SPECIES ASSOCIATIONS AND COMMUNITY COMPOSITION OF MIDDLE ATLANTIC BIGHT CONTINENTAL SHELF DEMERSAL FISHES[1]

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ABSTRACT

Cluster analyses of seasonal NMFS Groundfish Survey bottom trawl catches on the Middle Atlantic Bight continental shelf revealed consistent species associations and faunal zones over a 9-year period. Boundaries between faunal zones tended to follow isotherms and isobaths. During the late winter-early spring, the following faunal zones were found: Northern inner shelf, northern mid-shelf, southern inner- and mid-shelf, and outer shelf-shelf break. Five species groups were identified: A small cryophilic group restricted to the first zone, a cold-water boreal group found in the first two zones, a ubiquitous boreal/resident group containing the major dominants, a warm-temperate group confined to the warmer southern and outer shelf waters, and a group of slope residents confined to the deepest zone. During the fall, five faunal zones were found: Southern inner/mid-shelf, northern inner shelf, northern mid-shelf, outer shelf, and shelf break. Five species associations were largely analogous to those in the spring, with the following exceptions: The cryophilic group was absent, the ubiquitous group contained mixed boreal and warm-temperate elements, and a second outer shelf group was recognized. The most notable change in the distribution of groups from the spring was a general northward shift and a sharply defined inshore movement of the temperate group.

Communities of fishes on the continental shelf have rarely been studied beyond the compilation of species lists for given areas. This is enigmatic when one considers the large amount of survey data that has been collected from much of the world's continental shelf waters in connection with fishery exploration and monitoring. While trawl survey data have traditionally been collected with the primary aim of assessing commercially harvestable stocks, they also provide an excellent base for evaluating the interspecific relationships among trawlable organisms.

The few studies which have previously addressed community structure of open continental shelf fishes have found clearly definable species associations with distributions related to environmental parameters. Demersal fish species assemblages found using objective mathematical measures have been described for the continental shelves in the Gulf of Guinea (Fager and Longhurst 1968), northwest Pacific coast of the United States (Day and Pearcy 1968), and Campeche Bank off Mexico (Sauskan and Ryzhov 1977).

Since 1967 the National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) has conducted a semiannual bottom trawl survey of the continental shelf waters from Nova Scotia to Cape Hatteras (Grosslein 1969). This program has produced a data base which offers a unique opportunity for the analysis of the composition and variability of the fish communities in this region.

In the present study, that portion of these data collected in the Middle Atlantic Bight (Cape Cod to Cape Hatteras) during the cruises from fall 1967 through spring 1976 were analyzed with the aim of defining the composition of fish communities present within this area and how they vary geographically, thermally, and seasonally.

METHODS

Sampling

Groundfish Survey cruises were conducted by the National Marine Fisheries Service during the fall and spring from fall 1967 through spring 1976, aboard either the RV *Albatross IV* or RV *Delaware II*. The survey area extended from the 15-fathom (27 m) contour offshore to 200 fathoms (365 m). A stratified random sampling design was utilized, based on depth and geographical zones (Fig. 1). Catch data from strata 1-12 and 61-76 (Middle Atlantic Bight) were analyzed in the present study. Sampling intensity in each stratum was allocated according to the geographic area of each stratum

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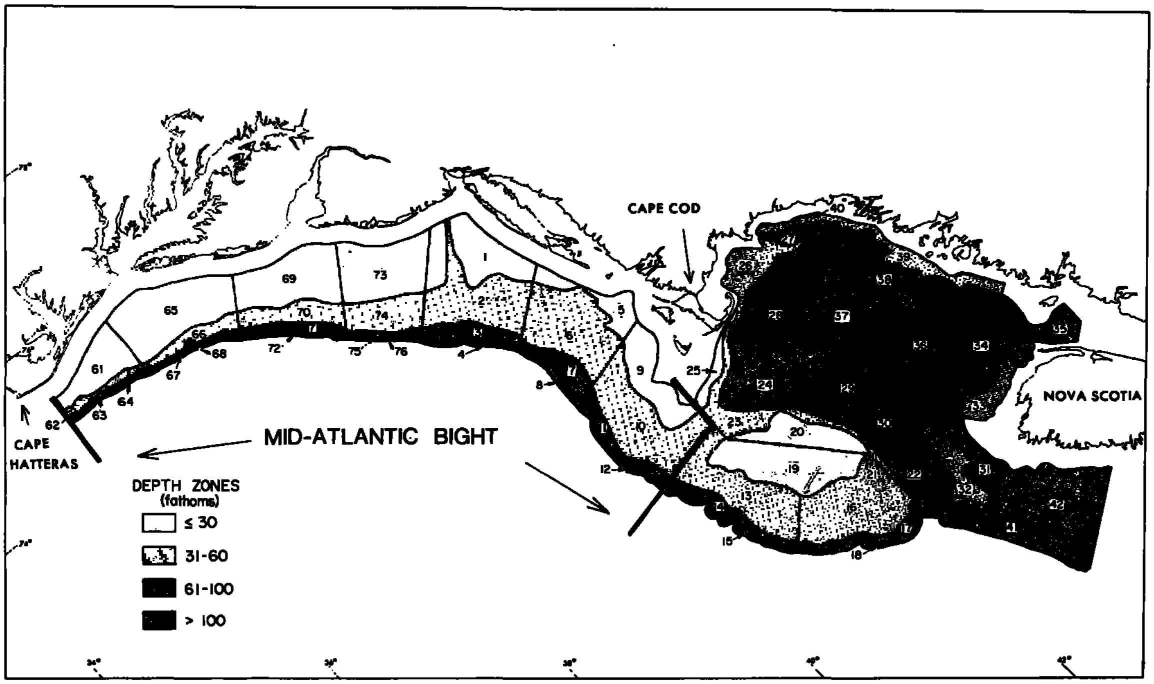


FIGURE 1.—Northwest Atlantic area sampled by NMFS Groundfish Survey. In the present study, data collected from the Middle Atlantic Bight area (strata 1-12, 61-76) between fall 1967 and spring 1976 were examined.

(2-16 stations per stratum). At each station a tow of ½-h duration at a speed of 3.5 kn was made along the bottom. A standard #36 Yankee trawl was utilized except during the spring cruises from 1973 to 1976, when a modified high-opening #41 Yankee trawl was used. The fishes captured were identified, counted, and weighed by species. A bathythermograph cast was made at each station. Further details of sampling design and sample processing may be found in Clark and Brown (1977) and Grosslein (1969).

Analyses

Clustering

Catch data were initially analyzed separately for each of 18 cruises, using numerical classification (clustering). Assemblages of fishes were defined by computing a similarity coefficient, $S_{(j,k)}$, among species from the species-station matrix and subsequently classifying species into clusters or groups (Sneath and Sokal 1973). Stations were clustered in the same manner from the inverted matrix, and species and station (site) groups were compared by nodal analysis (Lambert and Williams 1962). Matrix values entered were counts of individuals, as biomass measurements are overly influenced by the presence of relatively rare but large, motile fishes (which are poorly sampled by trawls) in the collections.

The similarity coefficient used was the Canberra metric (Lance and Williams 1967), which is particularly effective when the organisms under study are contagiously distributed (Clifford and Stephenson 1975) as most fishes are. Also, to further reduce the effects of contagion, the numerical abundance data were transformed [$\log_{10}(x + 1)$] before analysis (Taylor 1953). Species were eliminated from cluster analysis if they occurred at <5% of the stations occupied during a sampling period. Although this is a more severe data reduction than is commonly employed, examination of the raw matrix and trial runs at various cutoff levels indicated that species occurring below this level showed highly inconsistent distributions.

The clustering strategy used was flexible fusion with beta set at the conventional value of −0.25 (Boesch 1977). Calculations were performed on an IBM 370-115[3] at the Virginia Institute of Marine Science using the Fortran IV program COMPAH

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(Combinatorial Polythetic Agglomerative Hierarchical Program) developed at the institution. Output was in the form of similarity matrices and computer generated dendrograms.

The choice as to which branches in the dendrograms were to be identified as biologically significant groups was based on the following procedure. Each branch of the dendrogram, composed solely of fusions involving only one entity as at least one-half of each fusion, was considered to constitute a minimal grouping. The distribution of each minimal grouping was then map-plotted, with logarithmic keyed symbols being used for plots of abundances of minimal species groupings. The plot of each grouping was then compared with that of the grouping with which it next fused; if no significant differences in distribution were evident, the fusion was considered to be intragroup. This procedure was repeated until all minimal groupings had been fused into groups showing evident distributional differences. In cases where there was any doubt as to whether two groups should be fused, nodal analysis diagrams were generated and compared for the two cases and the decision producing the "crisper" result (Clifford and Stephenson 1975) utilized. While this method obviously involves some subjectivity in the recognition of groups, it has been pointed out by several authors that all methods of interpreting numerical classifications require a certain degree of subjectivity and that fixed stopping rules are especially inappropriate with fusion strategies which introduce a group size-dependent element into intergroup relative affinities (Boesch 1977; Pielou 1977; Clifford and Stephenson 1975).

Two methods of nodal analysis were performed. The patterns of "constancy" and "fidelity" of species groups to site groups were expressed as relative densities of cells of a two-way table (Stephenson et al. 1972). Constancy is the proportion of the number of occurrences of each species group in the site group to the total number of occurrences possible (Boesch 1977). The index has a value of 1 when all members of a species group occur in all collections in a site group and a value of 0 when a species group does not occur in a given site group. Fidelity is a measure of the degree to which species groups are limited to site groups. The fidelity index used in this study was the constancy of a species group within a site group divided by the average constancy over all site groups. This index is unity when the constancy of a species group in a site group is equivalent to its overall constancy, >1 when its constancy in the site groups is greater than that overall, and between 0 and 1 when its constancy is less than its overall constancy. A chi-square test was applied to the fidelity value of each cell to determine whether it varied significantly ($\alpha = 0.05$) from 1. Fidelity values significantly >1 indicate a positive association of species in a group with a site group, while values significantly <1 suggest a "negative" association. In the present analyses, a highly positive (or strong) association was inferred if the number of occurrences of a given species group within a site group was twice that necessary to produce a fidelity value significantly >1, and a highly negative association was assumed when the number of occurrences was less than half that necessary to produce a fidelity value significantly <1. All nodal diagrams were drawn with the width of the rows and columns proportional to the number of entities in the respective site and species groups.

Species Dominance

Numerically dominant species have been used by ecologists for many years to characterize communities (Thorson 1957), and changes in dominant species often reflect faunal changes. In the present study, we have compared patterns of species dominance among site groups. A species was included in dominance comparisons if it occurred among the five most abundant species in at least 20% of all the stations from a site group.

Faunal Affinities

The faunal affinities of fishes captured were determined by examining published records of their usual ranges of occurrence (Bigelow and Schroeder 1953; Leim and Scott 1966; Struhsaker 1969; Musick 1972). Most warm-temperate species had resident populations south of Cape Hatteras in the "Carolinian" faunal province (Hazel 1970) and had their normal northern range limit somewhere within the Middle Atlantic Bight south of Cape Cod. Boreal species had permanent populations north of Cape Cod, and most had their southern range limit somewhere within the Middle Atlantic Bight north of Cape Hatteras. A few boreal species transcend Hatteras through bathymetric submergence. Certain components of the fauna tended to be residents on the inner shelf (*Scophthalmus aquosus*) or outer shelf (*Paralichthys oblongus*). Many species were resident on the shelf edge and upper slope (Musick 1976).

Pooling of Within-Season Cruises

Size of the data matrix was too large for simultaneous clustering of either of the two multiple-year seasonal data sets. However, the results of the cluster, nodal, and dominance analyses of the individual cruises revealed a high degree of within-season repetition in the composition and distribution of species groups and in the faunal, geographic, and hydrographic attributes of site groups. Major repetitive species groups were recognized for each season, and site groups for each year were referred to generalized seasonal site groups. The validity of these groups was examined by subjecting the pooled seasonal data sets to nodal and dominance analyses based on these groupings and comparing these results to those for the individual cruises.

RESULTS AND DISCUSSION

Thermal Regime

The geographic patterns of bottom-water temperatures were variable among years within both of the sampling seasons, although these differences were minor compared with the seasonal variation within a given year. Variability among years within a season can be attributed to two sources: Climatic differences among years and sampling artifacts (i.e., differences in the dates and duration of the sampling periods, and stochastic differences arising from the location of stations and the temporal sequence in which they were done).

The spring cruises were conducted in March and April, the period during which water temperatures in the Middle Atlantic Bight are at a mini-

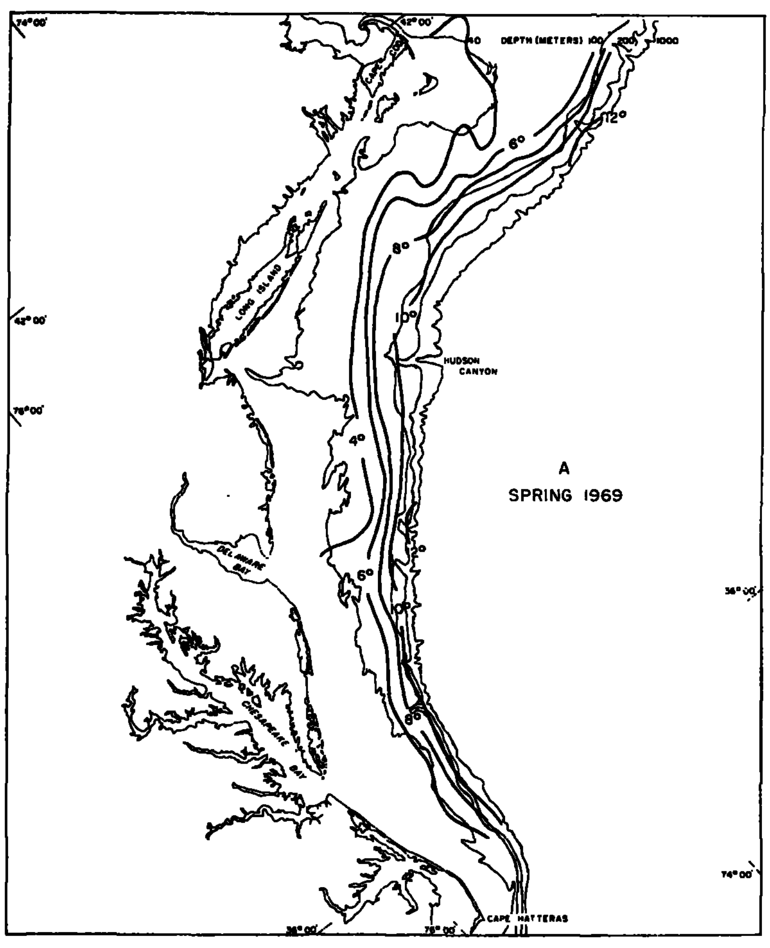
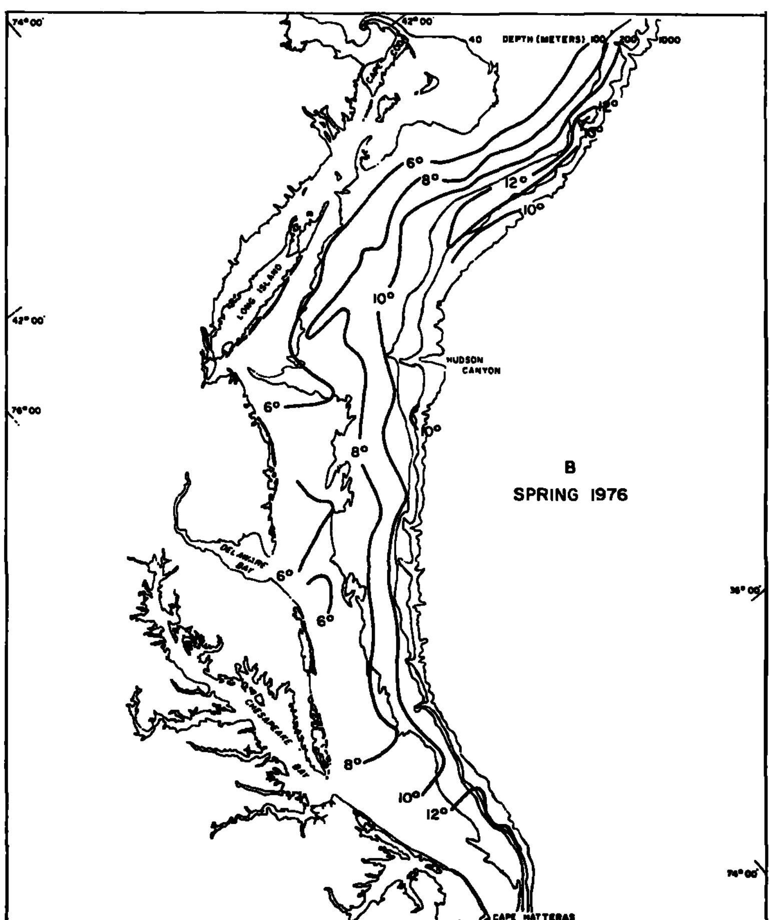


FIGURE 2.—Bottom isotherms for spring 1969 (A) and 1976

mum (Walford and Wicklund 1968), and therefore it is more appropriate to consider these cruises as having sampled the late winter distribution of fishes (Musick and Mercer 1977). There was a definite trend toward warmer temperatures during the study period for this season which cannot be completely attributed to sampling artifacts (Davis 1979). Bottom isotherms extrapolated from the collection data are shown for two cruises representative of the warmer (1976) and cooler (1969) extremes (Fig. 2). During the 1969 cruise, inshore and mid-shelf temperatures were <4°C north of Delaware Bay and between 4° and 6°C between Delaware Bay and Cape Hatteras, with an increasing gradient present along the entire outer shelf. In 1976 temperatures of <6°C were encountered only at northern inshore stations. South of Chesapeake Bay there was a southwardly increasing thermal gradient perpendicular to the shoreline, and the outwardly increasing gradient was distributed across a greater portion of the shelf. Bottom temperatures for the other spring cruises exhibited patterns intermediate between these two (Davis 1979).

Fall sampling cruises were conducted primarily in October. Because of water column turnover, this is the time of maximum temperature for mid-shelf bottom waters in this region (Bigelow 1933); however, coastal waters undergo rapid cooling during the fall (Parr 1933), initiating migrations for many fishes that spend the summer inshore. Bottom isotherms for a typical warm (1973) and cool (1971) fall sampling period are shown in Figure 3. In 1971 a strong thermal gradient was encountered along the mid-shelf from New York to Cape Hatteras. A pocket of cooler water (6°-9°C) was present northward and offshore of this gradient, where turnover was in progress or just beginning.



(B) extrapolated from NMFS Groundfish Survey cruises.

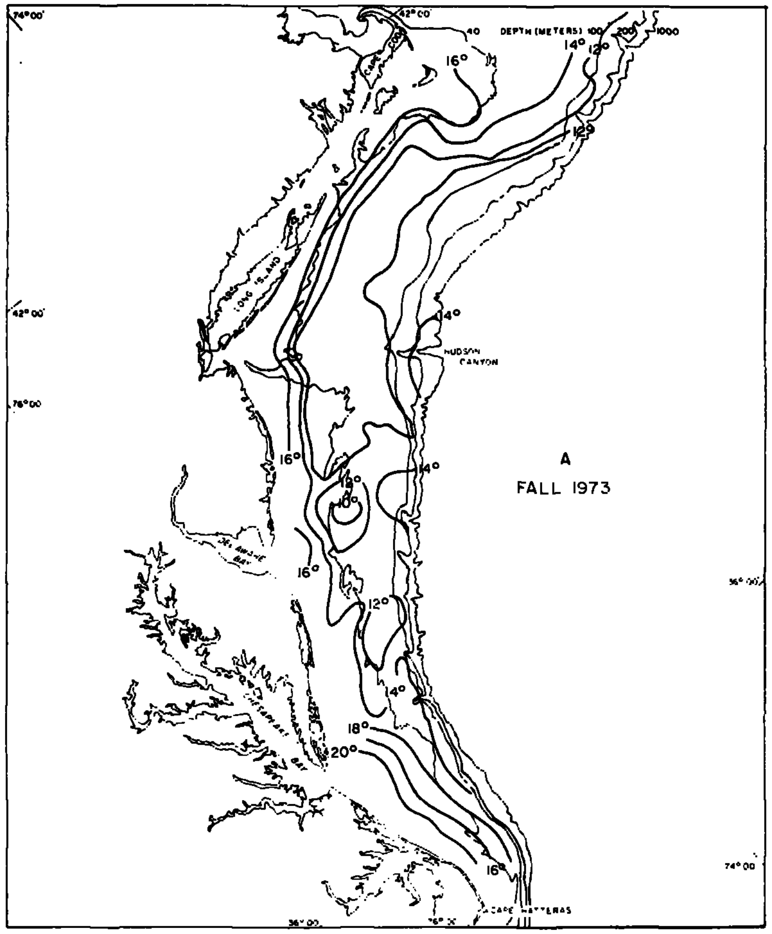


FIGURE 3.—Bottom isotherms for fall 1973 (A) and 1971

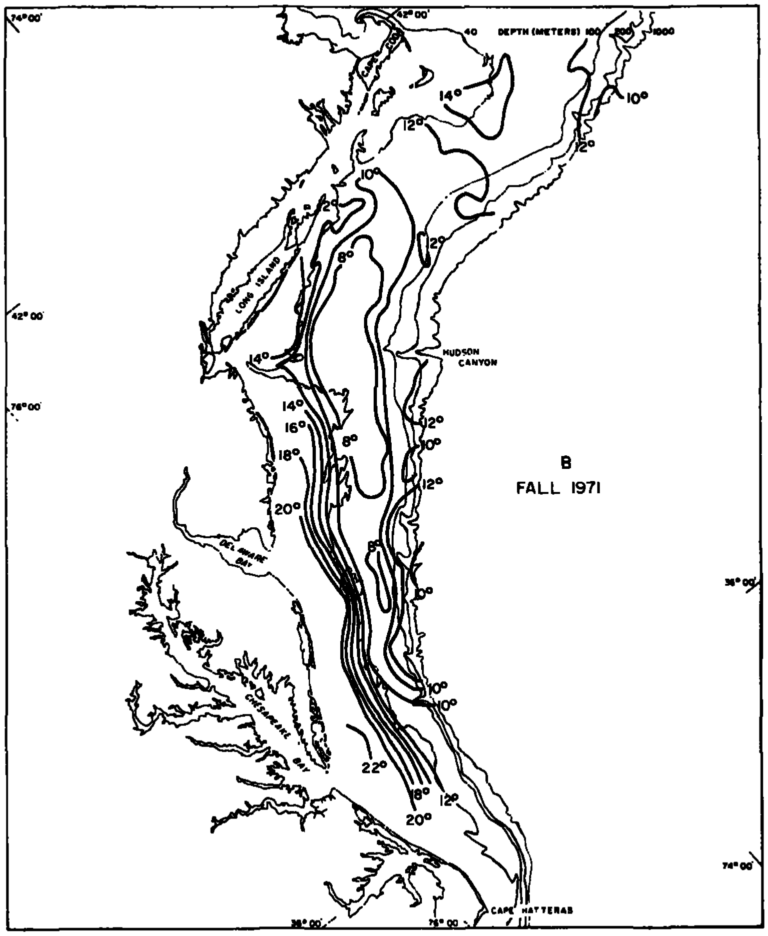
During 1973 bottom-water temperatures were less stratified and 2°-4°C warmer throughout most of the study area. Inshore temperatures exceeded 16°C along the entire Bight, with temperatures above 18°C occurring only south of Chesapeake Bay. The coolest temperatures were found again on the mid-shelf off New Jersey and Long Island, but the "pocket" was much less clearly defined and was composed of waters between 10° and 12°C, indicating that turnover had already occurred. The other fall cruises showed thermal regimes intermediate to those of 1971 and 1973 (Davis 1979).

Site Groups

Spring Cruises

Station groups based on cluster analysis were determined for the nine spring cruises (Colvocoresses and Musick 1979). Most groups were geographically contiguous and tended to be thermally and bathymetrically restricted. Site groups were not precisely comparable from one year to the next, but could, however, be categorized on the basis of faunal similarity, geographic location, bathymetry, and temperature.

During all nine cruises there was a group of site clusters of similar depth and temperature regimes which were contained between the shore and approximately the 8°C isotherm. The geographic extent of these groups varied from year to year, but generally covered the inner- and mid-shelf out to about 70 m from Cape Cod south to between Delaware Bay and Cape Hatteras, depending upon the southward extent of waters cooler than 8°C. These site groups were assigned to site group I (Fig. 4) for the pooled analyses. Adjacent to this group were



(B) extrapolated from NMFS Groundfish Survey cruises.

two other categories of groups: Northern outer shelf groups extending from the cold-water group to the shelf break (150 m) (pooled group II), and southern groups (pooled group III) which occupied the remaining shelf both outward and south of the 8°C isotherm. The boundary between these two categories was generally off the New Jersey coast, at which point there was often considerable overlap. The remaining outermost groups were located along the shelf break at depths of 150-350 m (pooled group IV).

In general, areas of geographic overlap between site groups can be related to variations in the thermal regime. For example, there is considerable overlap between groups I and III on the inner- and mid-shelf south of Delaware Bay. This area showed the greatest temperature variation among years, with group I station clusters predominating in the area in colder years and group III station clusters in warmer years. Hydrographic parameters and basic catch data for each stratum are summarized in Table 1. The hydrographic parameters (depth, temperature) within a site group are much better represented by the mean and standard deviation than by the range of values encountered. At a small percentage of stations only a few species were taken, and in cases where these species occurred within all or several strata, some misclassifications occurred. Because the incidence of these obvious misclassifications was low, they have been ignored rather than introducing an arbitrary system of reclassification. Virtually all extremely variant values of depth and temperature and strong deviation in geographic location within a site group were attributable to stations where only a few ubiquitous species were taken. Figure 5 illustrates temperature-depth envelopes for each site group. In order to reduce dis-

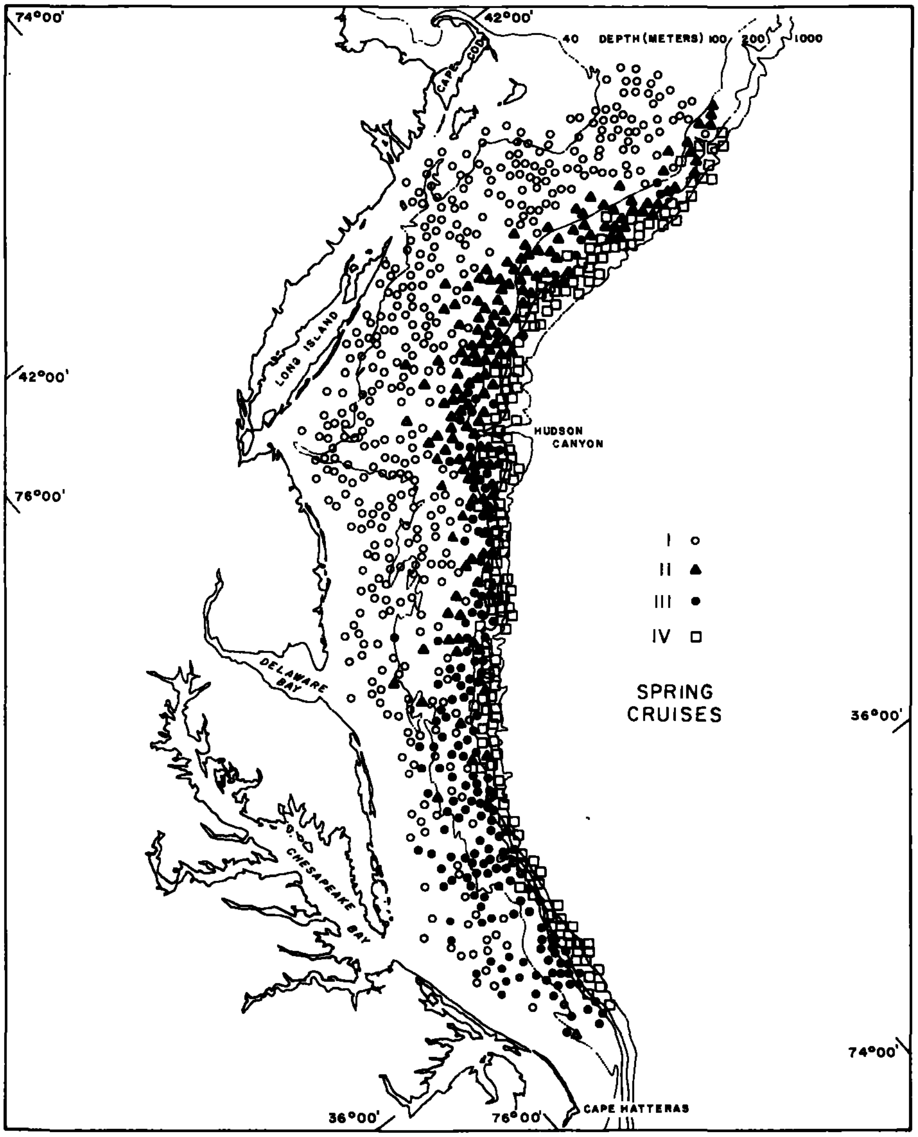


FIGURE 4.—Pooled site groups based on cluster analysis for spring NMFS Groundfish Survey cruises, 1968-76.

tortions introduced by misclassified stations, points which exceeded 2 standard deviations from either mean were not included. As may be seen by a comparison of Figures 4 and 5, groups I and IV are geographically, bathymetrically, and thermally discrete from one another with groups II and III occupying the intermediate area and somewhat overlapping the first two groups in terms of bathymetry and thermal regime. Groups II and III are largely separable on the basis of latitude (as well as faunal composition).

Fall Cruises

Station groups recognized from cluster analysis of the fall cruises (Colvocoresses and Musick 1979) were not as geographically contiguous or as thermally restricted as during the spring cruises, but could still be readily grouped into categories based on faunal attributes. During seven of the nine cruises there was a distinct southern inshore site group between shore and about 60 m extending from Cape Hatteras northward to the region off

TABLE 1.—Hydrographic and average catch parameters by site group for Spring NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1968-76. The 1968-72 cruises used a #36 Yankee trawl, the 1973-76 cruises a #41 Yankee trawl. Numbers in parentheses are retransformed values.

		I		II		III		IV	
Site group		1968-72	1973-76	1968-72	1973-76	1968-72	1973-76	1968-72	1973-76
No. of stations		237	188	92	90	138	53	110	112
Abundance	$\bar{x}$	2.19(154)	2.47(296)	2.40(252)	2.62(416)	2.17(149)	2.35(224)	2.16(144)	2.36(230)
log (x + 1)	SD	0.40	0.45	0.54	0.40	0.68	0.67	0.54	0.51
Biomass (kg)	$\bar{x}$	1.70(50)	1.97(95)	1.79(62)	2.14(138)	1.58(38)	1.92(84)	1.56(37)	1.65(45)
log (x + 1)	SD	0.40	0.36	0.54	0.43	0.59	0.51	0.57	0.46
No. of species	$\bar{x}$	10.1	12.4	9.7	12.1	8.1	8.8	9.1	13.1
	SD	2.8	3.0	2.9	2.5	2.9	3.3	3.3	4.3
Depth (m)	range	18-101	18-90	24-329	29-152	18-349	27-152	66-379	53-341
	$\bar{x}$	50.0	46.5	117.9	78.9	84.1	75.2	222.1	194.0
	SD	17.3	15.4	46.8	21.9	54.2	33.2	78.3	72.1
Temperature	range	2-9	3-11	4-14	7-16	5-13	5-14	5-16	5-15
(°C)	$\bar{x}$	4.6	6.0	10.0	9.6	8.9	10.2	10.1	11.4
	SD	1.5	1.5	2.1	2.0	2.2	2.1	2.0	1.6

Delaware Bay. This group was generally contained behind a strong thermal gradient and exhibited the warmest bottom temperatures in the study area. These groups were assigned to site group I for the pooled analyses (Fig. 6, Table 2). Extending northward from these groups along the inner shelf was a second, colder site group which tended to be constricted toward shore between northern Long Island and Cape Cod (group II). During 1973 and 1974, when thermal stratification was weaker and inshore water temperatures in the north were higher, there was no distinct break between northern and southern inshore station groups (groups I and II), but instead there were two station groups with members in both northern and southern inshore and mid-shelf waters. One group from each of these years was assignable to each of the two major pooled groups based on faunal similarity; but such assignment, of course, led to the geographical overlap between groups I and II seen off Long Island and Chesapeake Bay in Figure 6.

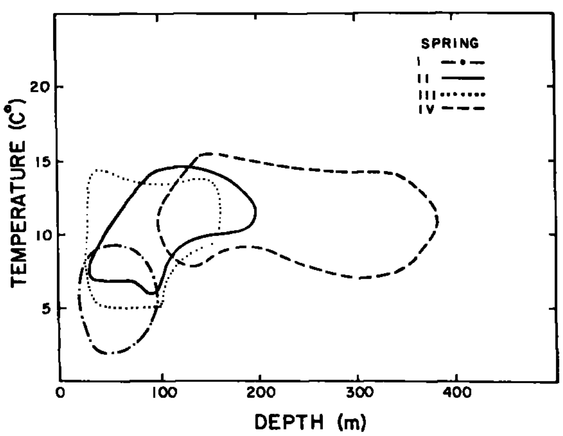


FIGURE 5.—Temperature-depth envelopes for pooled spring site groups, Middle Atlantic Bight area, 1968-76. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

One or two site groups each year occurred on the northern mid-shelf primarily between 35 and 90 m, in the region of the coolest shelf waters (group

TABLE 2.—Hydrographic and average catch parameters by site group for Fall NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1967-75. All cruises used a #36 Yankee trawl. Numbers in parentheses are retransformed values.

Site group		I	II	III	IV	V
No. of stations		114	176	209	382	114
Abundance	$\bar{x}$	2.19(130)	2.30(200)	2.20(249)	2.05(111)	1.92(84)
log (x + 1)	SD	0.73	0.59	0.57	0.67	0.54
Biomass (kg)	$\bar{x}$	1.55(36)	1.78(61)	1.73(54)	1.09(11)	0.86(6)
log (x + 1)	SD	0.58	0.56	0.59	0.56	0.39
No. of species	$\bar{x}$	8.2	10.8	10.8	6.8	9.3
	SD	3.7	3.6	4.1	2.9	3.7
Depth (m)	range	18-123	20-80	31-192	16-397	71-433
	$\bar{x}$	33.8	42.6	61.5	110.6	249.6
	SD	12.7	12.4	17.1	60.2	77.4
Temperature	range	8-23	6-25	5-22	6-21	6-18
(°C)	$\bar{x}$	16.7	13.4	10.7	11.7	10.4
	SD	3.5	3.5	2.6	2.2	1.9

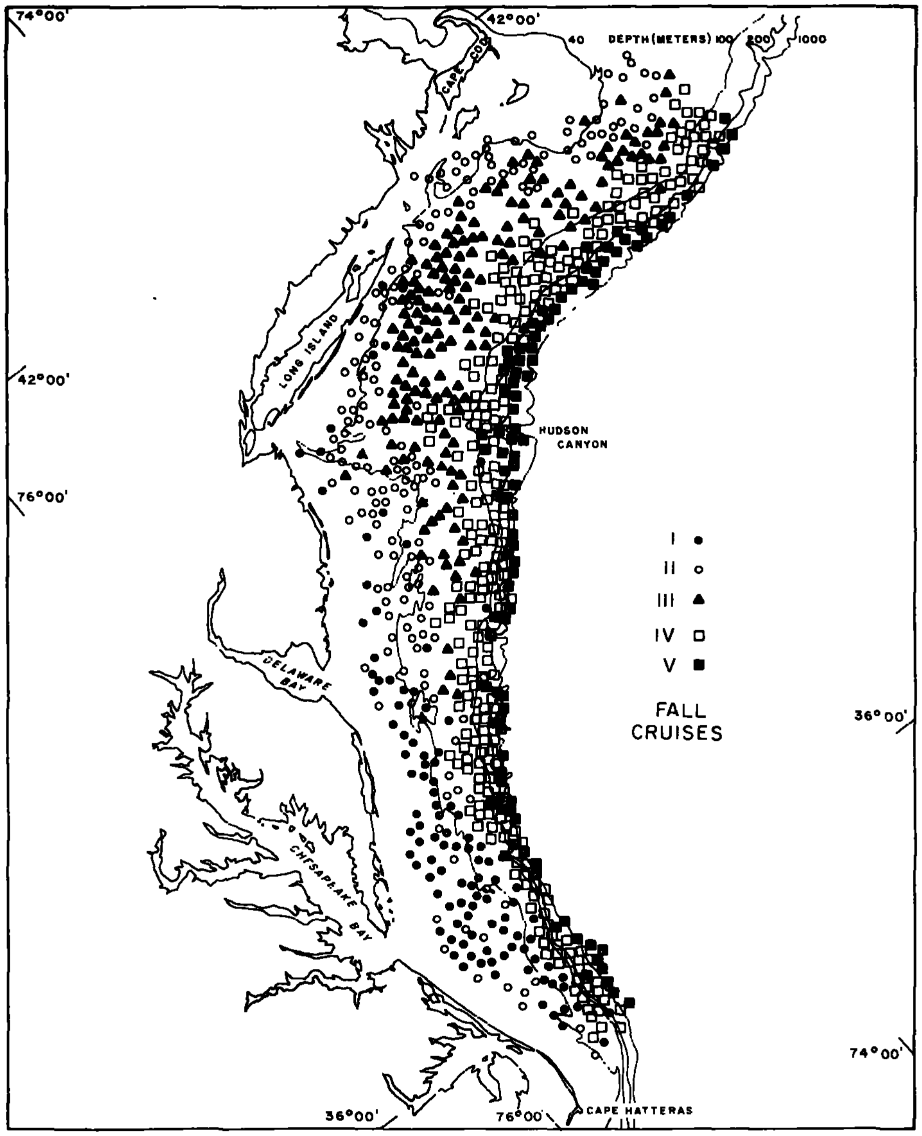


FIGURE 6.—Pooled site groups based on cluster analysis for fall NMFS Groundfish Survey cruises, 1967-75.

III). The remaining site groups could be classified as outer shelf-shelf break (group IV) or upper slope (group V). The outer shelf-shelf break group displayed a wide depth range and a temperature range very similar to groups II and III, but occurred consistently offshore of those two groups (Fig. 6). The upper slope group had the most restricted temperature range and was bathymetrically discrete from the inner- and mid-shelf groups. The temperature-depth envelopes for the first four site groups (Fig. 7) show a large amount of overlap in the shallower portion of the study area, but much of this overlap is an artifact of combining data across years and over a wide area (i.e., thermal ranges and boundaries between groups varied between years, and bathymetric boundaries varied with latitude).

Species Associations

Between 6 and 11 species clusters were recognized for each cruise (Colvocoresses and Musick 1979). As with the station clusters, although there was some variation in group composition and dis-

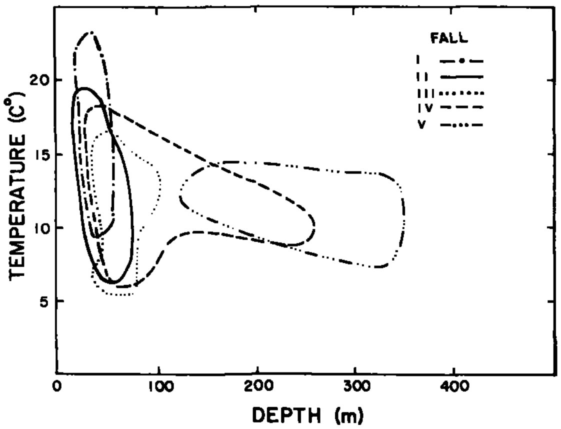
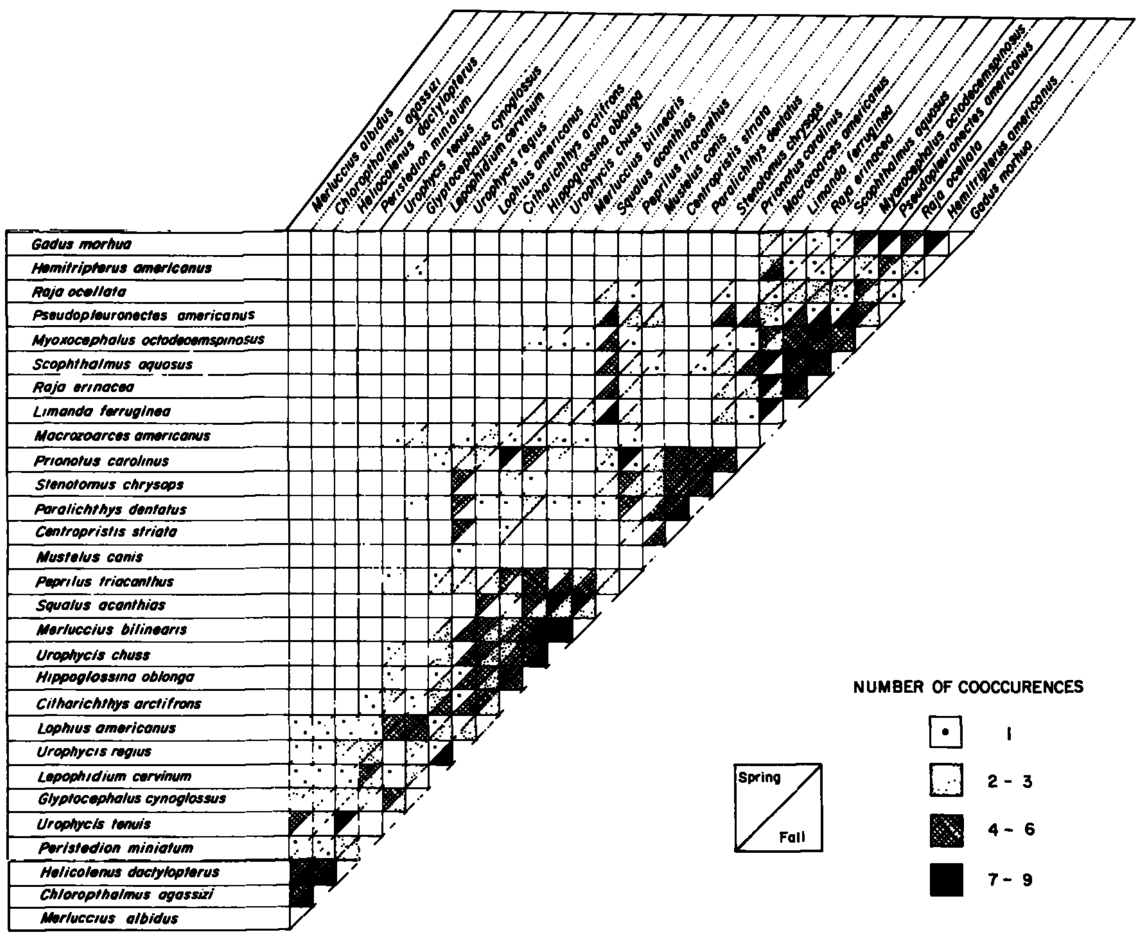


FIGURE 7.—Temperature-depth envelopes for pooled fall site groups, Middle Atlantic Bight area, 1967-75. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

tribution from year to year, the groupings were largely consistent over the 9-yr period of this study. Figure 8 shows the number of times the 30 most commonly occurring and dominant demersal species occurred within the same species group during the spring and fall cruises. The species are arranged so as to be closest to those species they occurred with most often in the clusters, i.e., so that the densest cells fall along the diagonal border of the diagram.

Four strongly recurring species groups are evident from this diagram. *Myoxocephalus octodecemspinosus, Scophthalmus aquosus, Raja erinacea*, and *Limanda ferruginea* frequently appeared in the same group during both seasons. In the spring they were often joined by *Macrozoarces americanus*, a species generally absent from the

FIGURE 8.—Cooccurrences within the same species cluster group for major species, spring and fall NMFS Groundfish Survey cruises, Middle Atlantic Bight area, 1967-76.



clusters in the fall, while *Squalus acanthias* and *Pseudopleuronectes americanus* were common co-group members during the fall cruises. In the spring the latter species regularly occurred in a separate group which included *Gadus morhua* and *Hemitripterus americanus*. Except for *Scophthalmus aquosus*, an inshore resident, all of these species are of boreal faunal affinity and are restricted to cold water (Bigelow and Schroeder 1953; Leim and Scott 1966).

Prionotus carolinus, *Stenotomus chrysops*, *Paralichthys dentatus*, and *Centropristis striata*, all warm-temperate species, were regularly classified in the same group during both seasons. During the fall this group was often joined by *Mustelus canis*, another warm-temperate species which was only rarely taken during the spring cruises. Two other warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, regularly cooccurred with this group in the spring.

Merluccius bilinearis and *Urophycis chuss* were the two most consistently cooccurring species, appearing in the same group in all but one cruise. These two species formed the core of a third species group which was ubiquitous in the spring and widespread across the deeper portion of the study area in the fall. Both of these boreal species have broader temperature tolerances than the cold-water groups noted above (Musick 1974; Bigelow and Schroeder 1953). Abundances of these two species were greater on the outer shelf and shelf break, and they often clustered with *Paralichthys oblongus* (= *Hippoglossina oblonga*), an outer shelf resident, and, in the fall, with *Citharichthys arctifrons*, a slope resident which also occurs on the outer shelf (Richardson and Joseph 1973) and *Lepophidium cervinum*, another outer shelf resident. The warm-temperate species *Peprilus triacanthus* and *Urophycis regia* were also common group members in the fall, while *Lophius americanus* regularly occurred in this group in the spring.

The fourth clearly defined recurring species group was an upper slope group composed of *Helicolenus dactylopterus*, *Chloropthalmus agassizi*, and *Merluccius albidus*, which appeared consistently during both seasons. *Urophycis tenuis* commonly cooccurred with members of this group during the spring, while in the fall this species was more widely distributed across the outer shelf and tended to appear in small groups with *Lophius americanus* and *Glyptocephalus cynoglossus*.

The major recurring species groups described above are listed for each season in Table 3. The groups are ordered in the same manner as the generalized station groups, that is, from shallowest to deepest (distribution) while still maintaining nearest neighbor intergroup relationships as determined in the clusters. Figures 9 and 10 show the distributional relationships between the major site and species groups as determined by nodal analyses. As noted above, these relationships are more sharply defined during the spring cruises than in the fall, but in both cases the nodal analyses show clear differences in the faunal composition of site groups and the distribution of species groups. The interrelationships seen here are also highly representative of those noted during analyses of the individual cruises.

Dominance

The dominant species for each of the pooled site groups are given in Tables 4 and 5. During the spring *Limanda ferruginea* was the major dominant at the cold-water, inshore site group (I), *Squalus acanthias* and *Merluccius bilinearis* were among the major dominants at all site groups, and *Peprilus triacanthus* was a major dominant at all but the cold-water site group. *Stenotomus chrysops* was a major dominant along the southern outer shelf (group III). In the fall, the southern inshore site group (I) was strongly dominated by three warm-temperate species: *Prionotus carolinus*, *Stenotomus chrysops*, and *Peprilus triacanthus*. These three species persisted as major dominants at the northern inshore site group, but were joined there in roughly equal dominance by three boreal species: *Limanda ferruginea*, *Squalus acanthias*, and *Merluccius bilinearis*. *Peprilus triacanthus* and the latter group were major dominants on the northern mid-shelf (group III). *Peprilus triacanthus* and *Merluccius bilinearis* were also major dominants at the outer shelf stations (group IV), where they were joined by *Urophycis regia*. The shelf-break stations (group V) were dominated by *Merluccius bilinearis*, *Citharichthys arctifrons*, and *Helicolenus dactylopterus*.

There were few major changes in species dominance throughout the study, and Tables 4 and 5 are representative of those for the individual cruises. *Merluccius bilinearis*, *Peprilus triacanthus*, and *Squalus acanthias* were consistently the three most dominant species during both major seasons. Although *Merluccius bilinearis* accounted for only around 10% of the individuals taken, it was the most consistently dominant

TABLE 3.—Major recurrent species groups, NMFS Groundfish Survey, Mid-Atlantic Bight area, 1967-76. Faunal affinity is designated after each species name: Boreal, Bo; warm temperate, WT; inner shelf resident, IS; outer shelf resident, OS; slope resident, Sl.

Spring cruises	Fall cruises
A	A
Gadus morhua Bo	*Centropristes striata* WT
Hemitripterus americanus Bo	*Mustelus canis* WT
Pseudopleuronectes americanus Bo	*Paralichthys dentatus* WT
	Prionotus carolinus WT
	Stenotomus chrysops WT
B	B
Limanda ferruginea Bo	*Limanda ferruginea* Bo
Macrozoarces americanus Bo	*Myoxocephalus octodecemspinosus* Bo
Myoxocephalus octodecemspinosus Bo	*Pseudopleuronectes americanus* Bo
Raja erinacea Bo	*Raja erinacea* Bo
Scopthalmus aquosus IS	*Scophthalmus aquosus* IS
	Squalus acanthias Bo
C	C
Lophius americanus Bo	*Citharichthys arctifrons* OS
Merluccius bilinearis Bo	*Lepophidium cervinum* OS
Paralichthys oblongus OS	*Merluccius bilinearis* Bo
Squalus acanthias Bo	*Paralichthys oblongus* OS
Urophycis chuss Bo	*Peprilus triacanthus* WT
	Urophycis chuss Bo
	Urophycis regia WT
D	D
Centropristes striata WT	*Glyptocephalus cynoglossus* Bo-Sl
Paralichthys dentatus WT	*Lophius americanus* Bo
Peprilus triacanthus WT	*Urophycis tenuis* Bo-Sl
Prionotus carolinus WT	
Stenotomus chrysops WT	
Urophycis regia WT	
E	E
Chloropthalmus agassizi Sl	*Chloropthalmus agassizi* Sl
Helicolenus dactylopterus Sl	*Helicolenus dactylopterus* Sl
Merluccius albidus Sl	*Merluccius albidus* Sl
Urophycis tenuis Bo-Sl	

species, reflecting a very uniform distribution. *Limanda ferruginea* was the only major species to undergo a notable change in dominance, showing a pronounced decline only during the last 2 yr of the study. Parrack[4] has carefully linked the decline of this valuable commercial species to overfishing.

Squalus acanthias and *Peprilus triacanthus*, two of the most dominant species, showed strong seasonal differences in the groups with which they clustered. *Squalus*, a boreal cold-water species, was widespread in the spring and occurred in the ubiquitous group, but during the fall cruises this species was restricted to the cooler waters on the northern shelf and generally clustered with the *Limanda*-dominated cold-water group. *Peprilus triacanthus* generally appeared in the same group as the other warm-temperate species in the spring when it was distributed along the outer shelf, but in the fall this species was widespread across the shelf and tended to be more concentrated in the cooler portions of the study area and usually clustered with the semi-ubiquitous *Merluccius bilinearis*-*Urophycis chuss* group. *Peprilus triacanthus* is considerably more tolerant of cooler temperatures than the other warm-temperate species encountered in this study (Horn 1970). *Urophycis regia*, another warm-temperate species which inhabits cooler waters (Struhsaker 1969), clustered similarly to *Peprilus triacanthus*, occurring with the warm-temperate group in the spring and with the semi-ubiquitous group in the fall; however, it appeared to have slightly narrower temperature tolerances, as it was more restricted to the southern portion of the outer shelf in spring and tended to be more concentrated in deeper, warmer waters in the fall.

Absolute abundances, both of total catches and of individual species, varied to a much greater extent than did the relative abundances between species throughout the study. Because abundance trends for the fall cruises have been well documented by Clark and Brown (1977) and the change

[4]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northw. Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

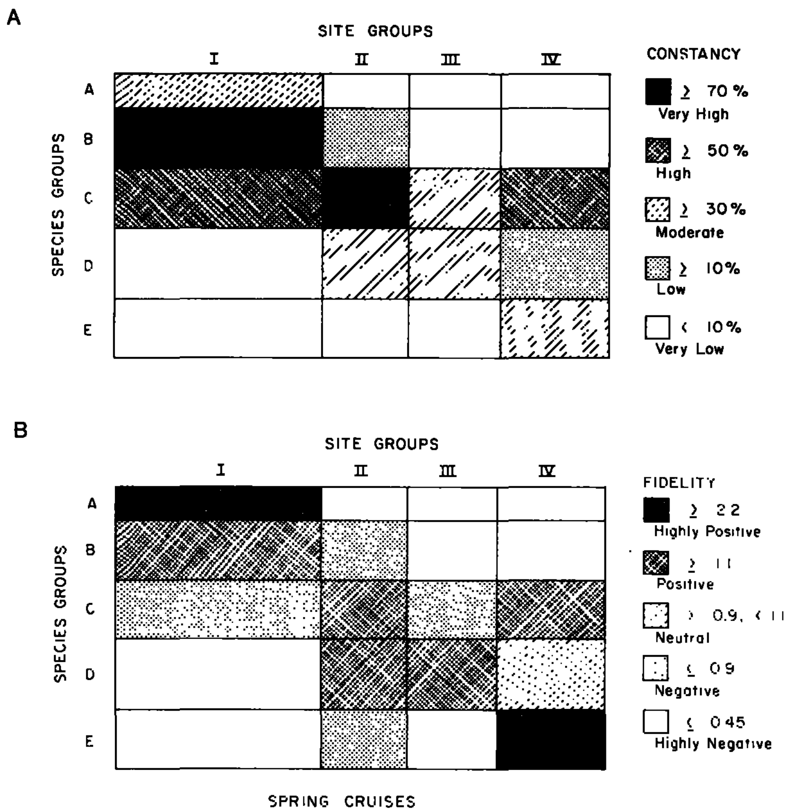


FIGURE 9.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey spring cruises, 1968-76.

TABLE 4.—Dominant species by site group for Spring NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1968-76. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I %	I $\bar{x}$%	II %	II $\bar{x}$%	III %	III $\bar{x}$%	IV %	IV $\bar{x}$%
Gadus morhua	Bo	A	44	1.4						
Pseudopleuronectes americanus	Bo	A	38	2.2						
Limanda Ferruginea	Bo	B	88	28.5	22	1.4				
Macrozoarces americanus	Bo	B	68	5.2						
Myoxocephalus octodecemspinosus	Bo	B	56	5.0						
Raja erinacea	Bo	B	77	11.9	52	1.5				
Scophthalmus aquosus	IS	B	70	4.7						
Hippoglossina oblonga	OS	C	29	1.1	84	7.6	44	2.4	63	5.2
Lophius americanus	Bo	C			58	0.7			53	1.4
Merluccius bilinearis	Bo	C	79	20.5	97	22.4	66	13.0	90	27.2
Squalus acanthias	Bo	C	73	11.1	87	30.0	82	24.6	58	12.2
Urophycis chuss	Bo	C	54	3.9	84	9.3	25	1.9	74	9.5
Centropristes striata	WT	D					40	4.2		
Paralichthys dentatus	WT	D					47	2.2		
Peprilus triacanthus	WT	D			75	14.8	57	12.3	56	19.4
Prionotus carolinus	WT	D			50	7.1	51	9.8		
Stenotomus chrysops	WT	D			24	2.1	50	15.6		
Urophycis regius	WT	D					48	7.2	35	2.0
Chloropthalmus agassizi	SI	E							31	1.6
Helicolenus dactylopterus	SI	E							59	6.7
Merluccius albidus	SL	E							38	3.1
Urophycis tenuis	Bo-SI	E							38	1.6

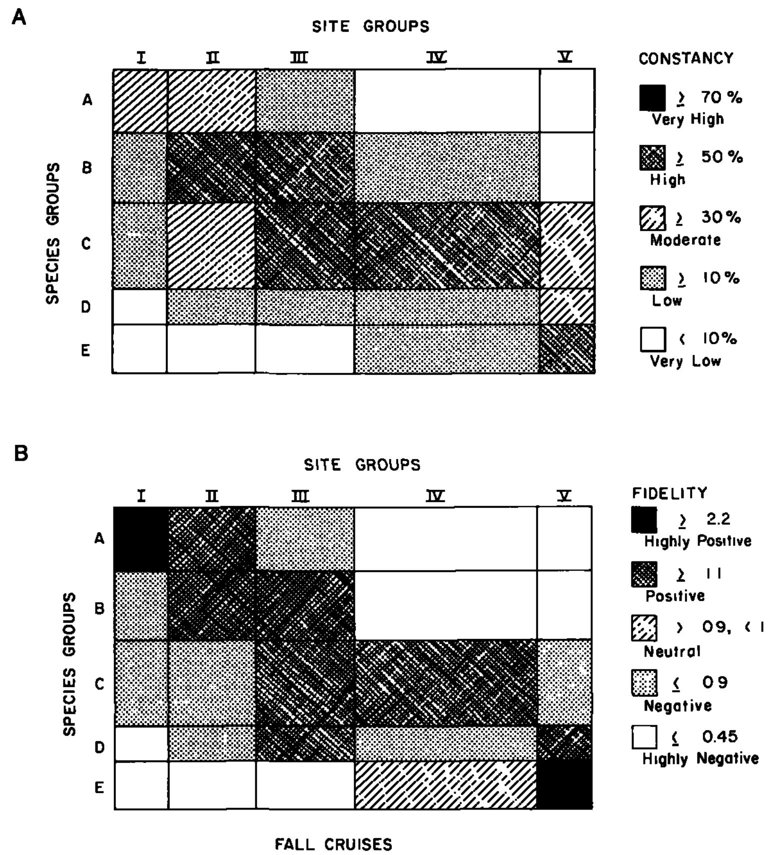


FIGURE 10.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey fall cruises, 1967-75.

TABLE 5.—Dominant species by site group for Fall NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1967-75. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I %	I $\bar{x}$%	II %	II $\bar{x}$%	III %	III $\bar{x}$%	IV %	IV $\bar{x}$%	V %	V $\bar{x}$%
Centropristes striata	WT	A	50	4.7								
Mustelus canis	WT	A	38	5.7								
Paralichthys dentatus	WT	A	61	6.7	51	13.5						
Prionotus carolinus	WT	A	75	33.3	61	10.1						
Stenotomus chrysops	WT	A	53	17.5	51	13.5	30	2.4				
Limanda ferruginea	Bo	B			65	14.1	79	18.0				
Myoxocephalus octodecemspinosus	Bo	B					52	2.7				
Pseudopleuronectes americanus	Bo	B			69	3.3	47	1.7				
Raja erinacea	Bo	B			64	3.8	58	2.7				
Scophthalmus aquosus	IS	B	52	2.9	62	3.4	25	1.0				
Squalus acanthias	Bo	B			69	16.8	77	11.3	23	5.1		
Citharichthys arctifrons	OS	C					35	2.7	49	6.4	68	11.8
Hippoglossina oblonga	OS	C			59	2.2	70	3.3	53	3.6	34	1.4
Lepophidium cervinum	OS	C							32	2.9	27	2.9
Merluccius bilinearis	Bo	C			67	10.2	92	23.0	80	20.8	58	11.3
Peprilus triacanthus	WT	C	59	15.8	65	11.1	72	19.6	65	26.5	28	5.1
Urophycis chuss	Bo	C			35	2.7	74	8.2	37	4.2	30	2.1
Urophycis regius	WT	C	40	6.5					57	14.8	40	7.9
Lophius americanus	Bo	D							31	2.2	57	3.0
Chloropthalmus agassizi	SI	E									44	5.9
Helicolenus dactylopterus	SI	E									84	21.2
Merluccius albidus	SI	E									65	7.7

in nets makes a similar analysis of the spring cruises tenuous at best, we will not consider the topic further other than to note that average abundance and biomass were higher in the northern and inshore portion of the study area during both seasons (Tables 1, 2).

CONCLUSIONS

Despite large variation in the abundances of individual species, cluster analyses of 9 yr of survey data have shown clear and consistent patterns of community composition and distribution among demersal fishes of the Middle Atlantic continental shelf. Allowing for thermal variation and misclassification of small catches, persistent site and species clusters have indicated the presence of four relatively constant and well-defined areas of faunal homogeneity in the spring and five more general areas in the fall, and five strongly recurring species associations during both seasons.

The spring site groups can be described approximately as northern inner- and mid-shelf (I), extending from shore out to about 60-80 m from Cape Cod to south of Delaware Bay; northern mid-shelf (II), occupying from around 60-80 m out to about 150 m from Cape Cod to Hudson Canyon; southern outer shelf (III), 60-150 m, from Delaware Bay to Cape Hatteras; and outer shelf-shelf break (IV), >150 m. The southern inner and mid-shelf is a thermally related transition zone between groups I and III. The outer shelf between Delaware Bay and Hudson Canyon was also a transition zone (between groups II and III), but this discontinuity does not appear to be related directly to temperature, but rather to the extent to which the northward migration of the warm-temperate species group has progressed by the time of the survey.

The five spring species groups contained one group specific to this season and four which contained common elements and properties with analogous fall groups. The first group (A) can be characterized as highly cryophilic, being virtually restricted to site group I and containing two members (*Gadus morhua* and *Hemitripterus americanus*) which were relatively absent from the study area during the fall. None of these species were major dominants, even within group I. The second group (B) is also composed of primarily boreal, cold-water species, but in this case is not completely restricted to site group I (although primarily distributed there) and contains the major dominant for that site, *Limanda ferruginea*. The third group (C) may be described as ubiquitous throughout the study area with moderate or better constancy to all site groups (Fig. 9). All members of this group are boreal or resident, and the major dominants, *Merluccius bilinearis* and *Squalus acanthias*, are the nuclear members. The fourth group (D) is composed entirely of warm-temperate members and is restricted to the warmer southern and outer shelf waters (site groups II-IV). *Peprilus triacanthus* and *Stenotomus chrysops* are the major dominants from this group. The last group (E) is composed strictly of weakly dominant slope species mostly confined to the shelf break site group (IV).

The spring warming trend noted during the study period appeared to have no major effect on the composition and distribution of fish communities in the area other than the latitudinal division between the inshore site groupings. The results of the present study are very much in accordance with the conclusions of Taylor et al. (1957) and Colton (1972) who found that while the ranges and distributions of certain species did shift with a changing thermal regime, there were no obvious overall changes in faunal composition. This is understandable when one considers that the average change encountered (about 2°C) is relatively small compared with the temperature tolerances of the species involved and the seasonal and geographic temperature variation encountered.

The five fall site groups can best be described as southern inner- and mid-shelf (I), extending out to about 60 m from Cape Hatteras to Delaware Bay and containing the area of warmest temperatures; northern inner shelf (II), extending northward from group I along a similar depth regime and containing cooler waters; northern mid-shelf (III), extending from group II out to about 90 m and occupying the area of the cold pool; outer shelf (IV), occupying the area between groups I and III and about 150 m; and shelf break (V), >150 m. While, again, with these groups there is some overlap (particularly with groups I and II as discussed above), their definition is fairly good considering the rapidly changing environmental conditions and migratory activity of fish during this period.

The fall species associations, as noted above, have much in common with those noted in the spring. The small cryophilic group is absent, but the terms applied to the other four spring groups may be applied here as well. An exclusively boreal-resident group (B) persists on the northern inner- and mid-shelf, including four members of the spring cold-water group B, one member of the cryophilic group, and *Squalus acanthias*, a ubiquitous dominant in the spring found only in the northern portion of the study area in the fall. The ubiquitous spring group (C) persists with *Merluccius bilinearis* the major dominant, and two other common members from the spring group, but the fall group is no longer exclusively boreal-resident in faunal affinity and the group is distributed primarily in more northerly and deeper waters. Two warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, join this group as major dominants, while the other warm-temperate species, dominated by *Prionotus carolinus* and *Stenotomus chrysops*, continue to occur in the same group (A) but show a dramatic change in distribution, occurring on the inner shelf rather than the outer as in the spring. The shelf break group (E) shows the same composition and distribution as in the spring, while the fifth group (D), which did not occur in the spring, is composed of nondominant eurybathyic species which occur sporadically across all but the southern inner site group.

It is obvious that although the two sampling periods included the two extremes of average water temperatures in the study area, the fall (warm extreme) is a much more dynamic period than the spring (cool extreme) for the fish communities in the region. This appears to be related in large part to the much less stable thermal regime encountered in the fall, particularly in shallower portions of the study area. Thermal gradients developed during the warmer months on the inner shelf are much stronger than those encountered on the mid-shelf during the spring, and because cooling waters mix or turn over while warming waters stratify, the fall gradients break down much more quickly than those in the spring. As a result, a fish community in this region may be subjected to rapidly changing environmental temperatures by a number of factors. A relatively small shift of water masses in the vicinity of a strong thermal gradient, migration across a gradient, or rapid cooling and mixing along the gradient all subject these communities to abrupt changes of temperature (Parr 1933), and it is not surprising that the site groupings based on faunal similarities found in the inner portion of the study area during the fall exhibited wide temperature ranges (Fig. 7). Parr (1933) pointed out that the temperature-related distributions of organisms in the vicinity of a strong thermal gradient may be more influenced by the magnitude of short-term temperature changes than by the actual temperatures encountered. This concept may well have application to the formation of the three innermost site groups identified during the fall; for although the groups strongly overlap with respect to the temperature ranges encountered, there is a considerable difference in the strength of the thermal gradients and presumably the short-term temperature variations encountered within each, with group I being primarily sited in the region of the sharpest gradients and group III being located in the most thermally stable area.

The distributional patterns noted in this paper lead to the conclusion that continental shelf demersal fish communities in the Middle Atlantic Bight are largely structured by temperature on the inner- and mid-shelf and by depth on the outer shelf and shelf break. This is not at all unexpected considering the sedimentary and topographical uniformity of the inner- and mid-shelf (Emery and Uchupi 1972) and the large annual variation in bottom-water temperature in the inshore region, with the converse holding true along the outer shelf and shelf break. Scott (1982) found the distributions of a number of groundfish species on the Scotian Shelf to be related to bottom sediment type. Although substrate preference indices were not generated during the present study, comparisons of species group distribution with bottom sediment type maps do not indicate any strong species group-sedimentary relationships. This contrast may be the result of two major differences between the continental shelves in the Middle Atlantic Bight and off Nova Scotia; there is a much more variable sedimentary environment and a considerably smaller annual range of bottom-water temperatures on the Scotian Shelf.

Tyler (1971) examined latitudinal variation in the regular and seasonal components of several nearshore Atlantic marine fish communities, and concluded that the proportion of seasonal and occasional components to regular components varied directly with annual variation in water temperature. The results of the present study are certainly in accord with this conclusion, in that the most highly variable area in terms of annual water temperature variation (the southern inner- and mid-shelf) was also the most variable area in terms of community composition, but it is also evident that Tyler's statement cannot be taken axiomatically. The outer shelf, although very homothermic, was also subject to considerable seasonal variation in community structure because of the changing relationship between the stable thermal regime on the outer shelf and the highly varying regime in adjacent inshore waters. During the spring, when inshore water temperatures were depressed well below those on the outer shelf, the outer shelf served as a refuge for the warm-temperate species association which occurs largely inshore when water temperatures there become elevated above those on the outer shelf.

It is also interesting to note that while for the most part the communities observed here are structured by species associations that behave as a group in response to environmental variation, two of the most successful species (*Peprilus triacanthus* and *Squalus acanthias*) are those which show the least permanent group affinities. As noted above, the success of *P. triacanthus* may be due in part to the species' very wide thermal tolerance, but *S. acanthias* was one of the more thermally restricted species encountered in the study, being restricted to waters less than 14°C.

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