LONG-TERM RESPONSES OF THE DEMERSAL FISH ASSEMBLAGES OF GEORGES BANK

WILLIAM J. OVERHOLTZ[1] AND ALBERT V. TYLER[2]

ABSTRACT

The resilience of demersal fish assemblages on Georges Bank was investigated with data from seasonal bottom trawl surveys conducted by the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Massachusetts, from 1963 to 1978. Cluster analysis proved to be a useful statistical method for delineating assemblage boundaries and associated species. Assemblages persisted over the long-term and changed spatial configuration only slightly on a seasonal basis. Declines in biomass, numerical density, and changes in relative abundance occurred ranging from mild to severe. Assemblage changes were probably triggered by intense fisheries as well as inherent trophic dynamics of component species. Results have useful multispecies management connotations. The assemblage concept appears to be an appropriate operational or conceptual framework for further management and modeling applications.

Most community ecological studies have necessarily concentrated on the short-term aspects or seasonality of assemblages. Typically 1 to 3 yr of field measurements are analyzed with information theory, niche breadth procedures, or multivariate statistical methods. Demersal fish assemblages in particular have been investigated in a number of locations [see studies by Tyler (1971), Oviat and Nixon (1973), Stephenson and Dredge (1976), Hoff and Ibara (1977), Gabriel and Tyler (1980), and Inglesias (1981)]. The recurrent theme in most of these studies centers around seasonally varying diversity because of environmentally induced migration, temperature usually acting as the dominant driving variable.

Unfortunately, many interesting questions cannot be addressed in these studies because of their short-term horizon. It is important to consider the long-term ramifications of fishery system responses. The temporal scale referred to here as "long-term" does not refer to geologic time, but rather ecological time, the span of years during which the actions of fishery ecologists evoke system responses. Fishery ecologists are limited in their ability to function within this time frame. For instance, a plant ecologist could predict with some certainty the type of forest that would eventually occupy a cleared site, if left undisturbed, but comparable knowledge for fishery systems is lacking, especially in the marine environment.

Are fish assemblages stable? How do they respond to exploitation? Holling (1973) investigated system responses to man's activities, showing that in closed systems, such as freshwater lakes, the propensity to remain stable is high, but not infallible. Smith (1972) critiqued the Great Lakes experience, concluding that the activities of man, notably fishing and pollution, when coupled with biological interactions, caused significant community alterations in this system. Few marine studies, with the exception of Soutar and Isaacs (1969), Sutherland (1980), DeVries and Pearcy (1982), and some general overview papers (Brown et al. 1976; Richards et al. 1978), have stressed the long-term temporal and spatial aspects of marine system response.

Longer term temporal and spatial questions were examined with data from research conducted at the Northeast Fisheries Center (NEFC) (Grosslein 1969). Concentrating on Georges Bank, we used cluster analysis to produce yearly fall and spring dendrograms for the period 1963-78 and 1968-78, respectively. Assemblages were defined, component species were identified, distributional maps plotted, and the information was examined to elucidate long-term temporal and spatial patterns. Further analyses led to trajectories of species catch-per-unit-effort (CPUE), assemblage total biomass, estimates of intra-assemblage diversity, and other measures of community response. It is suggested that fishing, coupled with interspecific interactions, appeared to have played a major role in determining trends in the Georges Bank assemblages.

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[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; present address: Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; present address: Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada.

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METHODS

Georges Bank, a large, submerged, marine plateau, is located off the northeastern coast of the United States (Fig. 1). It has been the site of an intense fishery for several centuries, and a large international fleet exploited the area from the 1960's to the mid-1970's. The NEFC has conducted annual bottom trawl surveys on the Northwest Atlantic continental shelf since the autumn of 1963. Annual spring surveys commenced in 1968 and, in addition, several summer and winter cruises have been undertaken on an intermittent basis. Surveys were conducted from Nova Scotia to Hudson Canyon from 1963 to 1966 and coverage was extended to Cape Hatteras beginning in 1967. Grosslein (1969) and Azarovitz (1982) described the details and justification for the surveys, but a brief summary is appropriate.

The objective of the surveys is to obtain statistically meaningful abundance estimates of the offshore marine fish populations in the aforementioned areas. Secondary objectives included the collection of data for distribution studies, age and growth determinations, predator-prey interactions, and a host of special purpose investigations. The potential area was divided into zones (strata) based on depth and biological considerations. Stratified random samples were selected with allocation to each strata proportional to its area. A 30-min sample with a standardized research bottom trawl and a 1.25 cm cod end liner was accomplished. All fish, as well as major invertebrates, were sorted to species, weighed, and measured, and some fish were sampled for other

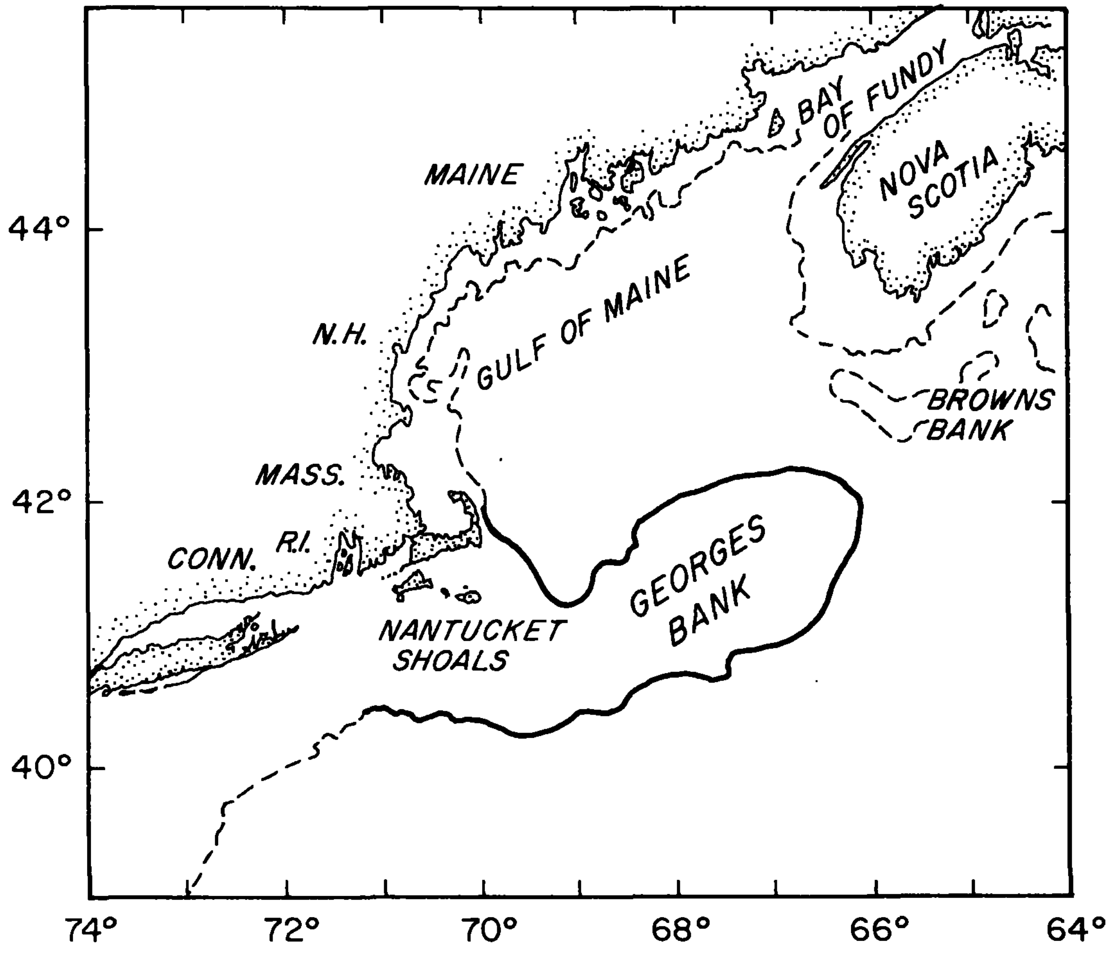


FIGURE 1.—Georges Bank and Gulf of Maine region with shoreline place names and other associated geographical landmarks.

analyses. Sampling frequency averages about one station for every 250 mi^2 or roughly 300 locations in a normal survey from Cape Hatteras to Nova Scotia.

Data from a selected portion of this time series was used in cluster analyses that defined demersal fish assemblages. Specifically, a group of 36 species representing the dominant fishes on Georges Bank, were chosen as the focus for the investigation (Table 1). This choice was based on a preliminary examination of the data to determine which species were most important in terms of biomass and numerical density. Catches (kg) for each of the species from every station in a particular cruise were organized into a data matrix and processed with an agglomerative cluster analysis program (Keniston 1978). To remove skewness in the species matrices, we transformed the data prior to clustering by using an ln $(x + 1)$ conversion. Station dissimilarities were calculated by using the Bray-Curtis dissimilarity index, an ecological distance measure that is sensitive to dominant species (Clifford and Stephenson 1975; Boesch and Swartz 1977).

TABLE 1.—Species cited by common name in the text.

Common name	Scientific name
Spiny dogfish	*Squalus acanthias*
Winter skate	*Raja ocellata*
Little skate	*Raja erinacea*
Smooth skate	*Raja senta*
Thorny skate	*Raja radiata*
Atlantic herring	*Clupea harengus*
Alewife	*Alosa pseudoharengus*
Offshore hake	*Merluccius albidus*
Silver hake	*Merluccius bilinearis*
Atlantic cod	*Gadus morhua*
Haddock	*Melanogrammus aeglefinus*
Pollock	*Pollachius virens*
White hake	*Urophycis tenuis*
Red hake	*Urophycis chuss*
Cusk	*Brosme brosme*
American plaice	*Hippoglossoides platessoides*
Summer flounder	*Paralichthys dentatus*
Fourspot flounder	*Paralichthys oblongus*
Yellowtail flounder	*Limanda ferruginea*
Winter flounder	*Pseudopleuronectes americanus*
Witch flounder	*Glyptocephalus cynoglossus*
Windowpane	*Scophthalmus aquosus*
Gulf stream flounder	*Citharichthys arctifrons*
Atlantic mackerel	*Scomber scombrus*
Butterfish	*Peprilus triacanthus*
Bluefish	*Pomatomus saltatrix*
Blackbelly rosefish	*Helicolenus dactylopterus*
Longhorn sculpin	*Myoxocephalus octodecemspinosus*
Sea raven	*Hemitripterus americanus*
Cunner	*Tautogolabris adspersus*
American sand lance	*Ammodytes americanus*
Atlantic wolffish	*Anarhichas luptus*
Ocean pout	*Macrozoarces americanus*
American goosefish	*Lophius americanus*
Short-finned squid	*Illex illecebrosus*
Long-finned squid	*Loligo pealei*

The resulting dissimilarity matrix was used in a group average fusion strategy to combine stations with similar species distributions (Clifford and Stephenson 1975). These station combinations were displayed in dendrograms, which were examined and assemblage groups were chosen by two criteria: large-scale separations, as shown in Figure 2, and dissimilarity levels. Stations from these assemblage groups were plotted on cruise maps from the original sampling plan and areas were delineated. This process was repeated for all spring and fall cruises to provide a consecutive series of maps, which were then examined for continuity (Fig. 3). Finally, data from several consecutive years were pooled to delineate assemblages designated, based on nearby geographic features or depth zones.

Species lists were prepared for the assemblages outlined in the pooled cluster results, and data were analyzed to further define the structure of each group. Length frequencies from species in the different assemblages were used to separate life history stages and catch-per-tow data were used to investigate trends in distribution and abundance. Examination of food habit data in the literature and NEFC documents gave further insight into assemblage structure. Trajectories of assemblage CPUE for selected species were plotted and examined for long-term trends. Total assemblage CPUE was also investigated and compared with previous trends reported by other authors for the region.

Gradient analyses were performed with the objective of explaining species distributions based on a set of location, physical, and chemical variables. Canonical correlations, using information on latitude, longitude, depth, bottom temperature, bottom oxygen, and bottom salinity, were employed to define possible gradients that might be useful indicators of species distribution (Pimentel 1979). Data for the autumn cruise were obtained from measurements of bottom temperature and depth made aboard the RV *Albatross IV* (U.S.A.) 20 October to 5 November 1976, and corresponding information on bottom salinity and oxygen from the RV *Anton Dohrn* (Federal Republic of Germany) 14 November to 1 December 1976. Information for the spring cruise was procured from measurements of bottom temperature and depth from the RV *Albatross IV*, 17 April to 3 May 1978, and salinity and oxygen data that was obtained from the RV *Argus* (Union of Soviet Socialist Republics) from 13 to 28 April 1978; these two data sets were chosen because they corresponded closely in time to the available station information.

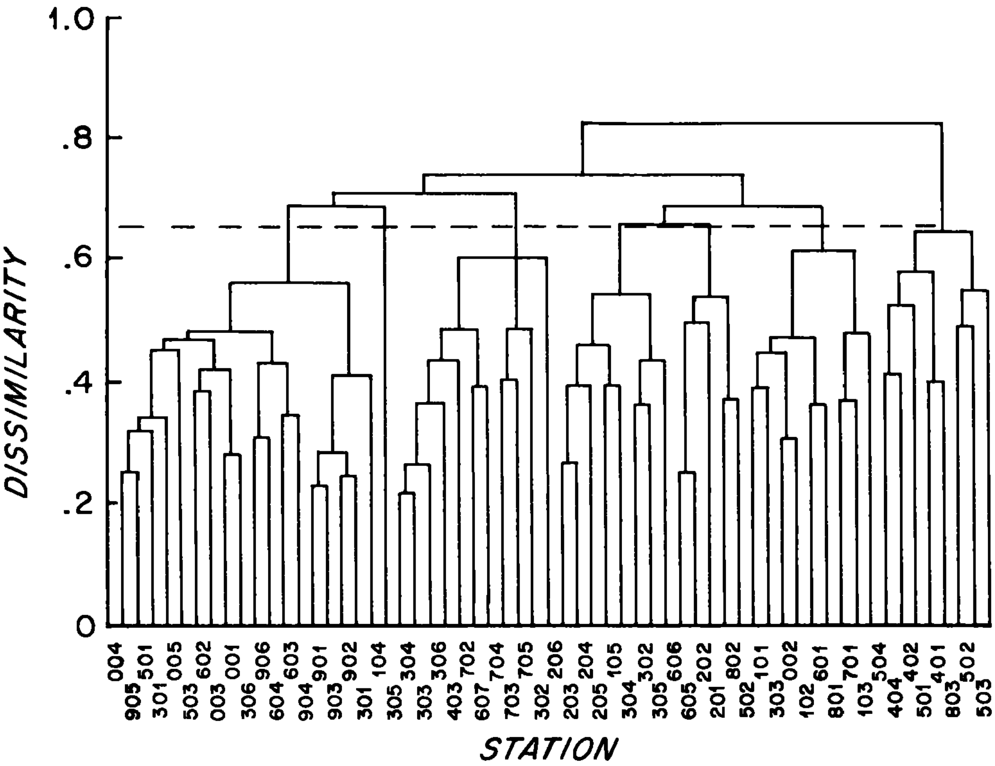


FIGURE 2.—Typical dendrogram, autumn 1966, showing cluster station groups and dissimilarities. Dashed line indicates a dissimilarity of 0.65.

RESULTS

Five important assemblage groups were present on Georges Bank from fall 1963 to 1978. For reference, we name these groups: Slope and Canyon, Intermediate, Shallow, Gulf of Maine Deep, and Northeast Peak. A consistent spatial pattern emerged as consecutive fall cruises were examined and plotted. The same five groups appear to have been present in similar locations since 1963. These five assemblages were present at the mid- and endpoints of the fall time series also (Fig. 3). The groups appear to change their spatial configuration slightly on an annual basis, but the general area of each group was maintained. Lists of the dominant species in each assemblage are given in Table 2.

The total area that each assemblage encompassed through time (years) was delineated by pooling the observations from consecutive years. Figure 4 shows an example of a representative assemblage from the spring and fall, respectively. The groups overlapped surprisingly little through time with the exception of a few border stations along adjacent assemblages.

TABLE 2.—Assemblage species associations from cluster results (demersal species only).

- Slope and canyon:
  - Silver hake
  - White hake
  - Red hake
  - Gulf stream flounder
  - Offshore hake
  - Fourspot flounder
  - Blackbelly rosefish
  - American goosefish
- Intermediate:
  - Winter skate
  - Little skate
  - Red hake
  - Silver hake
  - Atlantic cod
  - Haddock
  - Sea raven
  - American goosefish
  - Ocean pout
  - Longhorn sculpin
  - Yellowtail flounder
- Shallow:
  - Winter skate
  - Little skate
  - Silver hake
  - Atlantic cod
  - Haddock
  - Pollock
  - White hake
  - Red hake
  - Summer flounder
  - Yellowtail flounder
  - Winter flounder
  - Windowpane
  - Longhorn sculpin
  - Sea raven
  - Ocean pout
  - Sand lance
  - American goosefish
- Gulf of Maine Deep:
  - Thorny skates
  - American plaice
  - Witch flounder
  - White hake
  - Silver hake
  - Atlantic cod
  - Haddock
  - Cusk
  - Atlantic wolffish
- Northeast Peak:
  - Thorny skate
  - Atlantic cod
  - Haddock
  - Pollock
  - White hake
  - Winter flounder
  - Ocean pout
  - Longhorn sculpin

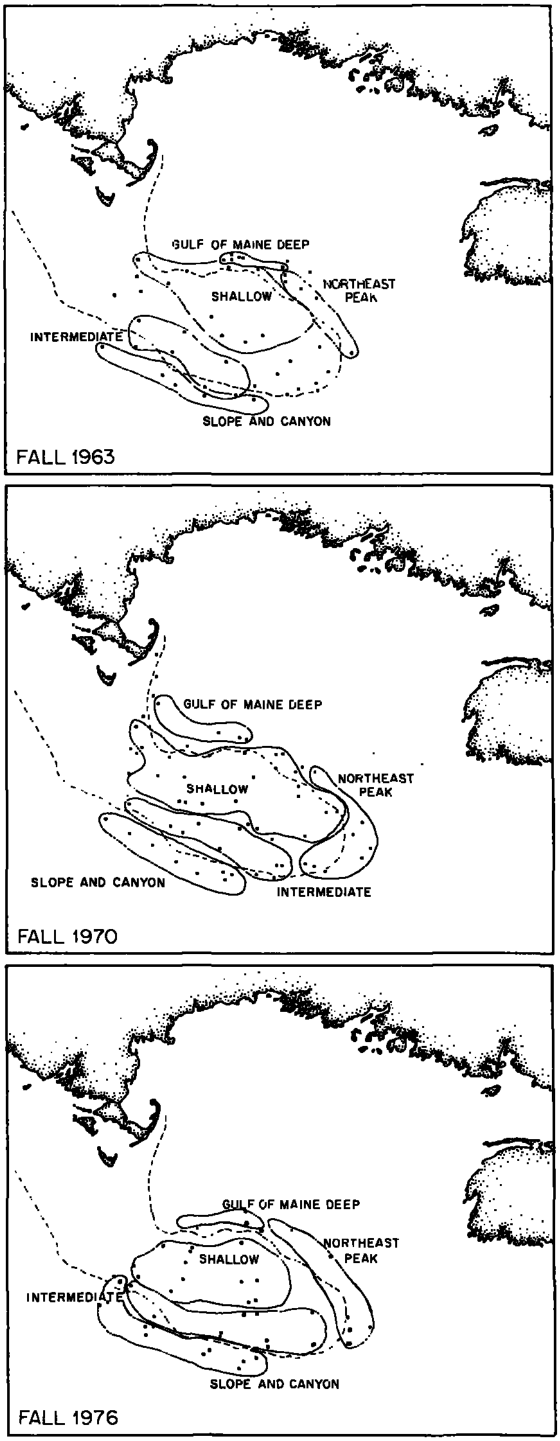


FIGURE 3.—Georges Bank assemblages for three autumn surveys 1963, 1970, 1976.

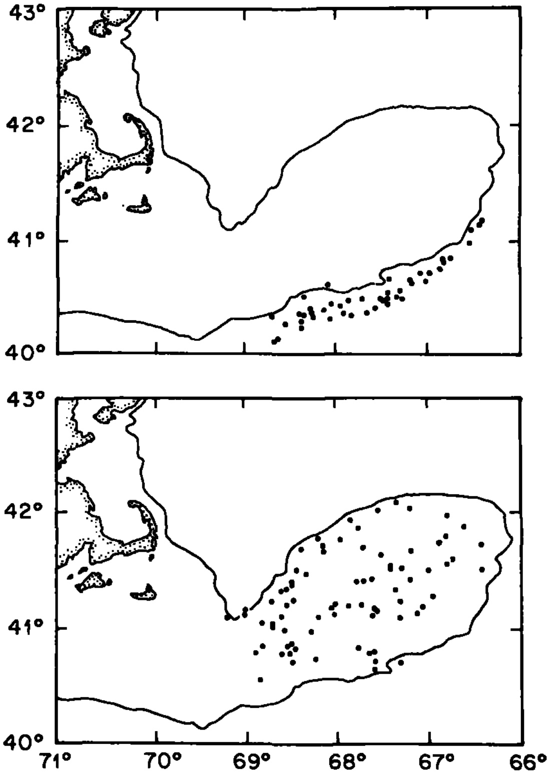
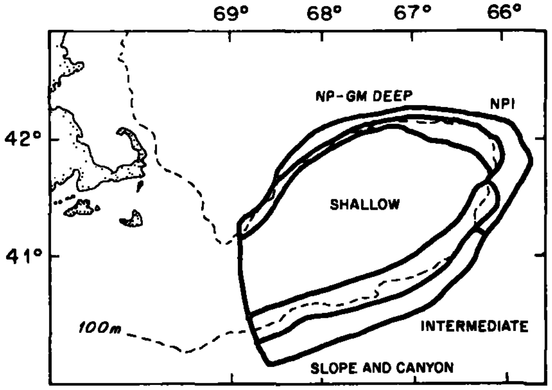
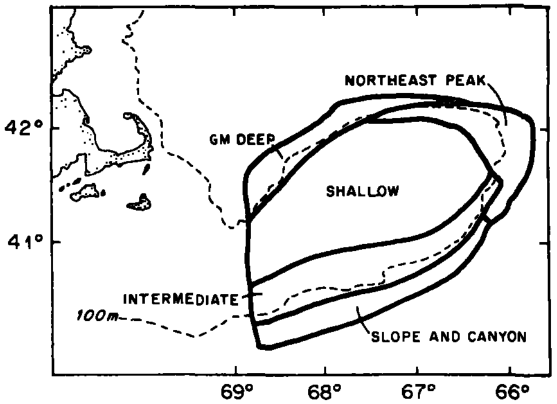


FIGURE 4.—Sample pooled station distributions for the Slope and Canyon assemblage, spring 1968-73 (top panel) and the Shallow assemblage, autumn 1963-67.

Data for all cruises were pooled by season and used to generate composite maps of general assemblage areas, for the spring and autumn (Fig. 5). The Slope and Canyon assemblage appears to encompass a similar area regardless of season, while some of the other assemblages changed slightly. The Shallow assemblage covered most of Georges Bank in the spring (Fig. 5) and was slightly smaller in the fall (Fig. 5). The Intermediate assemblage is somewhat larger in the fall (Fig. 5), suggesting a migration of the species in this area to shallower water as the year progresses. Assemblages in the spring appear to follow depth contours resulting in the elongate shape of the groups at this time (Fig. 5). The Northeast Peak Interior (NPI) and Northeast Peak-Gulf of Maine Deep (NP-GM Deep) assemblages show definite seasonal spatial changes when compared with the Gulf of Maine Deep (GM Deep) and Northeast Peak assemblages in the fall (Fig. 5). The general shape and location of the fall assemblages suggests that a different set of oceanographic and biological forcing factors are important in deter-



GEORGES BANK SPRING ASSEMBLAGES



GEORGES BANK FALL ASSEMBLAGES

FIGURE 5.—Composite maps showing seasonal changes in the Georges Bank assemblages and their approximate areas. NPI = Northeast Peak Interior; NP-GM Deep = Northeast Peak-Gulf of Maine Deep; GM Deep = Gulf of Maine Deep.

mining the distribution of fish. The Northeast Peak assemblage, for instance, spans several depth zones and encroaches on the Shallow assemblage, reducing its area during this part of the year.

The assemblage maps presented in Figure 5 were useful for organizing the 36 species of Table 1 into their corresponding demersal subunits (Table 2). Four basic species categories were defined in the various assemblages. These included ubiquitous species, resident species, periodics, and those resident species present in several assemblages during different parts of their life history. Ubiquitous species, such as ocean pout, goosefish, sea raven, and Atlantic cod, were found with regularity in almost all of the assemblages. Resident species, such as little skate, winter skate, longhorn sculpin, yellowtail flounder, winter flounder, American plaice, and witch founder, were present in only one or two assemblages in abundance. Periodic or seasonal migrants include bluefish, butterfish, and mackerel, as well as short-finned squid and long-finned squid. These species moved in and out of the various assemblages on a seasonal basis with temperature being a likely dominant force, and were often highly variable in terms of their abundance and were therefore not included in Table 2.

A number of species, including silver hake, red hake, white hake, and haddock, were present in more than one assemblage as different life history stages. Silver hake, for example, are found in the Slope and Canyon and Shallow assemblages, with adults on the average, occurring more frequently in the Slope and Canyon and Gulf of Maine Deep assemblage, while juveniles are more abundant in the Shallow assemblage. It appears that for many of the abundant fish species on Georges Bank, adults occupy the deeper peripheral assemblages while juveniles of these same species occupy the shallower zones during much of the year.

ASSEMBLAGE TRAJECTORIES

Assemblage CPUE indices were calculated for several of the spring and fall assemblages and used for evaluating temporal trends in total catch and catch by species. Assemblage CPUE declined dramatically in the mid-1960's to early 1970's in four of five Georges Bank assemblages in fall (Fig. 6). In particular, research catches in the Shallow, Northeast Peak, and Gulf of Maine Deep assemblages reached all-time lows in the early 1970's, coincident with large increases in international effort and landings at that time (Figs. 6, 7). International effort, measured in thousands of days fished, increased threefold over the period 1960-69 (Fig. 7). Assemblage biomass showed some signs of recovery in the late 1970's when good year classes of Atlantic cod, haddock, and other species occurred and international effort declined due to the Magnuson Fishery Conservation and Management Act of 1976 (Figs. 6, 7).

Research catch of silver hake, fourspot flounder, red hake, white hake, and black belly rosefish remained nearly stable over the spring period (1968-75), then increased abruptly after 1976 due to increases in the silver hake (Fig. 8A).

Total catch for the fall time series was also stable for most years, until 1972 when silver hake and red hake abundance fluctuated (Fig. 8B).

Figure 8C shows the trends in percent by weight for the five species during fall indicating a change in biomass dominance for silver hake and red hake. Blackbelly rosefish and fourspot flounder showed the

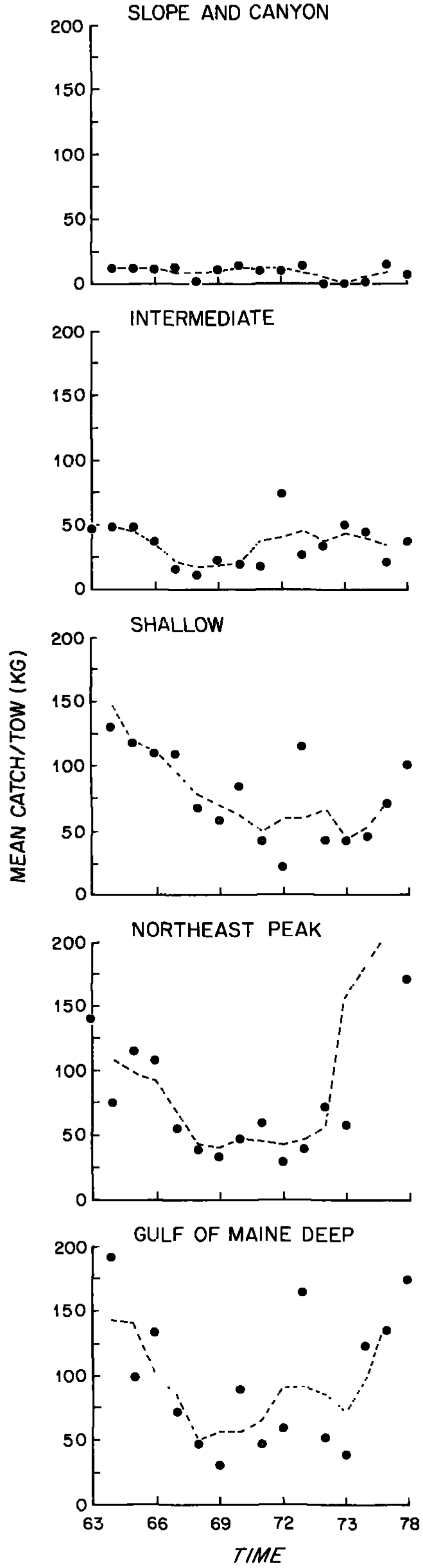


FIGURE 6.—Mean catch per tow (kg) from NEFC Georges Bank bottom trawl surveys for autumn 1963-78 for the five assemblages. Dashed line indicates a 3-yr moving mean of the plotted data points.

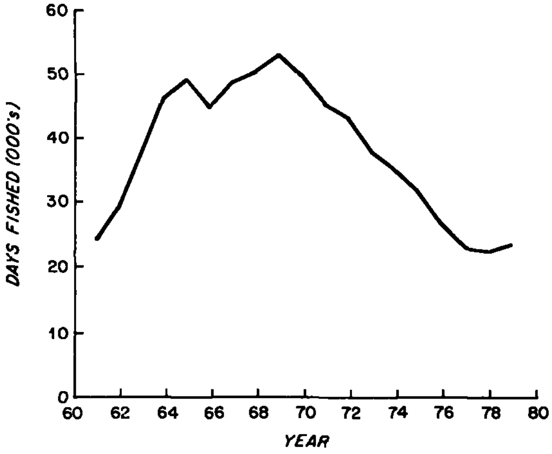


FIGURE 7.—Unstandardized effort data in thousands of days fished for the Georges Bank demersal fishery, all countries, for 1961-79, expressed as 3-yr moving means.

same trends as in the former case, but represented more of the catch on a percent weight basis in the later years of the fall time series (Fig. 8C). Gulf Stream flounder was actually one of the more important species numerically during the mid-years of the series (Fig. 8D). The same general trend for red and silver hake, and the other species is apparent in the percent by numbers data (Fig. 8D).

The shallow assemblage was much more diverse than the Slope and Canyon assemblage. The major species of importance were Atlantic cod, winter skate, longhorn sculpin, little skate, yellowtail flounder, and haddock. Mean catch per tow in the fall time series declined dramatically from 202 kg in 1963 to 22 kg in 1972 and subsequently rose to 99 kg in 1978 or about one-half the 1963 value (Fig. 6). Winter flounder, longhorn sculpin, and winter skate appear to have remained fairly constant in abundance over the spring time period, while Atlantic cod, windowpane flounder, and little skate displayed an increasing trend in biomass (Fig. 9A). Yellowtail flounder and haddock showed declining mean catches over this interval. The fall time series, since it is longer, clarifies some of the observed spring trends. Cod and winter flounder CPUE remained relatively stable over the fall period, while windowpane flounder, winter skate, and little skate appear to have increased from 1972 onward (Fig.

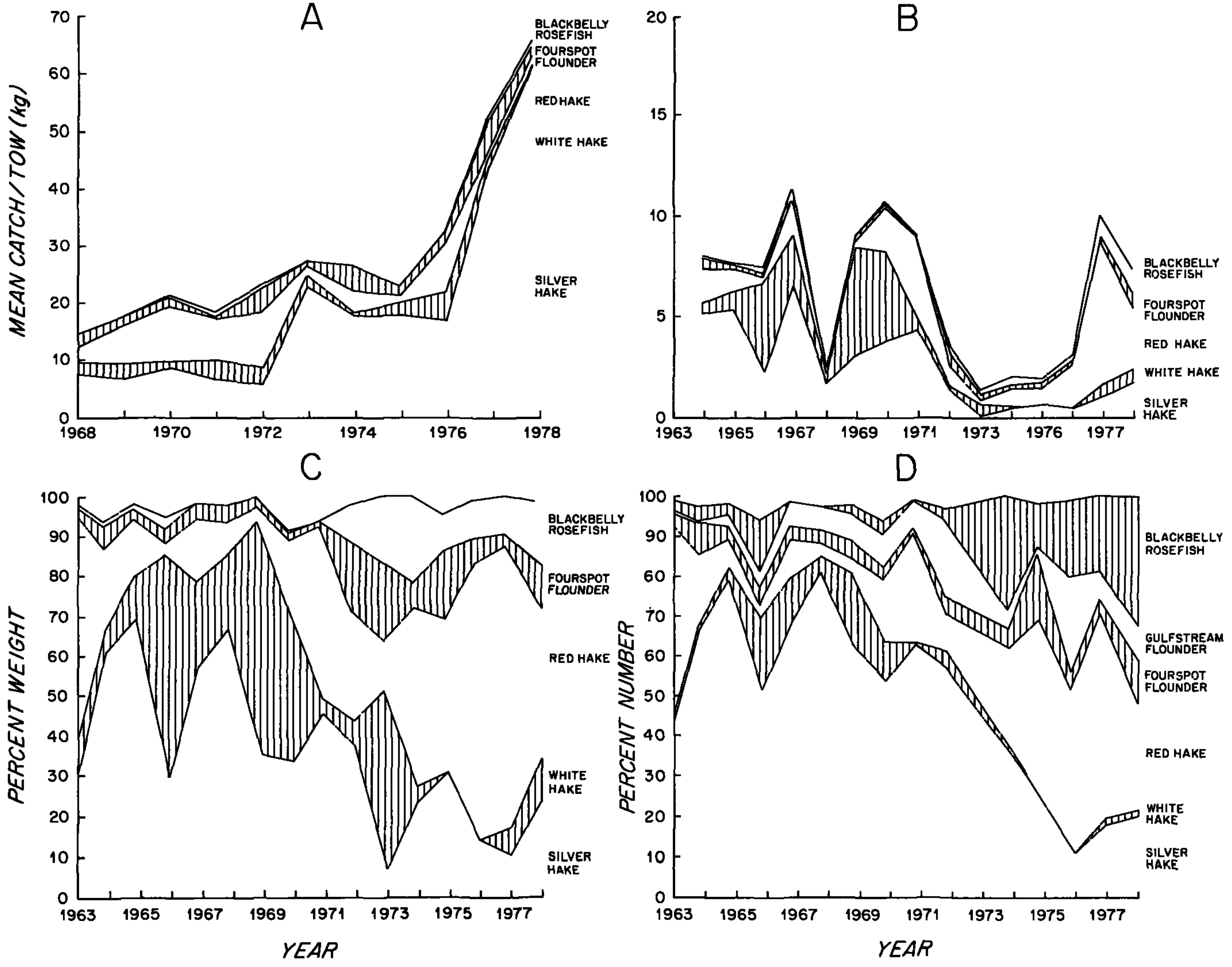


FIGURE 8.—Responses of species from the Slope and Canyon assemblage demersal fish community over the period 1963-78. Panels A and B express cumulative absolute abundance, mean catch/tow (kg) for spring 1968-78 and autumn 1963-78, respectively. Panels C and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

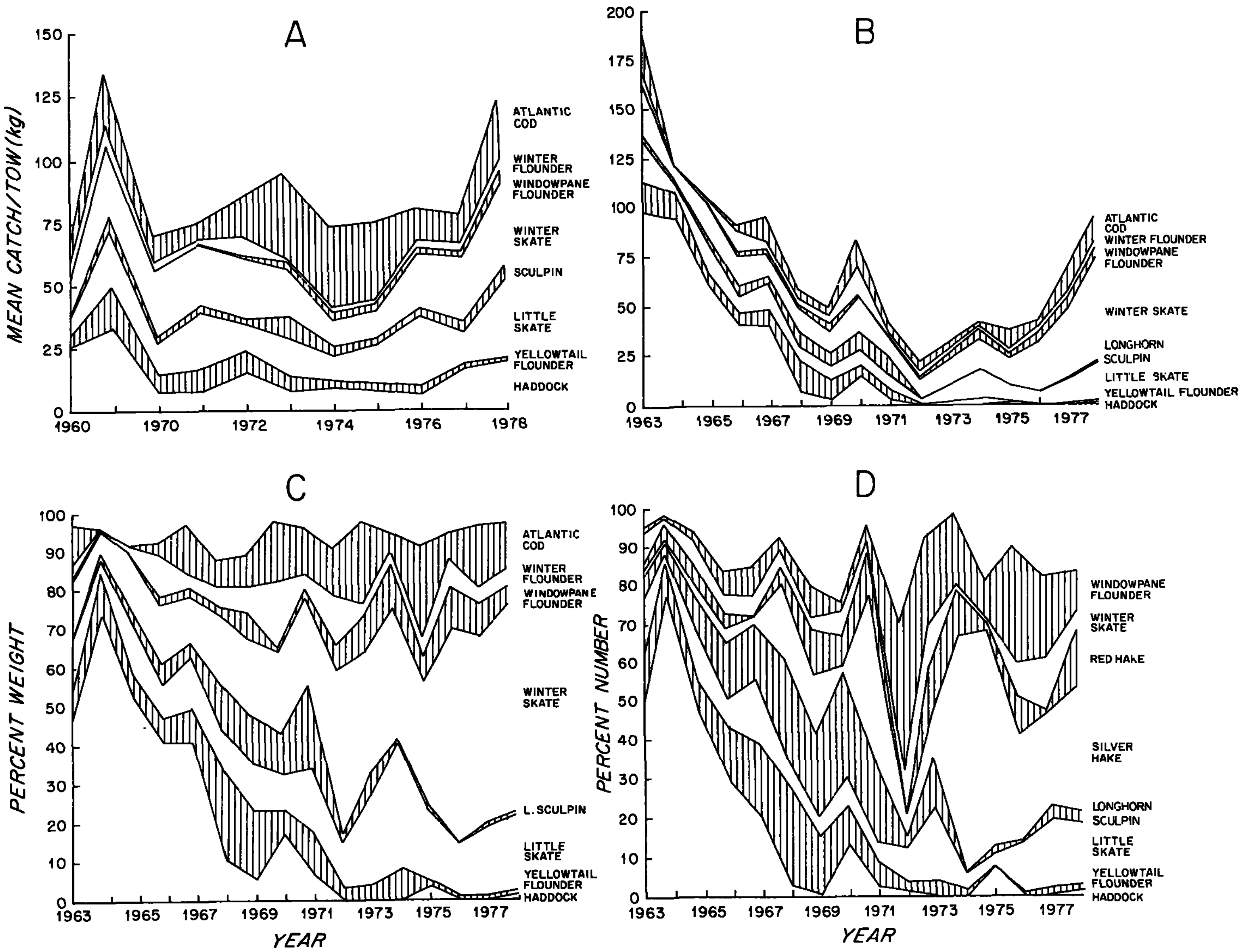


FIGURE 9.—Responses of species from the Shallow assemblage demersal fish community over the period 1963-78. Panels A and B express cumulative absolute abundance, mean catch/tow (kg) for spring 1968-78 and autumn 1963-78, respectively. Panels C and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

9B). Haddock CPUE, on the other hand, declined dramatically from 97.3 kg in 1963 to 0 in 1972, remaining at very low levels of abundance in the later years. Yellowtail flounder fluctuated from 15 kg in 1963 to a low of 6 kg in 1966, increased from 1966 to 1969, and declined through 1978 (Fig. 8B).

An examination of trends in cumulative percent by weight and number trajectories for the Shallow assemblage highlighted some interesting points. Atlantic cod comprised a fairly constant proportion of the species biomass for all the years except 1964 and 1965. Longhorn sculpin, yellowtail flounder, and to a lesser extent winter flounder, made up an increasing part of the biomass of this assemblage during 1966-71 and then all declined in importance (Fig. 9C). Haddock, as previously noted, experienced a pronounced decline in abundance from the early 1960's and was only present at very low levels from 1972 to 1978. Winter skates, little skate, and windowpane flounder accounted for an increasing percent of the biomass in this assemblage from the early 1970's onward (Fig. 9C).

When cumulative percent by number was investigated, silver hake and red hake became important (Fig. 9D). Silver hake was the numerical dominant through most of the mid- and late 1970's. This trend was due entirely to increased numbers of juvenile silver hake that represented a small amount of biomass. This same phenomenon applies to red hake, which enjoyed several periods of increased abundance as a proportion of the total numerical density from 1963 to 1978. Winter skate numbers remained relatively unchanging from 1963 to 1976 and then rose slightly in the late 1970's. Trends for windowpane flounder, longhorn sculpin, little skate, yellowtail flounder, and haddock follow the cumulative absolute and percent weight data (Fig. 9B, C, D).

The other Georges Bank assemblages were investigated using the same techniques, but on a much less intense scale. Total mean catch/tow for the Intermediate, Gulf of Maine Deep, and Northeast Peak assemblages is displayed in Figure 6 for the fall surveys 1963-78. The trends in total CPUE follow the same basic patterns for all three groups, a high initial period followed by a decline and subsequent recovery in the mid- to late 1970's.

General decreases in the catch of throny skates, haddock, and cod were responsible for the downward trend in CPUE for the Northeast Peak assemblage, but the recovery that occurred in the late 1970's was due primarily to increased haddock biomass (Figs. 6, 10). The Northeast Peak assemblage is fairly simple in species composition, and although some fluctuations in cumulative percent by weight occurred, the same four species remained dominant over the period (Fig. 10.)

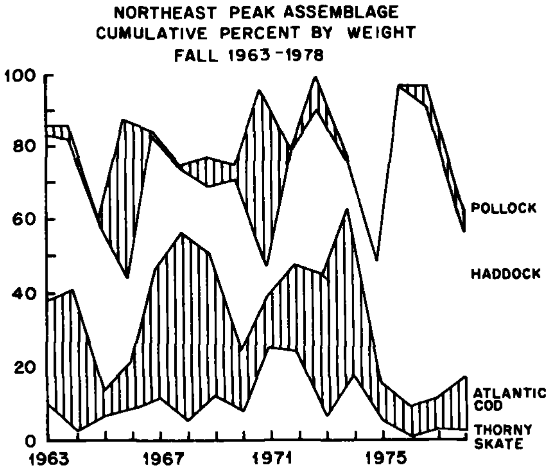


FIGURE 10.—Reponses of species from the Northeast Peak assemblage demersal fish community expressed as cumulative percent by weight for autumn 1963-78.

Time sequence cluster analyses were useful as further indicators of temporal trends in these groups. Species biomass for the Slope and Canyon assemblage did not appear to follow any clear long-term trend (Fig. 11). Enough fluctuation in CPUE occurred to mask any trend, and no clear pattern was established. This same analysis on the Shallow assemblage showed three distinct temporal clusters, composed of consecutive years (Fig. 11). Using this perspective and Figure 9, there appears to have been three periods of significant change in relative abundance during the fall time series; an initial period dominated by haddock, intermediate period with high yellowtail, longhorn sculpin, and winter flounder catches, and finally a group with little skate, winter skate, and windowpane flounder as the dominant species.

GRADIENT ANALYSIS

Gradient analyses of two selected Georges Bank data sets did not prove to be as useful as was hoped, but some information and insight were gained and the dimensionality of the large multivariate data sets involved was much reduced. The data set used in the fall 1976 canonical correlation analysis accounted for about 26% of the variation in species distribution for 32 selected species of interest. The variables included in the analysis were latitude, longitude, depth, bottom temperature, bottom salinity, and bottom oxy-

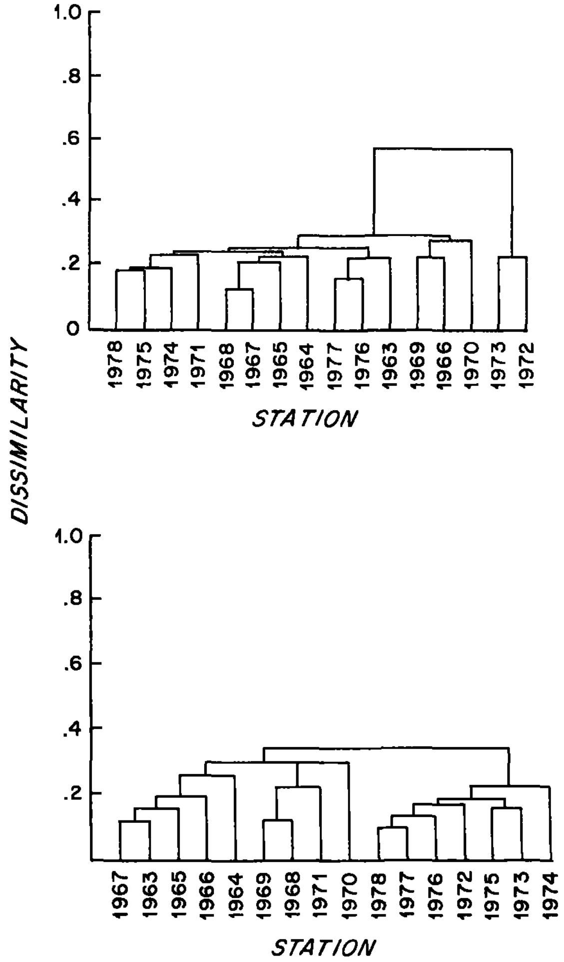


FIGURE 11.—Time sequence cluster analyses for autumn 1963-78 for the Slope and Canyon (top panel) and Shallow (bottom panel) assemblages on Georges Bank.

gen. The first three canonical axes accounted for 73.9% of this total, a cumulative redundancy of 19.0% (Table 3). The first canonical variable (CV) reflects the importance of depth and to a lesser degree bottom salinity, in determining the distribution of these species. Although none of the correlation loadings for CV1 are particularly high, the gadoids, as a group, show a positive trend. Many of the shallow-water species, such as little skate, winter skate, and most of the flounders, showed negative correlations with this canonical variable. The other two CV's reflect the location variables of latitude and longitude as well as bottom oxygen and salinity.

Since the gadoids and flounders appeared to show a group response to these distribution variables, we decided to use them in another analysis, excluding the other species (Table 3, Fall 1976 II). This data set explained 28.3% of the total variation in distribution for a selected set of 14 species (Table 3). The first canonical variable had a high correlation with latitude (r = 0.904) and the gadoids, as a group, were highly positively correlated with this CV (Table 3). It appears that although Georges Bank spans only about two degrees in total north-south latitudinal variation, this variable is useful for defining centers of gadoid biomass.

The third analysis did not reveal any new trends, accounting for 32.6% of the variation in species distribution. In general, then, although significant orthogonal canonical axes were defined in each of three data sets, the amount of variation that was actually explained was relatively small. There appear to have been trends in the distribution of some gadoid and flounder species, but the strength of these relationships was hardly firm. Most of the variation in species distribution was related to latitudinal, salinity, and depth differences.

DISCUSSION

Questions of community resilience (Pimm 1984) are meaningful because resource managers are faced with the dilemma of making decisions that may alter future community structure. Fishery managers, in particular, are unable to deal with the long-term consequences of their management decisions because they lack specific knowledge of ecosystem reponses. This idea may apply particularly to areas such as Georges Bank, where landings of each species are part of a multispecies otter trawl fishery. In this case the application of single species management to assemblages of fishes may result in simplification of the community such that less productive fish populations or those more vulnerable to fishing are reduced dramatically (Tyler et al. 1982). If this occurs, important trophic linkages may be precluded, economic viability may suffer, and management options may be removed indefinitely. At the present time the argument of these central issues is proceeding slowly in the literature and few, if any, management agencies are considering these types of questions in their decisions. We need, therefore, to begin to investigate the long-term temporal scale of communities so that ecologists and managers can begin to function in terms of ecological time instead of just a framework for short-term reaction.

Declines in total finfish abundance on the continental shelf of the northeastern United States reached unprecedented levels over the period 1965-74 (Brown et al. 1976). Not only had biomass declined,

TABLE 3.—Canonical variable (CV) loadings for fall 1976 and spring 1978 gradient analyses, with canonical correlation coefficients (Rc), amount of variation explained by *each canonical* axis (% variation), and total variation in species distribution explained by the environmental data.

	Fall 1976 I			Fall 1976 II			Spring 1978 I		
	CV1	CV2	CV3	CV1	CV2	CV3	CV1	CV2	CV3
Spiny dogfish	−0.509	0.149	0.232				−0.089	0.105	0.111
Winter skate	−0.263	0.342	−0.244				−0.176	−0.377	0.058
Little skate	−0.428	0.113	−0.163				−0.015	−0.437	0.142
Smooth skate	0.552	−0.117	−0.144				0.333	0.210	−0.204
Thorny skate	0.387	0.017	0.063				0.534	0.416	0.188
Sea herring	0.003	0.081	0.058				0.084	−0.147	0.068
Alewife	−0.023	0.097	0.161				0.433	0.086	0.104
Offshore hake	0.456	−0.408	−0.100	−0.147	0.613	0.284			
Silver hake	0.285	0.203	0.536	0.607	0.332	0.027	−0.237	0.637	−0.328
Atlantic cod	0.059	0.544	0.195	0.600	−0.263	0.048	0.262	−0.534	0.177
Haddock	0.370	0.525	0.131	0.647	−0.069	−0.235	0.383	−0.300	0.072
Pollock	0.337	0.158	0.199	0.439	0.274	0.167	0.425	0.209	0.015
White hake	0.564	−0.022	0.341	0.447	0.614	0.083	−0.030	0.527	0.055
Red hake	−0.109	−0.109	0.034	−0.220	−0.043	−0.460	0.303	0.616	0.057
American dab	0.281	0.048	0.362	0.395	0.365	0.141	0.409	−0.035	−0.026
Summer flounder	−0.245	−0.124	−0.102	−0.246	−0.111	0.126	−0.427	0.309	0.303
Fourspot flounder	−0.235	−0.265	0.210	−0.326	0.051	−0.588	−0.417	0.418	0.366
Yellowtail flounder	−0.158	0.324	−0.083	0.115	−0.419	−0.095	0.080	−0.442	0.144
Winter flounder	−0.145	0.364	0.078	0.295	−0.324	0.114	0.109	−0.301	0.040
Witch flounder	0.179	−0.267	0.140	−0.107	0.407	−0.187	0.368	0.138	−0.225
Windowpane	−0.326	0.165	−0.351	−0.087	−0.439	0.504	−0.527	0.041	0.251
Butterfish	−0.279	−0.415	0.405						
Blackbelly rosefish	0.359	−0.544	0.050				−0.295	0.529	−0.199
Longhorn sculpin	−0.078	0.432	−0.136				0.101	0.478	0.068
Sea raven	−0.034	0.432	−0.092				−0.500	0.034	0.194
Cunner	−0.082	0.198	0.023						
American sand lance	−0.134	0.043	−0.079				0.130	−0.125	0.224
Atlantic wolffish	0.011	0.240	0.106				0.233	0.073	0.358
Ocean pout	−0.043	0.265	0.122				−0.133	−0.316	0.034
American goosefish	0.145	−0.073	0.184				−0.261	0.414	−0.039
Short-finned squid	0.249	0.284	0.303				−0.275	0.169	0.072
Long-finned squid	−0.471	−0.239	−0.379				−0.256	0.399	−0.077
Variables									
Latitude	0.306	0.922	0.074	0.904	−0.333	0.066	0.878	0.012	−0.131
Longitude	−0.458	−0.164	0.597	−0.004	0.064	0.118	0.240	−0.032	0.474
Depth	0.885	−0.432	0.049	0.030	0.849	−0.071	−0.107	0.792	−0.448
Bottom temp.	−0.179	−0.696	−0.233	−0.590	0.258	0.366	−0.252	0.720	−0.465
Bottom salinity	0.463	−0.547	0.422	−0.107	0.753	−0.586	−0.374	0.909	−0.133
Bottom oxygen	−0.316	0.450	−0.581	0.041	−0.613	0.407	0.199	−0.908	0.144
RC	0.975	0.961	0.874	0.871	0.841	0.750	0.979	0.968	0.943
% variation	8.2	7.2	3.6	11.1	9.1	4.3	9.2	11.8	2.8
Significance	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Total variation		25.7			28.3			32.6	

but total effort on Georges Bank increased several times (Fig. 7). The assemblage trends examined in this paper can be linked to these high levels of effort.

During this time period, seasonal bottom trawl surveys monitored trends in finfish abundance over the area from the Gulf of Maine to Cape Hatteras. This survey proved invaluable to fish stock assessment work because changes in the relative abundance of most of the commercial species were followed closely and were highly correlated with commercial catch, effort, and other indices (Clark 1979). Other species of ecological, perhaps not commercial importance, were also routinely and closely monitored over this time. The spring and fall bottom trawl survey provided an excellent means for assessing community or assemblage responses over this time period.

Cluster analysis, with the Bray-Curtis dissimilarity index and group average fusion method, proved helpful for defining demersal fish assemblages on Georges Bank. Recent studies confirm the value and applicability of the Bray-Curtis index (Bloom 1981). This method provided a means for collapsing the multidimensional nature of the spring and fall Georges Bank survey cruises into smaller, more easily interpreted, units. It was then possible to investigate not only long-term temporal and spatial persistence questions, but also intraspecific responses within the particular assemblage of interest.

Not only did seasonal Georges Bank assemblages maintain their temporal integrity over the periods 1963-78 in the fall and 1968-78 in the spring, but they also appear to have retained their spatial configuration for the most part as well. The results of this study indicate that although changes in species composition and relative abundance occurred in varying degrees in all the assemblages, they remained continuous in time and space.

Although many of the species on Georges Bank are found in several assemblages, it appears that each of the five groups has enough large-scale variation in biomass, species composition, and relative abundance to make each of the assemblages unique. Also at least one or two dominant Georges Bank species occupy each assemblage, for example, the bulk of the haddock stock occurs in the Northeast Peak group. Thus, even though some assemblages changed dramatically in terms of species richness and relative abundance, the spatial integrity of each complex was preserved over time.

The energy budget of Georges Bank can serve as a plausible explanation for the particular species distributions we found. Georges Bank is a dynamic ecosystem driven by a complex and unique nutrient advection system. Its shallow topography and geographic location, with constant mixing of the water column and lack of stratification, does not lead to the usual nutrient limitation of primary productivity (Sutcliffe et al. 1976; Cohen et al. 1982). Instead of the usual spring and fall pulse in primary production, the region is characterized by high productivity from April to November. Yearly primary production levels are as high as 450 gC/m^2 per yr in the shallow (< 100 m) zone of Georges Bank (Cohen et al. 1982). This shallow mixed zone encompasses the same area as the Shallow and Intermediate assemblages delineated in our cluster analysis results. The area is dominated by fish that feed on invertebrates. Primary prey items for these species include euphausiids, copepods, mysids, amphipods, and other benthic invertebrates. This part of the ecosystem is fairly closely tied to primary production, and its component species may compete for food resources during their early life history (Pitt 1970; Bowman 1981; Overholtz 1982). Predation, too, may be an important biological mechanism for determing trends in this assemblage (Overholtz 1982). The other assemblages that we have described in this analysis occur along the fringes of Georges Bank at the shelf-slope interface. These shelf break groups contain the major adult demersal fish stocks found in the area with the exception of yellowtail flounder. These peripheral assemblages are dominated by large predators that are generally piscivorous, with little, if any, dietary overlap (Langton and Bowman 1981).

The gradient analyses suggest that about 25% of the total variation in species biomass distribution can be explained with the variables used in the study. This result was surprising at first, since we felt that the variables we used would explain much more of the variation than this. However, considering the fact that other important biological factors, such as predation, fishing, competition, and food preferences were not included in the analysis, it is probably a realistic percentage. Perhaps an analysis that included the whole east coast would account for much more variation because a wider range of conditions would exist.

Other studies that have successfully explained species distributions usually occur in habitats with very strong physical or chemical gradients, such as mountain forests or estuaries (Whitaker 1967; McIntire 1973). Either the actual gradients were not strong enough to explain more than a small percentage of the species distribution or those other factors were more important.

The questions of resilience and stability of demersal fish assemblages that were defined and investigated in this study have implications for the management of Georges Bank. This study provides a useful conceptual framework for managing many of the demersal fish stocks in this area. Not only were stable zones with specific resident fishes delineated, but they were present over the long-term record. Species components of fall assemblages are indicators of general distributions that represent the location of major fish stocks during the productive portion of the year. Long-term responses observed in the Georges Bank community indicate the propensity for adjustment or resilience (Holling 1973) that a particular assemblage might have. Assemblages on the periphery of Georges Bank might be less susceptible to changes in species composition and relative abundance because their component species are less trophically linked. The Shallow assemblage, on the other hand, appears to be particularly vulnerable to fishing and perhaps interspecific interactions. This type of knowledge will be helpful for understanding changes in fish abundance and community structure and for effectively managing fishery systems in the future.

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