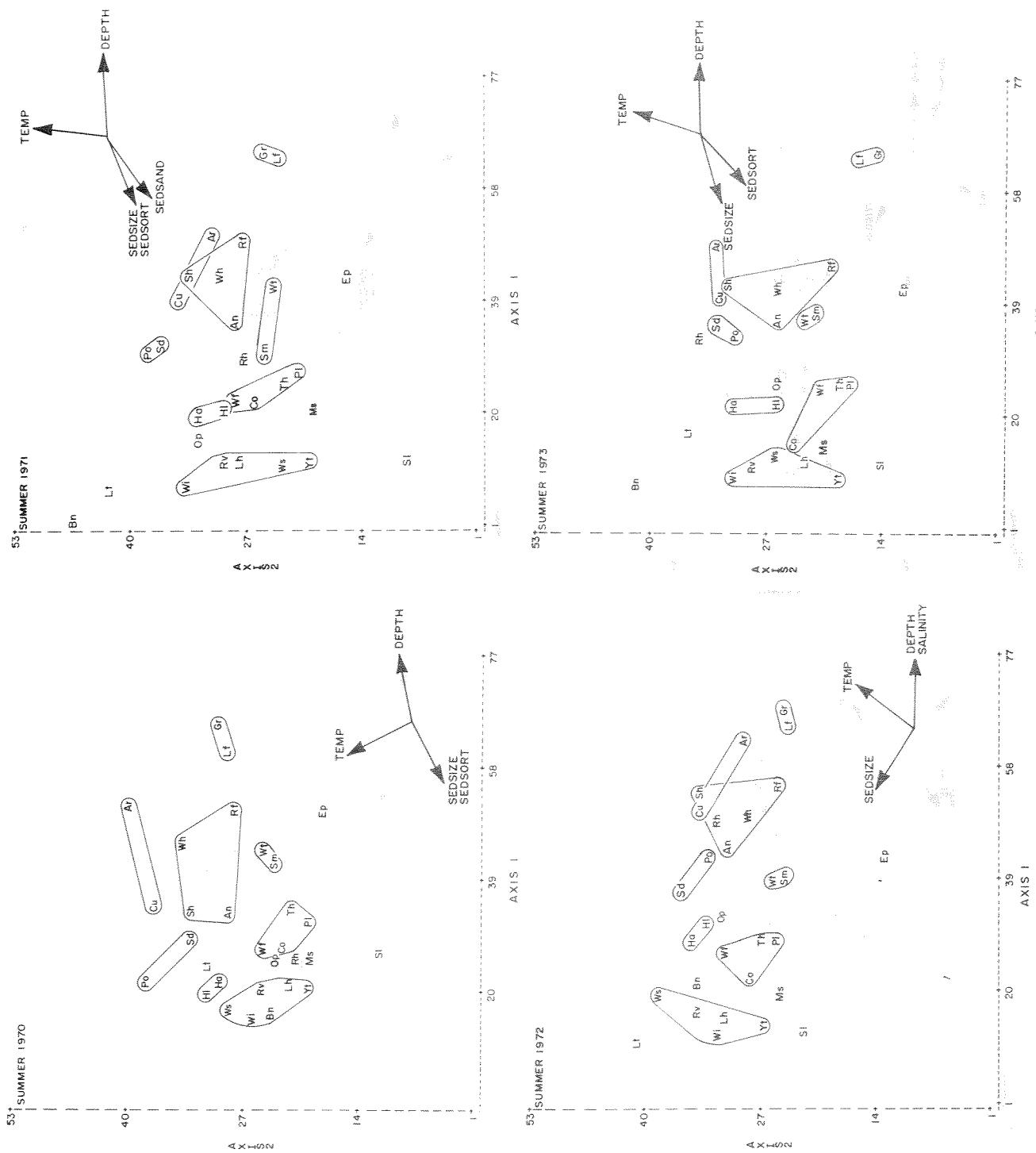


Fig. 103. See facing page for legend.

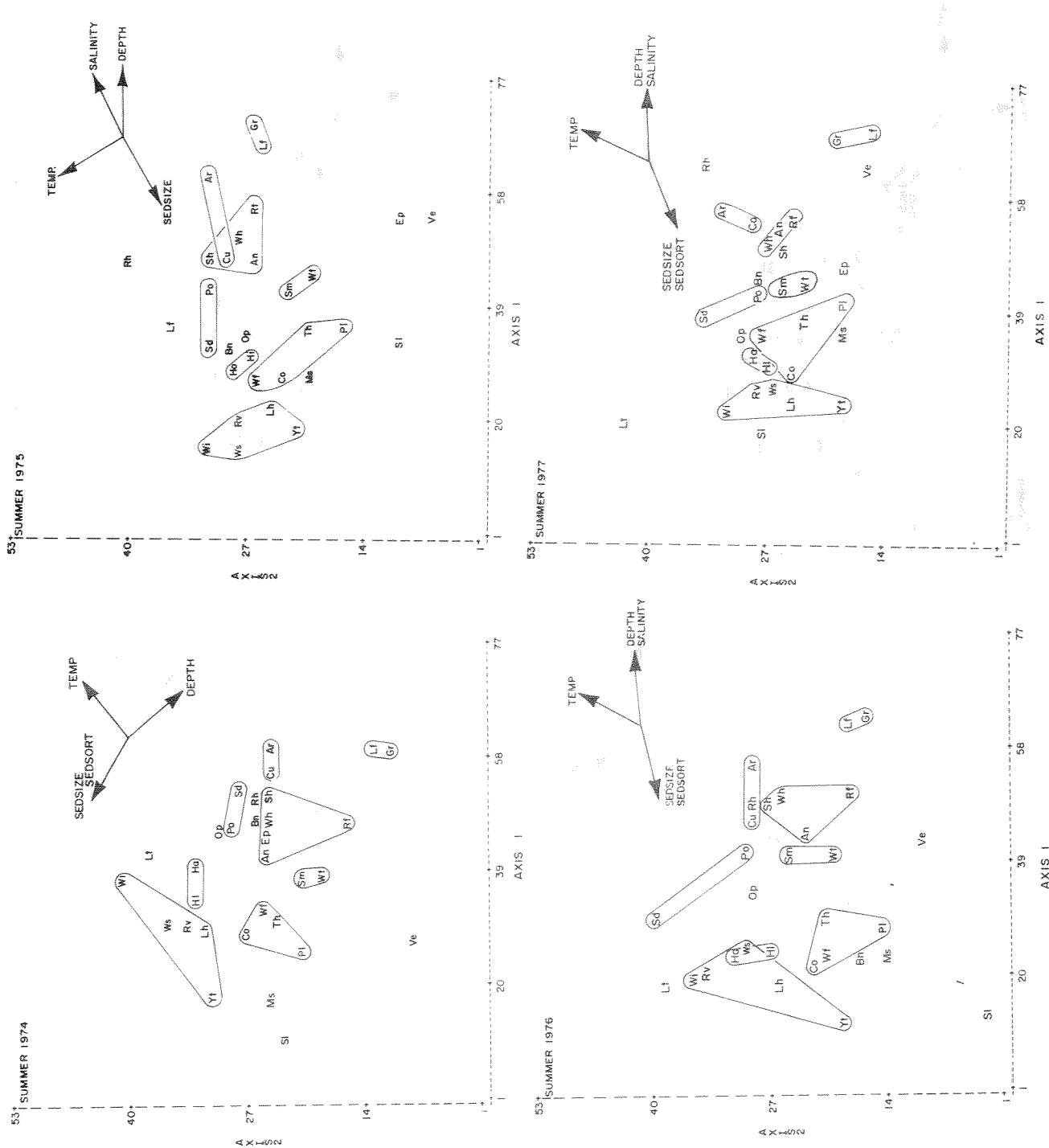


Fig. 103. (Continued)

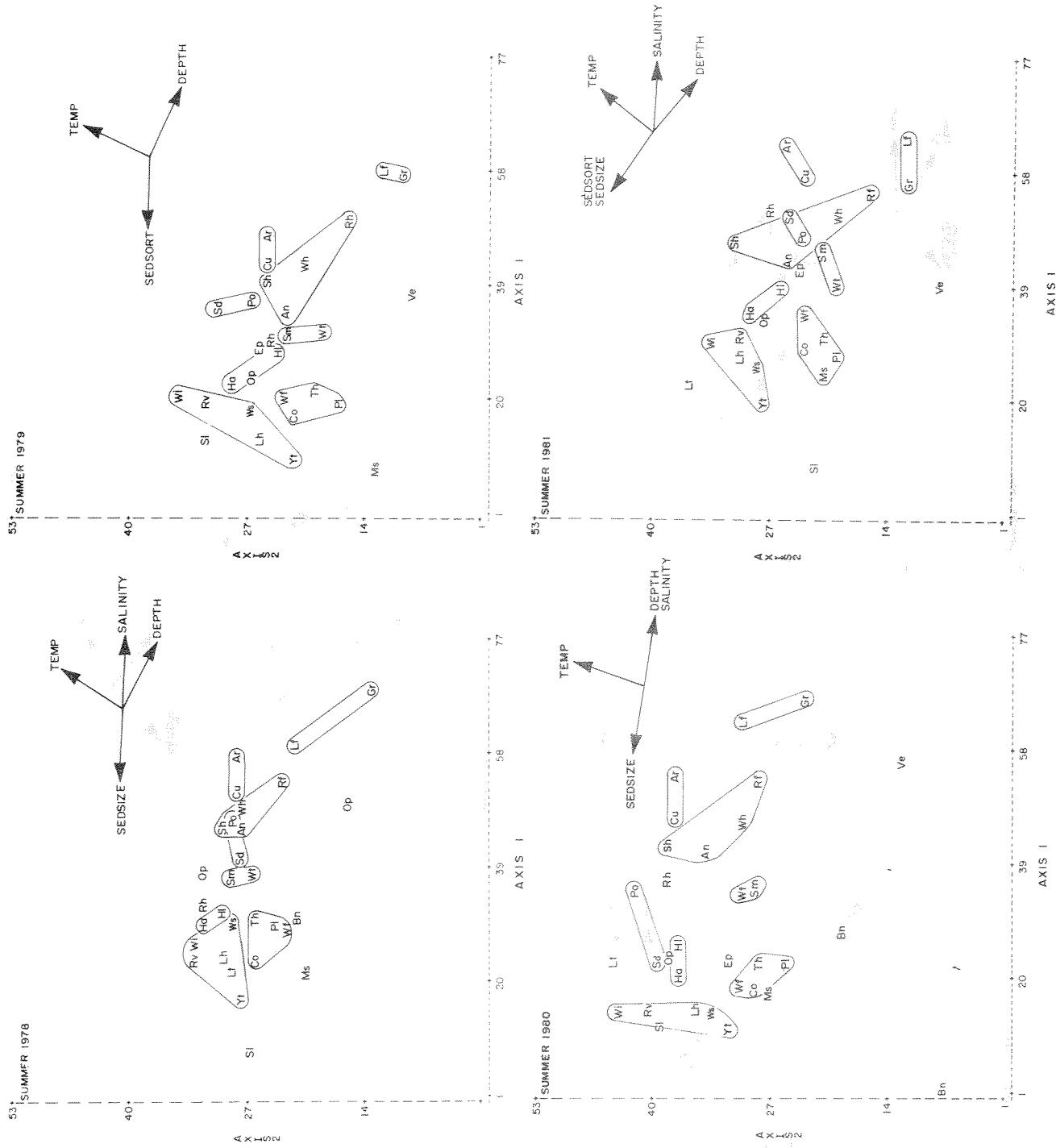


Fig. 103. (Continued)

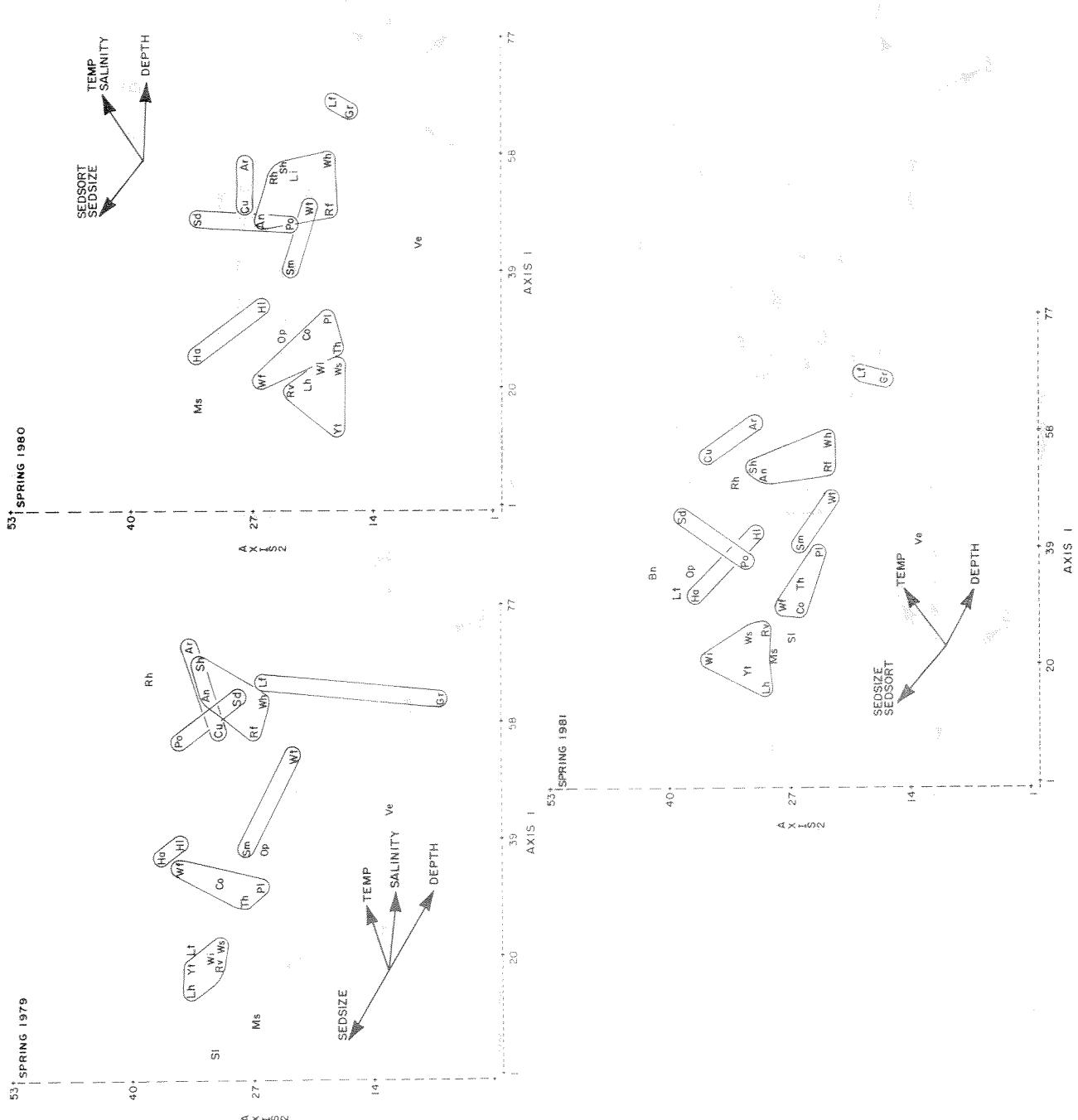


Fig. 104. The species' weighted mean positions in discriminant space during spring 1979-1981 (Codes as in Figure 103).

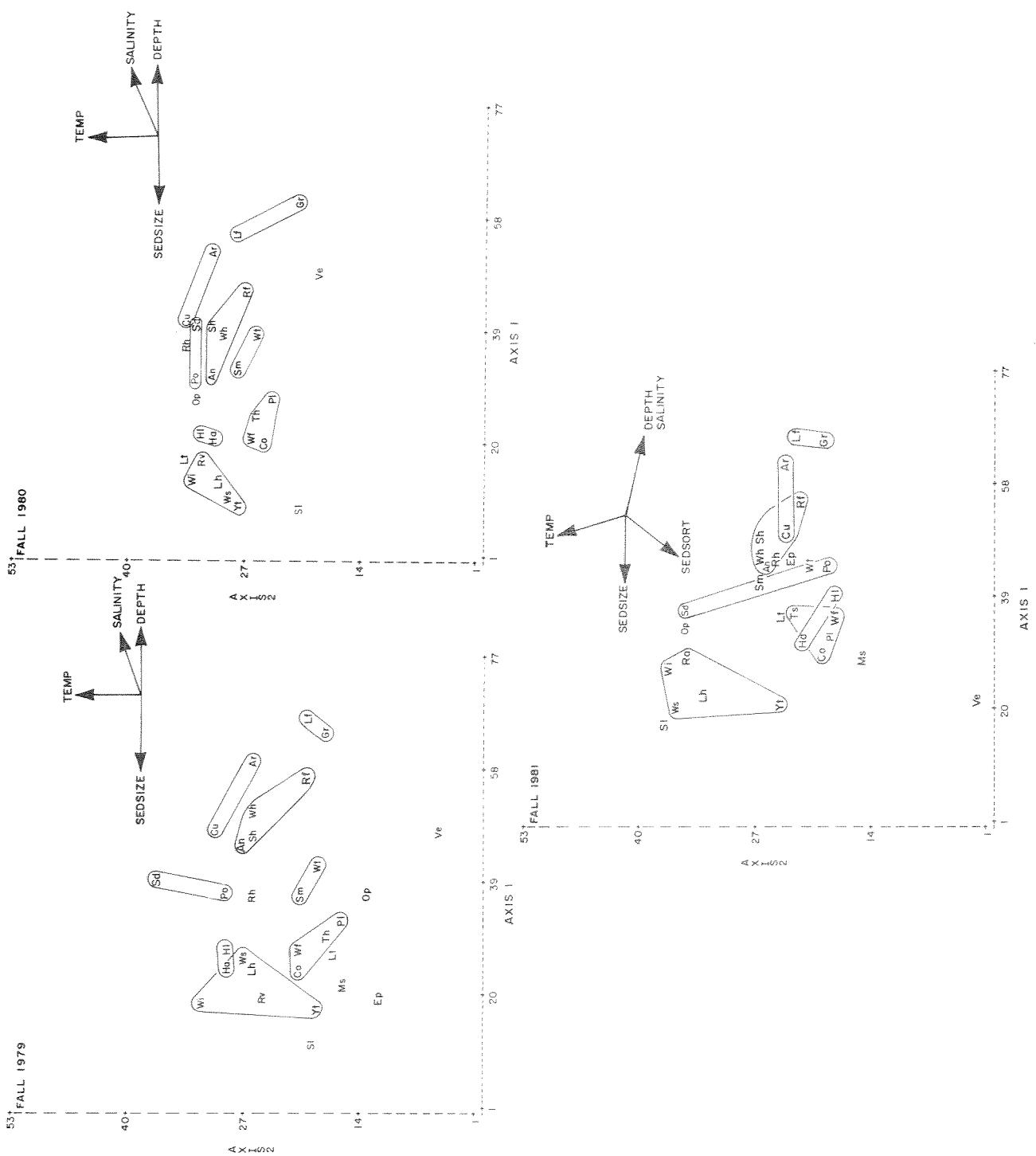


Fig. 105. The species' weighted mean positions in discriminant space during fall 1979-1981 (Codes as in Figure 103).

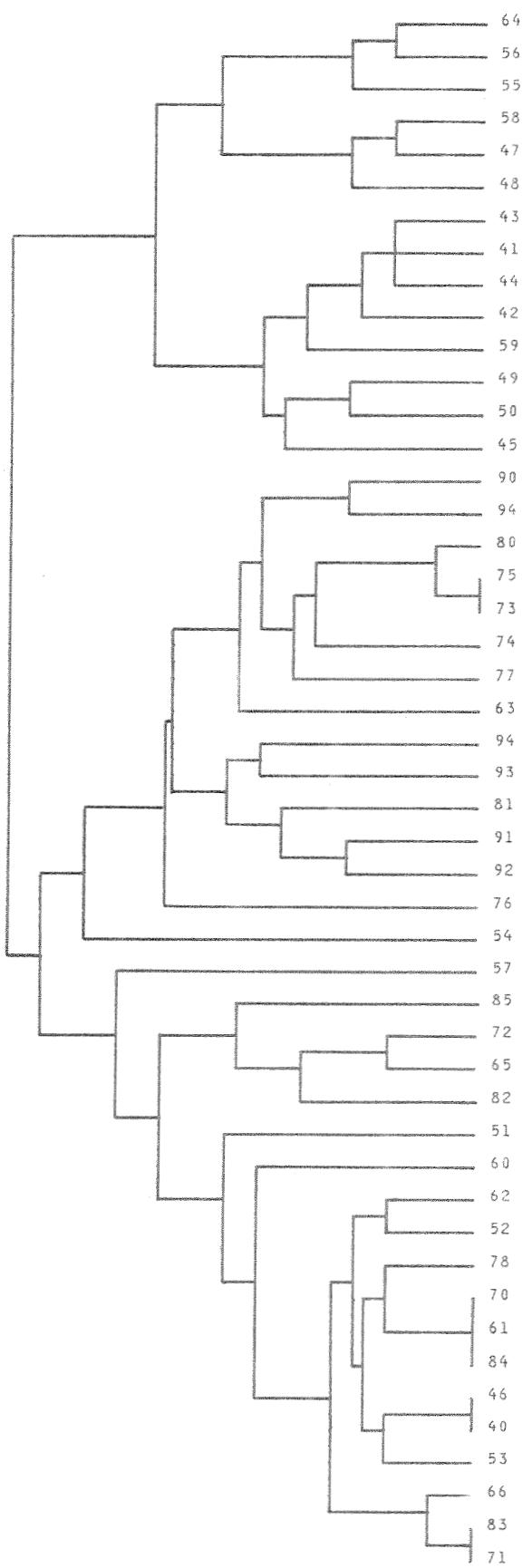
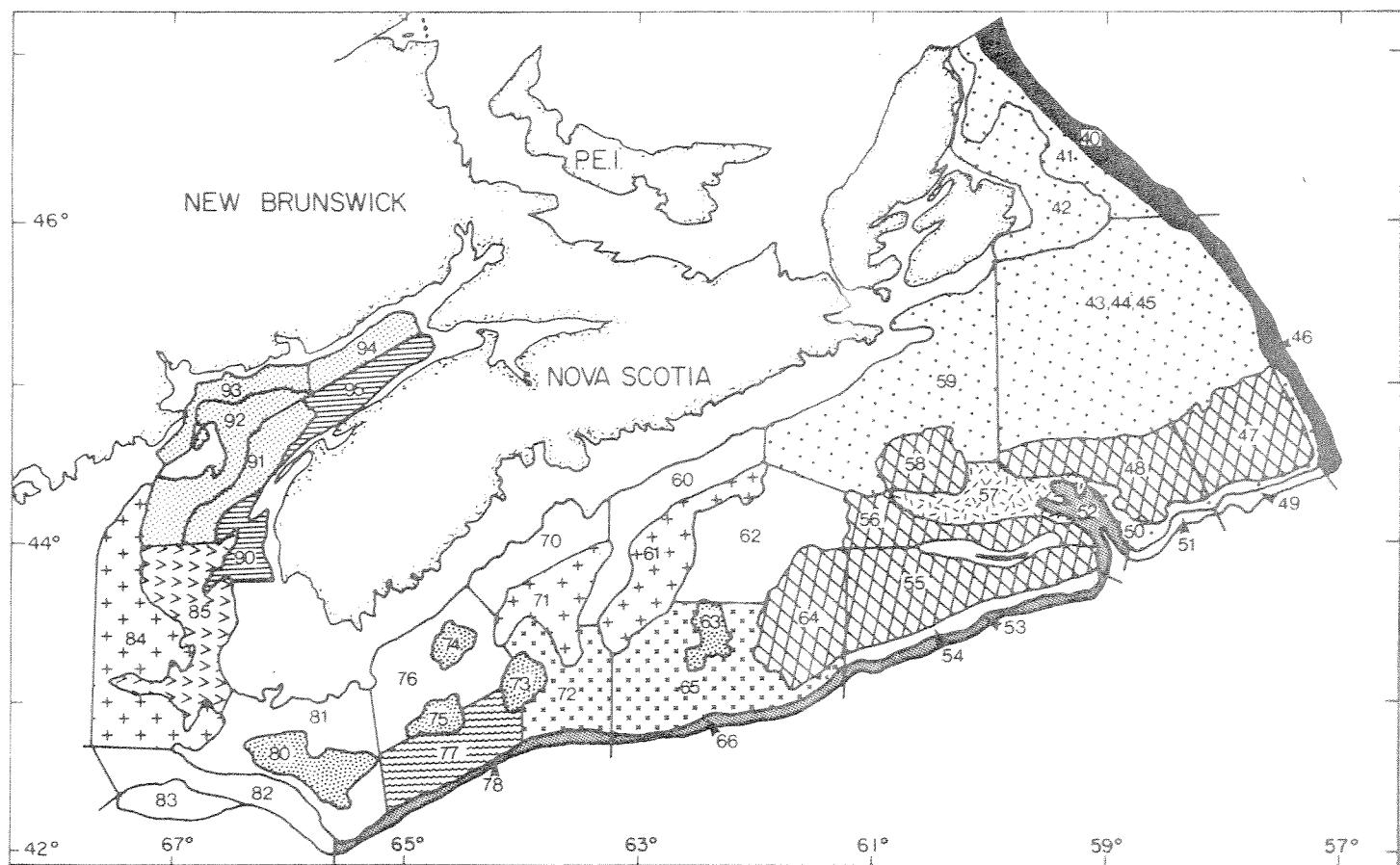


Fig. 106. Dendrogram showing the relationships among strata (Figure 2) based on the distances in Table 31. The strata are numbered as in Figure 2.



Stratum Group Name	Strata
NE Mixed	41, 42, 43, 44, 45, 50, 59
Cabot Slope	40, 46
East Banks	47, 48, 55, 56, 58, 64
Gully Plain	57
Central Plain	60, 62
Outer Plain	65, 72
Shelf Slope	52, 53, 66, 78
West Banks	63, 73, 74, 75, 80
Basins	61, 71, 84
West Plain	77
Yarmouth Plain	85
West Fundy	91, 92, 93, 94
South Fundy	90, 95
Not Included	49, 51, 54, 70, 76, 81, 82, 83

Fig. 107. The stratum groups based on stratum similarity within summer surveys (Figure 106) and geographic proximity.

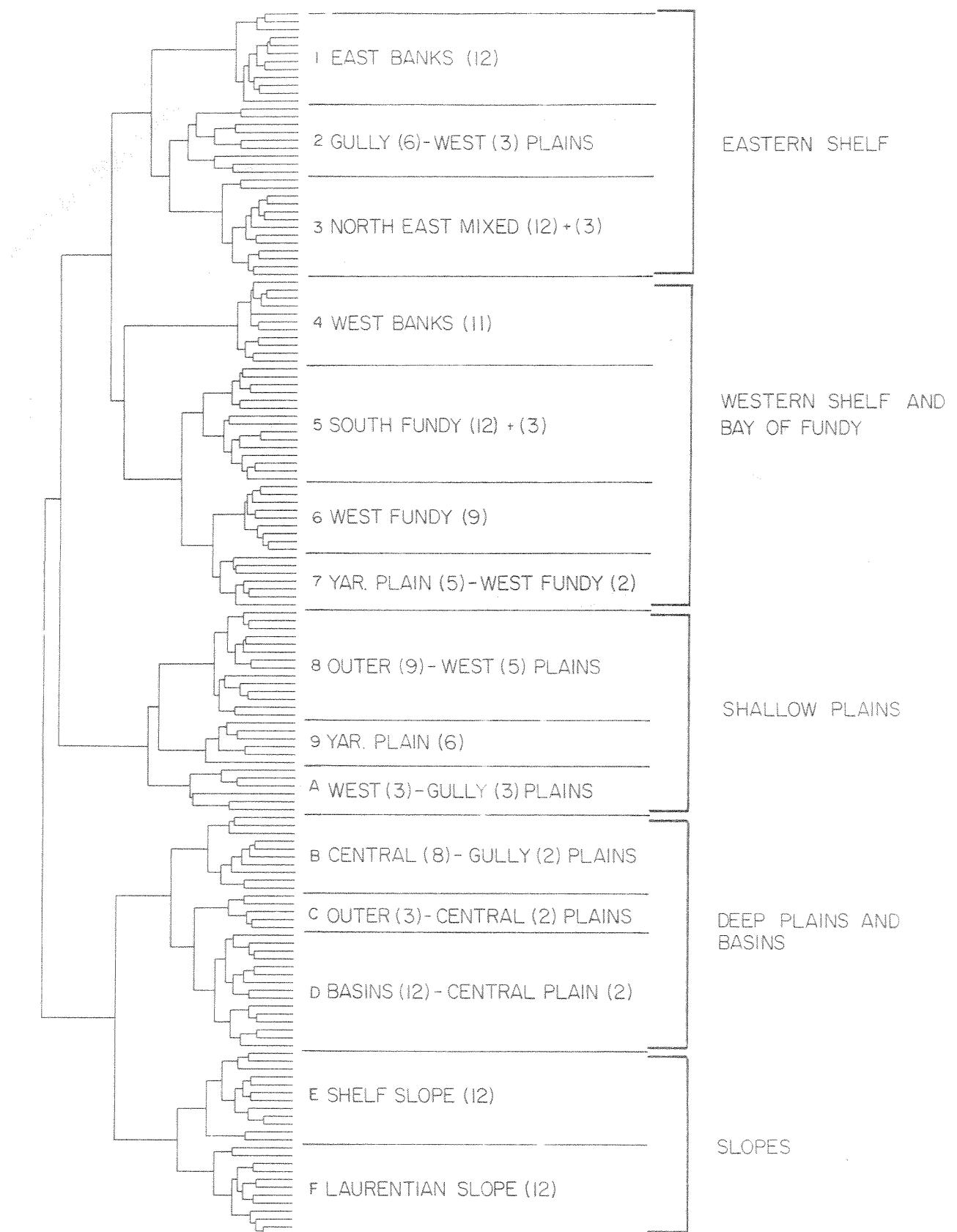


Fig. 108. The site dendrogram showing the relationships between stratum groups through time (the sequence of cases from top to bottom is the same as the sequence from left to right in Figure 110). The number/letter codes to the immediate right of the dendrogram serve as group identification in Figures 110-114. The numbers in parentheses show the number of years in which a particular stratum groups (e.g. West banks) are present in each cluster group (stratum/year group).

resulted from this analysis (Figure 109) differed slightly from those found in Figure 100. The groupings in Figure 100 are a summary of associations based on site by site information and, in our opinion, are more appropriate than those based on average abundance in stratum groups. Consequently, in the two-way table of relative species abundance in each stratum group (Figure 110) the species are in the same order as in Figure 100.

Table 30. Favorite site group for each stratum in each year.

Stratum	Year											
	70	71	72	73	74	75	76	77	78	79	80	81
40	1	1	5	7	6	1	1	1	1	1	4	4
41	2	2	1	6	1	3	1	4	4	6	1	1
42	2	2	2	6	1	3	4	5	4	6	3	1
43	2	2	1	6	1	3	4	5	4	6	1	1
44	2	2	1	6	1	3	4	4	4	6	3	1
45	1	2	5	6	1	3	4	4	2	1	4	1
46	1	1	5	7	6	1	1	1	1	1	4	4
47	2	3	1	6	2	4	4	5	4	6	3	1
48	2	3	1	6	1	3	4	5	4	5	3	1
50	2	2	2	6	1	3	4	1	2	2	4	1
51	1	1	4	6	4	3	1	1	1	1	4	4
52	1	1	5	7	6	4	1	1	1	2	4	4
53	1	1	5	7	6	1	1	1	1	2	4	1
54	1	2	5	2	4	4	3	5	1	4	1	1
55	2	3	2	1	2	4	4	5	3	5	1	2
56	2	5	2	6	2	4	4	5	3	5	1	2
57	1	2	1	6	6	4	1	1	4	2	1	3
58	2	3	2	6	2	4	4	5	4	5	3	1
59	2	2	1	6	1	3	4	4	1	6	4	4
60	3	1	5	7	6	2	1	1	1	3	1	4
61	1	1	5	7	6	1	1	3	1	2	4	4
62	3	1	5	7	6	5	1	1	1	2	4	4
63	3	2	1	2	2	5	3	6	1	4	1	2
64	2	5	1	6	2	4	4	1	3	5	1	2
65	3	5	4	7	6	5	3	3	3	2	1	4
66	1	1	4	7	6	1	1	1	2	2	4	4
70	1	1	5	7	6	1	1	3	1	2	4	4
71	1	1	4	7	6	1	1	3	2	2	4	4
72	3	5	4	7	6	5	1	3	3	4	1	4
73	3	5	3	2	3	5	3	6	4	4	1	2
74	3	4	3	2	3	5	3	1	3	2	1	2
75	3	5	3	2	3	5	3	6	4	4	1	2
76	2	5	5	7	3	5	1	1	4	2	1	2
77	3	5	4	2	3	5	3	1	4	2	1	4
78	1	1	5	7	6	2	1	3	3	2	4	4
80	3	5	3	2	3	5	3	6	3	4	1	2
81	3	5	3	6	3	4	1	3	3	2	1	2
82	3	4	4	7	6	2	1	3	3	2	4	4
83	1	1	4	7	6	1	1	3	2	2	4	4
84	1	1	5	7	6	1	1	3	1	2	4	4
85	3	4	4	7	6	5	3	6	1	2	1	1
90	3	5	2	2	3	4	3	6	3	5	1	2
91	3	5	5	2	3	1	2	3	3	2	1	2
92	3	5	5	6	3	1	2	3	3	2	4	1
93	3	5	2	6	1	4	2	1	3	2	1	1
94	3	5	3	2	6	4	2	1	3	4	1	2
95	3	5	2	3	3	5	2	6	3	5	1	2

The groups of stratum groups which result from the clustering shown in Figure 108 are subsequently used as input to discriminant and principal coordinate analyses and are hereafter referred to as stratum/year groups. The stratum groups contributing to each stratum/year group shown in the dendrogram (Figure 108) and the two-way table (Figure 110) are described in Table 33. Some groups (e.g. East Banks, NE

Mixed, Basins, Shelf Slope, and Cabot Slope) had relatively abundant populations of their characteristic species assemblages in all years, while others, especially the Plains groups, had more variable populations of major species (Figure 110).

Table 33. The consistency of stratum/year groups through time. Years is the number of years in which a stratum group (e.g. West Plain) appears in each stratum/year group in Figures 108 and 110. The group symbols are those used in Figure 111.

Group symbol	Stratum group	Years
1	East banks	12
2	Gully plain	6
	West plain	3
3	NE mixed	12
	Gully plain	1
4	West banks	11
5	South Fundy	12
	West banks	1
	West plain	1
	West Fundy	1
6	West Fundy	9
7	Yarmouth plain	5
	West Fundy	2
8	Outer plain	9
	West plain	5
9	Yarmouth plain	6
A	West plain	3
	Gully plain	3
B	Central plain	8
	Gully plain	2
C	Outer plain	3
	Central plain	2
D	Basins	12
	Yarmouth plain	1
	Central plain	2
E	Shelf slope	12
F	Cabot Slope	12

#### Stratum Groups Through Time in WDA Space

There is considerable overlap among stratum/year groups in weighted discriminant space (Table 34, Figures 111, 112), although careful inspection reveals that most groups are separated from each other by the first three discriminant axes. All possible pairwise combinations of stratum/year groups, and whether or not they are separated by the first three axes are shown in Table 35. Seventy of 105 possible combinations of groups are separated by axes 1 and 2, and 19 of the remaining 35 are separated by axes 1 and 3. Only 11 paired combinations of stratum groups remained

Table 31. Distances between strata based on the proportion of years in which each pair of strata had the same favorite site group.

Strata	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	
40	0.000 0.917 1.000 1.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 0.917																								
41	0.917 0.000 0.333 0.167 0.167 0.167 0.500 0.917 0.500 0.417 0.417 0.500 0.750 0.917 0.833 0.750 0.917 0.500 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.750																								
42	1.000 0.333 0.000 0.167 0.167 0.167 0.500 1.000 0.333 0.250 0.333 0.250 0.333 0.417 0.833 1.000 0.917 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.750																								
43	1.000 0.167 0.167 0.167 0.000 0.167 0.500 1.000 0.333 0.250 0.333 0.250 0.333 0.417 0.833 1.000 0.917 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.750																								
44	1.000 0.167 0.167 0.167 0.000 0.417 1.000 0.333 0.250 0.333 0.250 0.333 0.417 0.833 1.000 0.917 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.750																								
45	0.667 0.500 0.500 0.500 0.500 0.500 0.500 0.667 0.750 0.833 0.750 0.833 0.750 0.667 0.917 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.667 0.750																								
46	0.009 0.917 1.000 1.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 1.000 0.667 0.000 0.917																								
47	1.000 0.500 0.533																								
48	1.000 0.412 0.250																								
49	0.833 0.417 0.333																								
50	0.833 0.500 0.333 0.417 0.333																								
51	0.333 0.750 0.833																								
52	0.167 0.917 1.000 1.000 1.000 0.167																								
53	0.167 0.833 0.917																								
54	0.750 0.750 0.750 0.667 0.833 0.667 0.750 0.750 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.667 0.833 0.500																								
55	1.000 0.833 0.667 0.667 0.667 0.667 0.833 0.917 1.000 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.500 0.750																								
56	1.000 0.750 0.563																								
57	0.667 0.500 0.750 0.563 0.667 0.750 0.667																								
58	1.000 0.667 0.333 0.560 0.500 0.750 1.000 0.167 0.250 0.667 0.563 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
59	0.750 0.333 0.417 0.333 0.250 0.417 0.750 0.563 0.500 0.333 0.417 0.563 0.750 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.750																								
60	0.333 0.833 1.000 0.917 1.000 0.917																								
61	0.167 0.917 1.000 1.000 1.000 0.750 0.167 1.000 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167																								
62	0.250 0.917 1.000 1.000 1.000 0.833 0.250 1.000 0.167 0.250 0.667 0.563 0.750 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
63	0.917 0.750 0.917 0.750 0.835 0.917 0.917 0.833 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
64	0.917 0.667 0.750 0.283 0.667 0.833 0.500																								
65	0.750 0.917 1.000 0.917 1.000 0.917 0.750 1.000 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167																								
66	0.250 0.917 1.000 1.000 1.000 0.750 0.250 1.000 0.167 0.250 0.667 0.563 0.750 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
67	0.167 0.917 1.000 1.000 1.000 0.750 1.000 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167																								
68	0.833 0.833 0.917 0.833 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
69	0.917 0.917 1.000 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
70	0.167 0.917 1.000 1.000 1.000 0.750 0.167 1.000 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167 0.167																								
71	0.333 0.917 1.000 1.000 1.000 0.750 0.333 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
72	0.667 0.333 1.000 0.917 0.833 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
73	1.000 0.833 0.917 0.833 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
74	0.917 0.917 1.000 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
75	1.000 0.833 0.917 0.833 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
76	0.667 0.833 0.917 0.833 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
77	0.833 0.833 0.917 0.833 0.917 0.917 0.917 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833 0.833																								
78	0.333 0.917 1.000 1.000 0.750 0.333 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
79	1.000 0.917 1.000 0.917 1.000 1.000 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917 0.917																								
80	0.917 0.917 1.000 0.917 1.000 1.000																								

Table 31. (Continued)

Strain	64	65	66	70	71	72	73	74	75	76	77	78	80	81	82	83	84	85	90	91	92	93	94
40	0.917	0.750	0.250	0.167	0.333	0.667	1.000	0.667	0.833	0.333	1.000	0.917	0.563	0.333	0.167	0.750	0.667	0.533	0.750	0.917	0.833	1.000	
41	0.667	0.917	0.917	0.917	0.917	0.833	0.667	0.833	0.917	0.833	0.667	0.833	0.917	0.750	0.917	0.917	0.833	0.667	0.917	0.917	0.833	0.667	
42	0.750	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	0.917	0.833	0.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
43	0.583	0.917	1.000	1.000	1.000	0.917	0.833	0.917	0.833	0.750	0.833	1.000	0.917	0.833	1.000	1.000	1.000	1.000	0.833	0.917	0.833	0.667	
44	0.667	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	1.000	0.917	0.833	0.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
45	0.483	1.000	0.750	0.750	1.000	1.000	1.000	1.000	0.917	1.000	0.917	0.833	1.000	0.917	0.917	0.750	0.750	0.917	1.000	0.917	0.667	0.750	
46	0.817	0.750	0.250	0.167	0.333	0.667	1.000	0.667	0.833	0.333	1.000	0.917	0.583	0.333	0.167	0.750	0.667	0.533	0.750	0.917	0.833	1.000	
47	0.500	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	0.917	0.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.833	0.750	0.917	1.000	
48	0.583	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	0.917	0.833	0.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
49	0.667	1.000	0.833	0.917	0.917	1.000	0.917	0.833	0.917	0.833	0.917	0.917	0.833	0.917	0.917	0.917	0.917	1.000	1.000	0.917	1.000	0.917	
50	0.667	0.917	0.667	0.833	0.750	1.000	1.000	0.833	1.000	0.750	0.833	1.000	0.833	0.833	0.750	0.833	0.833	0.917	1.000	0.917	0.667	0.750	
51	0.833	0.833	0.417	0.500	0.500	0.750	1.000	0.917	1.000	0.667	0.833	1.000	0.667	0.500	0.500	0.833	1.000	1.000	0.833	0.833	0.917	1.000	
52	0.833	0.667	0.250	0.167	0.333	0.667	1.000	0.833	1.000	0.583	0.750	1.000	0.750	0.500	0.333	0.167	0.667	0.917	0.833	0.750	0.917	1.000	
53	0.917	0.750	0.250	0.167	0.333	0.750	1.000	0.833	1.000	0.583	0.833	1.000	0.833	0.583	0.333	0.167	0.583	1.000	0.750	0.833	0.750	1.000	
54	0.833	0.833	0.917	0.750	0.917	0.833	0.667	0.750	0.667	0.833	0.750	0.833	0.667	0.833	1.000	0.917	0.917	0.917	0.917	1.000	0.750	0.667	
55	0.333	0.833	1.000	1.000	1.000	0.833	0.833	0.750	0.833	0.750	0.917	0.917	0.750	0.667	0.917	0.917	0.667	0.500	0.917	0.500	0.917	0.917	
56	0.167	0.750	1.000	1.000	1.000	0.750	0.750	0.750	0.750	0.667	0.833	0.917	0.667	0.500	0.917	1.000	1.000	0.917	0.500	0.917	0.667	0.667	
57	0.583	0.750	0.583	0.667	0.667	0.750	0.750	0.833	0.750	0.833	0.667	0.667	0.917	0.583	0.667	0.750	0.667	0.750	0.917	0.500	0.583	0.500	
58	0.500	1.000	1.000	1.000	1.000	0.917	1.000	0.917	0.833	0.750	0.833	0.667	0.833	1.000	0.917	0.750	0.917	0.667	0.917	0.750	0.667	0.917	
59	0.667	0.917	0.833	0.750	0.833	0.917	1.000	1.000	0.917	0.833	0.750	0.917	0.750	0.667	0.917	0.917	0.667	0.500	0.917	0.500	0.917	0.917	
60	0.833	0.583	0.500	0.417	0.583	0.583	0.833	0.750	0.833	0.583	0.667	0.417	0.833	0.750	0.667	0.500	0.583	0.333	0.750	0.667	0.500	0.583	
61	1.000	0.583	0.250	0.000	0.167	0.583	1.000	0.917	1.000	0.917	0.667	0.833	0.917	0.667	0.500	0.917	1.000	1.000	0.917	0.667	0.750	0.500	
62	0.917	0.500	0.333	0.250	0.417	0.583	0.833	0.667	0.833	0.500	0.583	0.333	0.833	0.750	0.417	0.17	0.250	0.500	0.17	0.750	0.667	0.917	
63	0.667	0.667	1.000	0.917	0.750	0.667	0.333	0.750	0.583	0.917	0.667	0.833	1.000	0.917	0.500	0.500	0.667	0.917	0.500	0.667	0.917	0.500	
64	0.000	0.750	0.917	1.000	1.000	0.917	1.000	1.000	0.917	0.833	1.000	0.917	0.500	0.917	1.000	1.000	0.917	0.500	0.917	1.000	1.000		
65	0.750	0.000	0.583	0.583	0.500	0.167	0.583	0.500	0.167	0.583	0.583	0.500	0.500	0.500	0.500	0.500	0.500	0.583	0.583	0.583	0.583	0.583	
66	0.917	0.583	0.333	0.250	0.250	0.833	1.000	0.667	0.833	0.500	0.667	0.333	0.500	0.333	0.167	0.833	0.250	0.667	1.000	0.633	0.583	0.667	
70	1.000	0.583	0.250	0.000	0.167	0.583	1.000	0.917	1.000	0.667	0.833	0.167	1.000	0.750	0.417	0.167	0.667	1.000	0.667	0.583	0.667	0.917	
71	1.000	0.500	0.000	0.167	0.500	1.000	0.917	1.000	0.917	0.833	1.000	0.917	0.500	0.917	1.000	1.000	0.917	0.500	0.917	1.000	1.000		
72	0.750	0.167	0.583	0.583	0.500	0.000	0.583	0.667	0.583	0.583	0.500	0.500	0.500	0.500	0.500	0.500	0.583	0.667	1.000	0.667	0.583	0.667	
73	0.750	0.583	1.000	1.000	1.000	0.917	0.583	1.000	0.917	0.833	0.500	0.500	0.333	1.000	0.917	0.500	0.500	0.583	0.583	0.583	0.583	0.583	
74	0.667	0.583	0.833	0.917	0.667	0.333	0.667	0.833	0.500	0.667	0.667	0.667	0.333	0.500	0.333	0.167	0.667	0.917	0.500	0.667	0.583	0.667	
75	0.750	1.000	1.000	1.000	1.000	0.917	1.000	0.917	1.000	0.667	0.833	0.917	0.667	0.500	0.917	1.000	0.917	0.667	0.500	0.917	1.000		
76	0.583	0.583	0.667	0.667	0.750	0.583	0.500	0.500	0.583	0.667	0.667	0.667	0.500	0.750	0.667	0.667	0.500	0.667	0.750	0.667	0.667	0.667	
77	0.750	0.333	0.667	0.833	0.750	0.583	0.333	0.333	0.583	0.667	0.667	0.667	0.583	0.667	0.667	0.667	0.583	0.667	0.667	0.667	0.667	0.667	
78	0.917	0.500	0.333	0.167	0.250	0.500	1.000	0.633	1.000	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.750	0.667	0.667	0.667	0.667	
80	0.667	0.500	1.000	1.000	0.500	0.000	0.533	0.667	0.500	0.333	1.000	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	
81	0.500	0.500	0.833	0.750	0.500	0.500	0.500	0.500	0.417	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
82	0.917	0.333	0.417	0.417	0.333	0.333	0.917	0.667	0.517	0.750	0.667	0.250	0.833	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	
83	1.000	0.500	0.000	0.167	0.000	0.000	0.917	1.000	0.667	0.750	0.750	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
84	1.000	0.500	0.250	0.000	0.167	0.583	1.000	0.667	0.517	0.917	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
85	0.917	0.333	0.667	0.667	0.667	0.667	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500		
86	0.500	0.500	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
87	0.500	0.500	1.000	1.000	0.667	0.667	0.333	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
88	0.917	0.333	0.417	0.417	0.333	0.333	0.917	0.667	0.517	0.750	0.667	0.250	0.833	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
89	0.667	0.500	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667	0.667		
90	0.917	0.333	0.417	0.417	0.333	0.333	0.917	0.667	0.517														

Table 32. The species composition in the stratum groups over all summer surveys, 1970-1981 (Years = number of years in which the species occurred, average/tow = average number of individuals per tow).

Species	Years	Average/ Tow	Percent
<b>West Fundy</b>			
Redfish	12	12.7	14.1
White hake	12	11.3	12.6
Haddock	12	10.1	11.3
Cod	12	9.8	10.9
Spiny dogfish	12	9.3	10.4
Thorny skate	12	5.8	6.5
Plaice	12	4.9	5.5
Witch	12	4.5	5.0
Longhorn sculpin	12	4.2	4.7
Pollock	12	2.6	2.9
Sea raven	12	2.0	2.9
Silver hake	12	2.6	2.9
Winter flounder	12	2.2	2.5
Ocean pout	12	2.0	2.2
Smooth skate	12	1.8	2.0
Little skate	8	1.1	1.3
Winter skate	9	0.6	0.7
Cusk	10	0.5	0.6
Angler	12	0.3	0.3
Wolfish	11	0.2	0.3
<b>South Fundy</b>			
Haddock	12	125.1	58.4
Cod	12	18.6	8.7
Longhorn sculpin	12	17.9	8.3
Winter flounder	12	15.0	7.0
Spiny dogfish	12	7.6	3.6
Sea raven	12	5.9	2.8
Pollock	12	2.7	1.2
Thorny skate	12	3.3	1.5
White hake	12	2.4	1.1
Redfish	12	2.4	1.1
Ocean pout	12	1.9	0.9
Plaice	12	2.0	0.9
Witch	12	1.6	0.8
Winter skate	10	1.3	0.6
Yellowtail	8	1.3	0.6
Wolfish	12	1.0	0.5
<b>West Banks</b>			
Haddock	12	91.0	65.7
Spiny dogfish	8	18.3	13.2
Cod	12	10.1	7.3
Yellowtail	12	3.9	2.9
Wolfish	12	2.8	2.0
Halibut	12	2.0	1.5
Thorny skate	12	1.8	1.3
Plaice	12	1.6	1.2
Longhorn sculpin	12	1.5	1.1
Pollock	9	1.3	0.9
<b>Central Plain</b>			
Redfish	12	227.5	61.6
Silver hake	12	68.0	18.4
Haddock	12	20.0	5.4
Plaice	12	15.0	4.1
Pollock	12	11.5	3.1
Witch	12	7.3	2.0
White hake	12	5.9	1.6
Argentine	11	4.7	1.3
Red hake	7	1.9	0.5

Table 32. (Continued)

Species	Years	Average/ Tow	Percent
<b>Outer Plains</b>			
Haddock	12	46.5	39.68
Silver hake	12	29.5	25.2
Argentine	12	12.3	10.5
Redfish	8	5.5	4.7
Plaice	12	5.2	4.5
Pollock	12	3.9	3.4
Cod	12	3.3	2.8
White hake	12	2.0	1.7
Yellowtail	11	1.9	1.6
Thorny skate	12	1.7	1.4
Cusk	12	1.2	1.1
Witch	9	0.9	0.8
Red hake	5	0.7	0.7
Angler	10	0.6	0.5
<b>East Banks</b>			
Yellowtail	12	119.0	32.6
Cod	12	67.1	18.4
Haddock	12	40.6	11.1
Plaice	12	40.3	11.0
Sand lance	12	39.4	10.8
Longhorn sculpin	12	18.7	5.1
Thorny skate	12	16.1	4.4
Silver hake	12	11.1	3.0
Winter skate	12	2.8	0.8
Winter flounder	12	2.2	0.6
Witch	12	1.8	0.5
<b>NE Mixed</b>			
Plaice	12	78.8	34.3
Redfish	12	48.6	21.2
Cod	12	35.3	15.4
Sand lance	5	31.1	13.5
Thorny skate	12	8.7	3.8
Witch	12	5.2	2.2
Silver hake	11	4.2	1.8
Haddock	12	3.3	1.4
Eelpouts	9	3.0	1.3
Vahl's eelpout	7	2.5	1.1
Yellowtail	12	2.2	1.0
White hake	12	1.4	0.6
Smooth skate	12	1.4	0.6
Wolfish	12	1.0	0.5
<b>Cabot Slope</b>			
Redfish	12	405.9	77.3
White hake	12	38.8	7.4
Witch	12	35.6	6.8
Longfin hake	12	23.7	4.5
Cod	12	5.6	1.1
Grenadier	12	4.0	0.8
Plaice	12	3.7	0.7
Thorny skate	12	3.4	0.6
<b>Shelf Slope</b>			
Redfish	12	152.6	61.0
Longfin hake	12	23.7	9.5
Silver hake	12	22.5	9.0
Argentine	12	10.8	4.3
White hake	12	10.1	4.0
Plaice	12	8.4	3.4
Witch	12	5.7	2.3
Thorny skate	12	3.2	1.3
Grenadier	12	2.5	1.0

Table 32. (Continued)

Species	Years	Average/ Tow	Percent
<b>Shelf Slope (Continued)</b>			
Cod	11	2.4	1.0
Smooth skate	9	1.6	0.6
<b>Basins</b>			
Redfish	12	209.0	62.0
Silver hake	12	81.6	24.2
White hake	12	17.5	5.1
Spiny dogfish	12	7.0	2.1
Argentine	12	5.5	1.6
Plaice	12	3.4	1.0
Pollock	11	3.1	0.9
Witch	12	2.3	0.7
Thorny skate	12	1.6	0.5

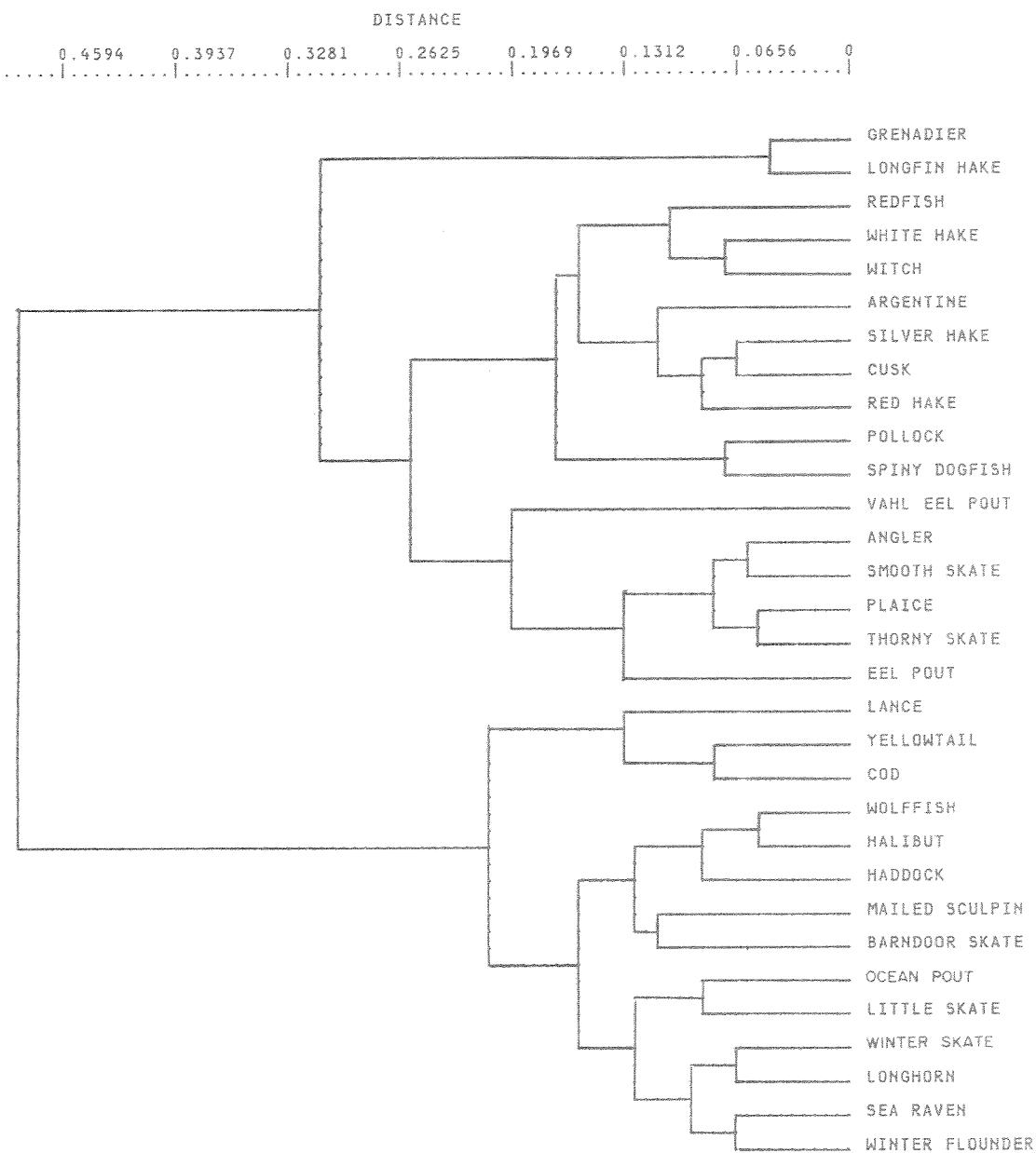


Fig. 109. The species dendrogram based on mean abundance of species in each stratum group in each summer survey.

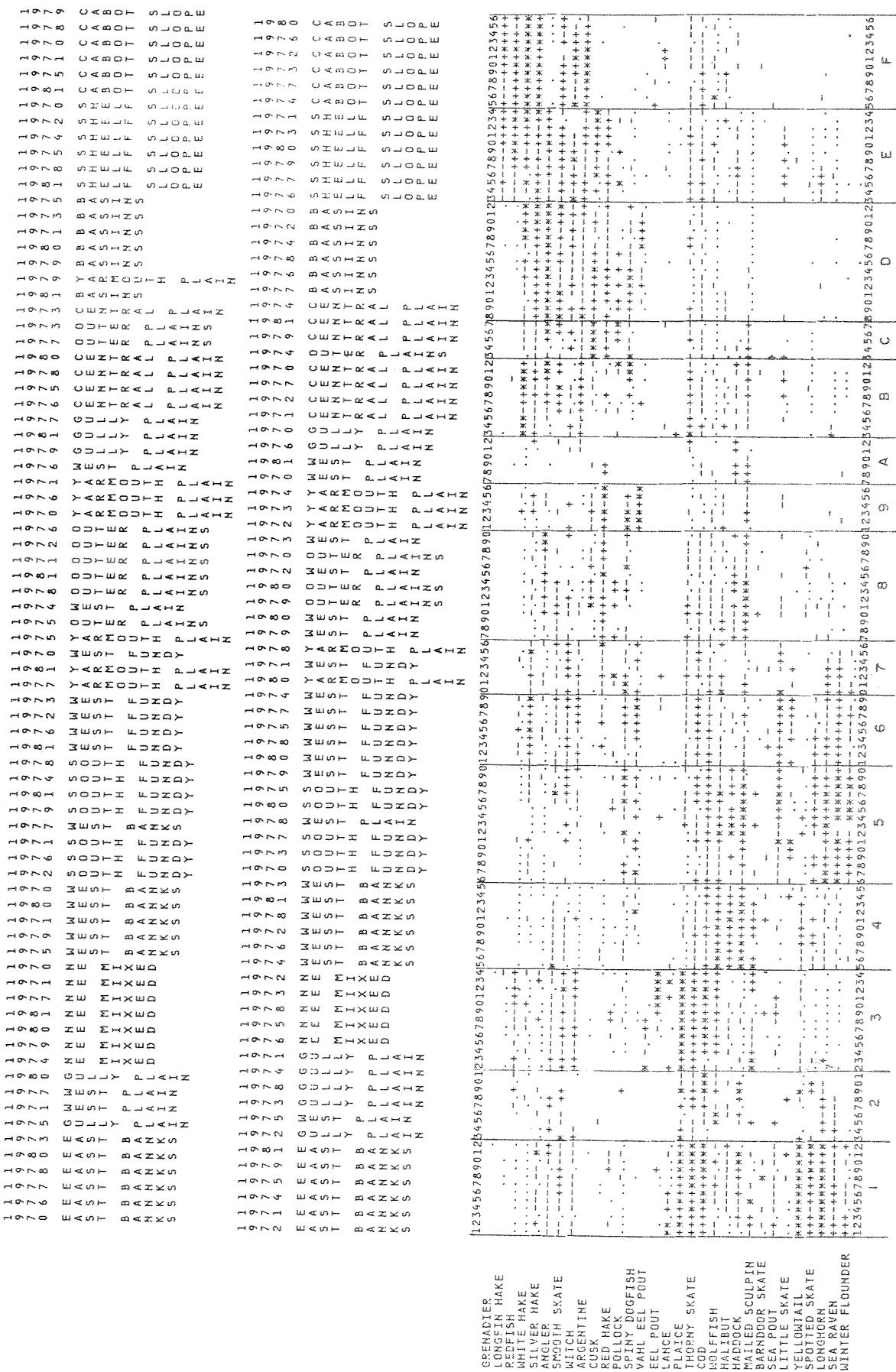


Fig. 110. The stratum/year groups (staggered across top) times species two-way table. The vertical lines break the table into groups identified by numbers and letters. These correspond to the codes in Figures 108, 111-114. The symbols within the table show abundance relative to the species mean: blank = 0; . = 0-0.5; - = 0.5-1.0; + = 1-2; \* = greater than 2.

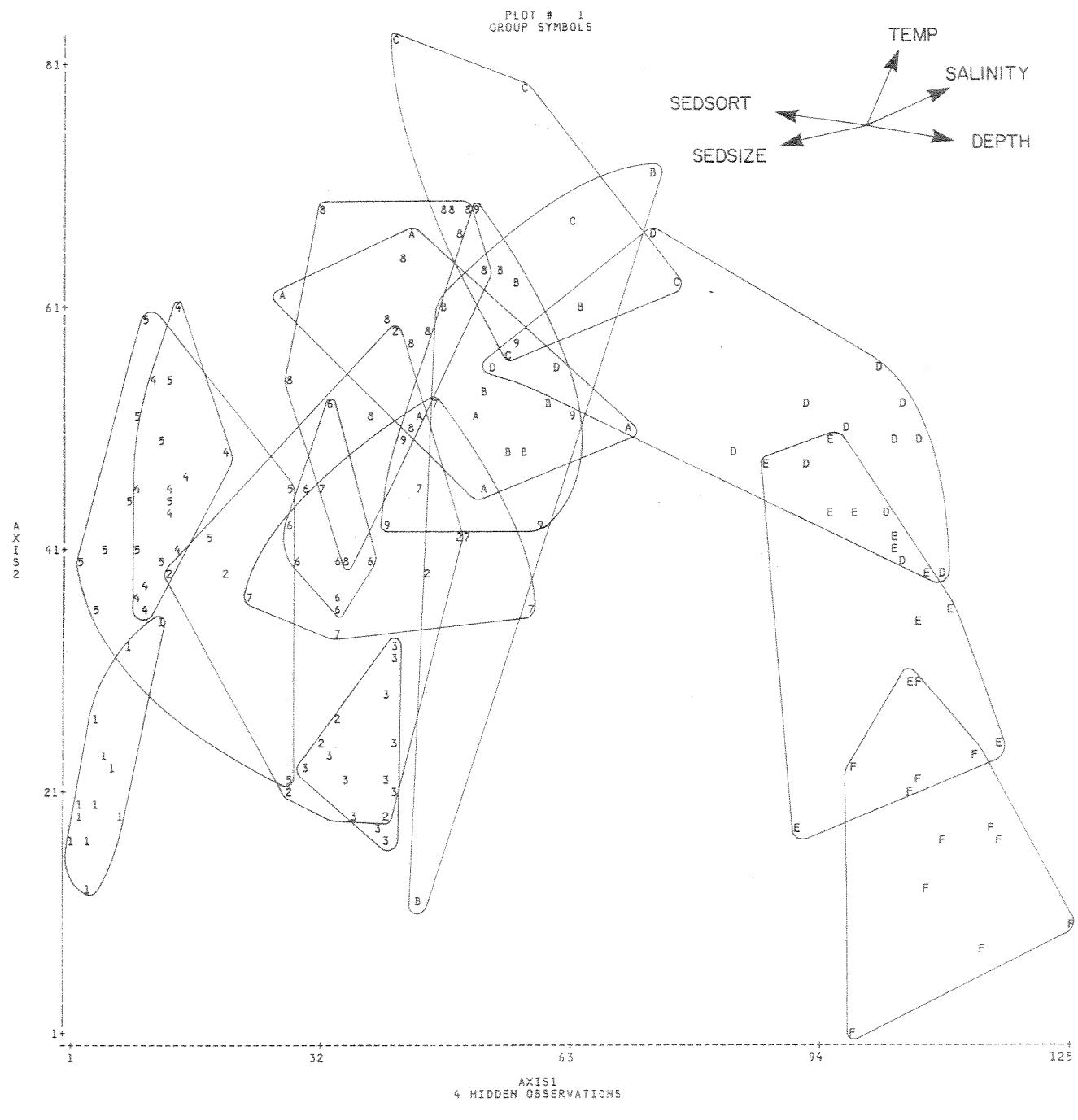


Fig. 111. The distribution of stratum/year groups in discriminant space defined by discriminant axes 1 and 2. The number/letter codes correspond to those in Figure 110.

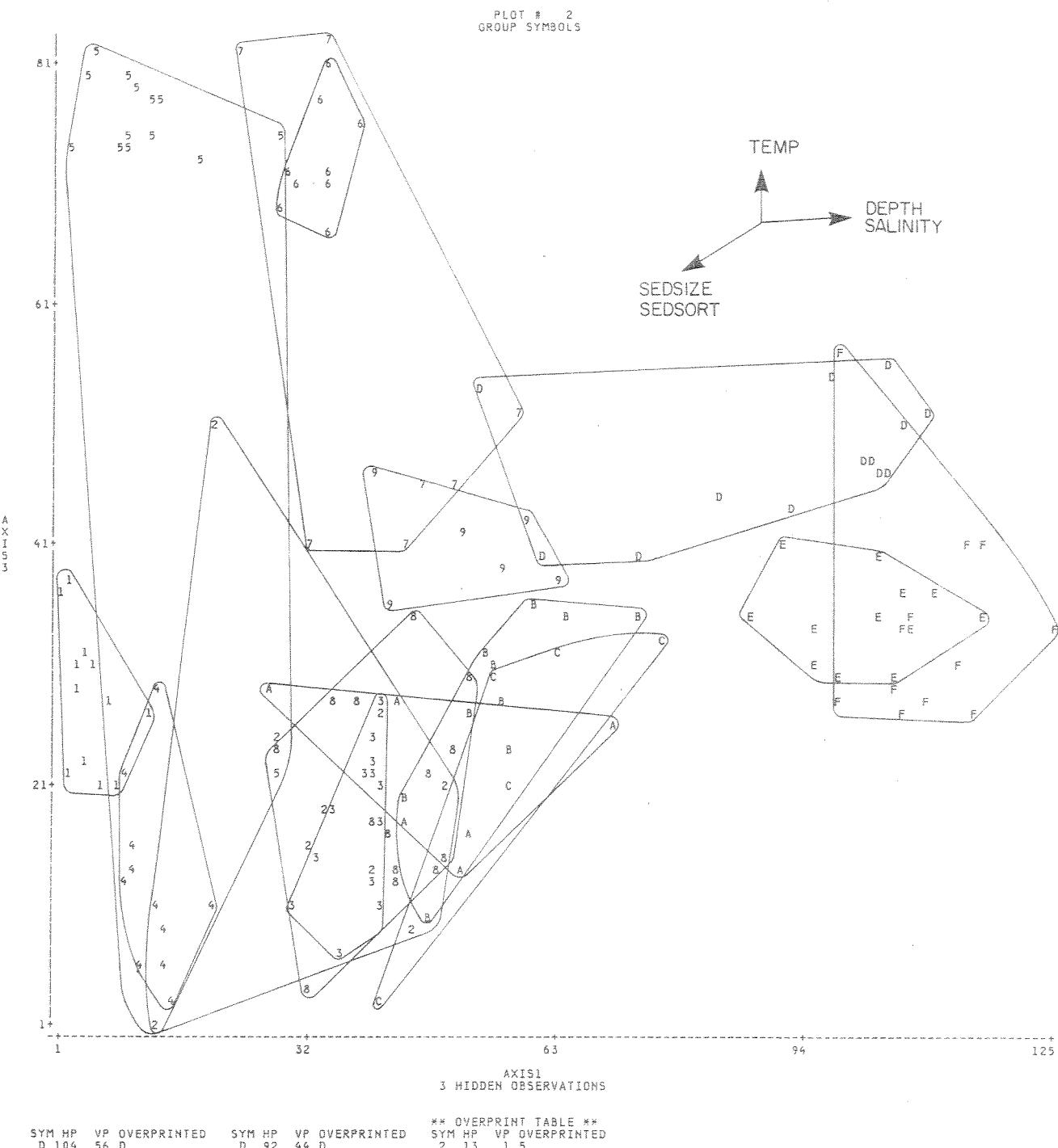


Fig. 112. The distribution of stratum/year groups in discriminant space defined by discriminant axes 1 and 3. The number/letter codes correspond to those in Figure 110.

unseparated in the discriminant space created by the first three axes.

Table 34. Coefficients of separate determination. These show the relative importance of each variable on each axis. The eigenvalues show the relative amounts of group separation accounted for by each axis.

Variable	Discriminant axes			
	Axis1	Axis2	Axis3	Axis4
1. Depth	36.3	16.4	0.5	17.6
2. Temp	0.2	24.4	20.5	0.4
3. Salinity	16.2	33.5	21.4	5.4
4. SEDSIZE	30.2	8.0	36.4	29.7
5. SEDSAND	3.8	4.1	4.4	29.8
6. SEDSORT	13.4	13.6	16.8	17.1
Eigenvalues	6.1	1.4	0.6	0.3
Percent of Group Separation	71.4	16.6	6.9	3.4

Stratum/year groups such as Cabot Slope, Shelf Slope, Basins, East Banks, and NE Mixed had the most distinct assemblages of species (two-way table), and also occupied the most distinct areas of the discriminant space. The Cabot Slope stratum/year group is characterized by relatively great depth, intermediate temperature, intermediate to high salinity, and small sediments. In relation to the Cabot Slope group, the other deep groups, the Shelf Slope and Basins groups, lie along gradients of slightly decreasing depth, increasing temperature, and increasing salinity, with no change in sediment size. The East Banks group is in an area of the space with the shallowest depth, low temperature, and low salinity, with the largest, most poorly sorted sediments. The NE Mixed group has shallow to intermediate depth, low temperature, low to intermediate salinity, and intermediate sized and sorted sediments. Environmental parameters within these groups are relatively stable.

Table 35. Separation of stratum/year groups in the environmental space defined by axes 1 to 3 of the WDA.

Main Group	Symbol				
	+ separate on axes 1 & 2				
East Banks	1	0	separate on axes 1 & 3		
Gully Plain	2	0			
NE Mixed	3	0			
West Banks	4	+	0		
South Fundy	5	0			
West Fundy	6	0	0	0	
Yarmouth Plain	7	0	0	0	0
Outer Plain	8	0	0	+ 0	0
Yarmouth Plain	9	0	0	0	0
West/Gully Plain	A	0	+ 0	+ 0	0
Central Plain	B	0	0	0	0
Outer/Central Plain	C	0	+ 0	0	0
Basins	D	0	0	0	0
Shelf Slope	E	0	0	0	0
Cabot Slope	F	0	0	0	0
	1	2	3	4	5
	6	7	8	9	A
	B	C	D	E	F

Most of the other groups are crowded into the left half of axis 1, and are spread out along axis 2. These are groups with a wide range of temperature, low to intermediate values of depth and salinity, and intermediate to high values of sediment size and sediment sorting. Within this region, the West Banks are separated from all

other groups except South Fundy, and Central Plains is well separated from Gully Plains, West Fundy, and Outer Plains.

Axis 3 separates several groups that overlap on axes 1 and 2. West Fundy and Gully Plain, for example, overlap completely along axes 1 and 2 yet are separated completely by axis 3. They have similar depth and salinity, but are separated on axis 3 by a combination of temperature, sediment size, and sediment sorting.

Further close inspection of Table 34 and Figures 111 and 112 will indicate which combinations of environmental variables are important in separating stratum groups. The two-way table (Table 110) can be used to identify each group's characteristic species assemblage, and then infer the physical habitat typical of each assemblage.

#### Principal Coordinates Analysis of Stratum/Year Groups Through Time

The purpose of this analysis is to determine if there is any major discrepancy between it and the discriminant analysis presented in the previous section. In principal coordinates analysis (PCOORD) the axes of the ordination space are defined by the species rather than the environmental variables as in the discriminant analysis.

The proportion of the total variability in the inter-sample distance matrix which is accounted for by the first five axes is shown in Table 36. The distributions of stratum/year groups in the space defined by the first three axes are shown in Figures 113 and 114. Each point corresponds to a single stratum/year group and the symbols are the same as used in the discriminant analysis. The position of each stratum year group in the principal coordinate space depicted is determined by its scores on axes 1 to 3.

Table 36. Principal coordinates analysis of stratum groups through time.

Axis	Eigenvalue	% of Variance	Cumulative
1	11.8	22.9	22.9
2	6.4	12.4	35.3
3	3.9	7.5	42.8
4	3.1	6.1	48.9
5	2.2	4.3	53.2

The degree of separation achieved for pairs of stratum groups on the first three axes is shown in Table 37. Of 105 possible combinations 85 are separate on axes 1 and 2, and 14 of the remaining 21 are separated on axes 1 and 3.

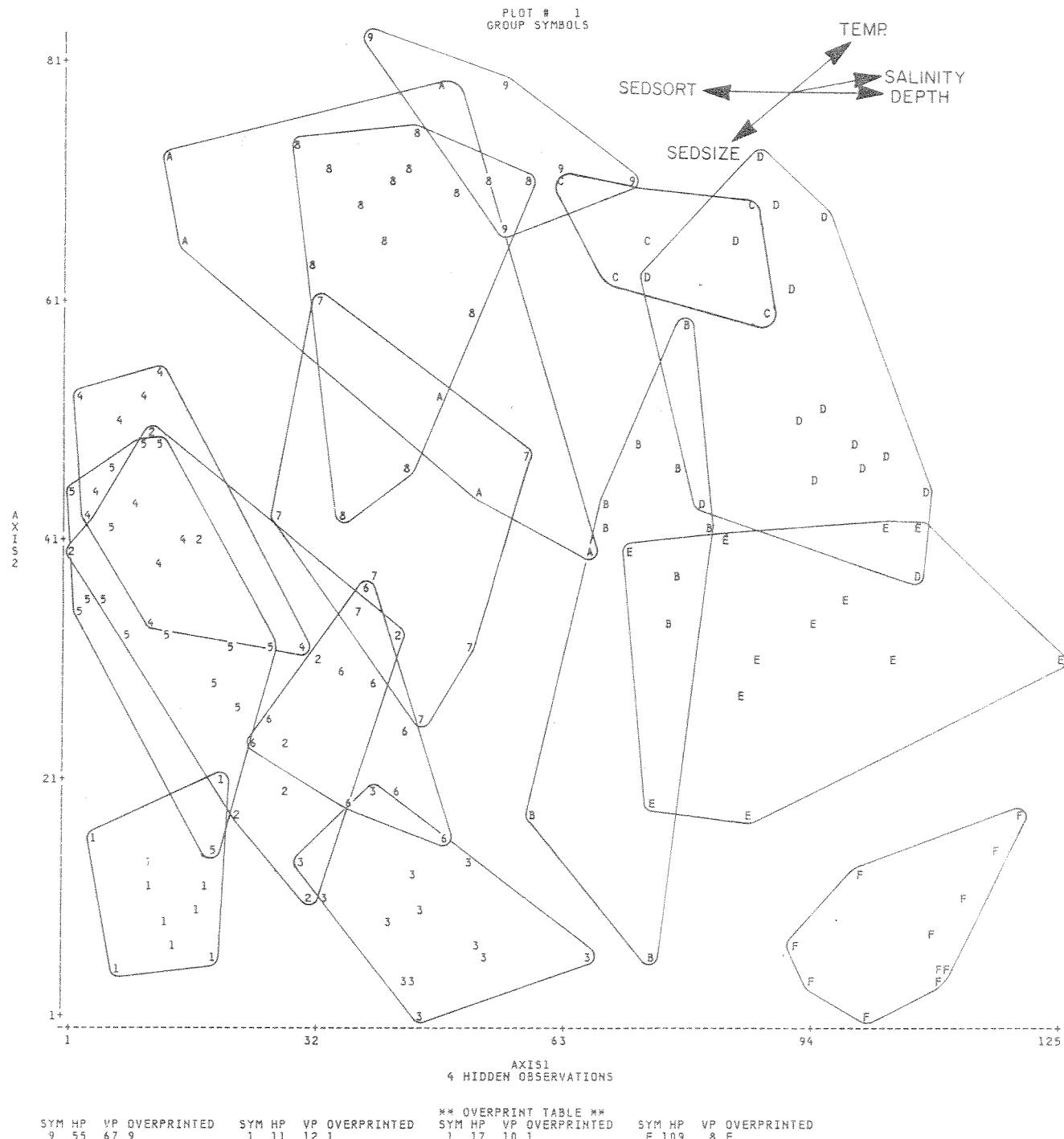


Fig. 113. The distribution of stratum/year groups in principal coordinate space defined by axes 1 and 2. The number/letter codes correspond to those in Figure 110.

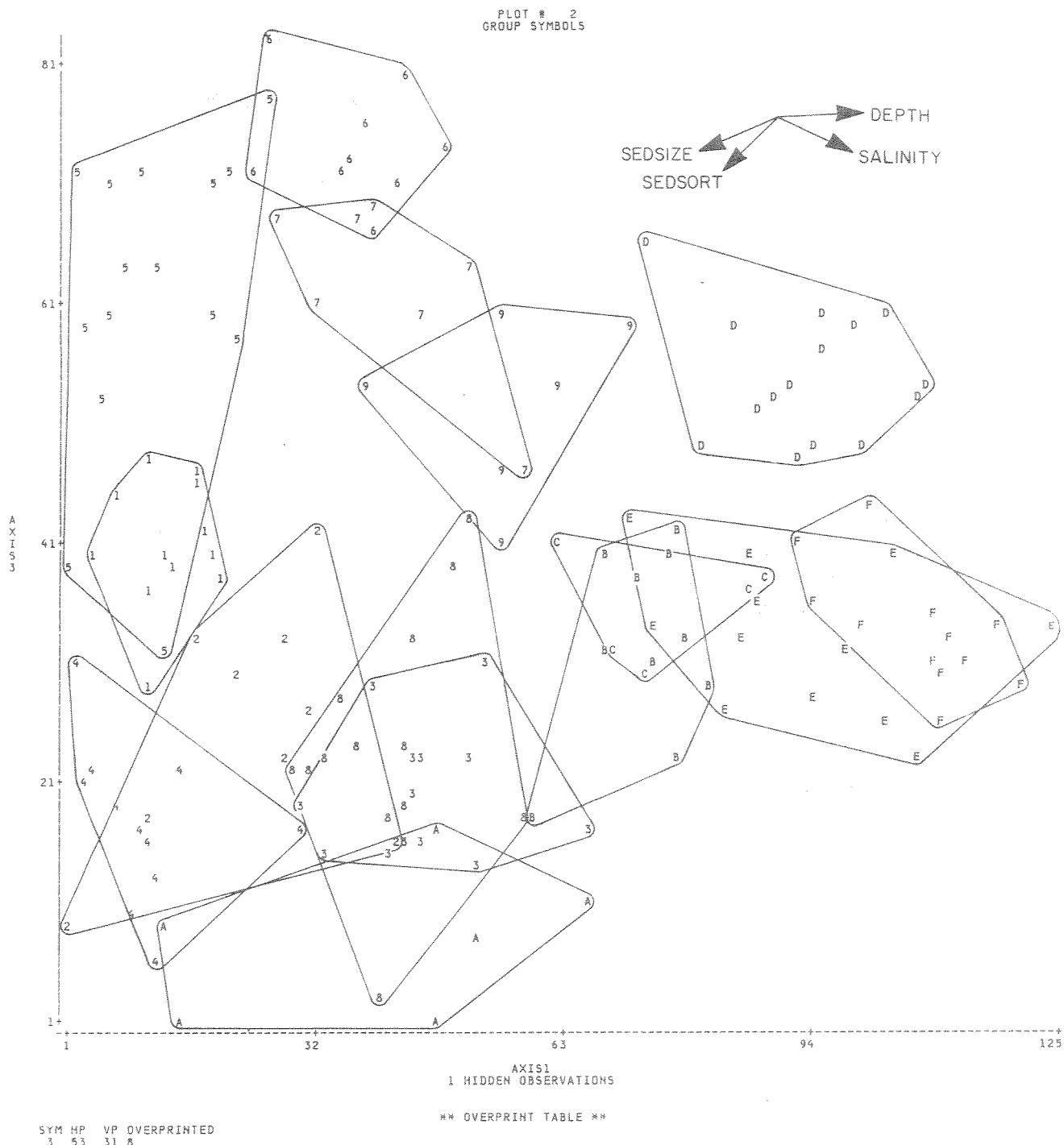


Fig. 114. The distribution of stratum/year groups in principal coordinate space defined by axes 1 and 3. The number/letter codes correspond to those in Figure 110.

Table 37. Separation of stratum year groups in the spaces defined by axes 1-3 of the principal coordinates analysis.

Main Group	Symbol
East Banks	1 + separate on axes 1&2
Gully Plain	2 0 0 separate on axes 1&3
NE Mixed	3 0
West Banks	4 0 0
South Fundy	5 0 0 0
West Fundy	6 0 0 0 0
Yarmouth Plain	7 0 0 0 0 0
Outer Plain	8 0 + + 0 0 0 0
Yarmouth Plain	9 0 0 0 0 0 0 +
West/Gully Plain	A 0 + + + 0 0 0 0
Central Plain	B 0 0 + 0 0 0 0 0 0
Outer/Central Plain	C 0 0 0 0 0 0 0 0 0 +
Basins	D 0 0 0 0 0 0 0 0 0 0
Shelf Slope	E 0 0 0 0 0 0 0 0 0 0 + 0
Cabot Slope	F 0 0 0 0 0 0 0 0 0 0 0 0 +
	1 2 3 4 5 6 7 8 9 A B C D E

The distribution of stratum groups in principal coordinate space is strikingly similar to their distribution in weighted discriminant space (Figures 111-114). On axis 1 in principal coordinate space the slopes and basins were well separated from the banks. Most of the separation within these two group types occurred on axes 2 and 3. The Bay of Fundy stratum groups separated most on axes one and three. These groups were also close to or overlapping the banks on axes 1 and 2 but were largely separated on axis 3. The least cohesive groups were comprised of stratum groups at intermediate depths, the plains.

The environmental gradients in both principal coordinates and discriminant space are similar to each other, and to these observed in individual surveys.

#### GENERAL DISCUSSION

The primary objectives of this study were to explore the spatial patterns of groundfish species and groups of species on the Scotian Shelf and in the Bay of Fundy. The two major parts of this study address these objectives from different viewpoints. In the first part the separate analysis of each survey allows the finest scale resolution of patterns of species distribution and environmental variables which is possible given the sampling design and gear. A preliminary assessment of how consistent these patterns are from year to year was made by comparing these results from survey to survey. The second major part attempts to address the question of temporal consistency or constancy more directly but loses spatial resolution as a result. We are aware that in aggregating sites within depth strata we may have cut across assemblage boundaries with the effect of blurring the natural spatial patterns. In the following discussions we will draw on the results from both parts as appropriate.

#### PHYSICAL VARIABLES

The interrelationships among the physical variables are evident from the discriminant coefficients and summary diagrams in discriminant space for each survey and the

analysis of stratum/year groups. As regards depth, temperature and salinity relationships at the bottom, the picture is consistent with that provided by previous studies (McLellan 1954a, McLellan 1954b). The distribution of stratum/year groups in environmental (discriminant) space, reflects the three layered structure of Scotian Shelf waters in summer (warm surface, cold intermediate, and warm deep layers), and the incursions of warm-saline slope-water onto the shelf in the region of the Scotian Gulf (Hachey 1937, Houghton *et al.* 1978)(Figure 111).

In summer the warm surface layer is seldom deep enough to affect bottom temperatures except in the shallowest areas of the banks. Consequently, the banks lie in the cool intermediate layers (Figure 111). However, the west banks are slightly deeper than the east banks, and thus lie closer to the deep warm layer. This, together with an along-shelf gradient of increasing temperature and salinity due to cross shelf mixing of slope water results in the complete separation of the east from the west banks on the temperature-salinity axis (Figure 111).

In the NE mixed area temperatures are similar to those on the neighboring banks but salinity is higher as would be expected owing to the greater depth. Other areas at similar, intermediate depths, all to the west, are warmer and for the most part more saline than the NE mixed area. This again reflects the influx of slope water over the middle of the shelf.

In deeper waters, slopes and basins, coolest temperatures are encountered in the Laurentian Channel, probably owing to the influence of the Labrador current. The Laurentian slope, the shelf slope and the basins lie along a gradient of increasing temperature and salinity, and decreasing depth.

The distribution of sediments on the Scotian Shelf have not previously been analysed as we have done. However, the tendency for sediment particle size to decrease with depth has frequently been noted (King 1971, Scott 1982). Our approach summarizes the important sources of variation in sediment type in three variables related to sediment particle size, sediment sorting and sand content and consequently overcomes the problem encountered by Scott (1982) in arranging the original sediment types in some meaningful order.

Previous analyses of the research vessel trawl surveys (1970-1979) on the Scotian Shelf have showed clearly that distribution of fishes is not random with regard to the environmental variables used in this study (Scott 1982a, 1982b). These analyses were carried out species by species and variable by variable, making it difficult to separate the relative effects of the variables in determining species' distributions. Although, we did not attempt a discriminant analysis among species using the environmental variables, the species relationships to these variables are clear from the plots of standardized abundances and species means in discriminant space for each year (Figure 103-106) and over all years (Figure

115). A further study of habitat selection is in progress and will attempt to quantify niche breadths and overlaps.

In this analysis, depth was consistently associated with the greatest proportion of biological change. This has also been observed by several previous studies of demersal fishes (e.g. Fager and Longhurst 1968, Day and Pearcy 1968, Wenner et al. 1980, Haedrich 1980, Overholtz 1982). In most instances there are a variety of factors associated with depth, for example light, salinity, turbulence, sediment type and pressure, which could cause biological change. In our study area, sediment particle size and salinity are associated with depth which itself could stand for several unmeasured factors. Temperature, whose relationship to depth is nonmonotonic, emerges as also being associated with a substantial proportion of biological change.

#### SPECIES GROUPS AND SPECIES INTERACTONS

One can seldom draw firm conclusions about species interactions by looking at their joint distributional patterns. The main problem with interpreting distributions is distinguishing the effects of species interactions from those of the abiotic environment. However, some indications about likely interactions worth exploring can be obtained in this way. The summer is likely to be a period of intensive feeding for most demersal fishes, therefore any effects of feeding interactions on distribution should be most visible at this time.

The two main types of interactions are predator-prey and competition. In the case of predator-prey relationships there should be considerable overlap in distribution. In the case of competition, distributions should be complementary (or reciprocal). However, some amount of overlap is to be expected at the edges of the distributions.

The study area is sufficiently large and heterogenous for there to be complete segregation among many pairs of species. However, the two-way tables from individual surveys show that this is seldom the case except at the extremes of the depth gradient. For example longfin hake and grenadier rarely encounter yellowtail flounder, longhorn sculpin or sea raven. Consequently, the possibility of interaction cannot be eliminated for many species pairs.

The likelihood of interaction between the members of any pair must be evaluated with reference to their biology. Closely related, or at least morphologically similar, species are the most likely candidates for competitive interactions. One example of complementary but overlapping distributions is the species pair yellowtail and winter flounder. These two flatfishes occur in the same species group indicating that they frequently occur together. The two way tables for each survey suggest that when one is abundant the other is not. This is evident also in Figure 110, which indicates that yellowtail does best on the banks, whereas winter flounder does best in the Bay of Fundy and off SW Nova Scotia. Figures 103 to 105 indicate that the species inhabit similar depths

but partition the habitat along the temperature gradient, with winter flounder predominating in warmer waters. The taxonomic and, consequently morphological similarity of these species would make them likely competitors. Stomach content data (Langton and Bowman 1981) show that these species do eat similar kinds of prey organisms. However, there are differences in the details of their diet which could be due either to distributional differences, or to differences in feeding adaptation. Closer examination of the food of coexisting individuals could distinguish between these possibilities.

An unexpected result was the association, though rather loose, between haddock and halibut. The two way tables indicate that halibut always occur where there are haddock, but not vice versa. This is suggestive of a predator-prey interaction.

#### Spatial Pattern and Its Temporal Persistence

The question of cluster validity is a difficult one (Dubes and Jain 1980). It is possible to consider clusters at any distance level. In this study where the samples are spatially aggregated the continuum of distance levels represents a continuum of spatial scales. The spatial scale of interest will depend on the objectives of the study. In this study we have concentrated on large to medium scale patterns, relative to the study area. Our primary criterion for cluster validity has been interpretability e.g. whether we could "see" biological differences between clusters in the two-way tables, and how well the clusters could be discriminated using environmental variables.

Pattern emerges at two interpretable scales. The largest scale pattern results in a division of the shelf into a deep water region including basins, an eastern region and a Western/Fundy region. Although the Fundy region is primarily associated with the western shelf, it is occasionally more similar to the Sable Island area of the eastern shelf. Extension of this approach to a larger scale would require a biogeographic consideration of the relationship of the Scotian Shelf to neighboring shelf areas.

At a smaller scale there was consistent discrimination between banks and plains within the larger areal units discussed above. Similarly, there appeared to be consistent discrimination between the north west areas of the Bay of Fundy and those in the south, adjacent to Nova Scotia. In the deep water, the basins, slope of the Laurentian Channel (Cabot Slope) and the slope of the shelf itself were frequently distinguishable.

Although the same broad spatial units (deep, eastern shelf, Sable-Western Banks, western shelf, Fundy) showed up year after year in the individual surveys as being relatively homogeneous within years, it was not possible to conclude from these analyses that they were similar through time. This, however, was demonstrated by the analysis of stratum groups through time in which several stratum groups proved to be more similar to themselves over time than to any other stratum groups at any

time. The stratum groups which were most distinctive in this regard were the deepest (the slopes and basins), the shallowest (the east and west banks, and the Bay of Fundy), and the area of mixed depths on the north east shelf extending north around Cape Breton. The medium depth stratum groups, or plains as we termed them, overlapped each other extensively, and overlapped the deep and shallow strata to a lesser extent.

#### RELEVANCE TO FISHERY MANAGEMENT OBJECTIVES

As we suggested earlier, natural groupings of species which are persistent through time may be relevant to fishery management. Even if biological interactions among the species are of no consequence in producing the patterns, the fact that there are areas of relatively homogenous species composition may be of value in allocating effort with the objective of optimising yield from mixed catch fisheries given the constraints of individual species quotas (Brown et al. 1979, Murawski et al. 1983). A study such as this one would be one of several aspects to be considered in developing a management scheme with the above objective. Other aspects would include the fishing patterns of the fleet, pragmatics of data collection and surveillance, and stock structure and migration.

A further possibility is that the pattern observed reflects some dynamical aspects of the fish community. Groups of fishes which occur together may be trophically linked. Tyler et al. (1982) have discussed a management approach based on assemblage production units (APUs) each of which is a trophically linked species group. They define an assemblage region as spatial unit within which one or more biological units, APUs, are represented.

The pattern of distribution of species among stratum/year groups in Figure 110 is compatible with the APU approach as presented by Tyler et al. (1982). Indeed, their formulation was partly based on analysis of research trawl catches on the Scotian Shelf in the 1960s (Knight and Tyler, 1973). The stratum groups in this analysis were defined on the basis of homogeneity of species composition within years. On the other hand, the stratum/year groups reflect homogeneity of species composition throughout time (Figure 110). In this presentation the stratum groups would be the equivalent of assemblage regions and the species groups within stratum groups would be the APUs. This would be assuming some functional significance of the groupings. Once again, the designation of assemblage regions and APUs would have to be made with reference to fishing patterns, stock boundaries, etc..

This approach assumes firstly that the APU is a functional unit with emergent properties which must be considered in managing the unit, and secondly that APUs with the same species composition in contiguous assemblage regions interact only weakly. To satisfy the latter assumption for the Scotian Shelf it would probably be necessary to define relatively large assemblage regions, such as: north eastern shelf, south western shelf, and Bay of Fundy.

These are rather similar to the existing single species NAFO boundaries. In the eastern half of the shelf one would not, for example, separate the banks from the area of mixed depths, because the cod/plaice group is present in both; the banks are distinguished only by the presence of the yellowtail/sea raven group in addition to the cod/plaice group.

In theory, by considering APUs within assemblage regions as the practical management units, there should be a significant reduction in the management error due to species interactions which are unaccounted for. This "multispecies" management structure would be analogous to the single species approach inasmuch as APUs would replace species and assemblage regions would replace stock boundaries. Single species assessments are critically dependent upon accurate definition of stock boundaries and upon realistic models of population dynamics. Similarly, the "multispecies" approach will require accurate definitions of assemblage regions and realistic models of community dynamics.

This study has made a preliminary step towards the definition of assemblage regions and species groupings on the Scotian Shelf, and in the Bay of Fundy. It provides a context within which existing "multispecies" models could be tried using existing data, or for modifying existing data collection procedures in order to obtain appropriate data. This process will lead to progressively more appropriate definition of the "system" until there is sufficient information to either reject the approach or proceed with practical application.

#### CONCLUSIONS

- 1) Natural groups of sites (trawl sets) occupy the same major areas year after year: Northeast shelf and Banquereau; Sable Island and Western Banks; slopes, basins and Scotian Gulf; western shelf; and Bay of Fundy. The interrelationships among these, as regards their assemblages of demersal fishes, are relatively consistent, but Bay of Fundy is most similar to the western shelf in some years and to Sable Island and Western Banks in others.
- 2) The environmental gradients along which the site groups are best separated are similar in all years. Depth, sediment particle size and salinity, usually in that order, comprised the axis which gave most of the group separation in each year. Temperature and salinity comprised the second most important axis.
- 3) The orientation of the species means with regard to the physical environment was similar in all years.
- 4) Groups of strata which were similar in species composition within years also grouped together through the 12 year period, further demonstrating the temporal consistency of the spatial patterns.

- 5) In general these spatio temporal groups were distinct in terms of their average environmental characteristics. The banks and the deep groups were most cohesive in this respect. This suggests that fish distribution is strongly environmentally aligned. However, it was not possible to distinguish the relative importance of the physical environment and biological interaction to groundfish distributional patterns.
- 6) The temporal persistence of the observed spatial patterns may be of value in managing technological interactions. In regard to defining functional assemblages of biologically interacting species, the units defined would be a starting point for further investigation of assemblage dynamics.

#### ACKNOWLEDGEMENTS

The data which are analysed in this report represent 12 years of diligent attention to detail on the part of a very large number of Marine Fish Division personnel. No sense of this is conveyed in the technical descriptions of the conduct of the more than 36 cruises and the subsequent coding, editing and custodianship of the resulting data. It is only here, tucked away at the end of this document that we are able to attempt to convey our admiration for the foresight of the scientists who planned this data time series, and for the diligence and dedication of the people who actually collected this information and brought it to the point where we could use it.

We also wish to thank some people more directly involved in the preparation of this report: Gary Paul for organizing and overseeing the preparation of the multitude of figures; Laurie Dauphinee and Keven Warner for drafting; Pat Simpson, Fran Holyoke and Mary Mingus for data preparation, and Valerie Myra for word-processing. Comments on the MS by Don Waldron and Ian Perry were most useful.

#### REFERENCES CITED

- Austin, M.P. 1976. On non-linear species response models in ordination. *Vegetation* 33: 33-41.
- Austin, M.P. and L. Belbin. 1982. A new approach to the inverse classification problem in floristic analysis. *Aust. J. Ecol.* 7: 75-89.
- Beals, E.W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. *The Wilson Bulletin* 72: 156-181.
- Beals, E.W. 1973. Ordination: mathematical elegance and ecological naivete. *J. Ecol.* 61(1): 23-35.
- Bigelow, H.B. 1927. Physical oceanography of the Gulf of Maine. U.S. Dep. Commer. Bur. Fish. Bull. 40: 511-1027.
- Bloom, S.A. 1981. Similarity indices in community studies: Potential pitfalls. *Mar. Ecol. Prog. Serv.* 5: 125-128.
- Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Brown, B.E., J.A. Brennan, and J.E. Palmer. 1979. Linear programming simulations of the effects of bycatch on the management of mixed species fisheries of the northeastern coast of the United States. *Fish. Bull.* 76: 851-860.
- Clifford, H.T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press: 229 pp.
- Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52(4): 567-576.
- Cooley, W.W. and P.R. Lohnes. 1971. Multivariate data analysis. John Wiley and Sons, New York,. 364 pp.
- Day, D.S. and W.G. Pearcy. 1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. *J. Fish. Res. Board Can.* 25: 2665-2675.
- Doubleday, W.G. 1981(ed.). Manual on groundfish surveys in the Northwest Atlantic. NAFO Sci. Coun. Studies. 2: 55 p.
- Drapeau, G. and L.H. King. 1971. Surficial geology of Yarmouth-Browns Bank map area. *Geol. Surv. Can. Pap.* 72-24, 6 p.
- Dubes, R. and A.K. Jain. 1980. Clustering methodologies in exploratory data analysis. *Advances in Computers.* 19: 113-229.
- Fader, G.B., L.H. King, and H.W. Josenhans. 1982. Surficial geology of the Laurentian channel and the western Grand Banks of Newfoundland. *Geol. Surv. Can. Pap.* 81-22, 37 p.

- Fader, G.B., L.H. King, and B. MacLean. 1977. Surficial geology of the eastern Gulf of Maine and Bay of Fundy. *Geol. Surv. Can. Pap.* 76-17, 23 p.
- Fager, E.W. and A.R. Longhurst. 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. *J. Fish. Res. Board Can.* 25: 1405-1421.
- Green, R.H. and G.L. Vascotto. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. *Water Res.* 12: 583-590.
- Gabriel, W.L. and A.V. Tyler. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. *Mar. Fish. Rev.* 1980: 83-88.
- Gauch, H.G. Jr. and W.M. Scruggs. 1979. Variants of polar ordination. *Vegetatio* 40: 147-153.
- Haedrich, R.L., G.T. Rowe, and R.T. Polloni. 1980. The megabenthic fauna of the deep sea south of New England, USA. *Marine Biology*. 57: 165-179.
- Halliday, R.G. and W.G. Doubleday. 1976. Catch and effort trends for the finfish resources of the Scotian Shelf and estimates of the maximum sustainable yield of groundfish (except silver hake). *ICNAF Sel. Pap.* 1: 117-128.
- Halliday, R.G. and P.A. Koeller. 1981. A history of Canadian groundfish trawling surveys and data usage in ICNAF Divisions 4TVWX. *Can. Spec. Publ. Fish. Aquat. Sci.* 58: 27-41.
- Heezen, B.C., M. Tharp, and M. Ewing. 1959. The floors of the oceans; Part 1, the North Atlantic. *Geol. Soc. Amer. Spec. Pap.* 65: 122 p.
- Hobson, E.S. and W.H. Lenarz. 1977. Report of a colloquium on the multispecies problem, June 1976. *Mar. Fish. Rev.* 39(9): 8-13.
- Houghton, R.W., P.C. Smith, and R.O. Fournier. 1978. A simple model for cross-shelf mixing on the Scotian Shelf. *J. Fish. Res. Board Can.* 325: 414-421.
- King, L.H. 1967. Use of a conventional echo sounder and textural analyses in delineating sedimentary facies. *Can. J. Earth Sci.* 4: 691-708.
- King, L.H. 1970. Surficial geology of the Halifax-Sable Island map area. *Mar. Sci. Pap.* 1, 16 p.
- Knight, W. and A.W. Tyler. 1973. A method for compression of species association data by using habitat preferences, including an analysis of fish assemblages on the southwest Scotian Shelf. *Fish. Res. Bd. Can. Tech. Rept.* 402. 15 pp.
- Langton, R.W. and R.E. Bowman. 1981. Food of eight northwest Atlantic pleuronectiform fishes. *NOAA Tech. Rep. NMFS SSRF - 749:* 16 p.
- MacLean, B. and L.H. King. 1971. Surficial geology of the Banquereau and Misaine Bank map-area. *Geol. Surv. Can. Pap.* 71-52, 19 p.
- MacLean, B., G.B. Fader, and L.H. King. 1977. Surficial geology of Canso Bank and adjacent areas. *Geol. Surv. Can. Pap.* 76-15, 11 p.
- McLellan, H.J. 1954a. Bottom temperatures on the Scotian Shelf. *J. Fish. Res. Board Can.* 11: 404-418.
- McLellan, H.J. 1954b. Temperature-salinity relations and mixing on the Scotian Shelf. *J. Fish. Res. Board Can.* 11: 419-430.
- Mercer, M.C. 1982 (ed.). Multispecies approaches to management advice: workshop report. *Can. Spec. Publ. Fish. Aquat. Sci.* 59: 1-15.
- Murawski, A.W. 1983 MS. Mixed species yield-per-recruitment analyses accounting for technological interactions. *Can. J. Fish. Aquat. Sci.* 41: 897-916.
- Murawski, S.A., A.M. Lange, M.P. Sissenwine, and R.K. Mayo. 1984. Definition and analysis of multispecies otter-trawl fisheries off the northeastern coast of the United States. *J. Cons. Int. Explor. Mer.* 41: 13-27.
- Orloci, L. 1975. Multivariate analysis of vegetation research. The Hague: Dr. W. Junk b.v., Publishers. 276 pp.
- Overholtz, W.J. 1982. Long-term temporal perspectives for the demersal fish assemblages of Georges Bank with implications for management and modeling. Ph.D. Thesis, Oregon State University. 243 pp.
- Scott, J.S. 1982a. Depth, temperature, and salinity preferences on common fishes on the Scotian Shelf. *J. Northw. Atl. Fish. Sci.* 3: 29-39.
- Scott, J.S. 1982b. Selection of bottom type by groundfishes of the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 39: 943-947.
- Sinclair, M., J.J. Maguire, P. Koeller, and J.S. Scott. 1984. Trophic dynamic models in light of current resource inventory data and stock assessment results. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* 183: 269-284.
- Smith, P.C. 1979. A proposal to study the circulation off Cape Sable, Nova Scotia. Bedford Institute of Oceanography Report, BI-R-79-5: 107 p.
- Smith, R.W. 1976. Numerical analysis of ecological survey data. Ph.D. thesis, Univ. of S. Calif., Los Angeles. 401 pp.

- Smith, R.W. 1981. The re-estimation of ecological distance values using the step-across procedure. EAP Technical Report No. 2. Ecological Data analysis, 1151 Avila Dr., Ojai, CA 93023.
- Smith, R.W. and D.E. Guggenheim MS. The measure of sample distinctness in ecology. In preparation.
- Sutcliffe, W.H. Jr., R.H. Loucks, and K.F. Drinkwater. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. *J. Fish. Res. Board Can.* 33: 98-115.
- Swan, J.M.A. 1970. An examination of some ordination problems by use of simulated vegetational data. *Ecology* 51: 89-102.
- Tyler, A.V., W.L. Gabriel, and W.J. Overholtz. 1982. Adaptive management based on structure of fish assemblages of northern continental shelves. *Can. Spec. Publ. Fish.* 59: 149-156.
- Uchupi, E. 1968. Atlantic continental shelf and slope of the United States - Physiography. *Geol. Surv. Pref. Pap.* 529-C. 30 p.
- Wenner, C.A., C.A. Barans, B.W. Stender, and F.H. Berry. 1980. Results of MARMAP otter trawl investigations in the south Atlantic Bight. V. Summer, 1975. South Carolina Marine Resources Center Tech. Rept. No. 45: 57.
- Whittaker, R.H., and W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. (II.) A gradient analysis of the south slope. *Ecology* 46: 429-452.
- Williams. 1971.

Williamson, M.H. 1978. The ordination of incidence data. *J. Ecol.* 66: 911-920.

## APPENDIX A: THE CALCULATION OF $B_{ijk}$ AND $W_{ijk}$

### CALCULATION OF $B_{ijk}$

#### General Overview

$B$  (for breadth) is a factor which equalizes the input to  $Q$  of species with different slopes or rates of change along a gradient of biological change.  $B$  is inversely proportional to slope when data have been standardized by species maximum, since a narrow breadth is usually associated with a steeper slope, and vice versa (Figure 6).

For each inter-sample comparison, a breadth measure for each species along a number of polar ordination axes (see Appendix B) is calculated. It is assumed that the ordination axes follow the major gradients of biological change in the survey area. The overall breadth value for the species is the weighted average of the breadths along all the ordination axes. The weights used in the average are proportional to the degree to which the two samples being compared extend into the ordination dimension in question.

#### Breadth Along a Single Ordination Axis

First we discuss the calculation of breadth along a single ordination axis. The method used depends on whether the samples being compared are on the same side of the species peak or whether they are on opposite sides of the peak.

#### Breadth When Both Samples Are on the Same Side of Species Peak

Figure A1a shows the parameters used to calculate breadth along an axis when both samples are on the same side of the species peak.  $S_{ap}$  is the score of the sample which contains the peak importance value for the species. If more than one sample contains the same peak value, the average score for all such samples is used.  $S_{ai}$  and  $S_{aj}$ , the scores for samples  $i$  and  $j$ , respectively, on axis  $a$ , are used to determine if the samples  $i$  and  $j$  are on the same side of the peak score ( $S_{ap}$ ), and if so, on which side they are found. Of all samples containing the species in question,  $S_{ar}$  is the score of the sample with the most extreme score on the pertinent side of the peak score. For example, in Figure A1a,  $S_{ar}$  is the sample with the lowest score, since both samples  $i$  and  $j$  are to the left of the peak. If both samples were to the right of the peak, the highest score would be used.

When both samples are on the same side of the species peak along axis  $a$ ,

$$bijka = |S_{ap} - S_{ar}|.$$

Note that  $bijka$  is the breadth or extent of the pertinent half of the species curve along the ordination axis. Only the half of the curve on which samples being compared are found is relevant here.

As discussed earlier, we are calculating breadth in order to get a measure of the general

rate at which the standardized species importance values are expected to be changing in the area of the comparison. We are purposely using an indirect means of estimating this rate of change. More direct methods would make the contribution of the X difference to the overall distance wholly dependent on  $|S_{ai}-S_{aj}|$ . For example, the actual rate of change (slope) between samples i and j for species k is:

$$\frac{|X_{ki}-X_{kj}|}{|S_{ai}-S_{aj}|}$$

Assuming unidimensional data, we would adjust the X difference for the rate of change by multiplying the X difference by the reciprocal of the slope (note that  $B_{ijk}$  is inversely proportional to the slope). The adjusted X difference would thus be:

$$\frac{1}{\text{slope}} \times X \text{ diff.} = \frac{|S_{ai}-S_{aj}|}{|X_{ki}-X_{kj}|} \times |X_{ki}-X_{kj}| = |S_{ai}-S_{aj}|.$$

Notice that the X difference cancels out and only the difference in scores remains. At this point we do not want the ordination space to directly determine the values of Q. Instead, our intention is that the ordination space supply a general orientation for an optimal use of the species importance values in the X difference.

#### Breadth With Samples on Opposite Sides of Species Peak

When the samples being compared are on opposite sides of the peak along a dimension or axis, the X difference will tend to decrease as one of the samples becomes more biologically dissimilar from the other. For example, in Figure A2a, note that if sample j were to be moved to the left (further from sample i), the X difference ( $|X_{ki}-X_{kj}|$ ) would decrease, even though the biological change is increasing. To compensate for the decreasing X difference, the breadth value must be increased. Note that the slope of the curve on the left side of the peak determines how rapidly the X difference decreases. The steeper the slope, the faster the decrease. Therefore, we would want the increase in breadth to be proportional to the slope. This can be accomplished by using  $|S_{aj}-S_{ar}|$  as the breadth. The effect of slope on  $|S_{aj}-S_{ar}|$  can be seen by comparing Figures A2a and A2b, where only the left hand slope differs.

To calculate  $|S_{aj}-S_{ar}|$ , note in Figure A2a that triangles  $r_{Bj}$  and  $r_{Bj}$  are similar. Thus, for species k,

$$\frac{X_{kj}}{|S_{aj}-S_{ar}|} = \frac{1}{|S_{aj}-S_{ar}|},$$

where  $X_{kj}$  is the transformed, maximum standardized species importance value for species k in sample j. With rearranging,

$$|S_{aj}-S_{ar}| = \frac{|S_{aj}-S_{ar}|}{X_{kj}}.$$

If  $X_{kj} > X_{ki}$ , then

$$b_{ijk} = \frac{|S_{aj}-S_{ar}(i)|}{X_{kj}},$$

while, if  $X_{kj} < X_{ki}$ , then

$$b_{ijk} = \frac{|S_{aj}-S_{ar}(j)|}{X_{ki}}.$$

Considering only samples in which species K is found,  $S_{ar}(i)$  is the score of the sample which has the extreme score on species i's side of the peak along axis a.  $S_{ar}(j)$  is analogous, but on species j's side of the peak. In the event that  $X_{kj} = X_{ki}$ ,  $B_{ijk}$  will be calculated as if  $X_{kj} > X_{ki}$  if  $S_{aj}$  is closer to  $S_{ap}$  than is  $S_{ai}$ . If  $S_{aj}$  is closer to  $S_{ap}$ , then  $b_{ijk}$  will be calculated as if  $X_{kj} < X_{ki}$ .

#### Weighting of Breadth Along Each Axis

An overall weighted-average breadth is finally calculated for each species. In the average, the breadths calculated on each axis are weighted by the extent to which the samples in question extend into that dimension of the ordination space. For example, in Figure Alb, samples i and j are more distant in position along axis 1 when compared with axis 2. Since the slope of the curve in the axis 1 direction is most relevant, the breadth along this axis will get much higher weight than that for axis 2. The extent to which two samples differ along axis a is simply

$$|S_{ai}-S_{aj}|,$$

where  $S_{ai}$  and  $S_{aj}$  are the ordination scores of samples i and j on axis a. In summary, the final weighted average breadth for a species in a particular sample comparison is

$$B_{ijk} = \frac{\sum_{a=1}^n |S_{ai}-S_{aj}| b_{ijk}}{\sum_{a=1}^n |S_{ai}-S_{aj}|}.$$

#### THE CALCULATION OF W<sub>ijk</sub>

When samples i and j are on opposite sides of the peak, there will be cases where the X differences can approach a value of zero. When the X difference gets close to zero, the product of  $B_{ijk}$  and the X difference will still be close to zero, so we cannot always depend on B to correct for this problem. The magnitude of the error resulting from this will depend on how far samples i and j are from the peak value. The further the sites are from the peak value, the greater the error.

Rather than trying to further correct for this distortion, we will downweight comparisons involving species with importance values on opposite sides of the species peak. The down-weighting will be greater for those

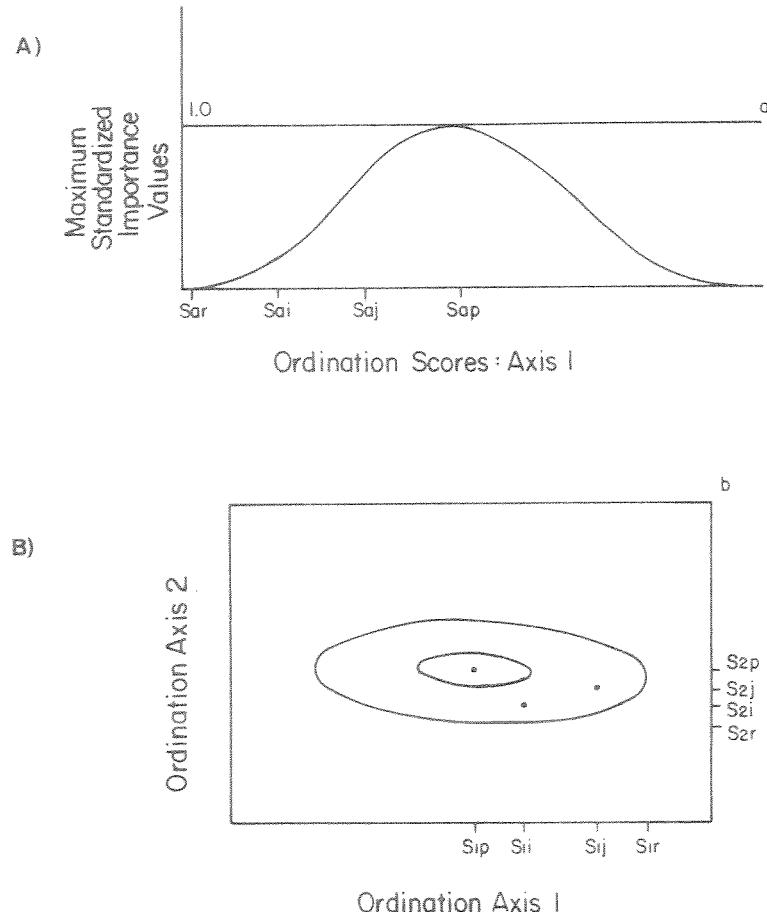


Fig. A1. The use of ordination scores and species importance values to locate samples i and j along the axes in relation to each species' peak abundance. a) and b) are one and two dimensional examples, respectively. Species importance values are used to identify positions of the peak ( $S_{ap}$ ) and endpoint ( $S_{ar}$ ) of each species' distribution.  $S_{ai}$  and  $S_{aj}$  are the axis scores for samples i and j, respectively.

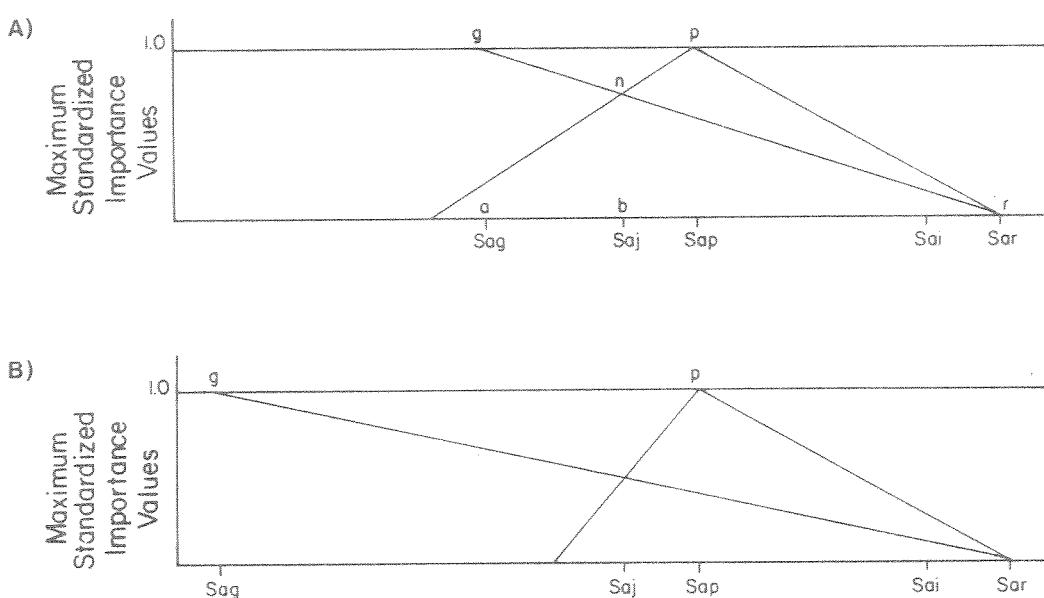


Fig. A2. Geometric interpretation of breadth when the samples being compared are on opposite sides of the peak along ordination axis a. : $S_{ai}-S_{ar}$ : is the breadth along axis a. Note how the slope of the species curve to the left of the peak affects the magnitude of the calculated breadth. The breadth for the case illustrated in b) is greater because the slope to the left of the peak is steeper. For simplicity, the species curves are depicted as straight lines.  $S_{ai}$  and  $S_{aj}$  are the scores of samples i and j, the samples being compared.  $S_{ap}$  is the score of the sample at the species peak.  $S_{ar}$  and  $S_{aq}$  are explained in the text.

comparisons in which the samples are both further from the peak value. The weighting is accomplished with Wijk.

The same ordination space used to calculate Bijk is used to calculate Wijk. Wijk is based on the position of the samples being compared relative to the position of the peak sample. This information can easily be found for each ordination axis by comparing the scores for the peak sample and samples in question. For example, in Figure Alb, it can be seen that samples i and j are on the same sides of the peak on both axes. This would be obvious from examination of the scores along these two axes.

In the case where the samples are on opposite sides of the species peak on axis a,  $W_{ijk}$  for axis a is calculated as:

$$W_{ijk} = \text{MAX}(Y_{ka}, Y_{kj}),$$

where  $Y_{kj}$  is the square-root transformed, weighted species-mean (of values 0) standardized importance value for species k in sample i. More explicitly,  $Y$  is calculated as follows:

$$Y_{ki} = \frac{T_{ki}}{\sum_{m=1}^p u_m T_{km} / \sum_{m=1}^p u_m},$$

where  $u_k$  is the uniqueness weight for sample m,  $T_{km}$  is the square-rooted species importance value for species k in sample m, and p is the number of samples with species importance values greater than zero. The weights in the standardization are a measure of each sample's biological uniqueness (Smith, 1976; Smith and Guggenheim, in prep.). The mean standardization can be affected by uneven sampling of habitats (Smith, 1976), and the weights correct for this. The species mean standardization gives higher values to species that have a well-defined peak in a limited range of habitats (Smith, 1976). These species are more sensitive indicators of overall biological change than are species with poorly-defined and/or widely dispersed peaks.

In summary, when the samples being compared are on opposite sides of the peak on axis a,  $W_{ijk}$  will be higher for species which are near their peak in at least one of the samples being compared, and lower when both samples have values further from the peak. Also, species with better defined peaks can have higher  $W_{ijk}$  values.

When both samples are on the same side of the peak on axis a, the  $W_{ijk}$  value will be the maximum  $Y_k$  value in all samples, that is, the peak value for that species. This will give highest  $W$  values to those comparisons with both samples on the same side of the species peak.

The final  $W_{ijk}$  is the weighted average of the  $W_{ijk}$  values. As with  $B_{ijk}$ ,  $|S_{ai-Saj}|$ , the degree to which i and j extend into dimension a, is used as the weight. Thus,

$$W_{ijk} = \frac{\sum |S_{ai-Saj}| W_{ijk}}{\sum |S_{ai-Saj}|}.$$

## APPENDIX B: THE ORDINATION SPACE USED TO CALCULATE $W_{ijk}$ AND $B_{ijk}$

### DEFINING A DISTANCE MEASURE

As noted in the text, the zero adjustment components ( $Z_{ij}$ ) are based largely on the  $E_{ij}$ 's, which are actually independent estimates of the inter-sample distances. We take advantage of this to use the  $E_{ij}$ 's to build an ordination space in which to orient the samples being compared in relation to species peaks and breadths.

The same properties that make  $E_{ij}$  ideal for calculating  $Z_{ij}$  (i.e. underestimated shorter distances), however, make  $E_{ij}$  a poorer measure from which to build an ordination space. Thus, instead of using  $E_{ij}$ , which utilizes only species that are absent from one of the two samples being compared, we use  $E'_{ij}$ , which utilizes all species absences. This improves the shorter distance estimates.

We refer to Figure A3 throughout the following discussion of the calculation of  $E'_{ij}$ . We represent  $M_{ki}$  (the degree of absence of species  $k$  in sample  $i$ ) as a negative importance value. A species can thus be used to detect biological change even after it reaches a value of zero, because it continues to become more missing (Swan, 1970). This is somewhat equivalent to extending the species curves below the abscissa as shown in Figure A3.

Figure A3 illustrates an important property of  $M_{ki}$ . The absolute values of the slopes of the curves below the zero line are approximately equal. This is due to the fact that the  $M_{ki}$  values are all calculated from the same inter-species distance matrix. Thus, when calculating  $E_{ij}$  or  $E'_{ij}$ , it is unnecessary to adjust for different rates of change (or slope) for the different species (as is necessary when calculating  $Q_{ij}$ ).

The formula for  $E'_{ij}$  is a weighted average very similar to that for  $E_{ij}$ :

$$E'_{ij} = \frac{\sum_{k=1}^s M'_{ki} M'_{kj}}{\sum_{k=1}^s M'_{ki} + \sum_{k=1}^s M'_{kj}},$$

where  $i$  and  $j$  are the samples being compared,  $s$  is the number of species that are absent in either one or both samples, and

$$M'_{ki} = M_{ki}$$

if species  $k$  is absent in sample  $i$  but not in sample  $j$ , and

$$M'_{kj} = M_{kj}$$

if species  $k$  is absent in sample  $j$  but not in sample  $i$ . If species  $k$  is absent in both samples  $i$  and  $j$ , then

$$M'_{ki} = M'_{kj} = |M_{ki} - M_{kj}|.$$

When species  $k$  is in one sample but not in the other, both  $M_{ki}$  and  $M_{kj}$  represent the distance below the zero line at the sample from which the species is missing (Figure A3). For example, when comparing samples 2 and 4 (Figure A3),  $M_{B4}$  is equivalent to the distance between points X and S.

If the species is missing from both samples, the difference in  $M$  values for that species at the two stations is used. For example, when comparing samples 1 and 2 (Figure A3),  $|M_{A1} - M_{A2}|$  equals the distance between points P and R. Note that using species missing from both samples in the calculation of  $E'_{ij}$  incorporates more information (compared to  $E_{ij}$ ) in the weighted average when the samples are biologically similar. This additional information should lead to better shorter distance estimates.

As with  $E_{ij}$ , the  $E'_{ij}$  formula is a weighted average, with each  $M'_{ki}$  value weighted by itself, and only the highest 50% of the  $M'_{ki}$  values included. This, of course, gives more weight to the larger  $M'_{ki}$  values. The importance of this weighting can be illustrated by comparing the relative contributions of species A and B to the contrast between samples 3 and 4 (Figure 9). Both species are absent from both samples. The values for  $M'_{B3}$  and  $M'_{B4}$  would not be good indicators of biological change since  $|M_{B3} - M_{B4}|$ , the vertical distance between points T and S, is approximately zero even though samples 3 and 4 are biologically dissimilar. This will occur whenever the samples are on opposite sides of the position where the species actually occurs. On the other hand,  $|M_{A3} - M_{A4}|$ , the distance between points U and W, is longer and more commensurate with biological change. This will occur when the samples are on the same side of the area of species occurrence. These longer, more appropriate,  $M'_{ki}$  values receive higher weight in the weighted average.

Finally, one may ask why we do not use  $E'_{ij}$  instead of  $D_{ij}$  as the final inter-sample distance value, since both are estimates of the distance. We prefer to base the shorter distances on the species actually present at the samples being compared. This seems preferable because it is much more direct and ecologically sensible.  $E'_{ij}$  is based on less and less information as more and more of the same species are found in samples  $i$  and  $j$ . This is because there will be fewer species absent. In the extreme case where two samples contain all species found in any of the samples surveyed, there could be no  $E'_{ij}$  calculated, since there would be no species absent.

When building the ordination space, we have no choice but to use  $E'_{ij}$ . We cannot use  $Q_{ij}$  since we are using the ordination space to calculate  $Q_{ij}$  in the first place. In any case,  $E_{ij}$  should be sufficient because the ordination space is used only for general orientation of samples relative to species' peaks in the corresponding biological space. This should not require extremely accurate distances.

## BUILDING THE ORDINATION SPACE

We use polar ordination (Bray and Curtis, 1957; Gauch and Scruggs, 1979) to quickly create an ordination space from the  $E'_{ij}$  distance matrix. Ordination axes are created by repeating two basic steps. 1) Two samples are chosen as endpoints for an axis. 2) An ordination score for each sample is then calculated from the distance between the sample in question and the two endpoints. Bray and Curtis (1957) accomplished this by hand, and Beals (1960) demonstrated how to accomplish this mathematically. The relationship between sample k and the endpoint (i and j) can be described geometrically (Figure A4). Here, i and j represent the endpoint samples, k is the sample for which a score is to be calculated, the D's are the distances between the corresponding samples, and  $S_k$  is the score of sample k.  $S_k$  is calculated as follows:

$$S_k = \frac{D_{ij}^2 + D_{ik}^2 - D_{jk}^2}{2 \times D_{ij}}$$

### The Selection of Endpoints for the First Axis

The longest distance is traditionally used to define the endpoints of the first axis. This can create difficulties when there are ties for the longest distance, or when one or both of the samples represented in the distance are extreme outliers. Choosing an outlier would tend to obscure information about the bulk of the samples.

We follow Beals' (1973) suggestion and consider the variability of the distances to each potential endpoint. Extreme outliers will have a lower variance of distances between themselves and other samples, because these distances will be uniformly long. We calculate an index,  $I_{ij}$ , for each potential sample pair. The sample pair with the highest index value is used as the endpoint pair.  $I_{ij}$  is calculated as:

$$I_{ij} = V_i V_j D_{ij},$$

where  $V_i$  is the variance of the distances between sample i and all other samples,  $V_j$  is the variance of the distances between sample j and all other samples, and  $D_{ij}$  is the distance between samples i and j.  $I_{ij}$  values should be highest for sample pairs which are distant but not extreme in position in relation to the rest of the samples.

### Selection of Endpoints on Subsequent Axes

Proposed methods of finding endpoints for subsequent axes are somewhat crude and subjective, and can lead to nonperpendicular or correlated axes (Bray and Curtis, 1957). Orloci (1975) presents a method for projecting onto perpendicular axes, but this still does not solve the endpoint selection problem.

We propose an objective and simple method of endpoint selection in two steps. First, the residual distance between two sites i and j ( $D'_{ij}$ ) is calculated as follows:

$$D'_{ij} = D_{ij} - |S_i - S_j|,$$

where  $D_{ij}$  is the distance used for endpoint selection and score calculation on the previous axis, and  $S_i$  and  $S_j$  are the scores of samples i and j on the previous axis. Once calculated,  $D'_{ij}$  is used (as  $D_{ij}$  was on the first axis) to find endpoints and calculate scores. The use of the residual distances assures that the scores on the different axes will be independent (Beals, 1973). All successive axes are based on the residuals from all previous axes.

### Choosing the Number of Axes

We can compute the amount of variation represented in each axis ( $V_a$ ) as:

$$V_a = \sum_{i=2}^n \sum_{j=1}^{i-1} |S_i - S_j|,$$

where n is the number of samples and  $S_i$  and  $S_j$  are the same as above. This is simply the amount of distance between samples along axis a. To obtain the percent of the total distances accounted for by the axis ( $P_a$ ), we can calculate

$$P_a = 100 \times \frac{V_a}{\sum_{i=2}^n \sum_{j=1}^{i-1} D_{ij}},$$

where  $D_{ij}$  is the distance between samples i and j in the original distance matrix. The cumulative percent of distance accounted for by all axes up to axis a is

$$C_a = \sum_{m=1}^a P_m.$$

The analyst can choose to compute ordination axes until a desired value of  $C_a$  is reached. For the present application, we have chosen to compute axes until  $C_a$  90%. If this results in more than 5 axes, we use axes up to a point where  $C_a$  80%. In any case, a maximum of ten axes are used.

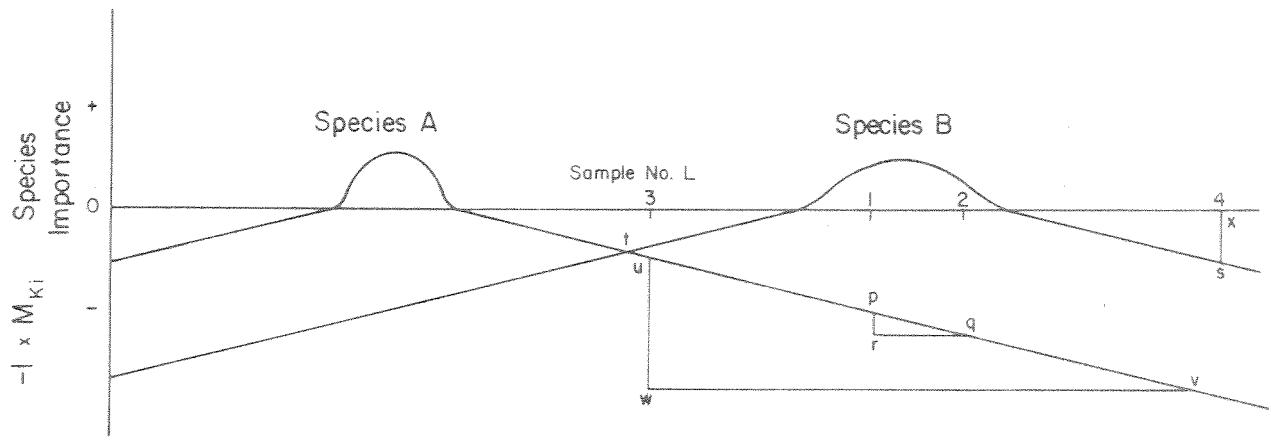


Fig. A3. Two of many hypothetical species along a single gradient of biological change, showing how  $M_{ki}$  values can be used to calculate  $E'_{ij}$ . See text for fuller explanation.

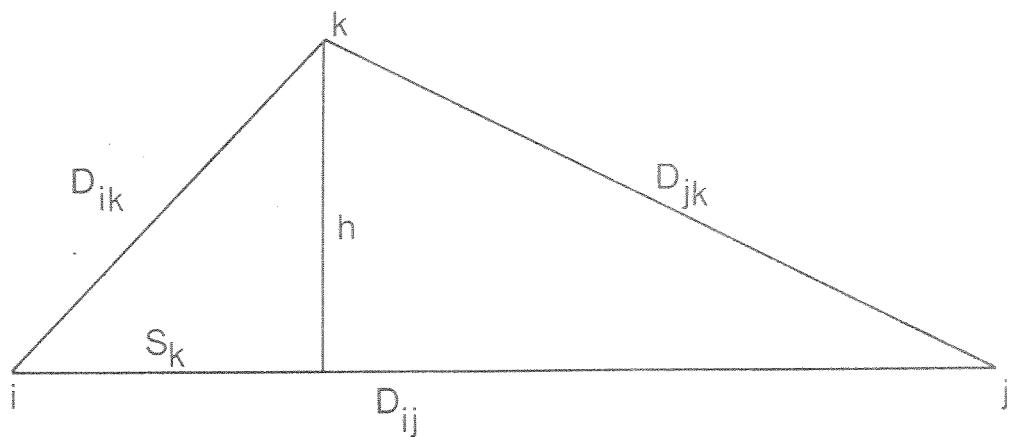


Fig. A4. Calculation of the ordination score for entity k on the axis with endpoints i and j. The D's are the distances between the corresponding entities and  $S_k$  is the score for k.