

AN ABSTRACT OF THE THESIS OF

William Joseph Overholtz for the degree of Doctor of Philosophy
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Albert V. Tyler

Questions of assemblage persistence, resiliency and continuity in time were investigated with data from seasonal bottom trawl surveys conducted by the Northeast Fisheries Center, Woods Hole, Massachusetts, from 1963-1978. Cluster analysis proved to be a useful statistical method for delineating assemblage boundaries and corresponding resident demersal fish components from Georges Bank, northeastern coast, USA. Assemblages were continuous and persistent over the long term and changed spatial configuration only slightly on a seasonal basis. Responses of assemblage species ranged from mild to severe with respect to declines in biomass, numerical density and changes in relative abundance. Assemblage directional changes were triggered by intense fisheries during this time period as well as inherent trophic dynamics of component species. This study has potentially important multispecies management connotations and the assemblage concept is a useful potential operational definition or working hypothesis framework for further

applications of management and modeling.

Linear programming analyses with catch maximization objective functions showed that the goal of attaining total summed quotas within specific assemblages was highly dependent on species composition, relative abundance and distribution. A multispecies model of the shallow assemblage on Georges Bank was constructed to answer specific questions concerning the assemblage species composition changes we had observed. We were interested in determining whether observed trends in species composition and abundance in this assemblage could in part be explained by simple ecological mechanisms. Results from model simulation runs indicate that competition and predation could account for some of the variability in biomass that we had observed in the shallow assemblage. These findings suggest that interspecific interactions may be important determinants of fish population abundance in this type of marine assemblage.

Long-term temporal perspectives for the demersal fish
assemblages of Georges Bank with implications for
management and modeling

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William Joseph Overholtz

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Associate Professor of Fisheries *W. J. Overholtz*
in charge of major

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

Date Thesis is presented

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Typed by researcher for

William Joseph Overholtz

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Long-term temporal perspectives for the demersal fish assemblages of Georges Bank with implications for management and modeling.

Overview

Exploitation of world marine fishery resources has progressed through a series of rapid changes since the early 1900's, where near shore species specific fisheries have been for the most part replaced by large scale otter trawl fleets that exploit many species in common. Gradually sophisticated domestic vessels were developed and large distant-water ships were able to leave their home countries to catch the many valuable fish stocks of former remote locations. Consequently, the landings from the oceans of the world rose dramatically from a few million tonnes to 50 million tonnes in the mid 1970's (Barney 1980). These trends developed largely through economic incentives and technological innovations, although biological and political considerations were also important.

The causes for these changes in world marine landings can perhaps best be described by using an example that illustrates the course of development for many fisheries. The haddock fishery of New England serves as a good case study. The salt cod industry on Georges Bank eventually gave way to the fresh fish market (Clark et al. 1982). The invention of better gear and preservation methods caused a subsequent increase in the supply of haddock. High domestic landings in the 1920's were followed by a period of lower catch, but rather tranquil equilibrium from 1935-1960 (Clark

et al. 1982). In the early 1960's a large distant-water fleet began exploiting the haddock stock, causing a precipitous decline in abundance during the period 1965-1966. The age structure of the stock was destroyed, recruitment failure resulted, and the population declined to extremely low levels. Some stock recovery occurred in the mid 1970's, but the species is now landed as one component of a multispecies otter trawl fishery. This same or a similar scenario aptly describes development of many of the large scale demersal fisheries of the world.

Concomitant to world fishery development, the science of fishery management progressed from its initial efforts to replenish removals and declines through stocking, to present thinking based on ecological principles, population dynamics, and assessment techniques. Management methodologies were developed and implemented to deal with problems as they arose on a domestic or international basis. For the most part simple yield models based on maximum sustained yield (MSY) were the main biological tool used to manage fisheries. Catch effort data and a simple logistic relationship gave an estimate of the MSY of a particular stock (Graham 1935, Schaefer 1954). Subsequent developments in this model led to refinements that increased its applicability to broader problems (Pella and Tomlinson 1969; Fox 1974). However, these models only described equilibrium fishery states and did not deal adequately with fluctuations in stock size caused by unequal year class strength.

A population dynamics approach, based on the tradeoff between

growth and mortality, provided the foundation for management with another model (Ricker and Foerster 1948; Beverton and Holt 1957). Although the latter provided for recruitment fluctuations, in practice the technique was applied to strictly equilibrium conditions, failing also therefore to account for the large variations in recruitment that occur in many marine fish populations.

As this evolutionary process continued a method known as an analytical assessment came into widespread use in the north Atlantic (ICNAF 1975). This technique involved the application of analytical models based on long-term age structure analysis (Gulland 1965; Pope 1972). The results of these virtual population and cohort analyses were then linked with recruitment estimates and used in models that predicted stock conditions based on different catch simulations (Anderson 1979; Clark et al. 1982).

This method was useful for dealing with the nonequilibrium conditions present in almost all marine fisheries. Although these procedures met with some success, they still all suffer from a number of problems. The nature of these methods is entirely single species oriented: they fail to account for interspecific interactions and exploitation of multiple stocks by common fisheries, and also have large data requirements. As a result some of the major fisheries of the world have declined (FAO 1977). The usefulness of the single species approach to fishery management has come under increasing criticism in the literature. Simple single species fisheries models, although appropriate at the time and still useful for the assessment of some fish stocks, are in many cases in-

adequate Larkin (1977); Gulland (1978); Sissenwine (1978). May et al. (1979) state that " MSY applied to each species individually cannot serve as a guiding principle when harvested species have strong interactions". Thus in many management situations it is necessary to account for interspecific and technological interactions (FAO 1977). Even nonequilibrium methods are inadequate here. The problems of modern day fisheries are much more complicated than in previous years when the catch was primarily one or two species. It is now necessary to begin to manage many fisheries on a multispecies or ecosystem basis.

Multispecies fisheries studies have proceeded along several different pathways, from simple extensions of single species surplus production models to complex ecosystem models that utilize size-selective predatory mechanisms .

It is possible that under certain conditions, surplus production models may be useful for providing estimates of yield from a complex of species (FAO 1977). Brown et al. (1976); Halliday and Doubleday (1976); and Pinhorn (1976) used this approach to model the total finfish biomass of several large ICNAF subareas and statistical areas in the northwest Atlantic. These studies showed that considerable overfishing of the total biomass in these areas occurred because the sum of the individual species quotas resulted in a catch that substantially exceeded the system yield predicted from these models. One of the main points illustrated was that due to species interactions or common exploitation, the total system yield was not necessarily equal to the sum of its component parts.

These studies served as a good preliminary foundation to system response, but in many ways they lack realism because a variety of species, regardless of their linkages, were lumped together in a composite analysis. An extension to the simple surplus production model described above involves the addition of interspecific interaction terms to the simple logistic model. A series of coupled differential equations is constructed for a particular group of species. Walter (1971); Pope (1976); May et al. (1979) used this idea to assess the yield potential of different fishery systems.

Another approach has been to use models that investigate interspecific interactions via their effect on the population dynamics of a species. Lett and Kohler (1976) studied the effects of competition and predation by Atlantic mackerel on the recruitment of Atlantic herring. Winters (1976) also studied herring and mackerel interactions, but he emphasized density dependent effects on growth, recruitment and maturation rates.

The most recent innovations in multispecies modeling and assessment use predatory mechanisms to model the various species being investigated. One of these methods uses predation coefficients in a modified cohort analysis or legion analysis (Pope 1979, Majkowski 1981, Sparre 1980). The other, more complex application, uses predatory mechanisms in a multispecies system model. This intricate numerical model describes species interactions in the North Sea by using size specific predation as the mechanism for interspecific interaction (Anderson and Ursin 1977). Unfortunately this type of model becomes large rapidly, and

frequently it is very difficult to track behavior of the system variables. It also suffers from the problem of too many un-estimatable parameters and processes, further complicated by large age class structure requirements.

Most of these multispecies methods in some way or another lack substance primarily because they lack organization. They are not based on principles of system organization and thus have no operational foundation or general paradigm to follow. To make progress in the area of multispecies and system modeling it is necessary to develop system perspectives (Overton 1975). For example, if one does not have an underlying concept of structure such as the unit stock definition (Cushing 1970) in single stock assessment work, it is impossible to go forward with further meaningful system analyses because we need knowledge of how the system and its subsystems are coupled together. The need for unifying concepts is clear, we cannot rely on the popular notion that modeling a system is merely an exercise in reconstructing the whole from the myriad of disorganized parts (Lane et al. 1975). We need to develop a more holistic approach to deal with the problems of fishery systems, to discover more about the internal and external structure of fisheries subsystem couplings. We need to ascertain the mechanisms that hold systems together and interface this with long-term temporal perspectives. If progress is to be made in understanding the intricacies of fisheries systems and their sub-units, it will be necessary to develop some simple and useful "working hypotheses".

Tyler (1971); Knight and Tyler (1973); Gabriel and Tyler (1980) cultivate the idea of fish assemblages as useful devices for studying communities of fishes. The term assemblage has been used by many authors, but here it refers to a group of species that are distributed in the same geographic area and habitat type for most of the year. The species are subject to the same environmental regimes, utilize common feeding areas and in many cases are linked trophically. There are many fields of study, such as community ecology, assessment and modeling, where this concept provides the organizational opportunity for further analyses. In this context then it was the goal of this study to develop and investigate the usefulness of applying the assemblage concept to the demersal fish community of Georges Bank.

Chapter 1: Georges Bank Demersal Fish Assemblages, Cluster
Results and Community Ecology.

Introduction

The concept of co-occurring groups of organisms called communities has long permeated the literature and plant ecologists can claim most of the credit for the original interpretations. This occurred because terrestrial plant ecosystems dominate the landscape, providing an accessible group of species for observation and study. Scientists could readily observe the long-term nature of a climax forest or the successional changes that ushered it into being. As notoriety for this paradigm increased, plant and animal ecologists began to apply the idea to groups of species they observed in a variety of ecohabitats, resulting in a voluminous number of definitions, terms and descriptions. Mills (1969) provides a nice review of this progression and also eliminates associated confusion by clarifying and combining the conceptual thoughts of several authors to produce a useful definition of a community. This discussion of course presupposes the existence of discrete communities of species, while in fact two different viewpoints exist. The continuum school embraces the idea that species are distributed rather loosely along geographic and environmental gradients while the zonal school espouses sharp discontinuities between associations (Krebs 1978).

As community interpretations became prevalent it was necessary to change emphasis from a strict observational perspective to one involving some statistical rigor, so that the existence and com-

parison questions could be investigated. Tyler (1974) examined a number of statistical community methodologies, emphasizing that cluster analysis is particularly useful for resolving group definition problems. The contagious distribution of benthic species is well documented and demersal fish in particular are often distributed in a non-random fashion (Taylor 1953; Tyler 1974; Pennington and Grosslein 1978). Investigating these associations to determine whether species are aggregated has important fishery management consequences (Gabriel and Tyler 1980). Regardless of whether the discrete or continuous hypothesis is accepted, the species in question can still be classified into useful assemblages (Krebs 1978).

Most community ecological studies have necessarily concentrated on the short term aspects or seasonality of species assemblages. Typically one to three years of field measurements are analyzed with information theory, niche breadth procedures or multivariate statistical methods. Demersal fish assemblages have been investigated in a number of locations Tyler (1971); Oviat and Nixon (1973); Stephenson and Dredge (1976); Hoff and Ibara (1977); Gabriel and Tyler 1980; Inglesias (1981). The recurrent theme in most of these studies centers around seasonally varying diversity due to environmentally induced migration, temperature acting as the dominant driving variable. Gabriel and Tyler (1980) stress bathymetric effects on distribution as well as the operational or organizational aspects of the assemblages they investigated. Unfortunately many interesting questions cannot be addressed in these studies. Are the assemblages actual aggregations? Are they

spatially continuous in the long-term temporal scale? It is important for a number of reasons to consider the long-term ramifications of fishery system responses, especially where mans' activities are involved. The temporal scale here does not refer to geologic time, but rather ecological time, the span of years during which the decisions of fishery ecologists evoke system responses. Fishery managers are limited in their ability to function within this time frame. For instance, a plant ecologist could predict with some certainty the type of climax forest that would eventually occupy a cleared site, if left undisturbed, but I know of no such analogous ability for fishery biologists, especially in the marine environment.

Are fish assemblages stable? Do they persist over time? How does a system respond to exploitation? Holling (1973) investigated system responses to mans' 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. Other investigators (Dix 1957; Mech 1962) have studied succession in forests and animal interactions with vegetation communities respectively. Very few marine studies with the exception of Soutar et al. (1969); Sutherland (1980) and some general overview papers Brown et al. (1976); Richards (1978); and Grosslein (1980) have stressed the long-term temporal and spatial aspects of marine system response. A few sets of appropriate marine fish data do ex-

ist, but have not been investigated with a community approach (Richards et al. 1978; Pope 1979; Azarovitz 1981). Important temporal and spatial questions were examined with data from research conducted at the Northeast Fisheries Center (Grosslein 1969). Concentrating on Georges Bank, I used cluster analysis to produce yearly fall and spring dendrograms for the period 1963-1978 and 1968-1978 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.

Methods:

Standardized research otter trawl surveys of the northwest Atlantic continental shelf from Nova Scotia to Hudson Canyon began in the autumn of 1963, were extended southward to Cape Hatteras, North Carolina in 1967 and occurred in consecutive years to the present. Spring surveys commenced in 1968, encompassed the same area and also had yearly coverage. In addition several summer and winter cruises were undertaken during this time on an intermittent basis. Grosslein (1969) and Azarovitz (1981) describe the details and justification for the surveys, but a brief summary is appropriate.

The objective of the surveys was 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 based on the proportion of total area in the strata and 2 by 2.5 minute blocks served as the site locator. Loran bearings were employed to locate the station and a 30-minute sample with a standardized research bottom trawl with a 1.25-cm codend liner was accomplished. All fish as well as major invertebrates were sorted to species, weighed, measured, and sampled for other analyses. A complete log for each station was recorded and later processed on shore for use in fishery analyses.

Occasionally catches were so large that it was impossible to obtain the entire breakdown, in these cases appropriate subsampling methods were employed and station totals were calculated for those particular species. Due to time and financial considerations, sampling frequency averages about one station for every 200 square miles or roughly 400 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 38 species representing the dominant fishes on Georges Bank, were chosen as the focus for the investigation. 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. Biomass rather than numbers was chosen as the unit of study, because it is the measurement of most interest to the biologist and fisherman. 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 I transformed the data prior to clustering by using a $\ln(x+1)$ conversion. This is a standard statistical method for damping skewness in contagiously distributed biomass data (Elliot 1971, Pennington and Grosslein 1978). Station dissimilarities were calculated by using the Bray-Curtis dissimilarity index, a widely used ecological distance measure that is sensitive to dominant species (Clifford and Stephenson 1975, Boesch and Swartz 1977). The dissimilarity matrix produced with

this distance coefficient was used in a group average fusion strategy to combine stations with similar species distributions (Clifford and Stephenson 1975). This fusion technique combines the stations that are most alike, through an iterative averaging process until all the stations are linked. These station combinations were displayed in dendrograms, a graphical method useful for the separation of cluster groups. Dendrograms were examined and assemblage groups were chosen by two criteria, large scale separations 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 the years in the spring and fall data set so that a consecutive series of maps was available. These yearly assemblage maps were then inspected for spatial similarities over the time sequence to see if there was any continuity. Finally, assemblage stations from several consecutive years were pooled in order to have enough points to delineate a map of each area and assemblage names were chosen based on nearby geographic features or depth zones.

This set of hierarchical cluster methods has been shown to be generally useful for classifying contagious bottom trawl data (Stephenson and Dredge 1976; Gabriel and Tyler 1980), but it was helpful to have an objective spot check of cluster results. To ascertain whether meaningful groups were being produced, a multivariate analysis of variance was used to test cluster differences for two cruises, (conducted in years 1966, 1973), chosen at random from the fall data set. As a further check, a discriminant analysis of the same data sets was used to produce

several scatter plots that were helpful for gauging group separation. Subsequent to these analyses, winter and summer cruises that were available on a more intermittent basis, were examined for agreement with the previous spring and fall results. Assemblage species lists were prepared from the areas outlined in the pooled cluster results and further analyses yielded information on the structure of each group. Length frequencies from species in the different assemblages were used to separate life history stages and mean catch per tow showed trends in distribution and abundance. Examination of food habits data 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. To track possible temporal directional biomass changes in the Shallow and Slope and Canyon assemblages, I used CPUE vectors from each fall survey in another cluster analysis to see if any clear time trends in species composition and abundance were apparent.

Several measures of community response were employed to answer intra-assemblage dynamics questions. McIntosh information indices were utilized to monitor diversity changes in several Georges Bank demersal fish assemblages (McIntosh 1967). Data sets representing numerical densities of selected species from the Slope and Canyon, Northeast Peak (NP), and Shallow assemblages for the fall time series were proportionalized to remove the effect of sample size from the analysis (Karentz and McIntire 1977), and used in diversity estimates. The McIntosh diversity index is given as follows:

The McIntosh diversity index is given as follows:

$$MDI = N - \sqrt{\sum_{i=1}^s n_i^2}$$

Where:

N =total number of all species

n_i =number of species i

s =number of species

This index is not only sensitive to species richness and relative abundance, but it also tracks density, an important measurement in exploited fish populations.

Several gradient analyses were also performed with the objective of trying to explain species distributions based on a set of location, physical, and chemical variables. Canonical correlation analyses 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 (Pimental 1979). Data for the autumn cruise was obtained from measurements of bottom temperature and depth made aboard the RV Albatross IV, USA, Oct 20 to Nov 5, 1976 and corresponding information on bottom salinity and oxygen from the RV Anton Dohrn, Federal Republic of Germany, Nov 14 to Dec 1, 1976. Information for the spring cruise was procured from measurements of bottom temperature and depth from the RV Albatross IV, April 17 to May 3, 1978 and salinity and oxygen data that was

obtained on the RV Argus, Union of Soviet Socialist Republics, from April 13-28, 1978. These two data sets were chosen because they were the only available source of salinity and oxygen data that corresponded even somewhat closely in time to the available station information. 33 species were used in the fall 1976 part I analysis, 14 selected gadoids and flounders in the 1976 part II breakdown and 29 species in the spring analysis.

Results

Figure 1 shows Georges Bank with other important geographic locations and (Table 1) lists the major species that were used in the various statistical and community ecological analyses. These 38 species were deemed the principal fishes after carefully examining the data set and deciding that if a species was not present in 3 or more tows and or represented at least 2 kg total biomass, it was not included in the investigation. It was beyond the scope of this work to address the problem of rare species simply because the nature of the study was not conducive to a clear resolution of this particular problem. Dendrograms, of the type displayed in Fig 2, were produced from species-station matrices and used to define assemblage groups. The type of large-scale difference observed at a dissimilarity of 0.7 in Fig 2 was used to separate the groups. For the purposes of this study, coarse separations were the desirable product because an area wide assemblage plan for Georges Bank would be too complicated if all the cluster subunits were included.

Cluster group sites were highlighted on original cruise station maps and outlined to give a rough approximation of spatial and geographic zones (Fig 3). Figure 3 shows the distribution of the five most important assemblage groups present on Georges Bank in the fall of 1963. For reference, I name these groups: Slope and Canyon, Intermediate, Shallow, Gulf of Maine Deep, and Northeast Peak. As subsequent fall cruises were examined and plotted, an interesting spatial and temporal pattern began to emerge. The same

Figure 1. Georges Bank with associated geographical landmarks.

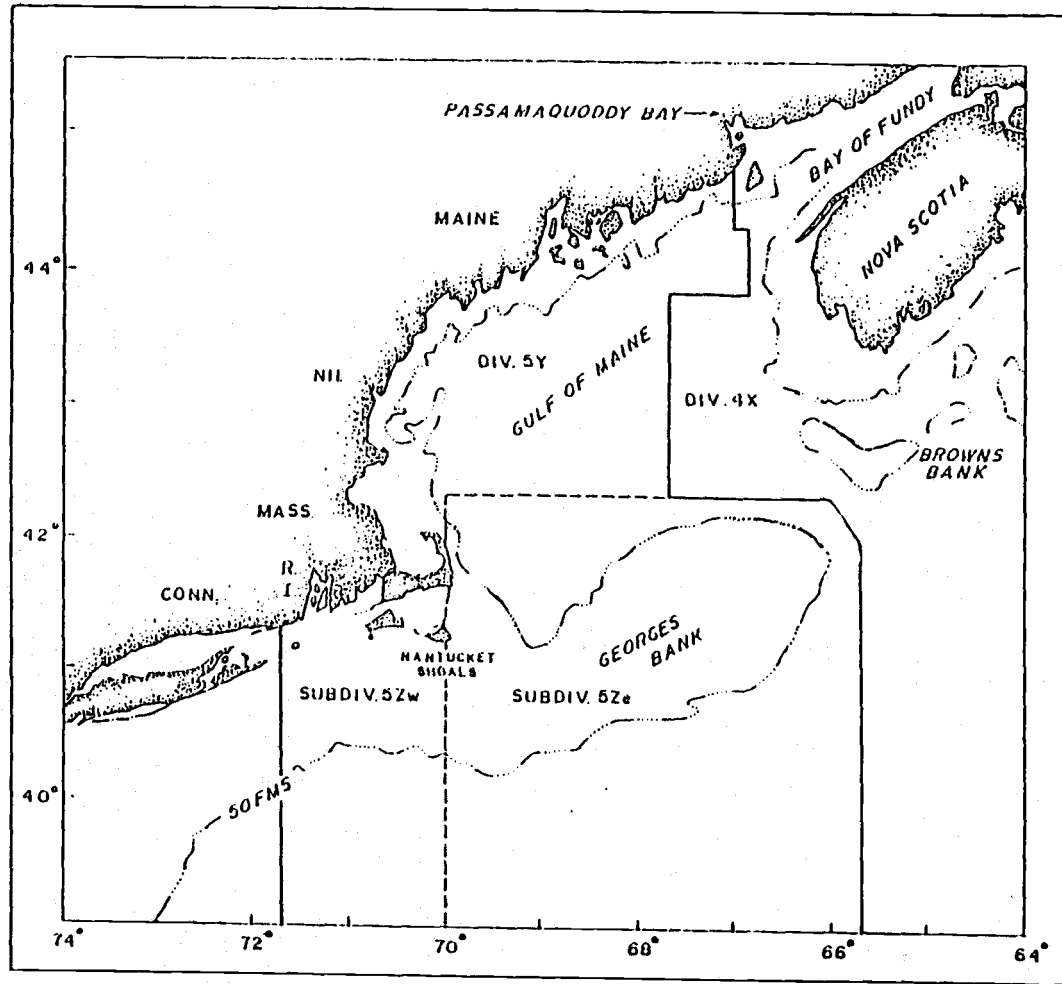


Table 1: Species cited by common name in the text (AFS 1980)

Spiny dogfish	(<i>Squalus acanthias</i>)
Winter skate	(<i>Raja ocellata</i>)
Little skate	(<i>Raja erinacea</i>)
Smooth skate	(<i>Raja senta</i>)
Thorny skate	(<i>Raja radiata</i>)
Sea herring	(<i>Clupea harengus</i>)
Alewife	(<i>Alosa pseudoharengus</i>)
Offshore hake	(<i>Merluccius albidus</i>)
Silver hake	(<i>Merluccius bilinearis</i>)
Atlantic cod	(<i>Gadus morhua</i>)
Haddock	(<i>Melanogrammus aeglefinus</i>)
Pollock	(<i>Pollachius virens</i>)
White hake	(<i>Urophycis tenuis</i>)
Red hake	(<i>Urophycis chuss</i>)
Cusk	(<i>Brosme brosme</i>)
American plaice	(<i>Hippoglossoides platessoides</i>)
Summer flounder	(<i>Paralichthys dentatus</i>)
Fourspot flounder	(<i>Paralichthys oblongus</i>)
Yellowtail flounder	(<i>Limanda ferruginea</i>)
Winter flounder	(<i>Pseudopleuronectes americanus</i>)
Witch flounder	(<i>Glyptocephalus cynoglossus</i>)
Windowpane flounder	(<i>Scophthalmus aquosus</i>)
Gulfstream flounder	(<i>Citharichthys arctifrons</i>)
Atlantic mackerel	(<i>Scomber scombrus</i>)
Butterfish	(<i>Poronotus triacanthus</i>)
Bluefish	(<i>Pomatus saltatrix</i>)
Redfish	(<i>Sebastes marinus</i>)
Blackbelly rosefish	(<i>Helicolenus dactylopterus</i>)
Mailed sculpin	(<i>Triglops ommatistius</i>)
Longhorn sculpin	(<i>Myoxcephalus octodecemspinosus</i>)
Sea raven	(<i>Hemitriperus americanus</i>)
Cunner	(<i>Tautoglabris adspersus</i>)
American sand lance	(<i>Ammodytes americanus</i>)
Atlantic wolffish	(<i>Anarhichas lupus</i>)
Ocean pout	(<i>Macrozoarces americanus</i>)
American goosefish	(<i>Lophius americanus</i>)
Short finned squid	(<i>Illex illecebrosus</i>)
long finned squid	(<i>Loligo pealei</i>)

Figure 2. Typical dendrogram, Fall 1966, showing station cluster groups

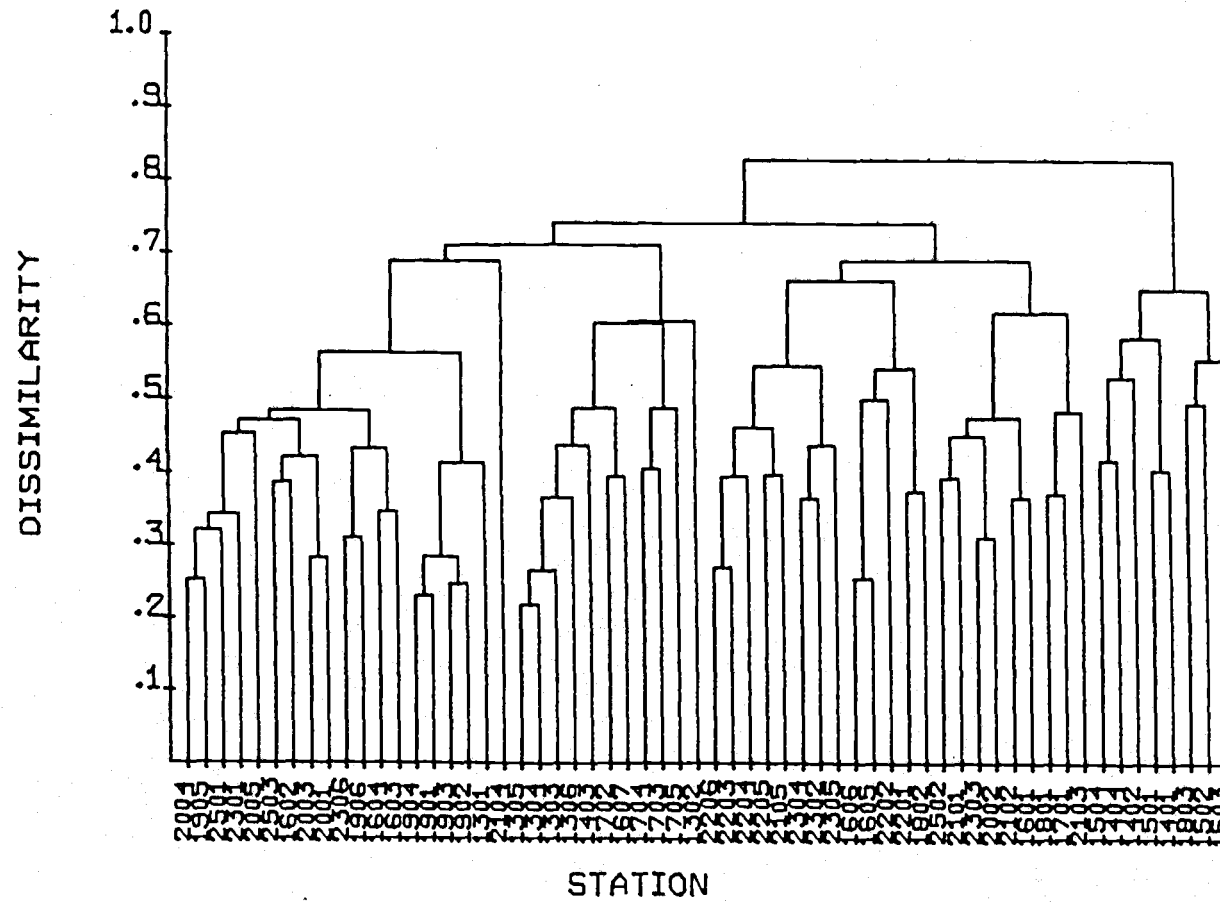
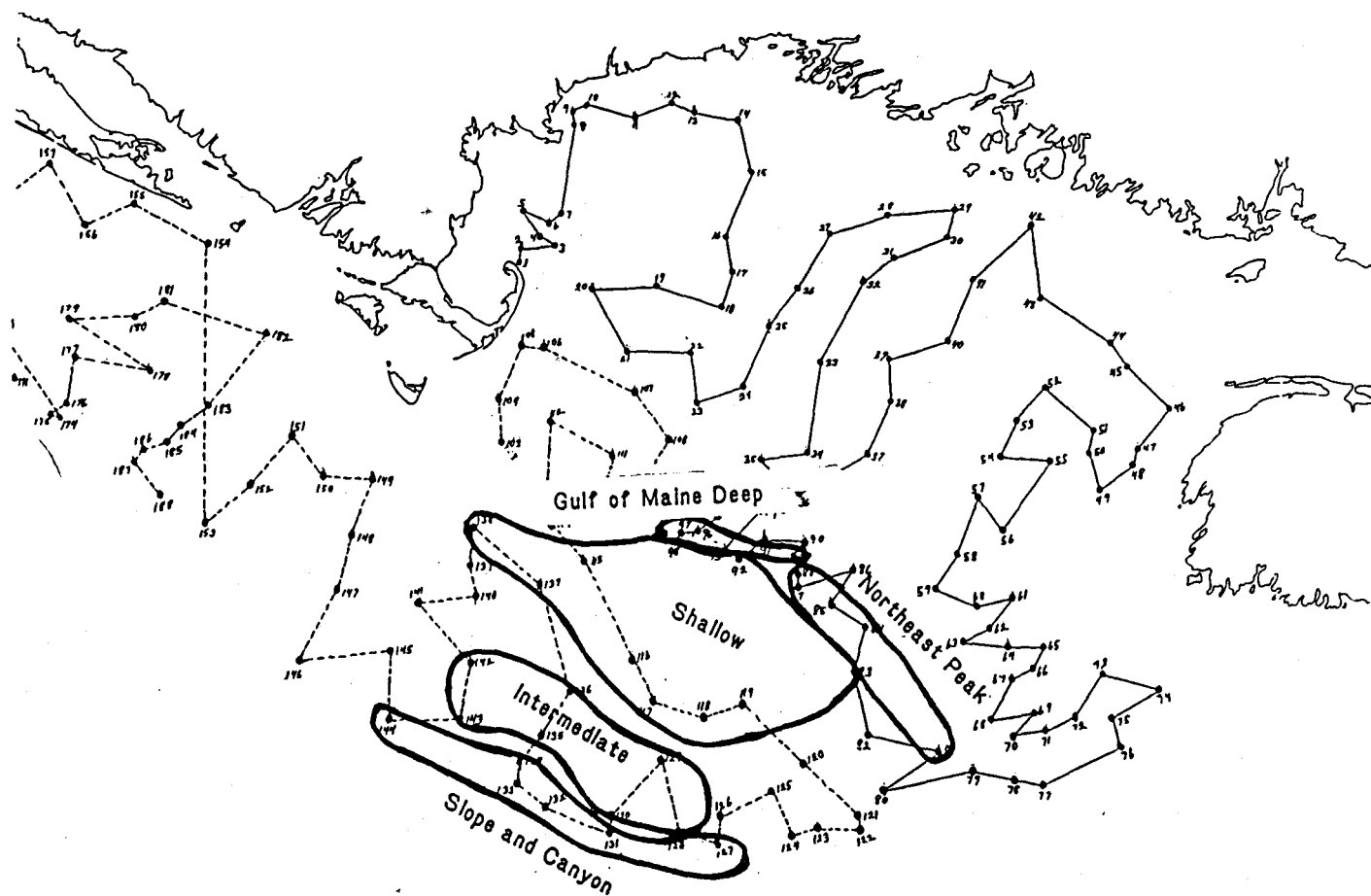


Figure 3. Cluster groups from Fall 1963 as roughly outlined on the original cruise track.



five groups appear to have been present in similar locations since 1963. Figures 4 and 5 solidify this point by showing the distribution of the 5 assemblages during years that occurred at approximately mid and endpoints of the fall time series. The groups appear to change their spatial configuration slightly on a year to year basis, but it is difficult to attribute this to a change in species abundance since the number of stations was not constant and they were chosen by stratified random methods. Species compositions of the assemblages are given in (Table 3).

It was desirable to delineate the total area that each assemblage encompassed through time (years). Pooled consecutive years of intra-assemblage stations yielded plots for the spring and fall represented by Figures 6-10 and 11-15 respectively. The groups overlapped surprisingly little through time with the exception of a few border stations along adjacent assemblages. It appears that the Shallow and Intermediate assemblages were somewhat dynamic with respect to each other and the assemblages that occupy the western part of the bank also intermingle slightly. The Shallow assemblage contains two large shoals (unsampled areas) represented by the openings present in Figs 8 and 13 for spring and fall respectively. This area, known as Cultivator Shoals, has never been sampled by the groundfish surveys.

Composite maps of general assemblage areas for the spring and autumn time series are shown in Figs 16 and 17 respectively. The Slope and Canyon assemblage appears to encompass a similar area regardless of season while other areas show slight seasonal

Figure 4. Cluster groups from Fall 1970 as roughly outlined on the original cruise track

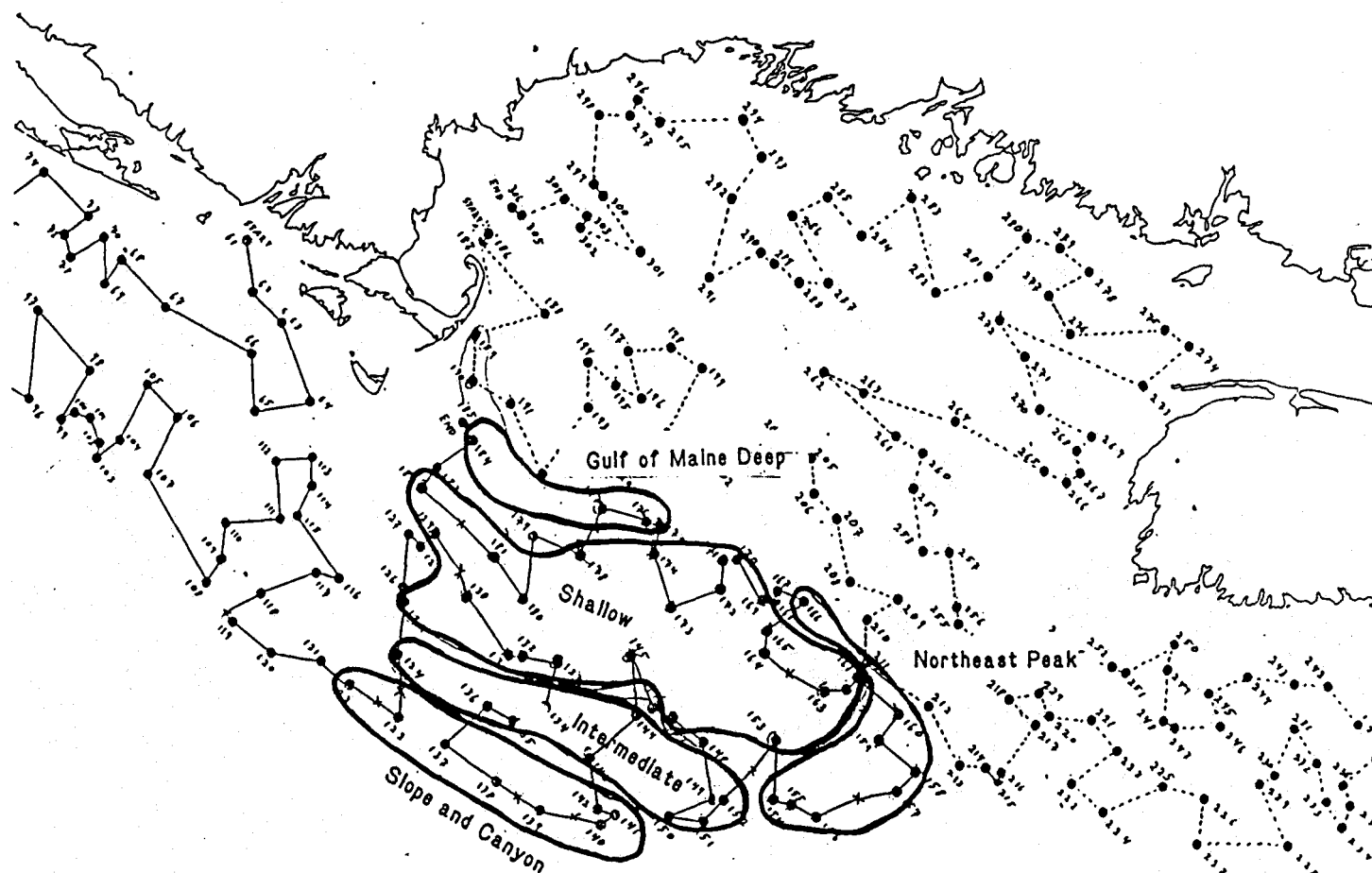


Figure 5. Cluster groups from Fall 1976 as roughly outlined on the original cruise track.

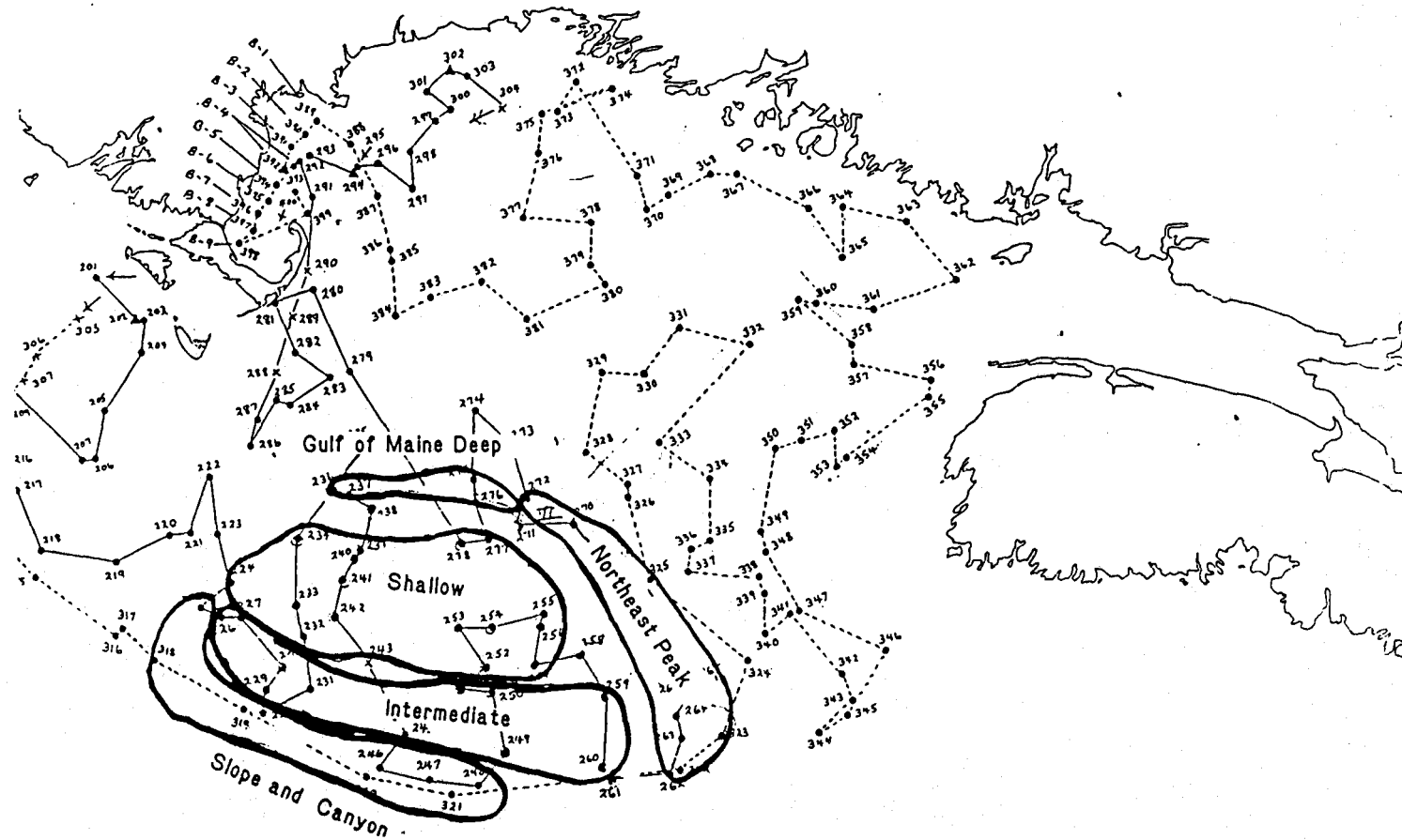


Figure 6. Pooled station distribution for the Slope and Canyon assemblage, Spring 1968-1973

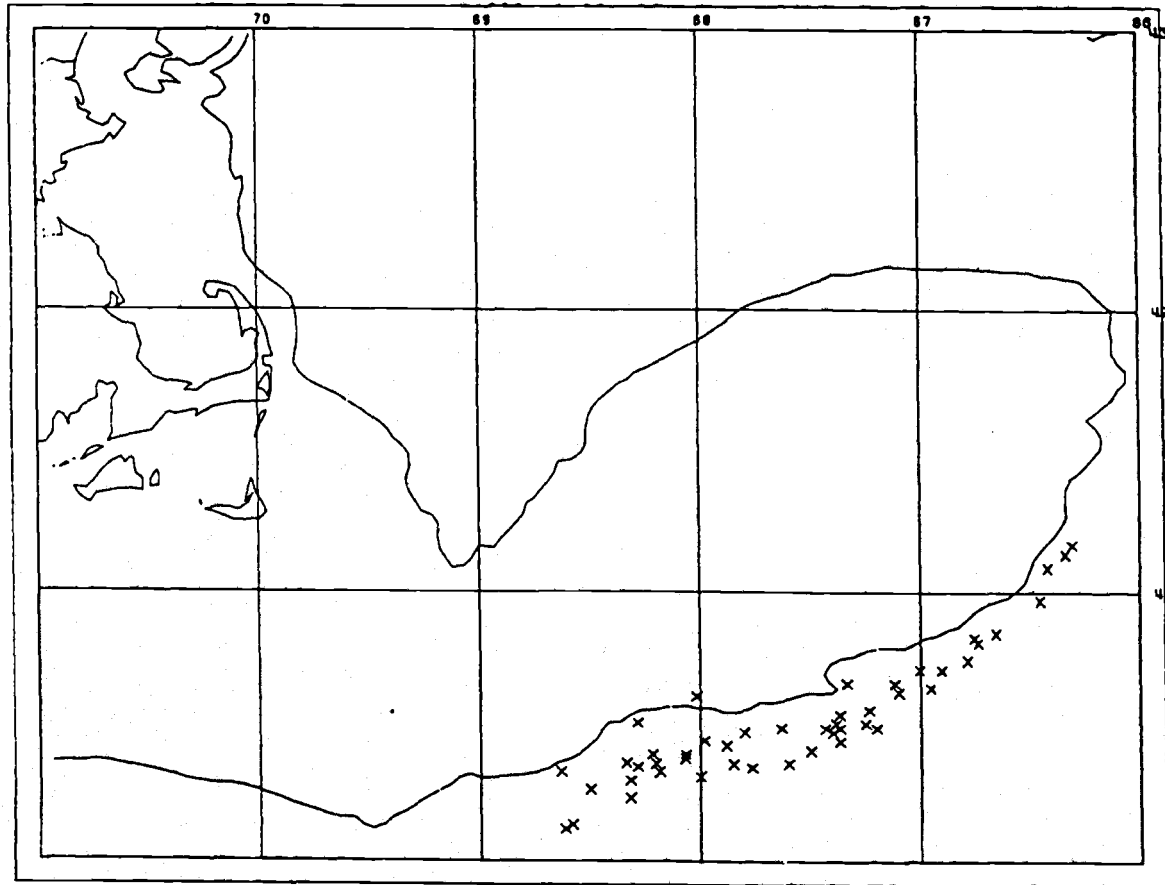


Figure 7. Pooled station distribution for the Intermediate assemblage,
Spring 1968-1973

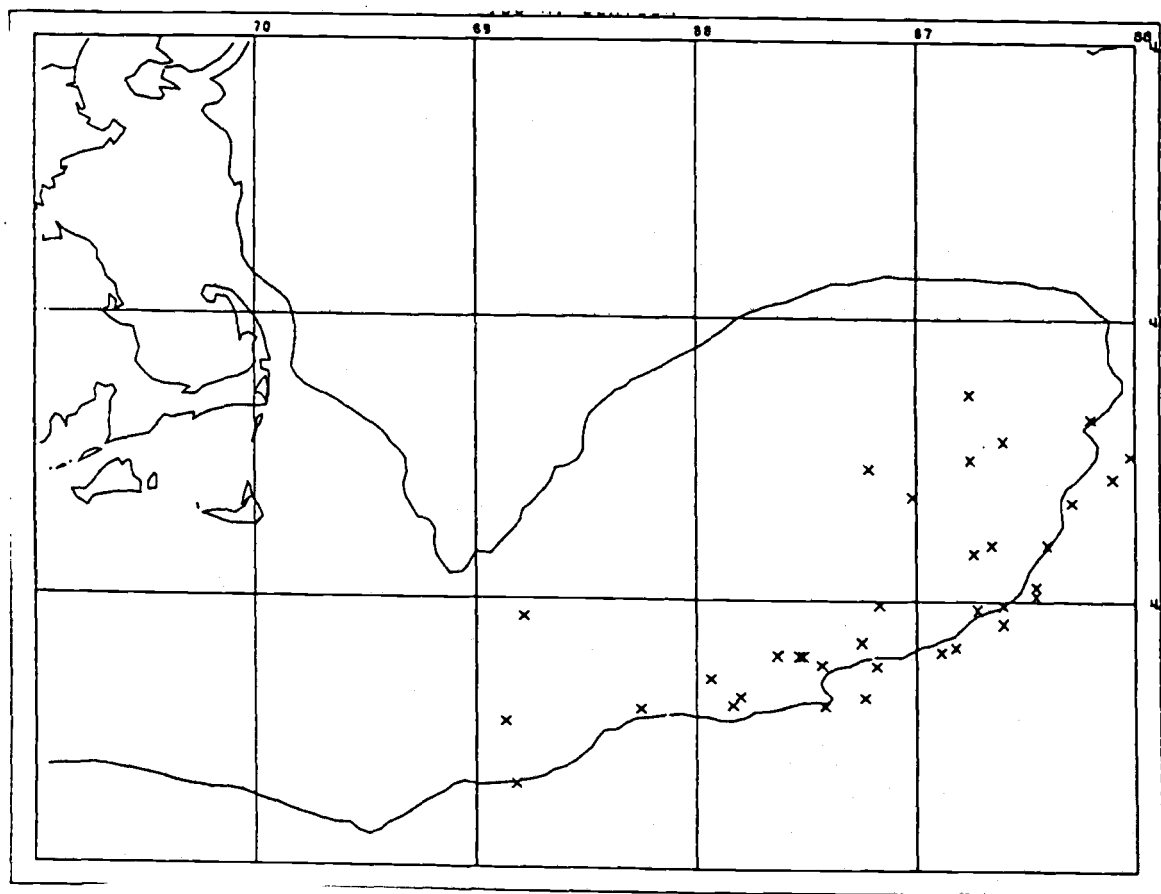


Figure 8. Pooled station distribution for the Shallow assemblage, Spring 1968-1971

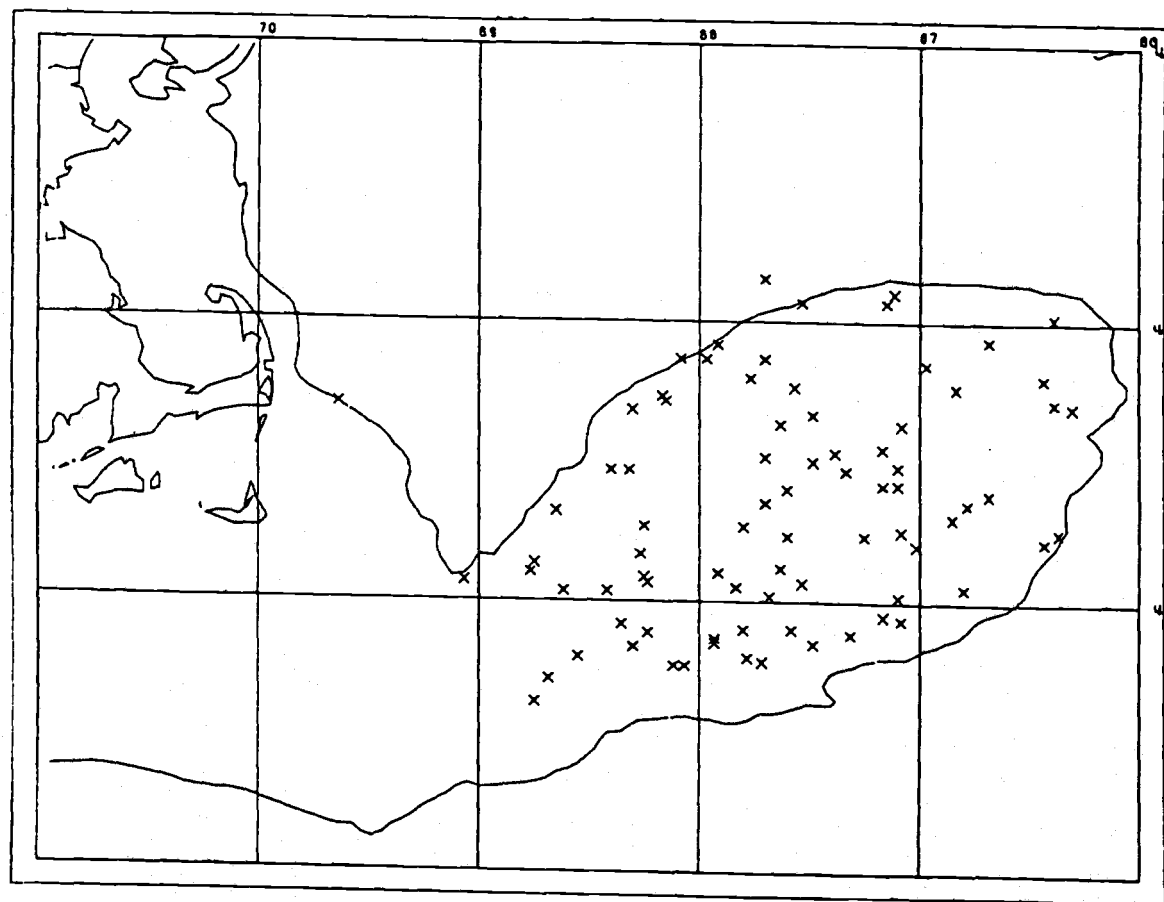


Figure 9. Pooled station distribution for the Northeast Peak Interior assemblage, Spring 1968-1972

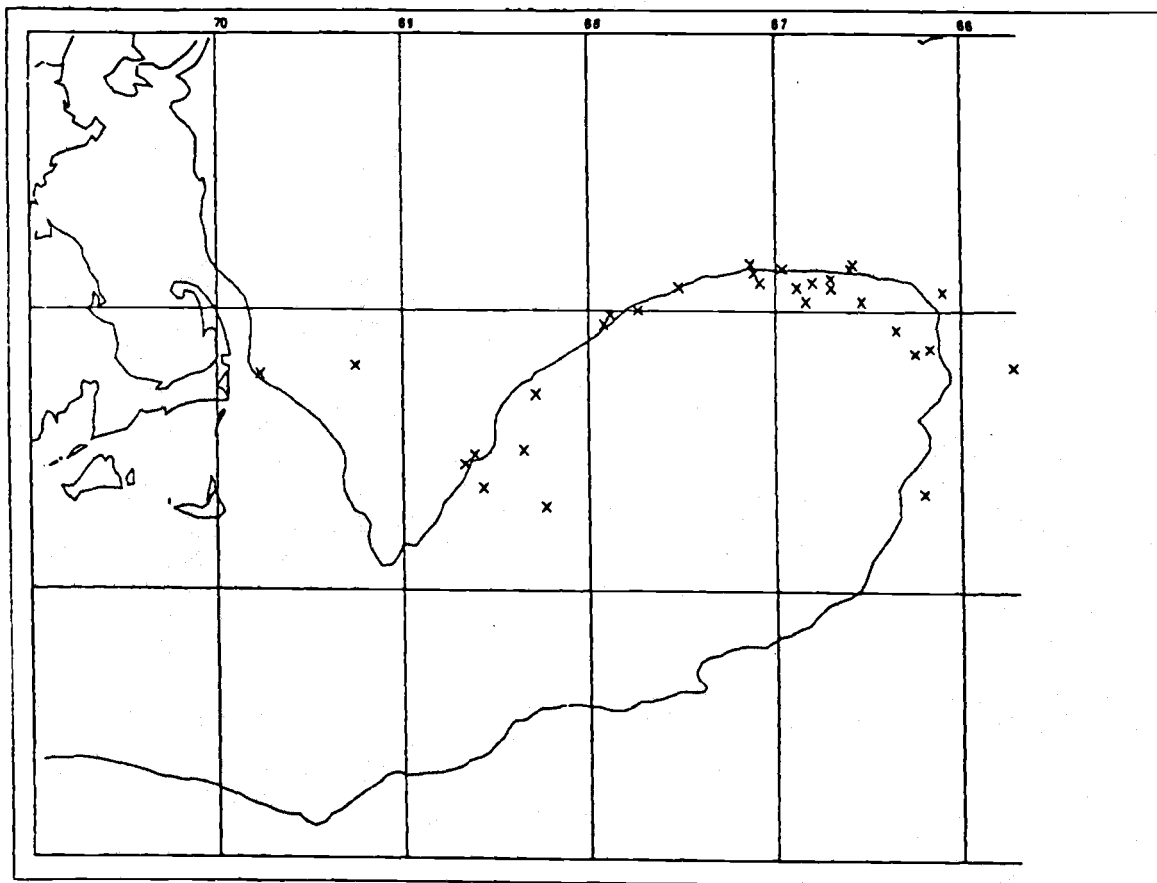


Figure 10. Pooled station distribution for the Northeast Peak-Gulf of Maine Deep assemblage, Spring 1968-1974

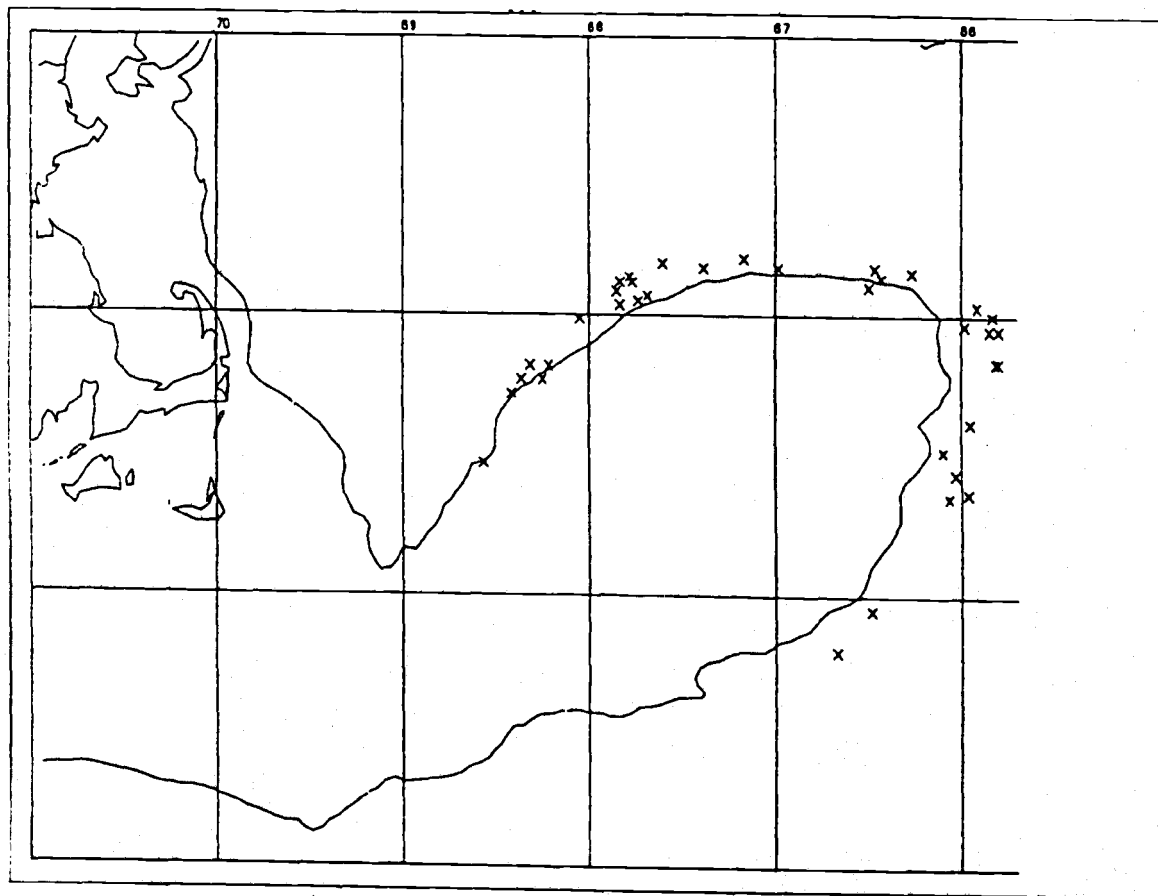


Figure 11. Pooled station distribution for the Slope and Canyon assemblage, Fall 1963-1968

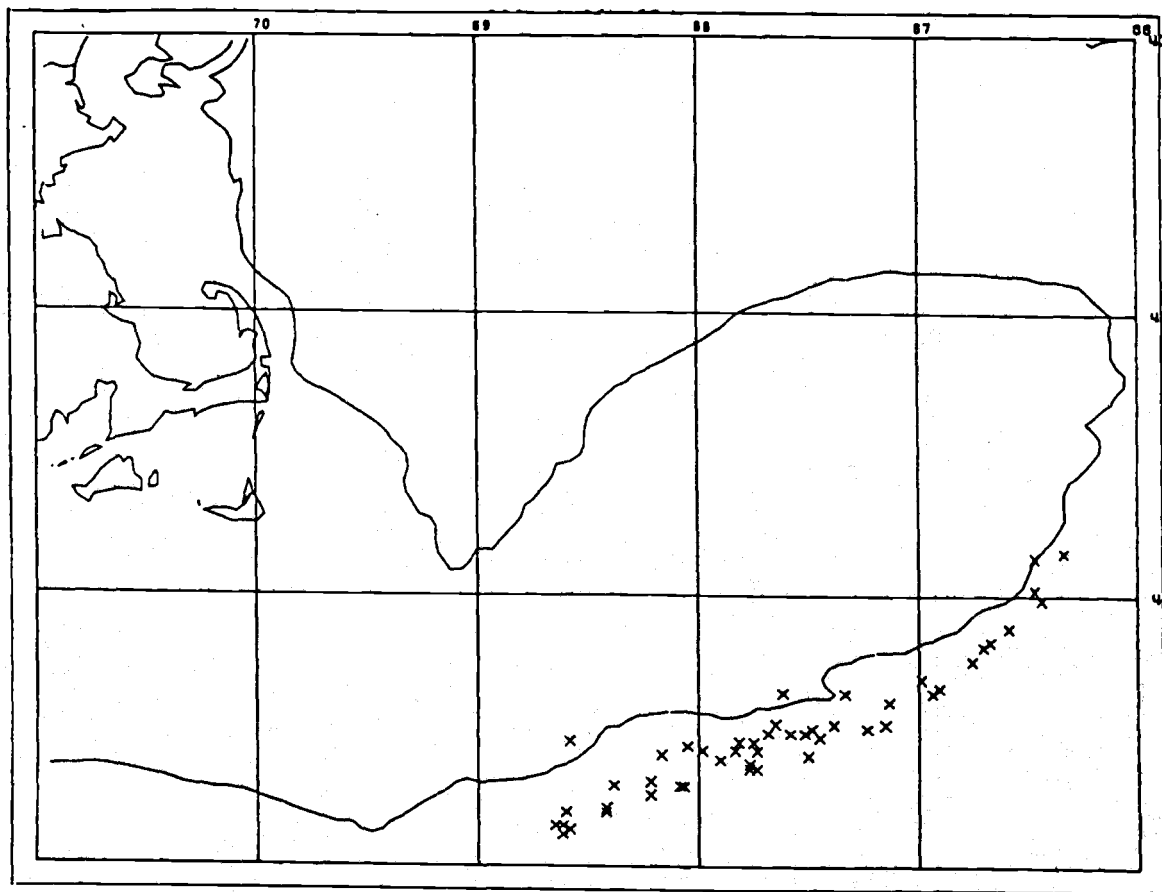


Figure 12. Pooled station distribution for the Intermediate assemblage,
Fall 1963-1970

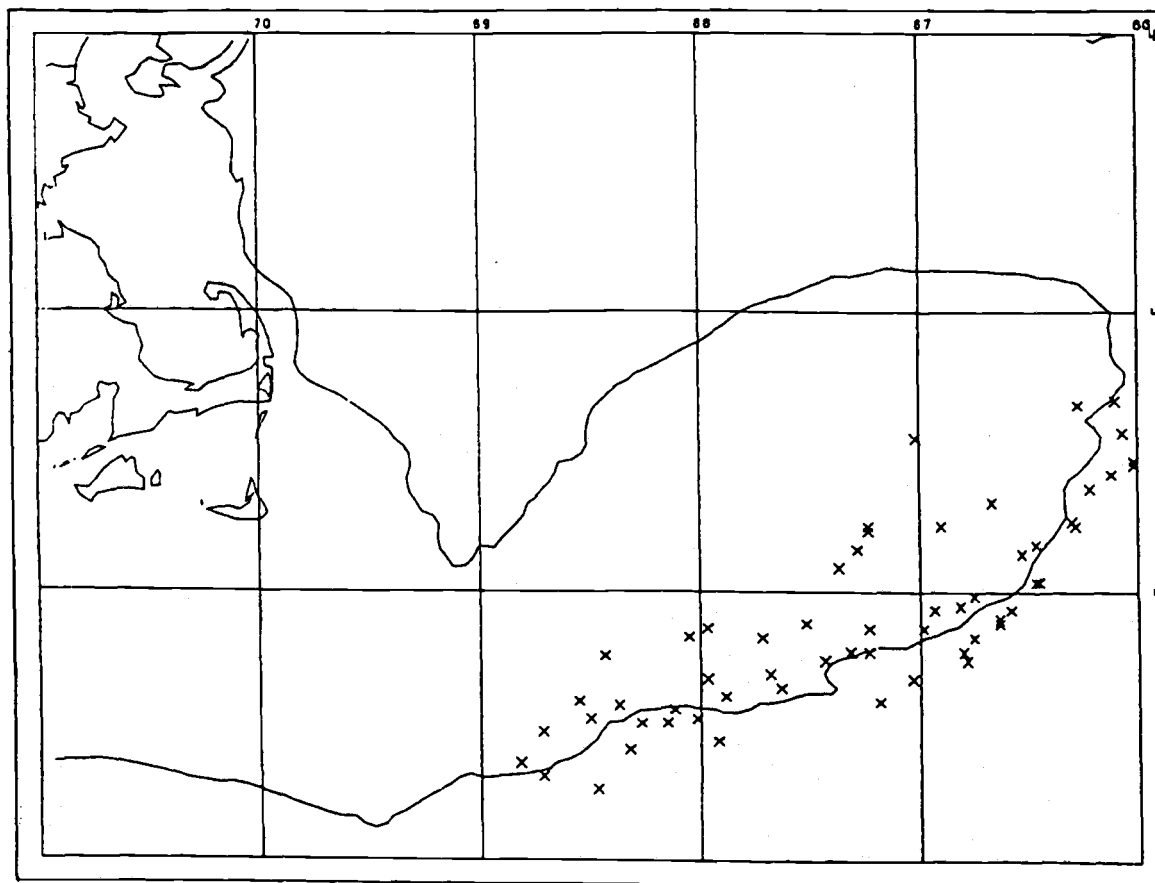


Figure 13. Pooled station distribution for the Shallow assemblage, Fall 1963-1967

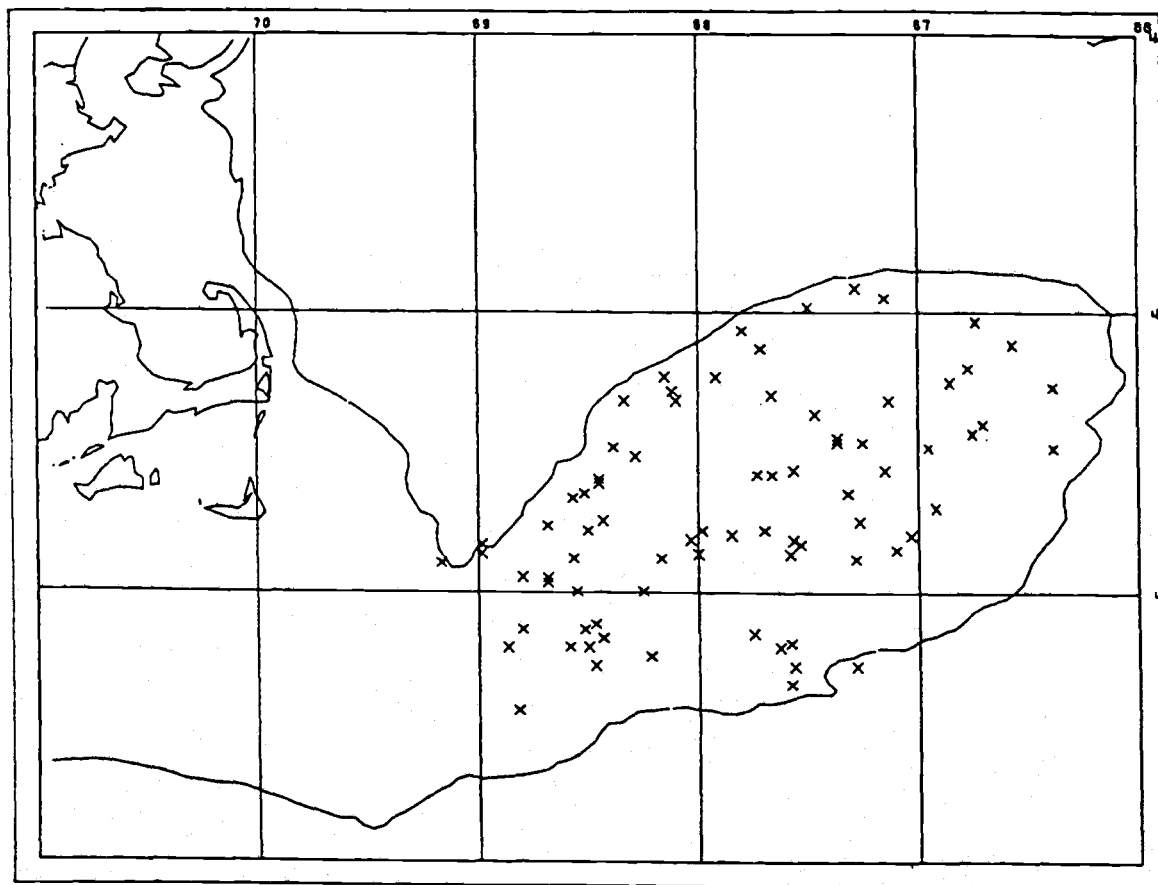


Figure 14. Pooled station distribution for the Northeast Peak assemblage,
Fall 1964-1970

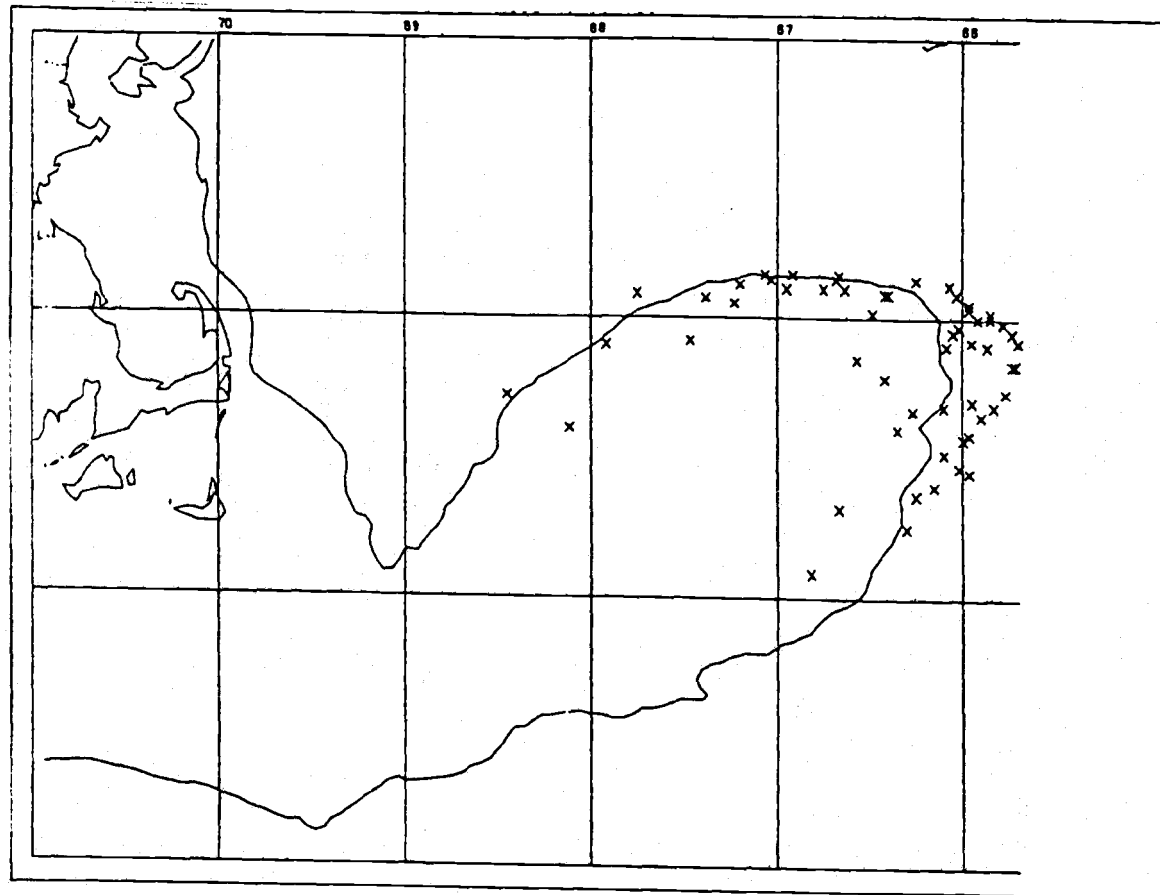
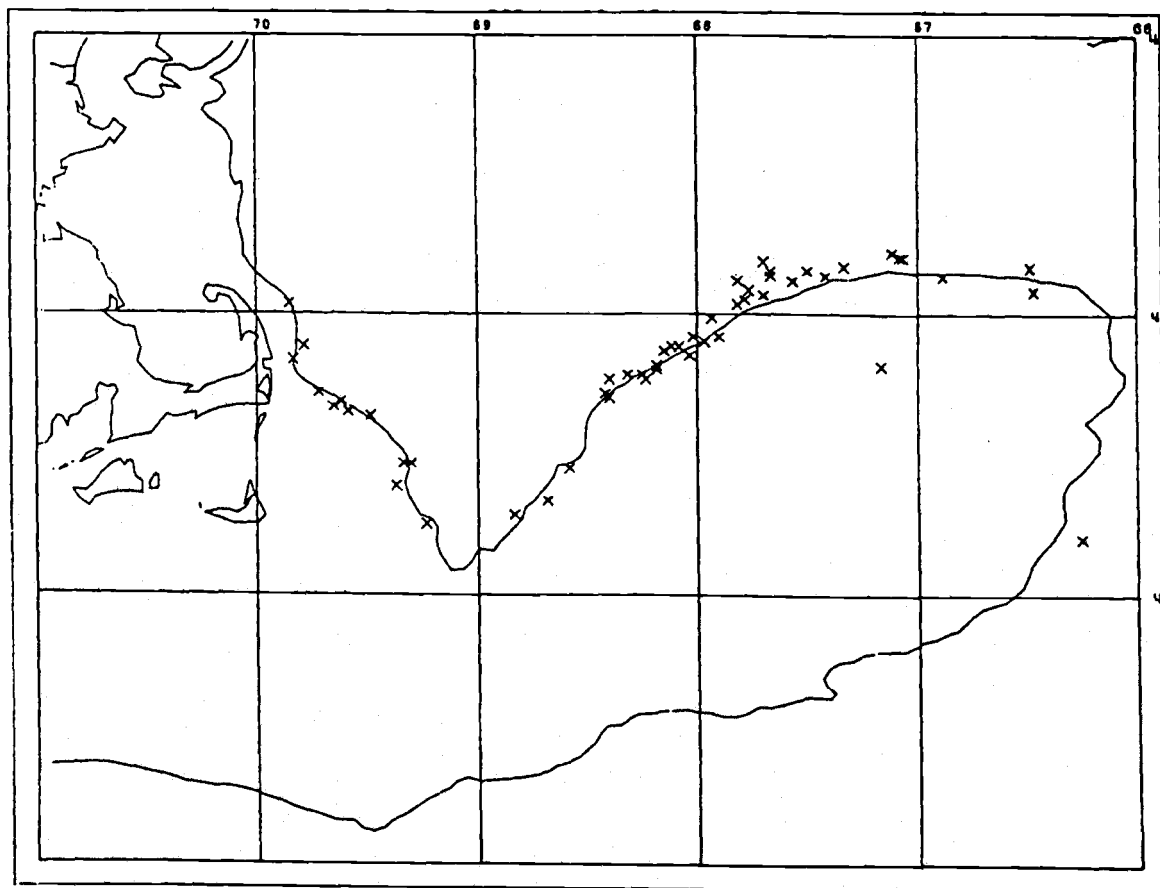


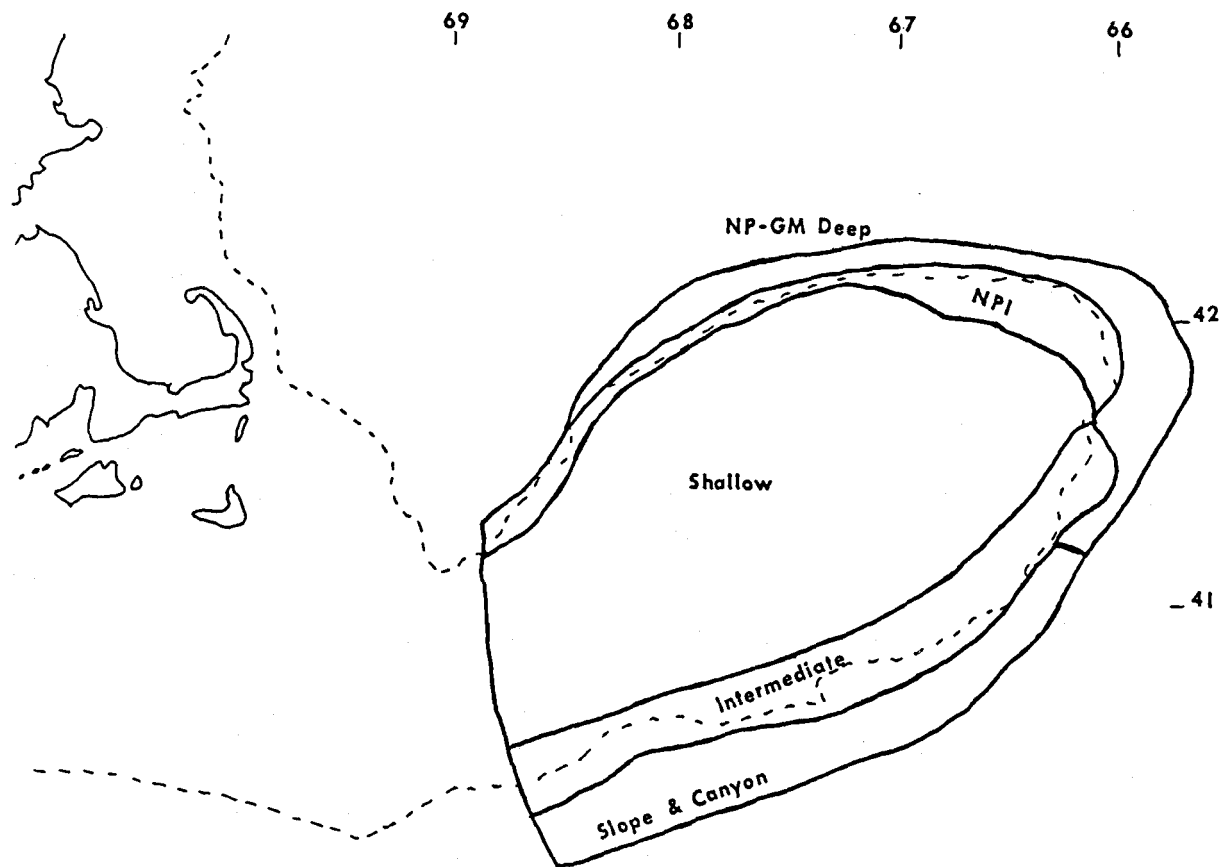
Figure 15. Pooled station distribution for the Gulf of Maine Deep assemblage, Fall 1963-1971



changes. The Shallow assemblage covered most of Georges Bank in the spring (Fig 16), but yielded some of its' area to the Intermediate and Northeast Peak assemblages in the fall (Fig 17). The Intermediate assemblage is about 2 times larger in the fall (Fig 17), suggesting a slight migration of this species complex toward 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 16). 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 (Figs 16 and 17). The general shape and location of the fall assemblages suggests that a different set of oceanographic and biological forcing factors are the important determinant of distribution. 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.

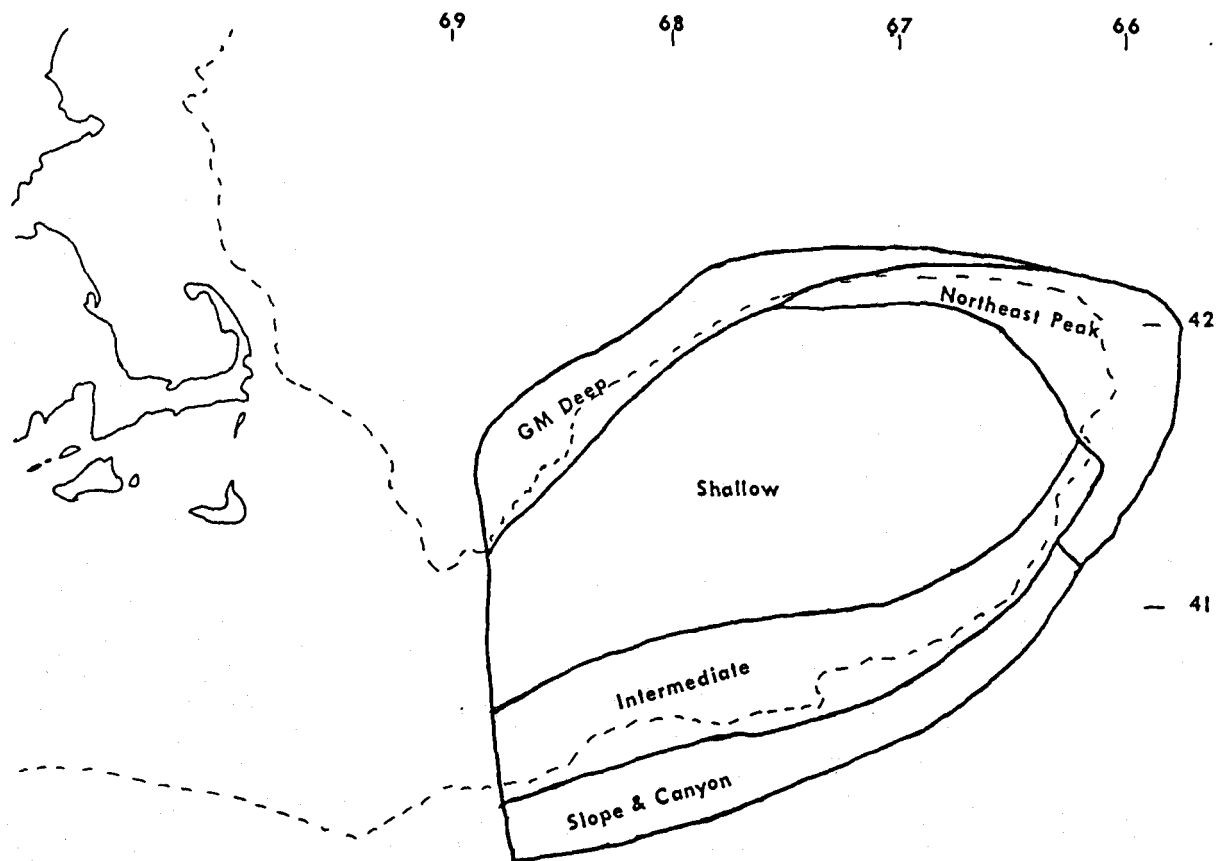
A suggested method for validating the authenticity of cluster groups was to use several random cruises in multivariate analyses of variance to assess if statistical differences between assemblages existed. Results from this analysis are presented in Table 2, showing a clear trend between the assemblages in question. The groups then have dissimilar species composition and biomass. Further proof of this is shown in Fig 18, a discriminant function map (Nie et al 1975) with group centroids, where group separation is also suggested. These analyses, although somewhat predisposed, help reinforce the idea that meaningful and useful community

Figure 16. Composite map of Spring Georges Bank assemblages..



Georges Bank Spring Assemblages (100 m. contour)

Figure 17. Composite map of Fall Georges Bank assemblages.....



Georges Bank Fall Assemblages (100m. contour)

Table 2: Results of multivariate analysis of variance
for fall 1966, 1973 data.

Year	Wilks Lamda	Approx F	DF	Significance Of F
1966	.00464	2.35566	102	.00001
1973	.00023	5.14327	143	.00001

groups were produced with this clustering procedure.

The assemblage maps presented in (Figs 16 and 17) were useful for organizing the 38 species of (Table 1) into their corresponding assemblage subunits (Table 3). There are four basic categories of Georges Bank species that are present in the various assemblages. These include several ubiquitous species, resident species, periodics and those present in several assemblages, but as different life history stages. 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 flounder were present in only one or two assemblages in abundance. Periodic or seasonal migrants include bluefish, butterfish, 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 (Fig 19). A number of species including silver hake, red hake, white hake, and haddock, were present in more than two assemblages 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 assemblage, while juveniles are more abundant in the Shallow assemblage. (Figs 20 and 21) show silver hake length frequencies from these assemblages, emphasizing this differential life history distribution. White hake adults similarly are found in the Slope and Canyon

Table 3: Assemblage species associations from cluster results

Slope and Canyon:

Silver hake
White hake
Red hake
Gulfstream flounder
Offshore hake
Fourspot flounder
Blackbelly rosefish
Goosefish

GM Deep:

Thorny skate
American plaice
Witch flounder
White hake
Silver hake
Cod
Haddock
Cusk
Atlantic wolffish

Intermediate:

Winter skate
Little skate
Red hake
Silver hake
Cod
Haddock
Sea raven
Goosefish
Ocean pout
Longhorn sculpin
Yellowtail flounder

Northeast peak:

Thorny skate
Cod
Haddock
Pollock
White hake
Winter flounder
Ocean pout
Longhorn sculpin

Shallow:

Winter skate
Little skate
Silver hake
Cod
Haddock
Pollock
White hake
Red hake
Summer flounder
Yellowtail flounder
Winter flounder
Windowpane flounder
Longhorn sculpin
Sea raven
Ocean pout
Sand lance
Goosefish

Figure 19. long finned squid research catch/tow (kg) , Fall 1963-1978

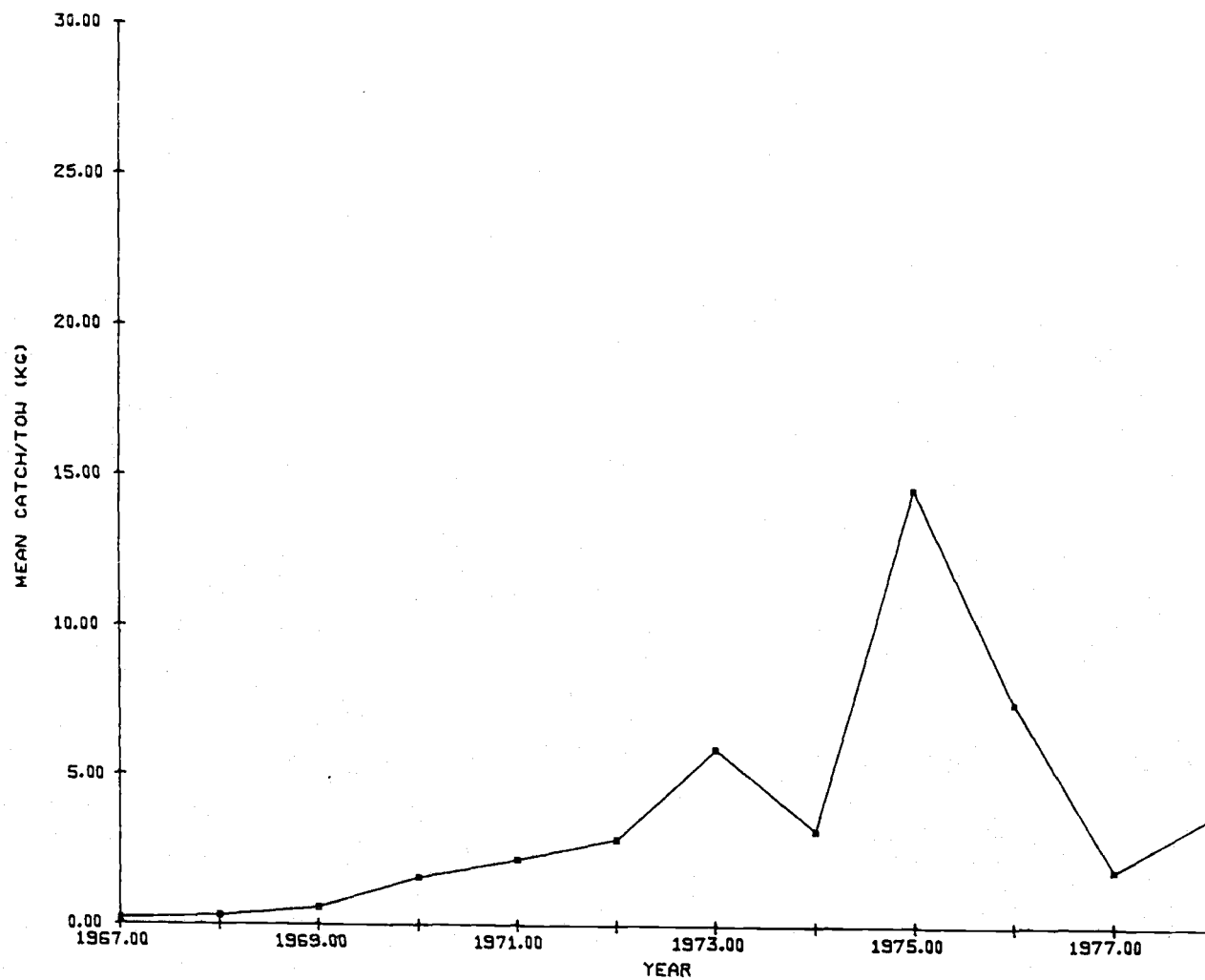


Figure 20. Silver hake length frequency from the Slope and Canyon assemblage, Fall 1969, N=200

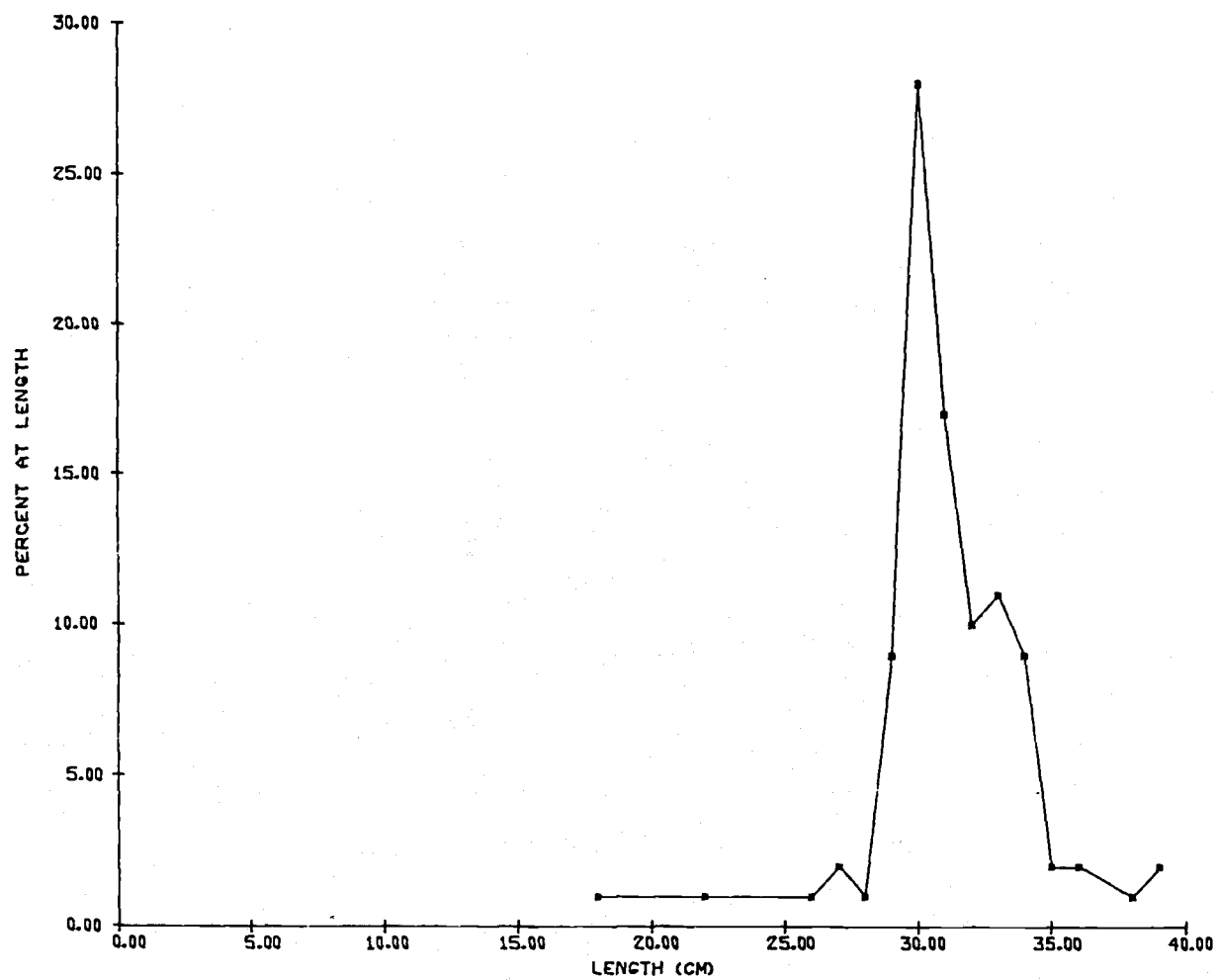
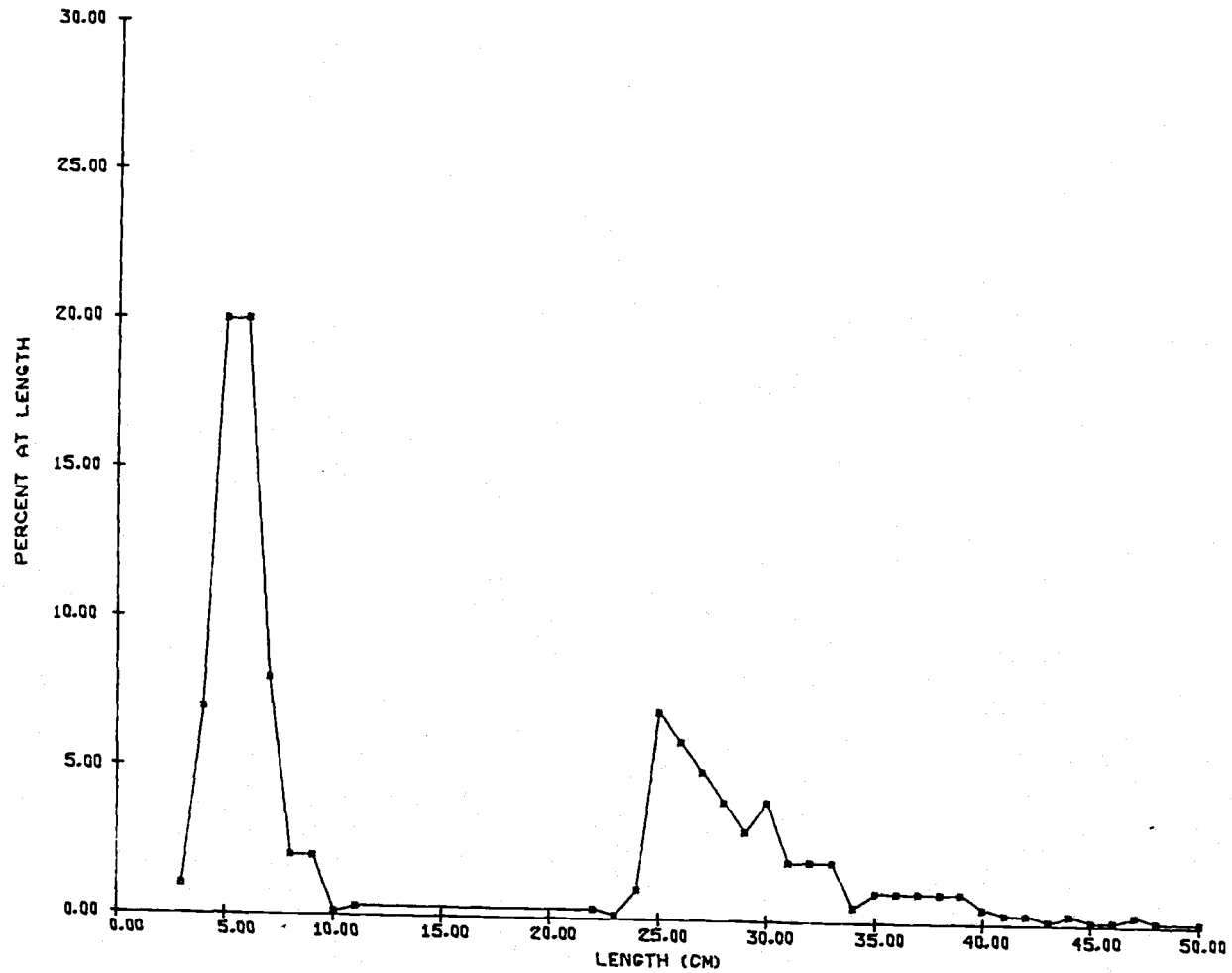


Figure 21. Silver hake length frequency from the Shallow assemblage, Fall 1969, N=635.



assemblage while the smaller fish tended to concentrate in the Shallow assemblage (Figs 22 and 23) respectively. Atlantic cod can be contrasted to these species with length frequencies that show similar length distribution in the Shallow and Northeast Peak assemblages (Figs 24 and 25) It appears that for many of the abundant fish species on Georges Bank, adult stocks 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 were useful for studying temporal trends in both total assemblage catch as well as CPUE for the intra-assemblage species. The spring trend for the Slope and Canyon assemblage in terms of total catch of silver hake, fourspot flounder, red hake, white hake, and blackbelly rosefish remained nearly stable over the period 1968-1975 and increased to over twice this level by 1978 (Fig 26). This abrupt increase can be almost entirely attributed to increased catches of silver hake in those later years. The total catch for the fall time series shows a similar stable trend for most years with the exception of the years 1974-1976 (Fig 27). A clearer perception of these overall catch trends was obtained by examining trends in the individual species catches. For the spring period 1968-1978, the catch of blackbelly rosefish, fourspot flounder, and white hake remained almost constant with very small fluctuations (Fig 28). Red hake and silver hake on the other hand, although initially equally abundant, showed some rather pronounced changes in biomass. Red

Figure 22. White hake length frequency from the Slope and Canyon assemblage, Fall 1969, N=120

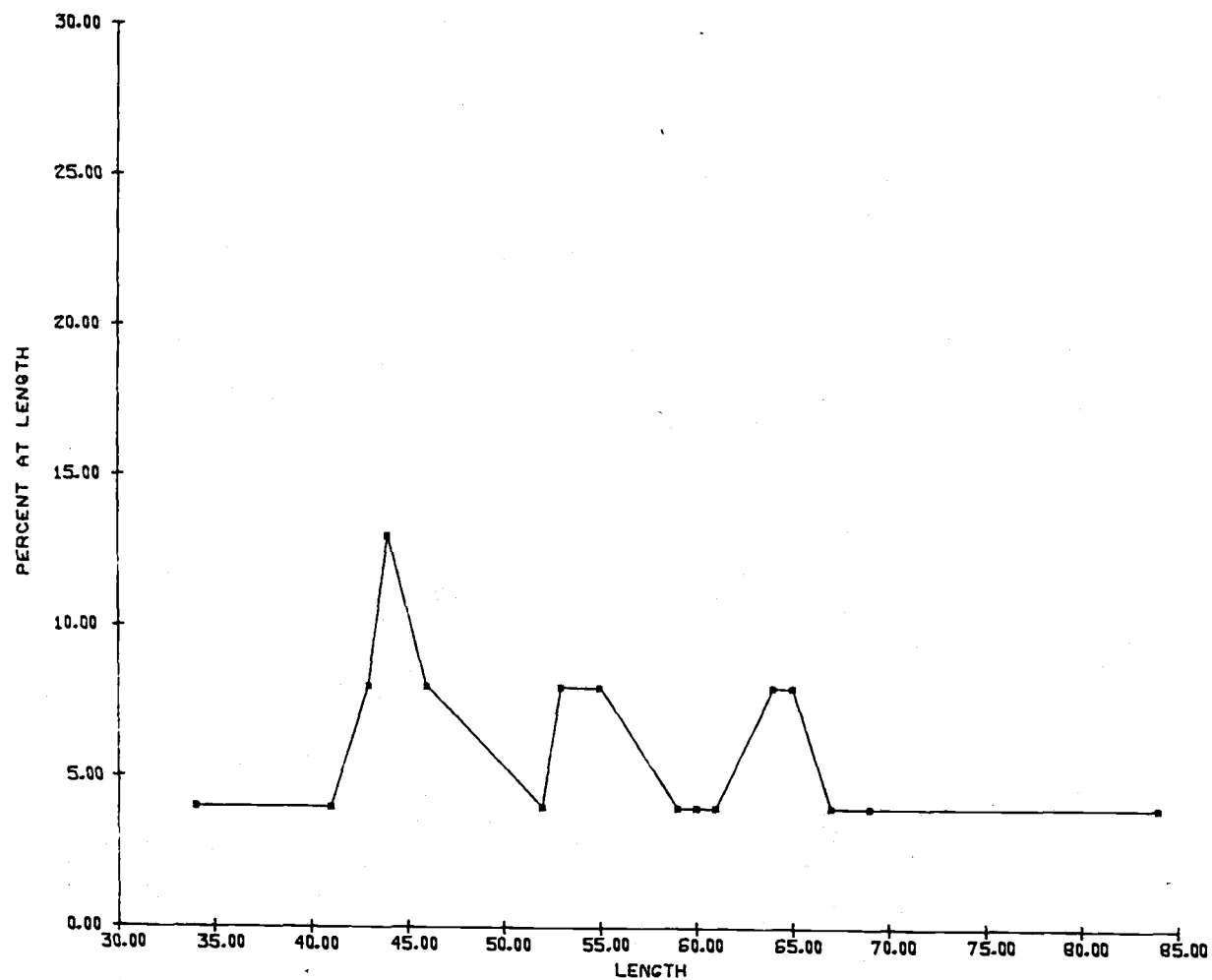


Figure 23. White hake length frequency from the Shallow assemblage, Fall 1969, N=190

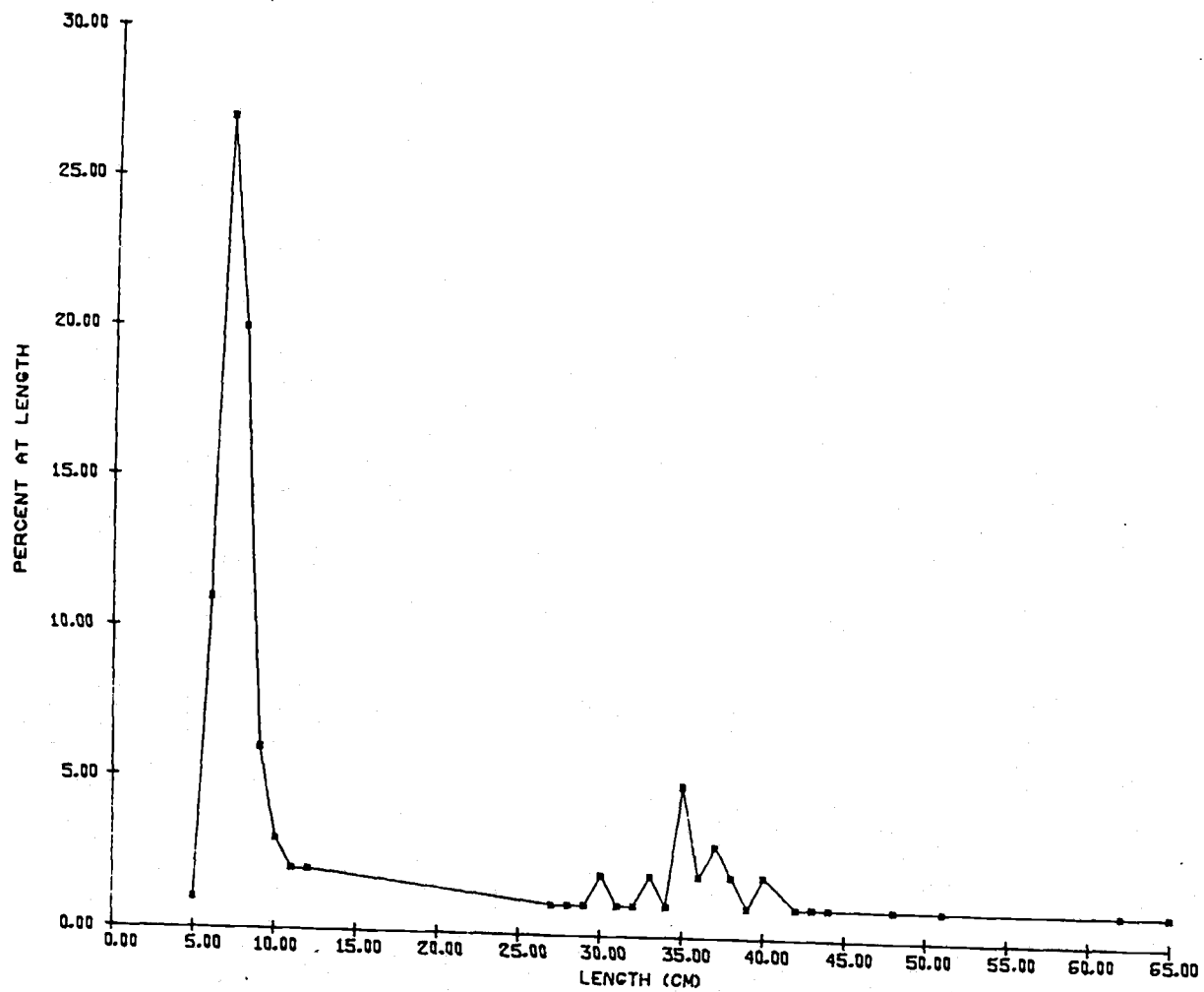


Figure 24. Atlantic Cod length frequency from the Shallow assemblage, Fall 1969, N=29.

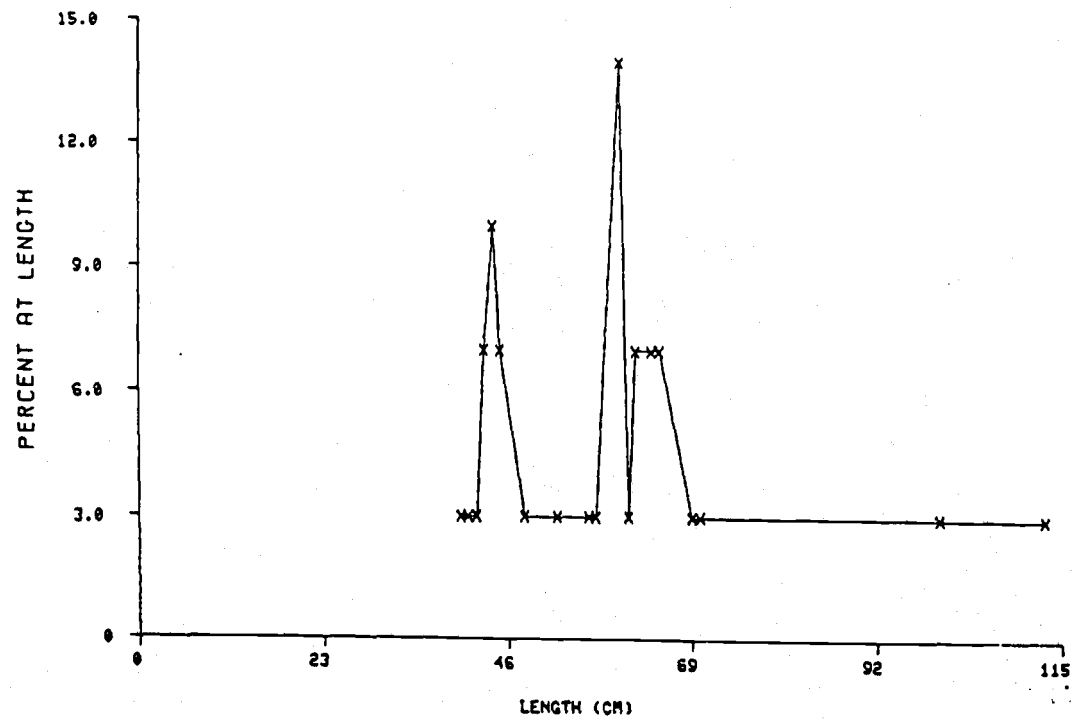


Figure 25. Atlantic Cod length frequency from the Northeast peak assemblage, Fall 1969, N=92.

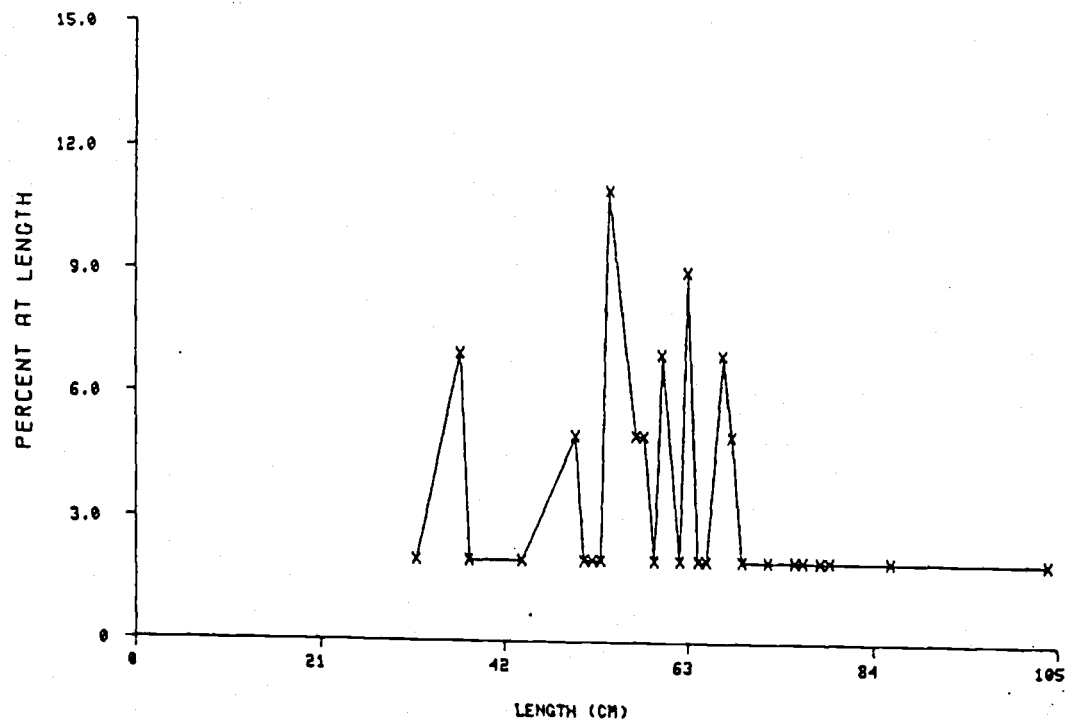


Figure 26. Slope and Canyon assemblage total mean catch/tow (kg), Spring 1963-1978, for selected species

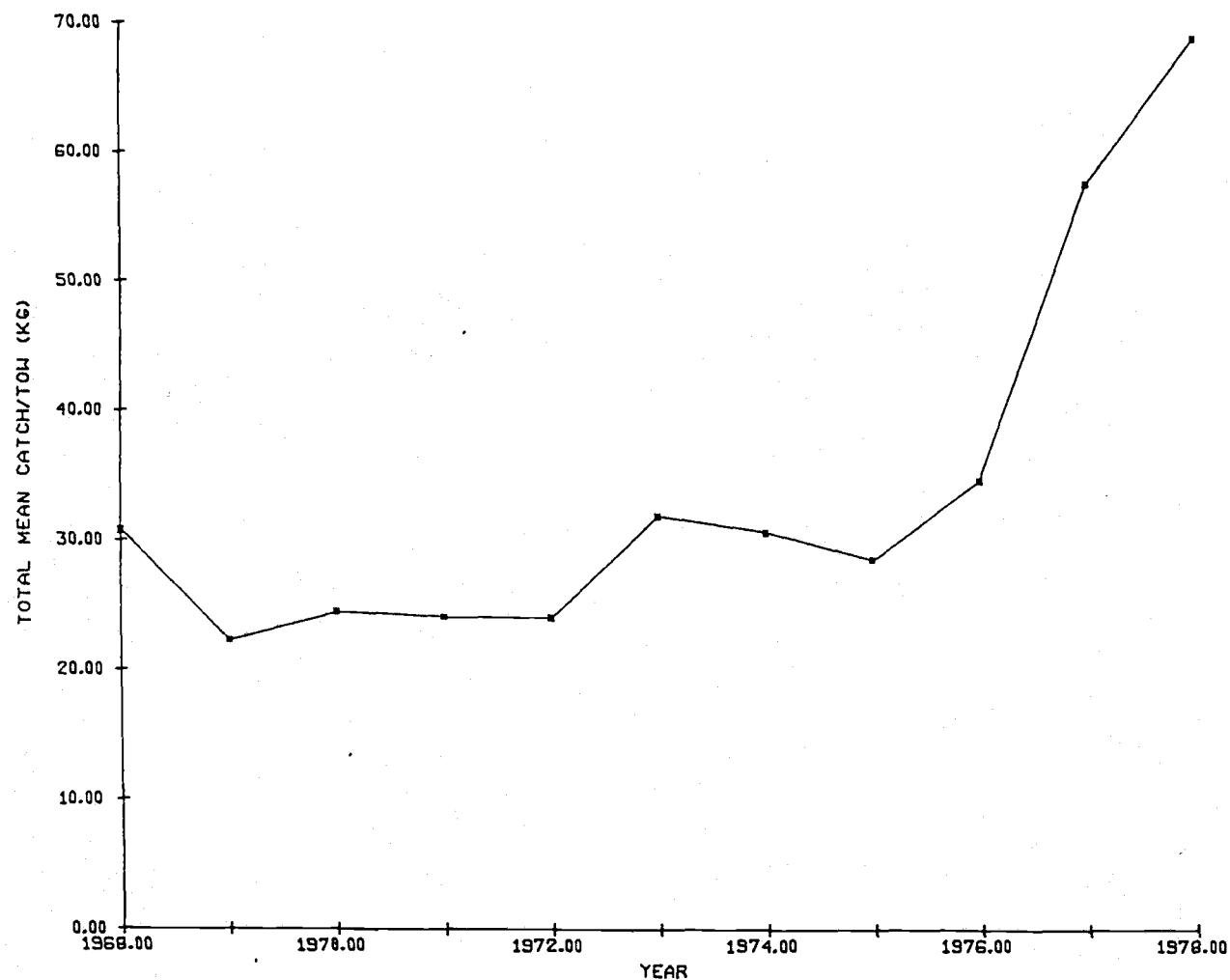


Figure 27. Slope and Canyon assemblage total mean catch/tow (kg), Fall 1963-1978, for selected species

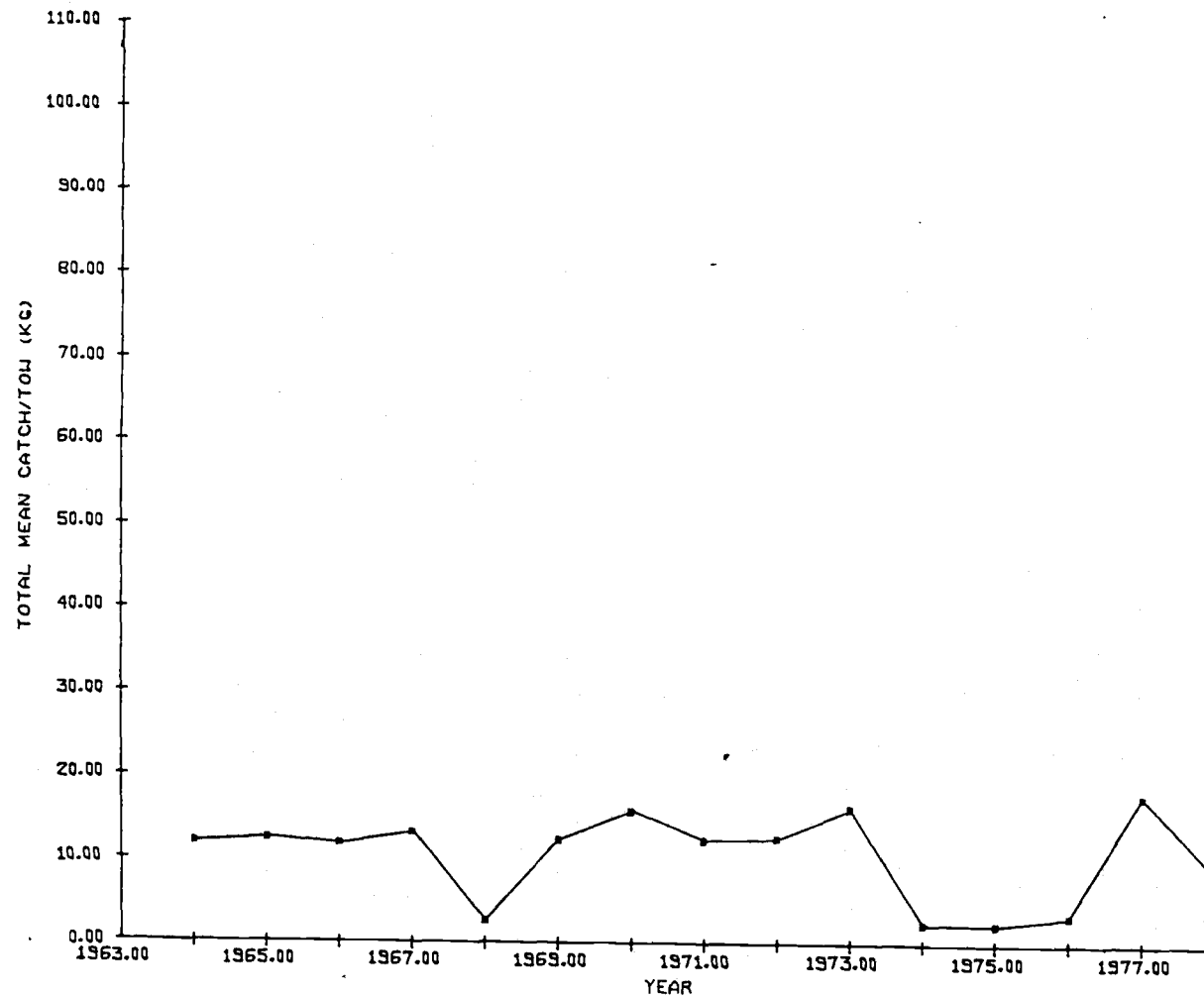
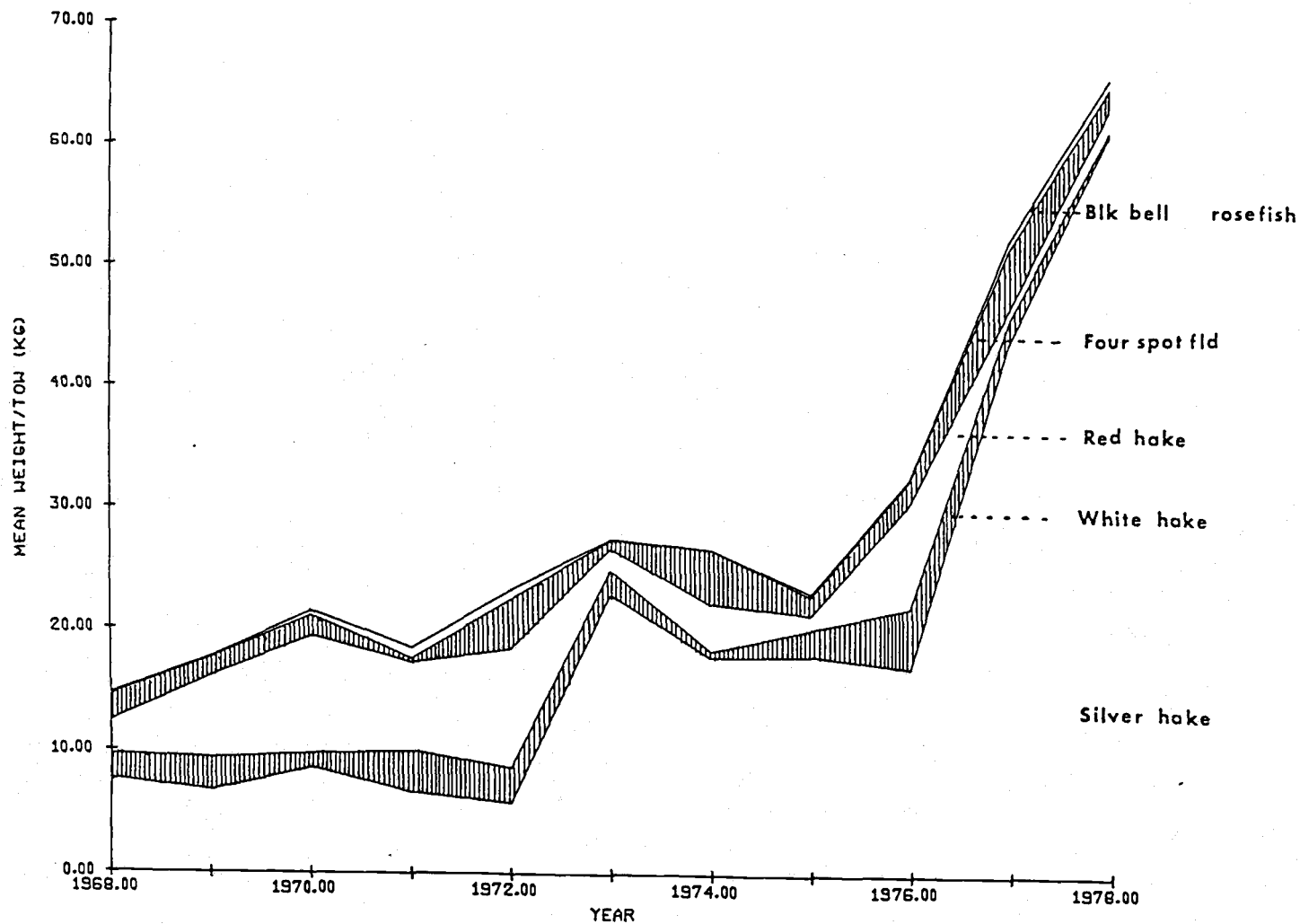


Figure 28. Slope and Canyon cumulative absolute abundance, mean catch/tow (kg), Spring 1968-1978



hake decreased in abundance from 1972-1976 and reached very low levels by 1978 (Fig 28). Silver hake showed an increasing trend from 1972-1976 and dominated the assemblage in 1977-1978 (Fig 28).

The fall trend in absolute abundance for fourspot flounder and blackbelly rosefish remained fairly constant at low levels of abundance except for an increased value for blackbelly rosefish in 1977-1978. White hake in contrast to the spring picture was one of the more dominant species in this assemblage from 1964 to 1971 and decreased in importance in the later years. Silver hake and red hake displayed a reversed trend when compared to the spring time series, silver hake exerting biomass dominance from 1964 to 1973 , yielding to increasing amounts of red hake in the research catch thereafter (Fig 29). When Slope and Canyon species trajectories based on percent weight and percent number for the fall were examined, a similar and perhaps clearer pattern emerged. Fig 30 shows the trends in percent by weight for the five species indicating the switch in biomass dominance for silver hake and red hake as well as the position of importance that white hake played in the earlier years of the series. Blackbelly rosefish and fourspot flounder showed the same trends in abundance as in the absolute abundance case, but these two species clearly represented more of the catch on a percent weight basis in the later years of the fall time series (Fig 30). Gulfstream flounder was actually one of the more important species numerically, during the mid years of the series (Fig 31, Table 4,7). The same reversing trend for red and silver hake is apparent, as is the clear numerical domination of silver hake in the early to mid 60's (Fig 31). Fluc-

Figure 29. Slope and Canyon cumulative absolute abundance, mean catch/tow (kg), Fall 1963-1978

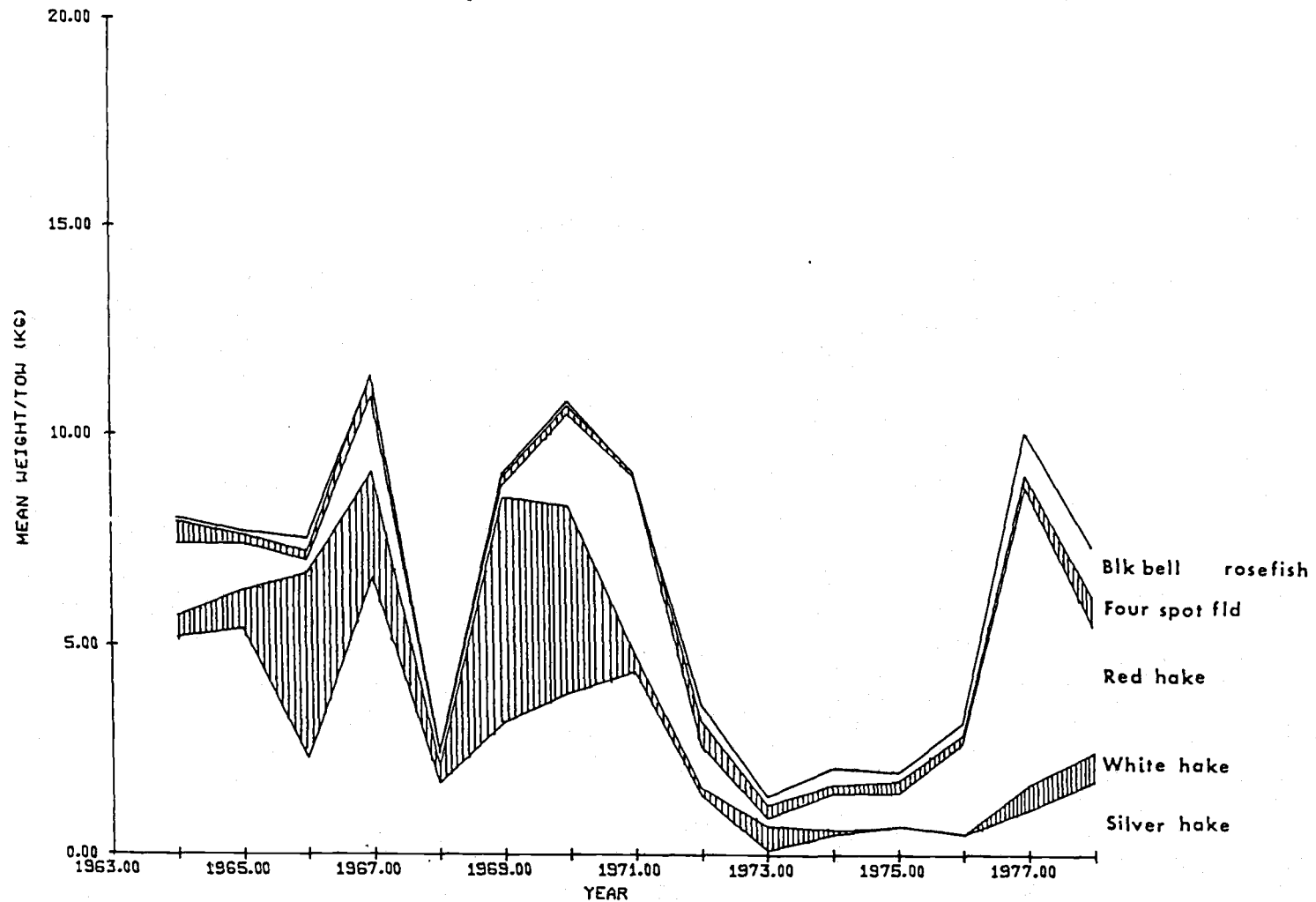


Figure 30. Slope and Canyon cumulative percent by weight, Fall
1963-1978

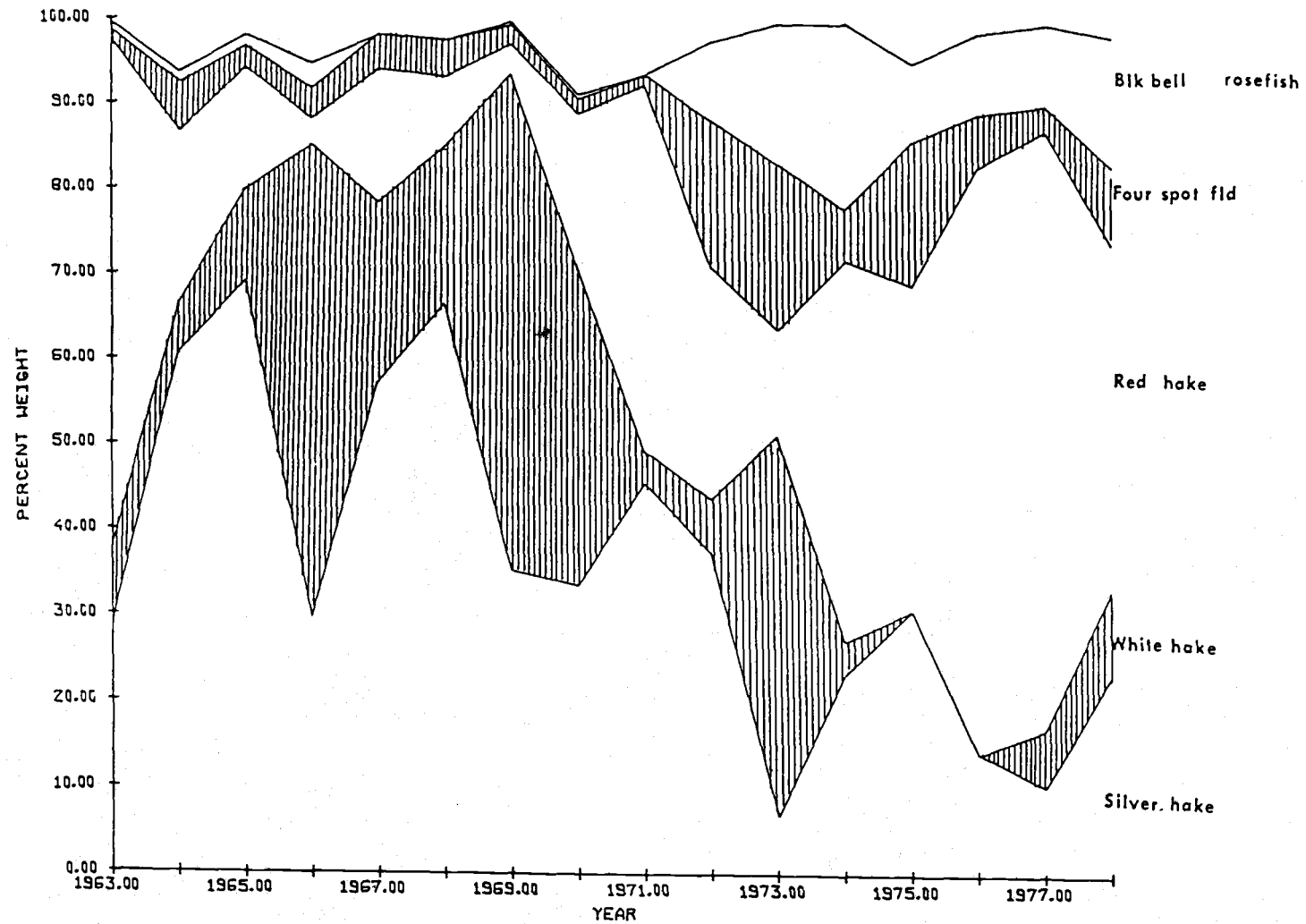


Figure 31. Slope and Canyon cumulative percent by number, Fall
1963-1978

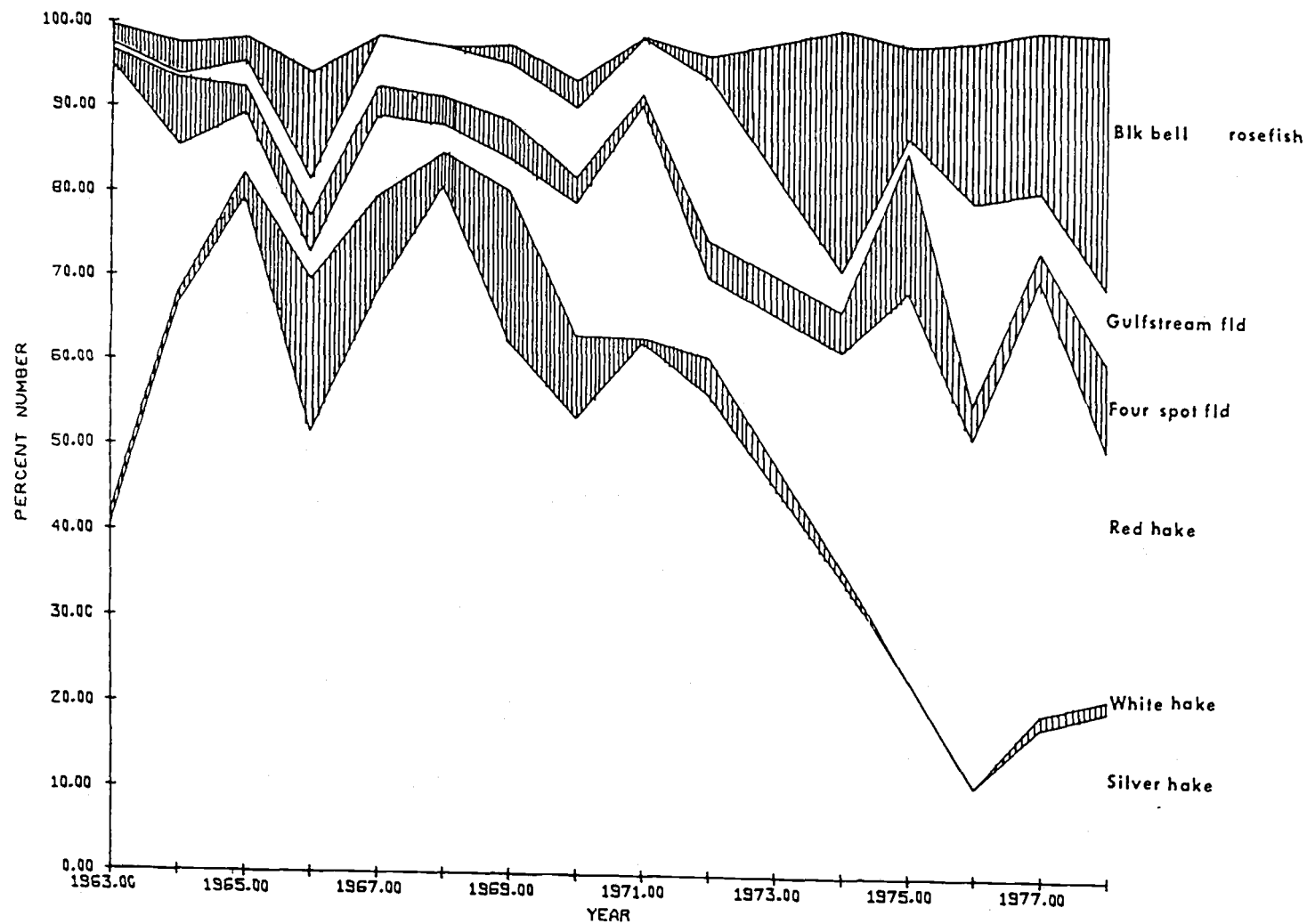


Table 4. Slope and Canyon Assemblage Proportion of Total Species Composition
By Number for Selected Species, with McIntosh Diversity Indices (MDI)

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Silver hake	.368	.432	.665	.308	.533	.649	.824	.411	.539	.503	.031	.272	.079	.108	.138	.152
White hake	.013	.009	.024	.108	.089	.032	.094	.074	.065	.004	.006	.010	.000	.000	.011	.011
Red hake	.483	.112	.060	.019	.074	.027	.020	.120	.235	.043	.006	.195	.152	.405	.389	.219
Fourspot flounder	.016	.052	.026	.025	.027	.027	.023	.023	.012	.037	.075	.036	.055	.041	.025	.078
Gulfstream flounder	.007	.003	.026	.025	.047	.048	.035	.063	.058	.850	.270	.036	.006	.276	.034	.066
Blackbelly rosefish	.019	.024	.024	.076	.000	.000	.012	.025	.001	.046	.107	.221	.037	.187	.145	.226
N	2287	660	388	315	257	188	257	567	778	563	159	195	164	148	442	1135
No. species	23	19	21	20	15	14	21	18	23	16	13	20	11	7	18	24
MDI	1436.65	484.29	212.44	265.19	176.65	106.31	213.19	443.95	504.50	381.09	121.37	161.75	134.37	108.09	348.72	973.43

Table 5. Shallow Assemblage Proportion of Total Species Composition by Number For Selected Species, with McIntosh Diversity Indices (MDI)

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Winter skate	.099	.017	.064	.048	.051	.044	.032	.065	.031	.106	.103	.016	.012	.088	.135	.054
Little skate	.163	.021	.134	.074	.168	.066	.053	.076	.049	.085	.187	.043	.030	.130	.186	.158
Silver hake	.021	.009	.034	.039	.021	.194	.157	.018	.436	.057	.106	.603	.552	.269	.241	.322
Atlantic cod	.019	.000	.001	.026	.091	.012	.007	.059	.013	.047	.035	.001	.008	.009	.031	.013
Haddock	.445	.780	.471	.290	.203	.027	.006	.133	.023	.013	.002	.000	.076	.000	.001	.014
Red hake	.008	.035	.052	.038	.002	.044	.115	.078	.108	.003	.131	.118	.019	.096	.008	.127
Yellowtail flounder	.129	.083	.080	.140	.186	.258	.146	.096	.065	.025	.039	.016	.003	.007	.011	.013
Winter flounder	.016	.000	.005	.053	.024	.022	.019	.080	.017	.040	.014	.002	.018	.070	.032	.027
Windowpane flounder	.016	.008	.024	.062	.075	.031	.082	.024	.038	.384	.228	.179	.097	.303	.206	.116
Longhorn sculpin	.056	.030	.082	.146	.141	.259	.207	.266	.204	.028	.126	.004	.020	.006	.003	.030
N	2836	4330	2762	3206	3063	3822	4054	3350	3874	1098	4791	11645	6286	1391	2873	8652
No. species	24	19	23	21	23	20	25	24	23	20	22	20	23	17	23	21
MDI	2109.40	1650.40	2037.95	2738.30	2628.75	3126.72	3538.08	2916.59	2894.84	867.38	4097.53	6842.47	4114.39	1108.13	2416.19	7170.41

Table 6. Northeast Peak Assemblage Proportion of Total Species Composition by Number For Selected Species, with McIntosh Diversity Indices (MDI).

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Thorny skate	.010	.038	.038	.023	.032	.017	.017	.059	.099	.051	.042	.068	.027	.002	.013	.007
Atlantic cod	.044	.052	.031	.048	.095	.131	.030	.032	.071	.187	.145	.163	.014	.090	.055	.063
Haddock	.787	.647	.403	.131	.155	.099	.025	.123	.164	.118	.263	.085	.108	.882	.769	.629
Pollock	.004	.014	.007	.191	.003	.009	.010	.011	.293	.034	.032	.014	.000	.000	.066	.020
Mailed sculpin	.006	.016	.051	.226	.530	.313	.803	.313	.226	.429	.002	.294	.000	.000	.029	.044
Longhorn sculpin	.071	.031	.263	.104	.022	.045	.016	.333	.022	.084	.031	.097	.057	.013	.038	.025
N	2225	425	744	1463	317	352	1896	751	464	1102	524	503	859	2633	4604	1845
No. species	28	22	24	28	13	19	27	22	20	22	25	23	20	14	22	25
MDI	829.93	242.25	558.49	1249.40	214.72	300.07	665.50	578.27	379.75	832.17	439.55	430.81	574.79	563.46	1837.0	1070.1

Table 7. Slope Canyon Assemblage Mean Number/Tow, Fall 1963-1978, for Selected Species

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Silver hake	*	25.91	36.29	12.13	19.57	13.56	9.22	25.89	69.83	47.17	1.00	4.82	2.60	2.29	10.17	9.05
White hake	*	0.55	1.29	4.25	3.19	0.67	2.67	4.67	0.67	0.33	0.20	0.18	0.00	0.00	0.83	0.63
Red hake	*	6.73	3.29	0.75	2.71	0.56	0.56	7.56	30.50	4.00	0.20	3.45	5.00	8.57	28.67	13.05
Fourspot flounder	*	3.09	1.43	1.00	1.00	0.56	0.67	1.44	1.50	3.50	2.40	0.64	0.82	0.86	1.83	4.63
Gulfstream flounder	*	0.18	1.43	1.00	1.71	1.00	1.00	4.00	7.50	23.50	8.60	0.64	0.11	5.00	4.00	3.95
Blackbelly rosefish	*	1.45	1.29	3.00	0.00	0.33	0.33	1.56	0.17	4.33	3.40	3.91	0.55	4.00	10.67	13.47

Table 8. Shallow Assemblage Mean Number Per Tow, Fall 1963-1978, for Selected Species

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Winter skate	25.55	5.62	13.69	8.50	6.74	7.64	6.45	10.22	0.32	6.47	27.44	10.76	4.47	7.69	17.64	14.47
Little skate	42.09	7.15	28.54	13.22	22.35	11.41	10.65	13.09	1.20	5.16	49.72	29.29	11.00	11.31	24.23	42.75
Silver hake	3.45	2.85	7.31	6.94	2.74	33.68	31.90	3.48	3.35	3.47	28.16	413.24	204.18	23.38	31.45	86.94
Atlantic cod	4.91	0.08	0.31	4.61	12.13	2.00	1.45	8.00	0.00	2.34	9.28	0.65	3.12	0.75	4.05	3.63
Haddock	114.82	259.92	100.08	1.72	27.04	4.77	1.25	11.35	1.80	0.79	0.50	0.12	28.24	0.00	0.14	3.88
Red hake	2.09	11.54	11.00	6.78	0.30	7.73	23.30	12.52	1.95	0.16	34.78	80.71	7.18	8.31	1.05	34.22
Yellowtail flounder	33.66	27.54	17.00	25.00	24.83	44.82	29.60	13.52	19.45	1.53	10.39	11.29	1.29	0.63	1.50	3.59
Winter flounder	4.09	0.15	1.00	9.39	3.17	3.82	3.85	12.74	0.00	2.42	3.73	1.35	6.65	6.06	4.23	7.31
Windowpane flounder	4.09	2.77	5.08	11.06	10.00	5.45	16.65	5.26	0.25	23.42	60.72	122.82	35.71	26.33	26.91	31.34
Longhorn Sculpin	14.45	9.92	17.46	26.06	18.78	44.91	41.95	42.48	5.80	1.74	33.44	2.65	7.41	0.56	4.32	8.16

Table 9. Northeast Peak Assemblage Mean Number/Tow, Fall 1963-1978, for Selected Species

Species	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Thorny skate	3.83	2.67	7.00	3.78	2.50	1.00	2.54	5.50	7.67	11.20	3.67	6.80	3.29	1.50	5.80	1.30
Atlantic cod	16.50	3.67	5.75	7.78	7.50	7.67	4.39	3.00	5.50	41.20	12.67	16.40	1.71	59.25	25.20	11.60
Haddock	293.17	45.83	75.00	21.33	12.25	5.83	3.62	11.50	12.67	26.00	23.00	8.60	13.29	580.50	354.00	116.10
Pollock	1.67	1.00	1.25	31.00	0.25	0.50	1.46	1.00	22.67	7.60	2.83	1.40	0.00	0.25	30.60	3.70
Mailed sculpin	2.33	1.17	9.50	36.67	42.00	18.33	117.15	29.38	17.50	94.60	0.17	29.60	0.00	0.00	13.20	8.20
Longhorn sculpin	26.50	2.17	49.00	66.89	1.75	2.67	2.39	31.25	1.67	18.60	2.67	9.80	7.00	8.25	17.70	4.60

tuations in white hake numbers appear to mimic the percent weight information as do the trends for blackbelly rosefish, except that this later species apparently has undergone a pronounced increase in numbers since 1972.

Total catch for the Shallow assemblage during the spring 1968-1978 showed a fairly stable trend between 1970 and 1977 (Fig 32). This assemblage was much more diverse in its demersal fish community than the Slope and Canyon assemblage. The major species of importance were Atlantic cod, winter flounder, windowpane flounder, winter skate, longhorn sculpin, little skate, yellowtail flounder, and haddock. When the fall time series for this assemblage was examined a better time perspective was obtained. Mean catch per tow declined dramatically from 202 kg in 1963 to 22 kg in 1972 and subsequently rose to 99 kg in 1978 or about 1/2 the 1963 value (Fig 33). Trends in absolute abundance for the individual species (Fig 34) showed different responses depending on the species of interest. Winter flounder, longhorn sculpin and winter skate appear to have remained fairly constant in abundance over the time period, while Atlantic cod, windowpane flounder, and little skate displayed an increasing trend in biomass (Fig 34). Yellowtail flounder and haddock showed declining mean catches over this interval (Fig 34). Again the fall time series, being the longer of the two, served to clarify some of the observed spring trends. Figs 35 and 36 are exactly the same except the 1973 point has been removed in Fig 36. This expanded view of species temporal responses shows that cod and winter flounder CPUE remained relatively stable over this time period. Windowpane flounder,

Figure 32. Shallow assemblage total mean catch/tow (kg), Spring 1968-1978, for selected species

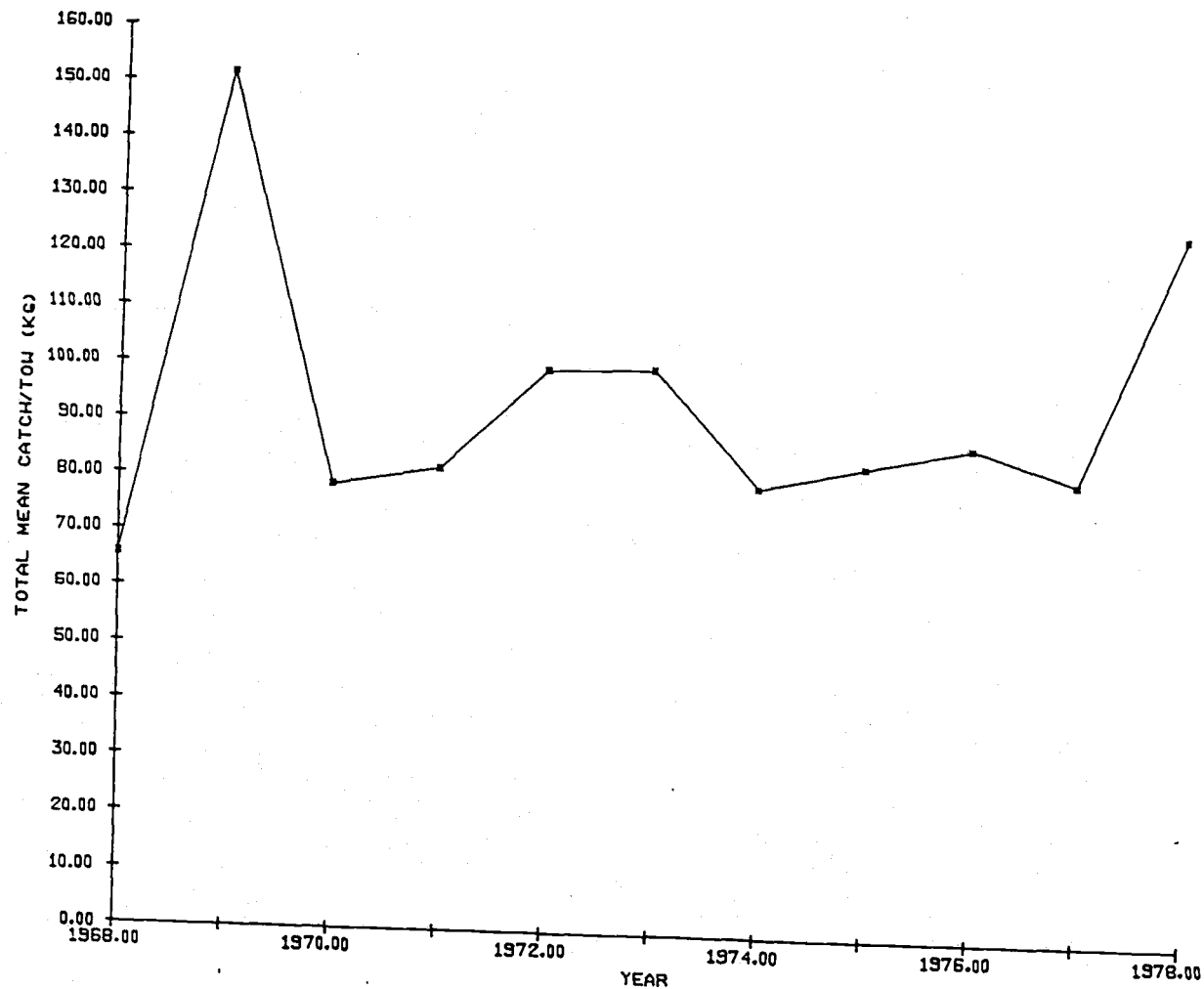


Figure 33. Shallow assemblage total mean catch/tow (kg), Fall 1963-1978, for selected species

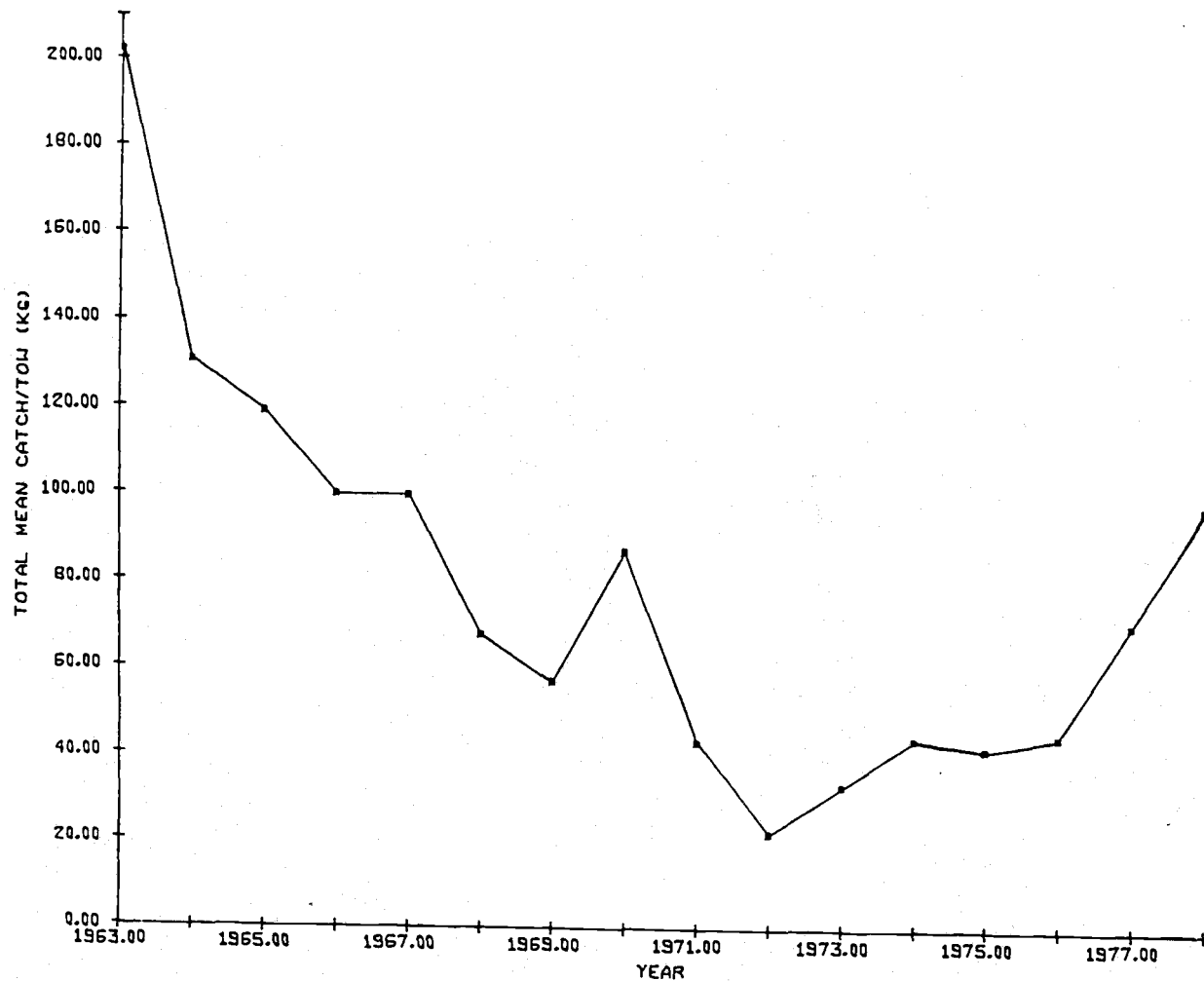


Figure 34. Shallow assemblage cumulative absolute abundance, mean catch /tow (kg), Spring 1968-1978

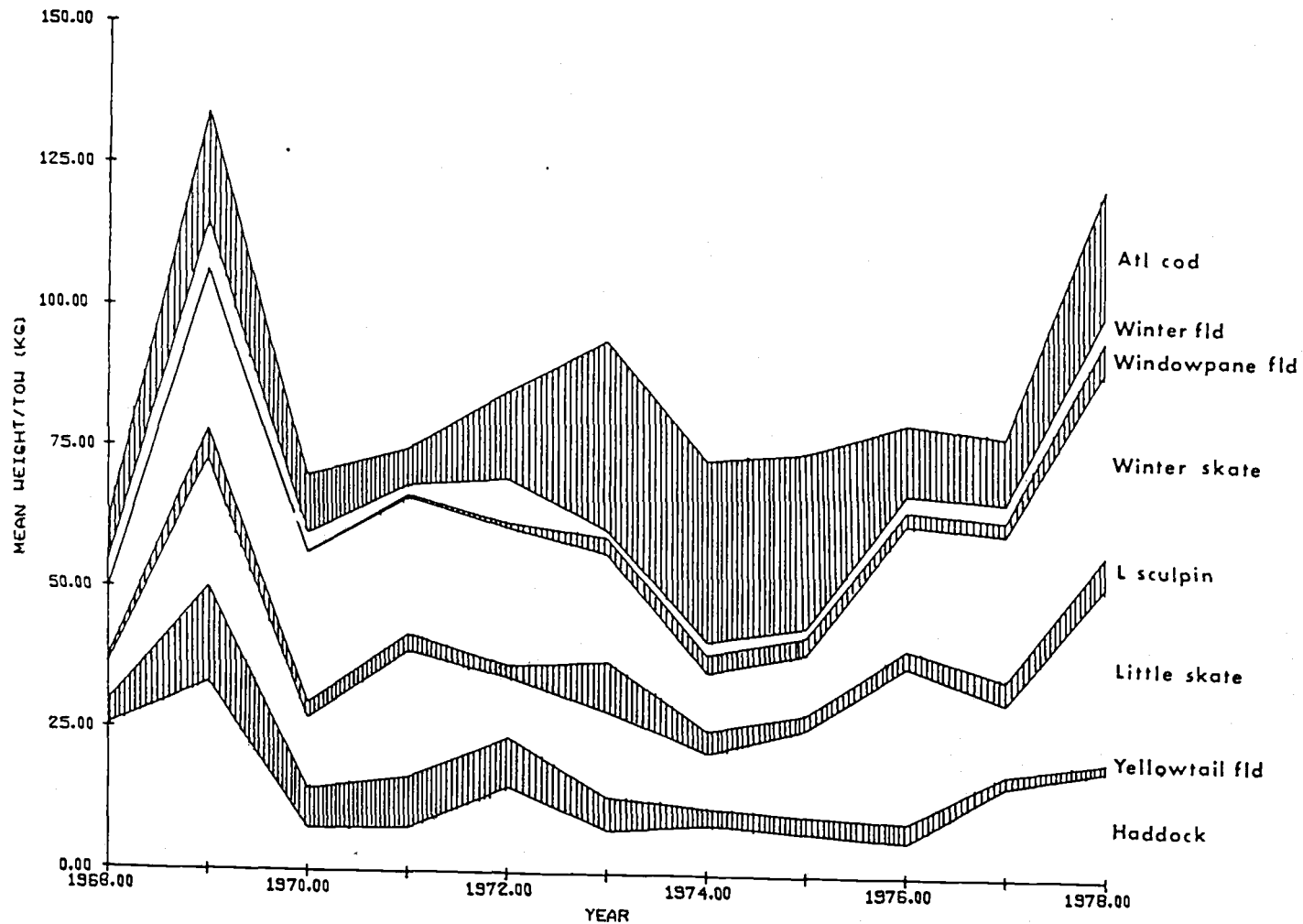


Figure 35. Shallow assemblage cumulative absolute abundance, mean catch/tow (kg), Fall 1963-1978.

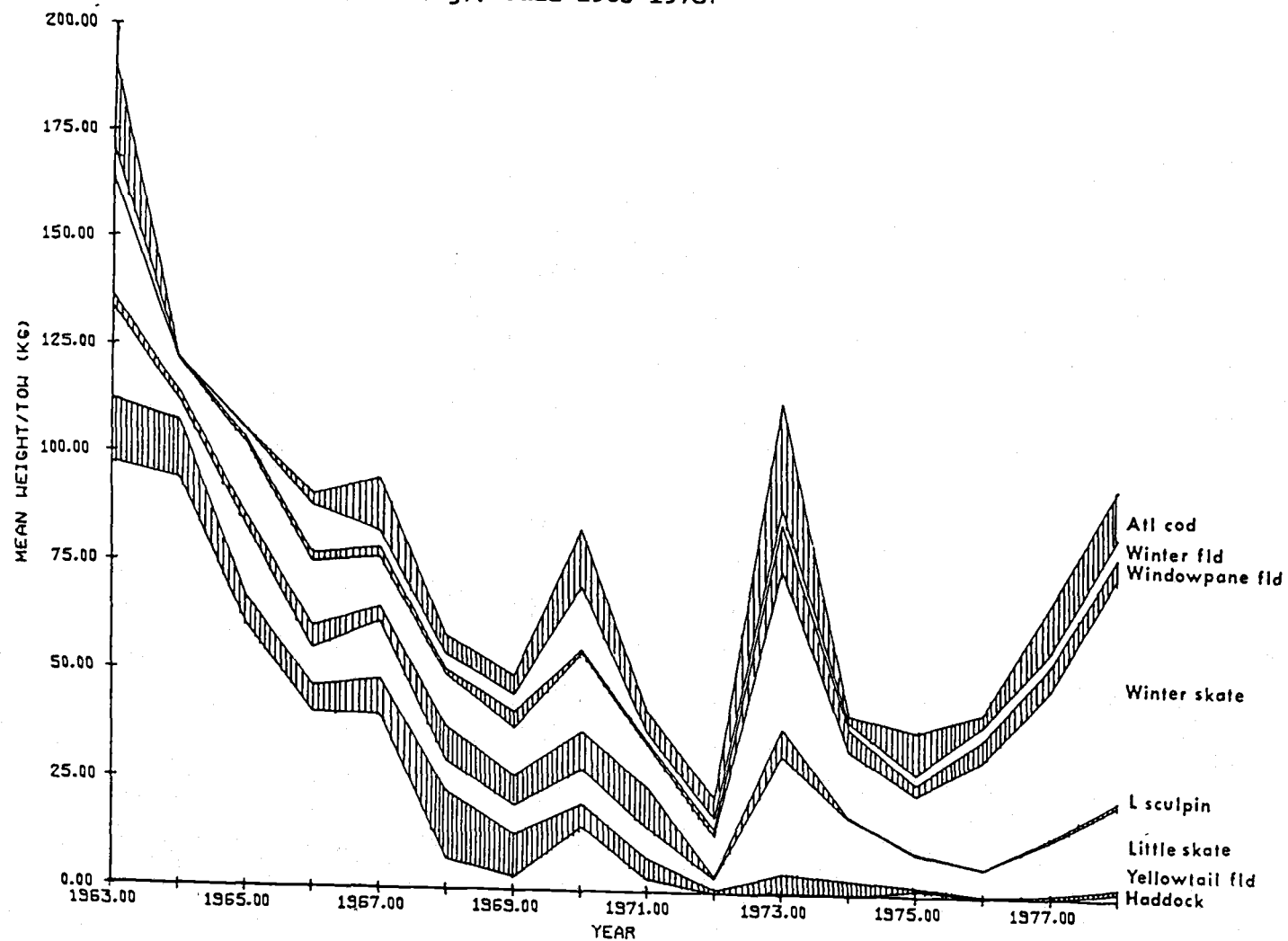
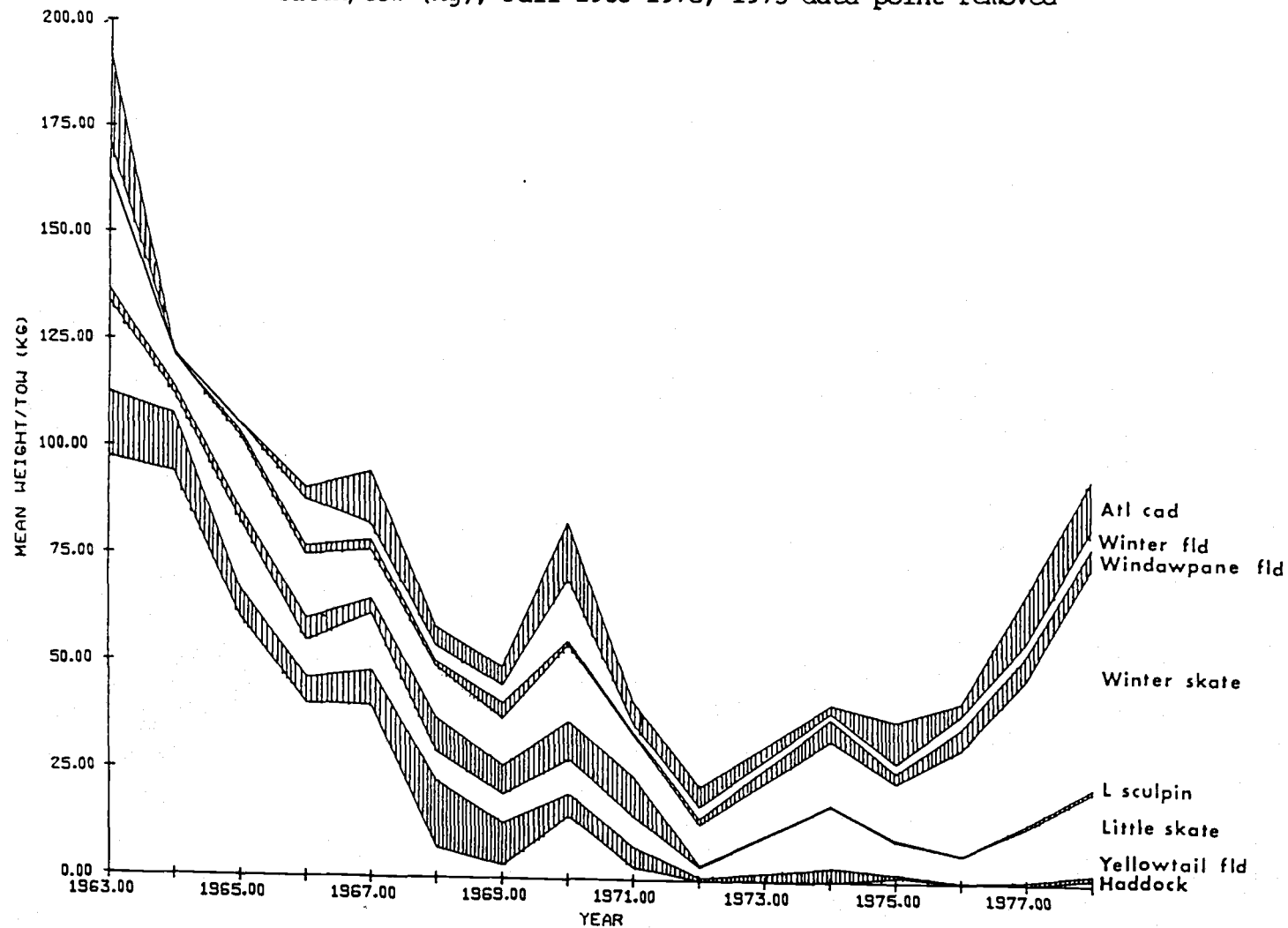
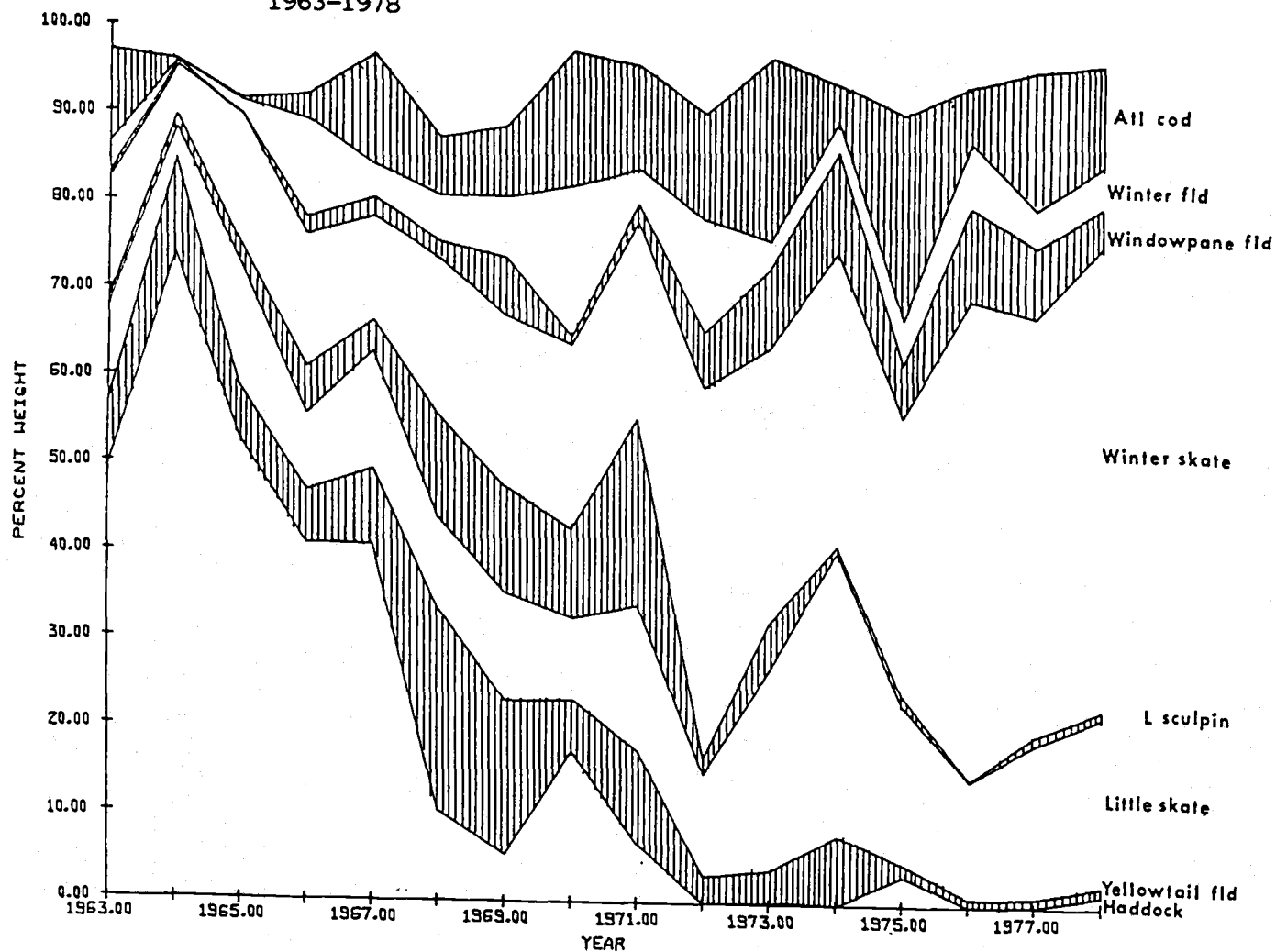


Figure 36. Shallow assemblage cumulative absolute abundance, mean catch/tow (kg), Fall 1963-1978, 1973 data point removed



winter skate and little skate appear to have increased since 1972. 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 (Fig 36). Yellowtail flounder fluctuated from 15 kg in 1963 to a low of 6 kg in 1966, experienced a gradually increasing trend from 1966-1969 and began a precipitous decline that lasted through 1978 (Fig 36). The decline in the haddock biomass was the undisputed cause of the trend in total catch observed in (Fig 33). As with the Slope and Canyon assemblage some interesting species trends were revealed in cumulative percent by weight and number trajectories for the Shallow assemblage. Most of the species followed the same directional changes as observed in the previous cumulative absolute abundance analysis, but the changes were accented for some species. 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 1966-1971 and then all declined in importance (Fig 37). Haddock as previously noted, experienced a pronounced decline in abundance from the early 60's and was only present at very low levels from 1972-1978. 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 37). When cumulative percent by number was investigated, silver hake and red hake became important while cod had very low densities and therefore do not appear in the analysis. Silver hake numbers showed a general increasing trend throughout the time in-

Figure 37. Shallow assemblage cumulative percent by weight, Fall
1963-1978



terval and were the numerical dominant through most of the mid and late 70's. This trend was due entirely to increased numbers of juvenile silver hake that represented an insignificant 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 70's. Trends for windowpane flounder, longhorn sculpin, little skate, yellowtail flounder, and haddock match favorably with the cumulative absolute and percent weight data (Fig 38, Table 5,8).

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, GM Deep and Northeast Peak assemblages is displayed in (Figs 39,40,41). respectively for the fall surveys 1963-1978. 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 70's. Decreased CPUE for the intermediate assemblage can be attributed to a general decline in all the species present, while the recovery period was produced by increased catches of winter skate, little skate, red hake, and longhorn sculpin. Trends in total catch in the GM Deep assemblage were also produced by general declines in the total demersal community, but thorny skate, cod, haddock, pollock, and white hake decreases were the most important contributors. General decreases in the catch of thorny skates and cod were partly responsible for the downward slide in CPUE for the

Figure 38. Shallow assemblage cumulative percent by number, Fall
1963-1978.

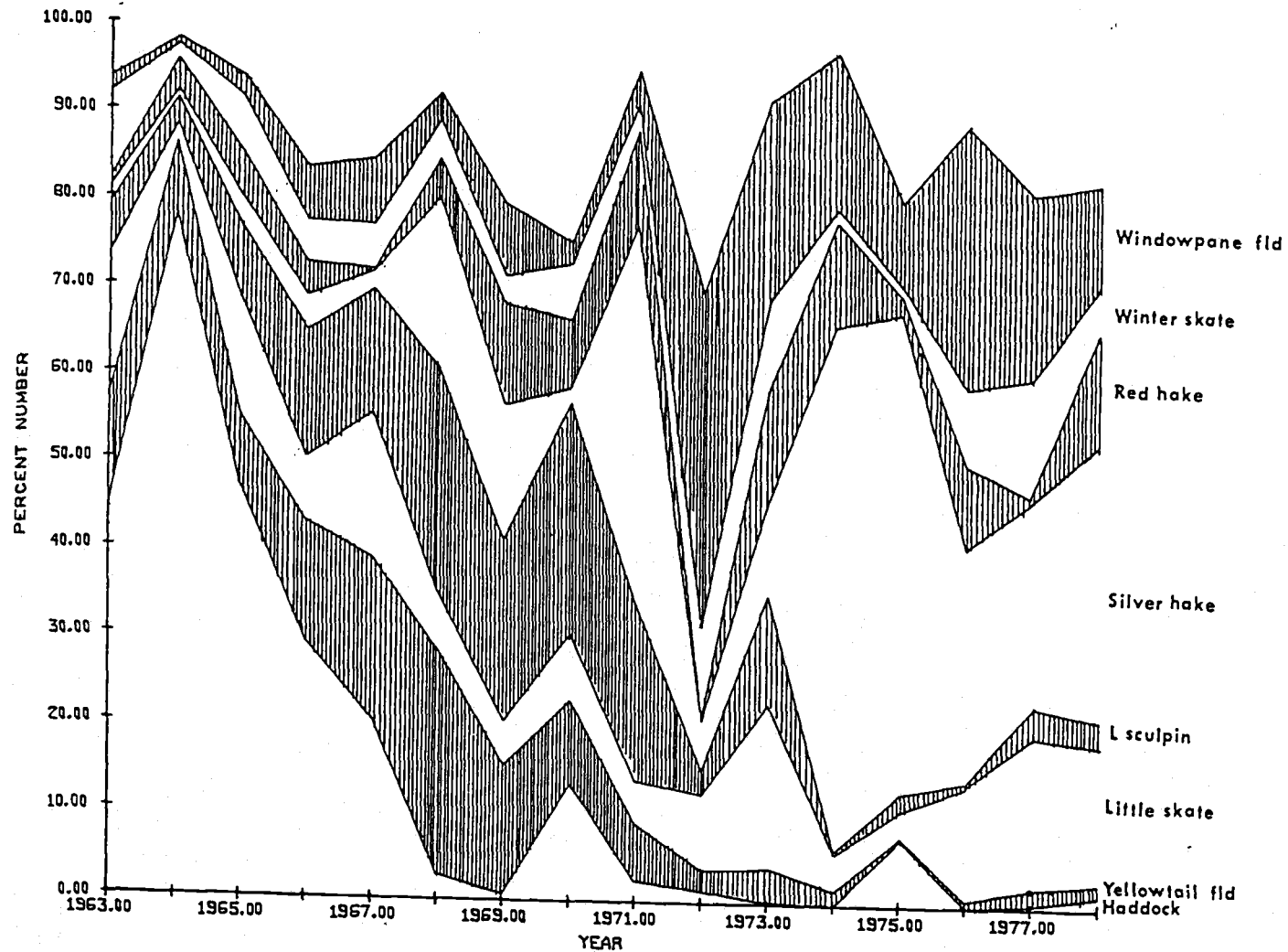


Figure 39. Intermediate assemblage total mean catch/tow (kg), Fall
1963-1978

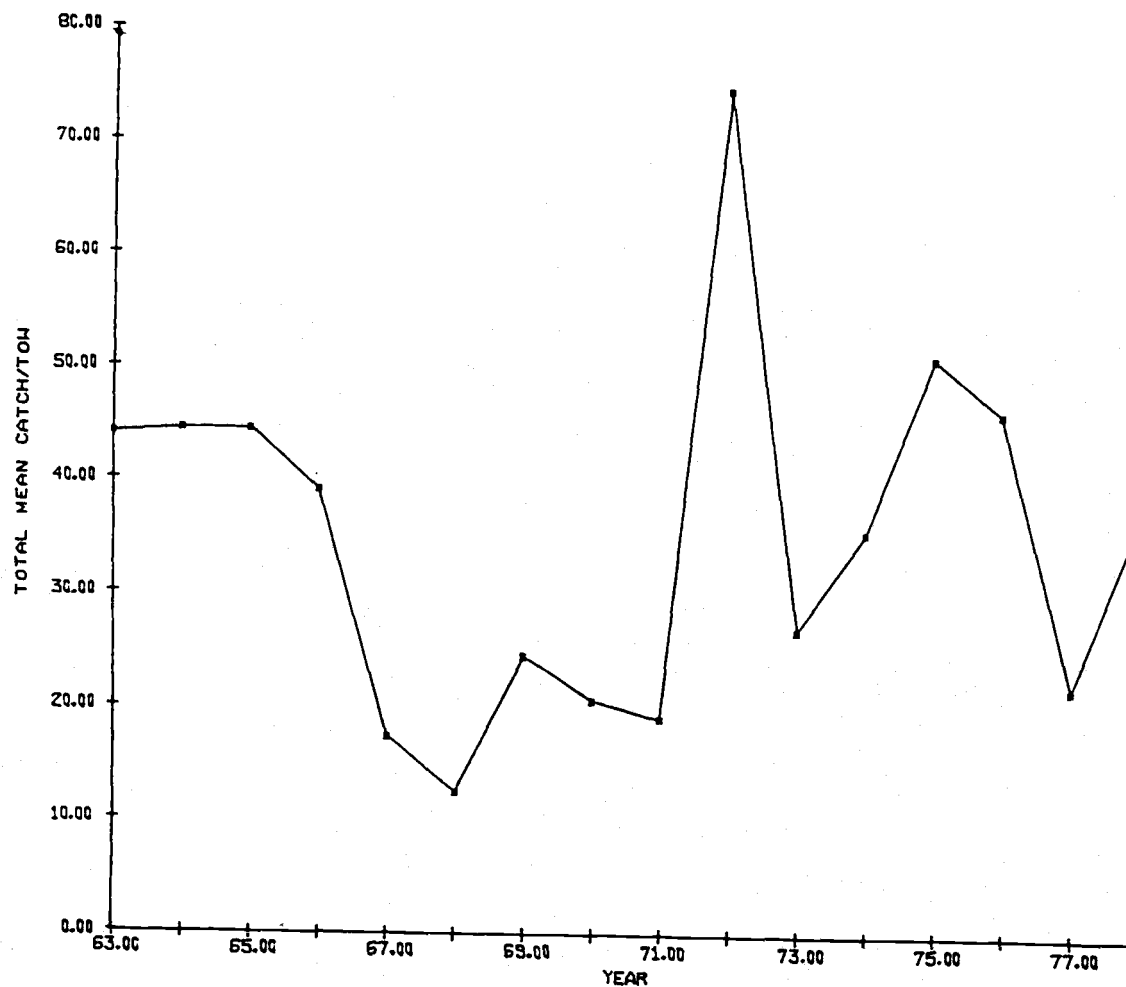


Figure 40. Gulf of Maine Deep assemblage total mean catch/tow (kg), Fall 1963-1978, for selected species

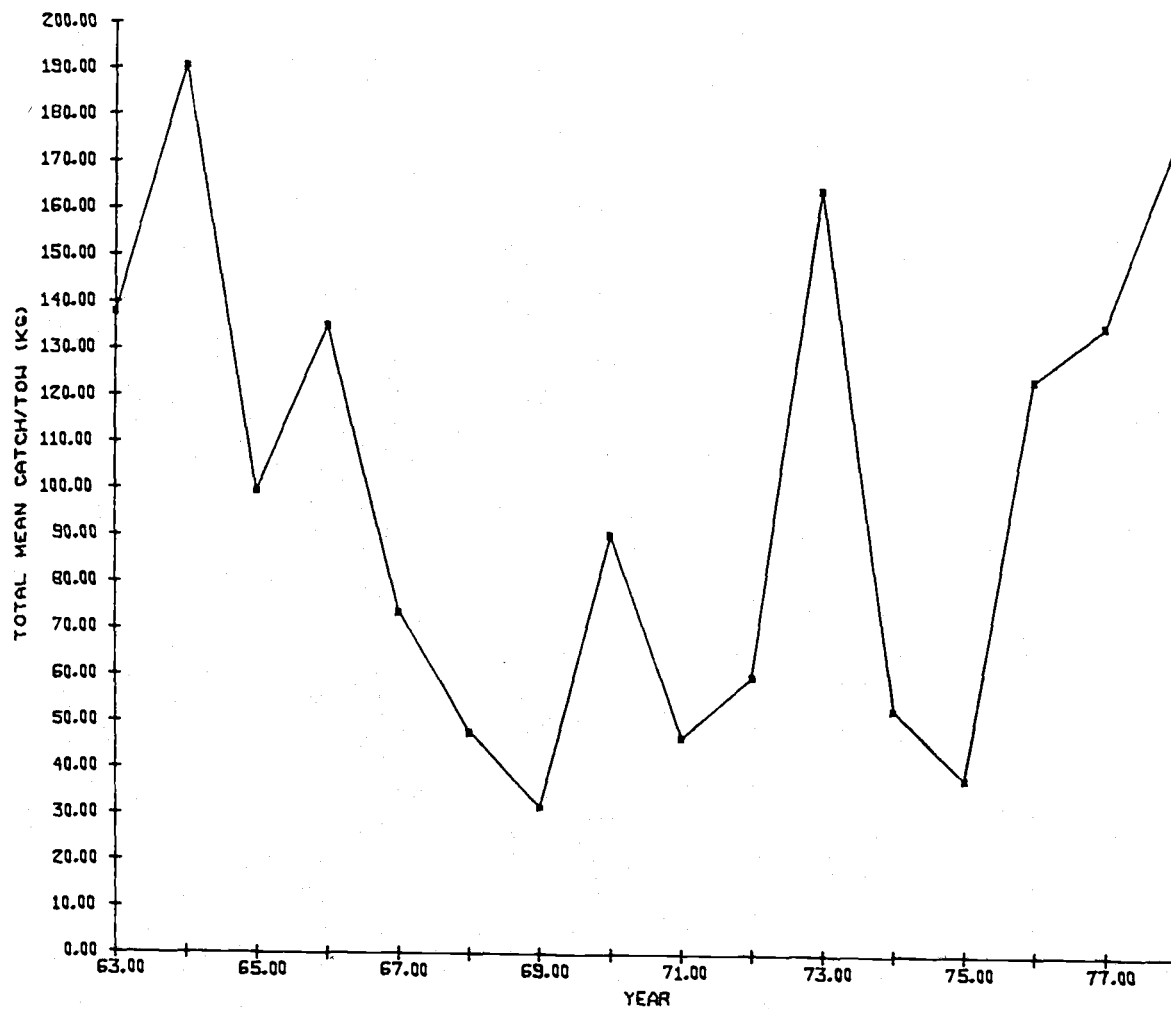
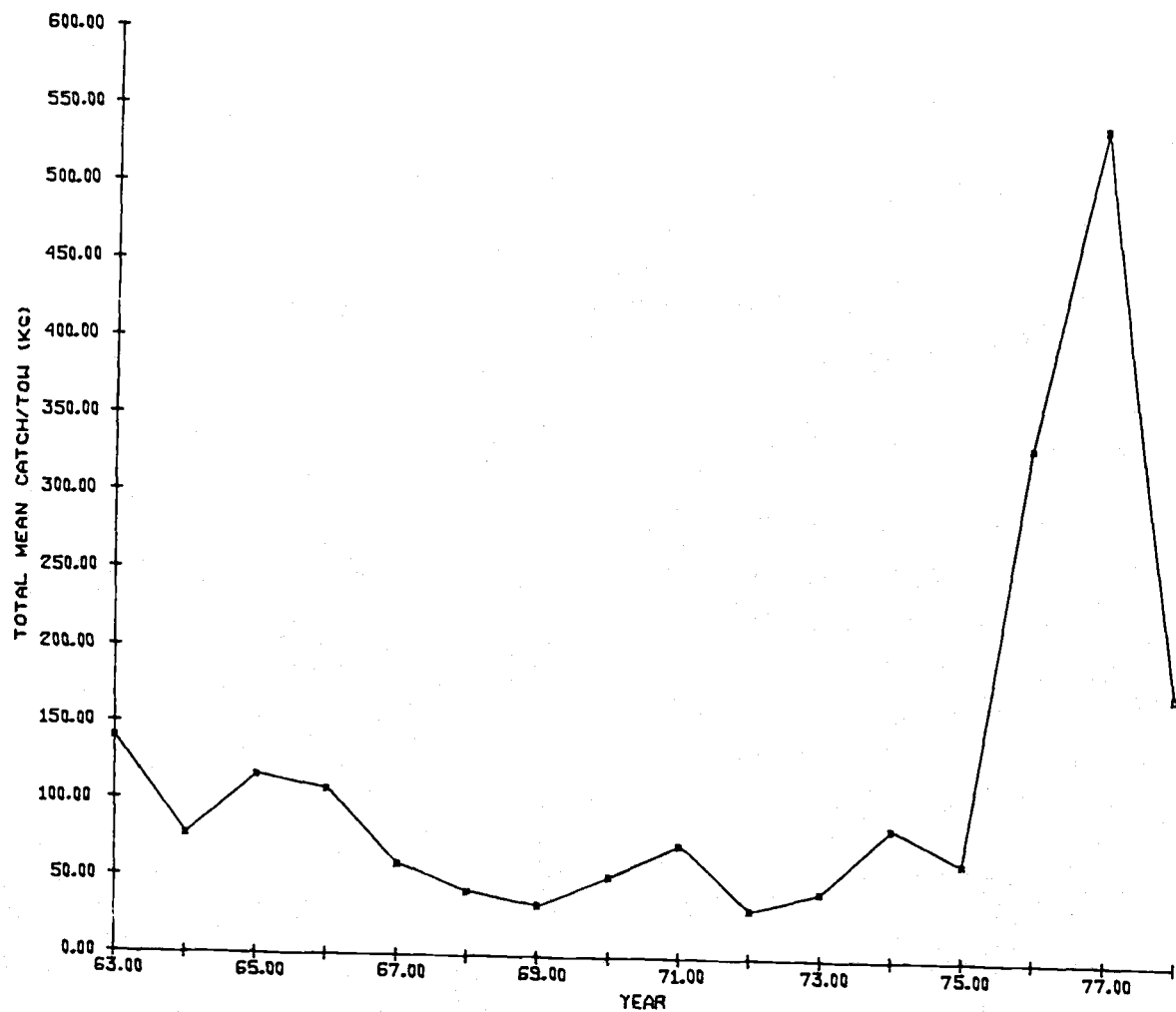


Figure 41. Northeast peak assemblage total mean catch/tow (kg), Fall 1963-1978, for selected species



Northeast Peak assemblage, but fluctuations in the haddock stock were responsible for this as well as the succeeding recovery that occurred in the late 1970's. Spring information from this assemblage basically mirrors the trends observed in the fall time series with the exception of a sharp decline in 1970 (Fig 42). When cumulative absolute abundance data for the GM Deep assemblage, fall 1963-1968, were examined, an interesting trend was observed. With the decline of haddock and thorny skate in the early 1960's, the assemblage CPUE for the other species had the opportunity to equilibrate, such that by the late 1970's, the catch of all the important species was much more equally distributed (Fig 43). The Northeast Peak assemblage in contrast was much simpler in species composition and although some fluctuations in cumulative percent by weight occurred, the same four species remained dominant over the period (Fig 44).

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 temporal trend, although some nearly consecutive blocks of years did cluster together (Fig 45). When the results of this dendrogram are interpreted by using Fig 29 the reasons for this emerge. Enough fluctuation in CPUE occurred to mask any trend, the dendrogram shows the years that are similar, but does not establish any coherent pattern that can be usefully followed in the long-term. Conversely, this same analysis on the Shallow assemblage, showed three distinct temporal clusters, and interestingly enough the within group structure was composed of consecutive

Figure 42. Northeast Peak assemblage total mean catch/tow (kg), Spring 1968-1978, for selected species

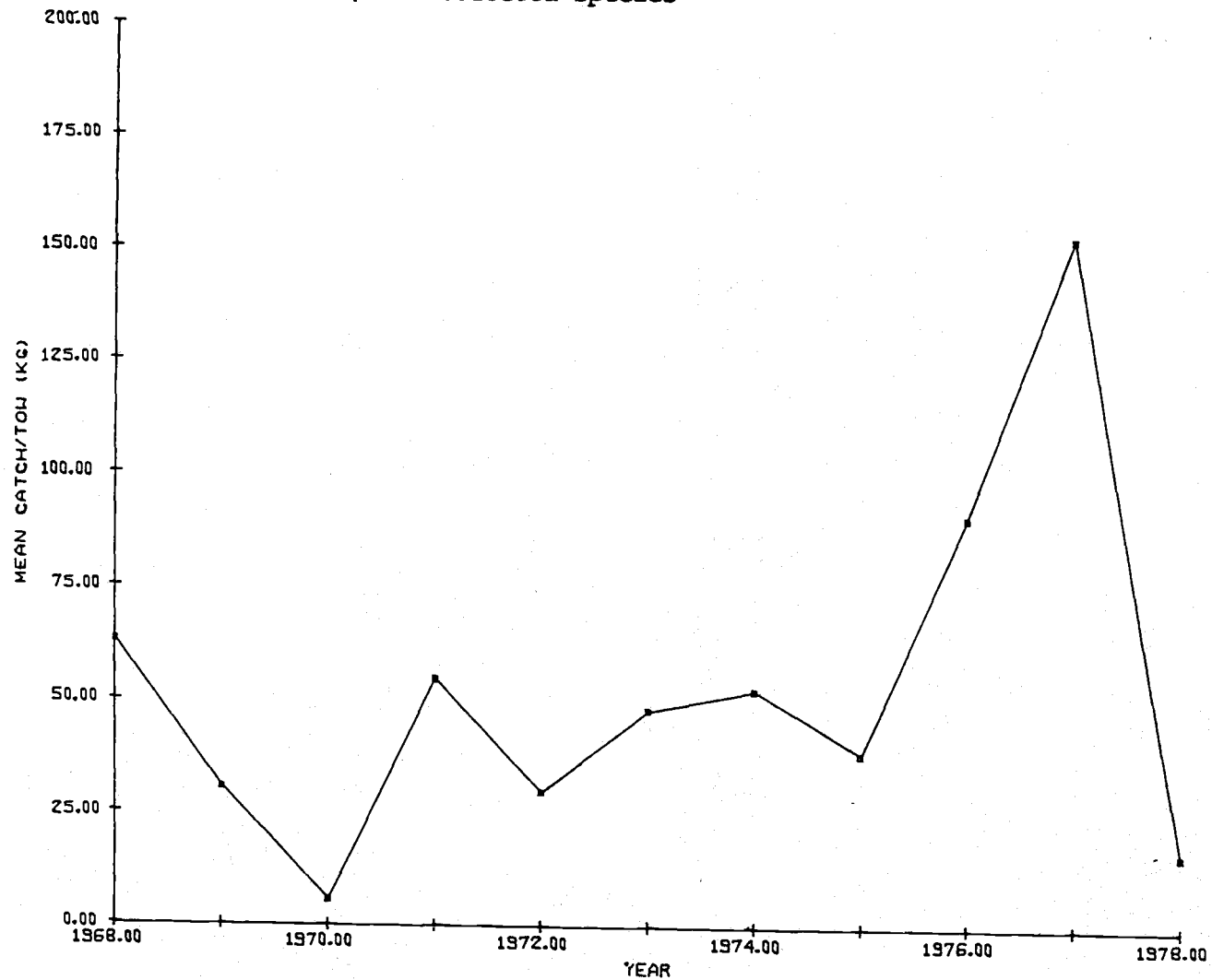


Figure 43. Gulf of Maine Deep assemblage cumulative absolute abundance, mean catch/tow (kg), Fall 1963-1978

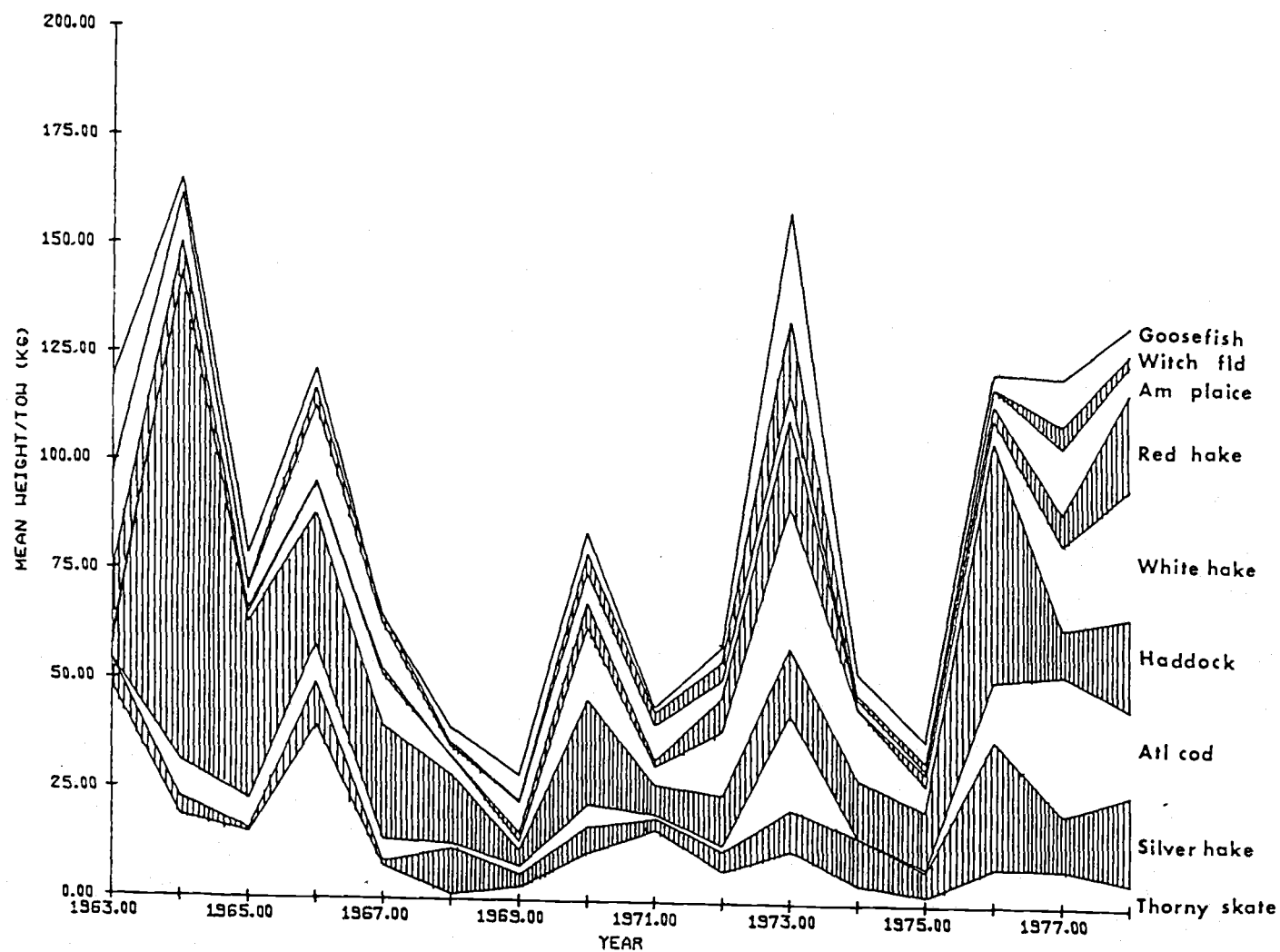


Figure 44. Northeast Peak assemblage cumulative percent by weight, Fall 1963-1978.

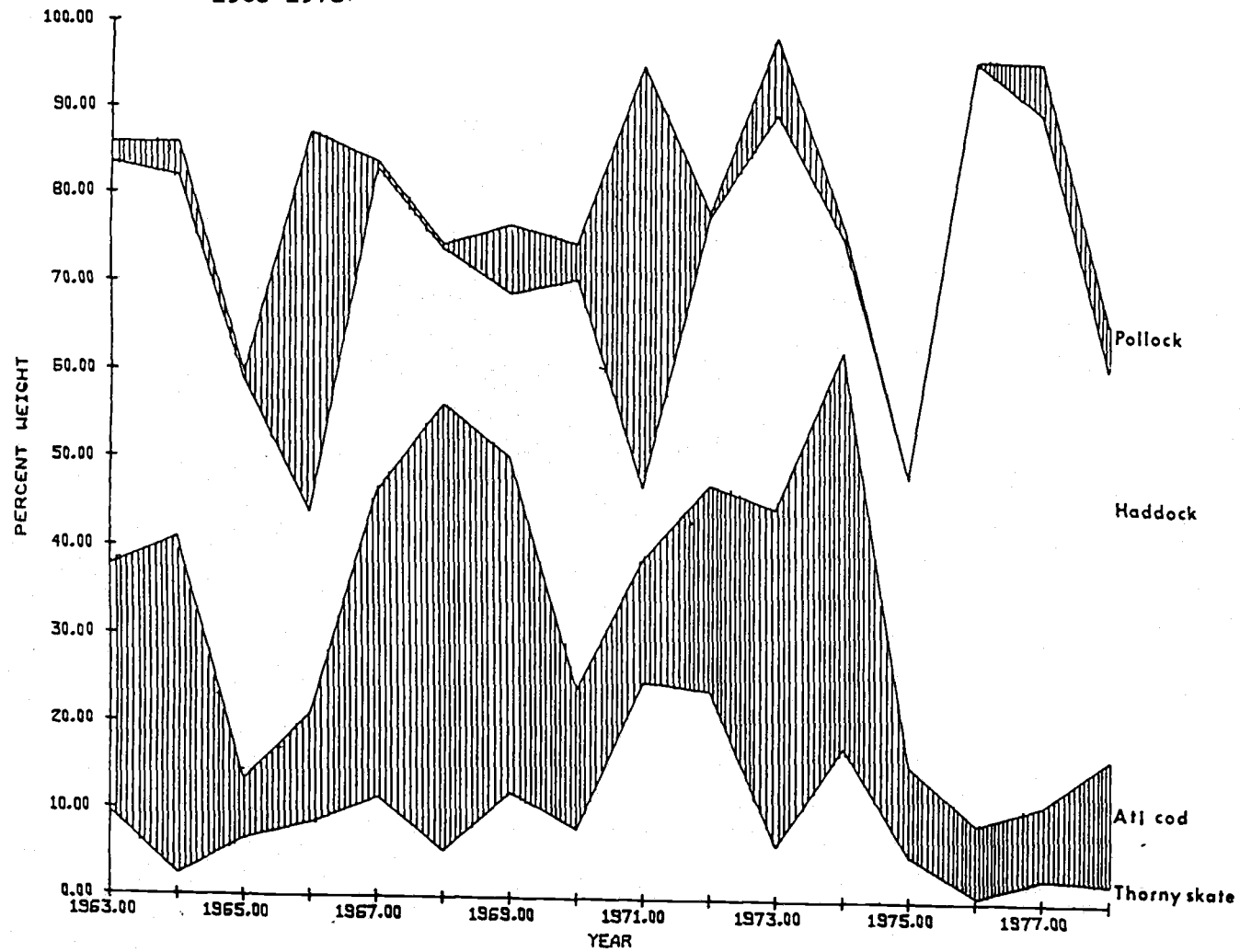
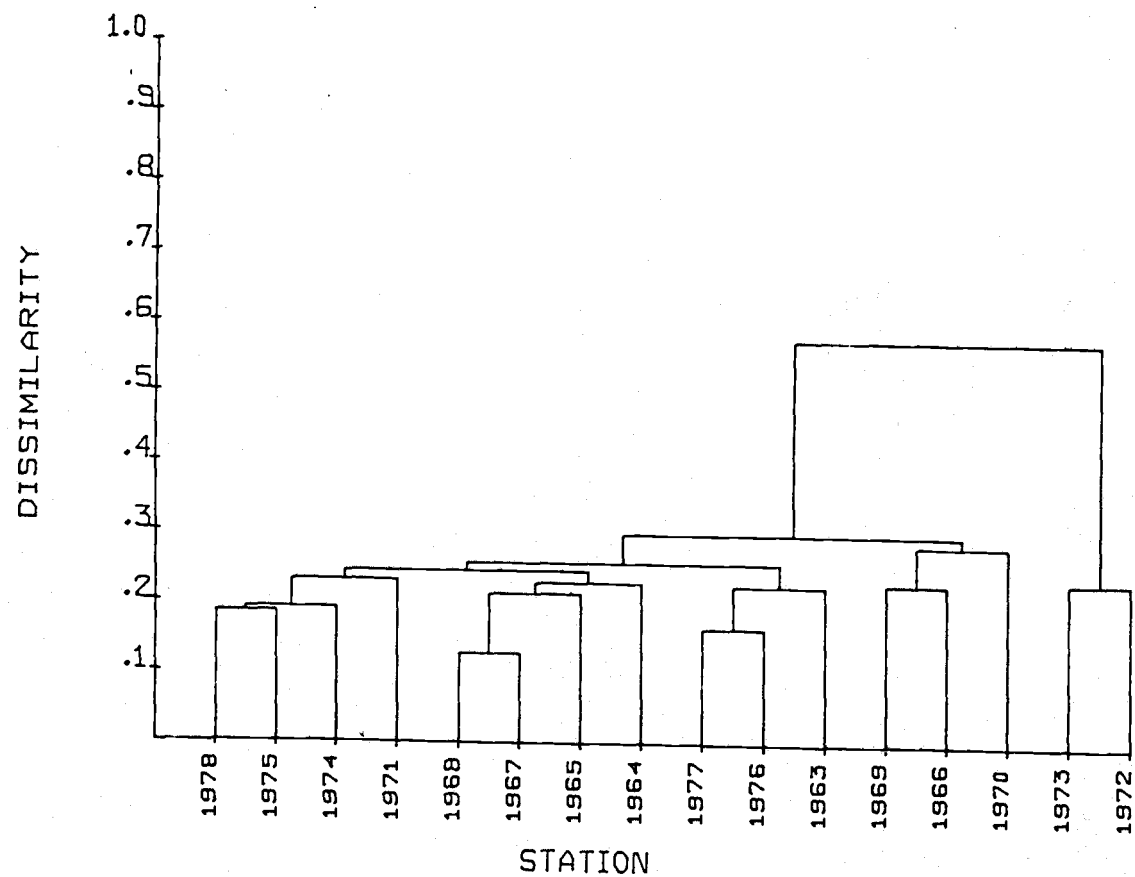


Figure 45. Slope and Canyon time sequence cluster analysis dendrogram,
Fall 1963-1978



years (Fig 46). Using this perspective and Figs 36 and 37, there appear to have been three periods of significant species relative abundance and composition change during the fall time series ; an initial period dominated by haddock, intermediate period with high yellowtail ,longhorn sculpin and winter flounder catches and a final group with little skate, winter skate and windowpane flounder comprising the dominant biomass.

Diversity

McIntosh information indices, representing the intra-assemblage change in diversity by numbers of fish over the autumn period 1963-1978, were used to follow trends in the Slope and Canyon, Shallow and Northeast Peak assemblages. These analyses were useful for following changes in density and relative abundance over the long-term. The indices in many cases followed trends in biomass, but in several important instances they yielded new insight into assemblage changes.

Diversity in the Slope and Canyon assemblage dropped from a peak value of 1438 in 1963 to a low of 106 in 1968, followed by an increasing trend with a peak at 505 in 1971, a decline to 108 in 1972 and a rapid rise to 973 in 1978 (Fig 47, Table 4). This trend was caused primarily by fluctuations in total numbers of fish caught and to a lesser extent by species and relative abundance shifts (Table 7). The peak 1963 value represented 2287 specimens and 23 species, and the subsequent low value in 1968 had only 188 fish comprising 14 taxa. Silver hake and red hake dominated the assemblage in 1963 and were found in large numbers while in 1968,

Figure 46. Shallow assemblage time sequence cluster analysis dendrogram,
Fall 1963-1978

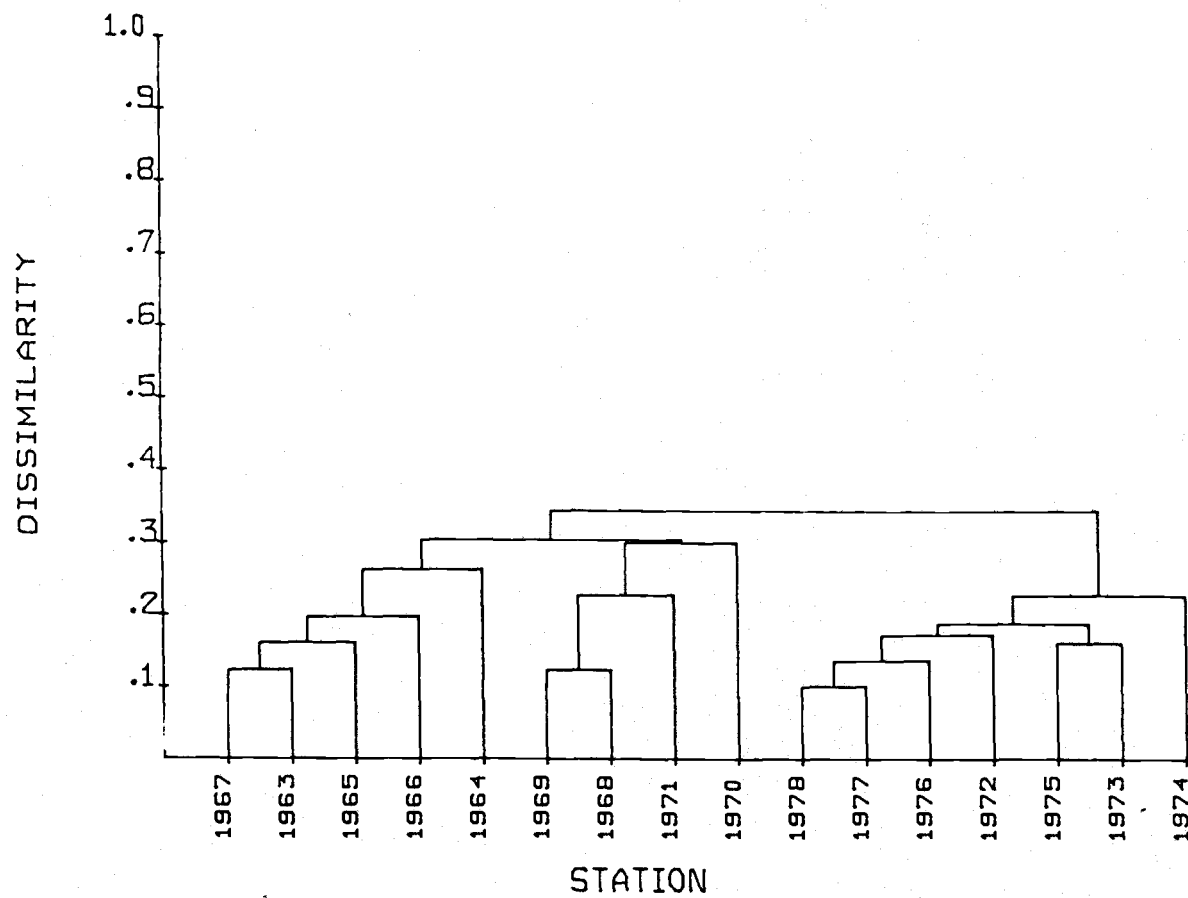
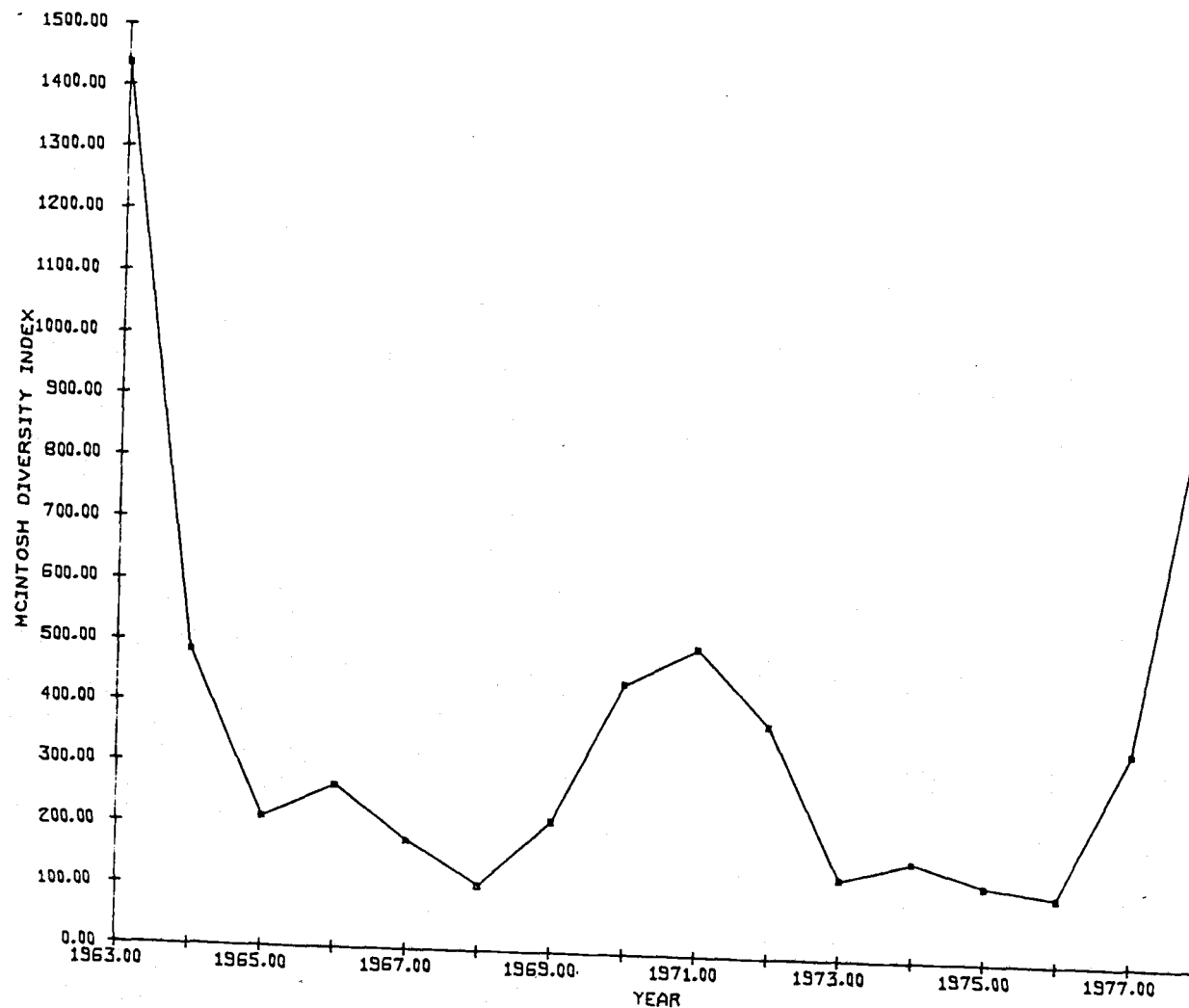


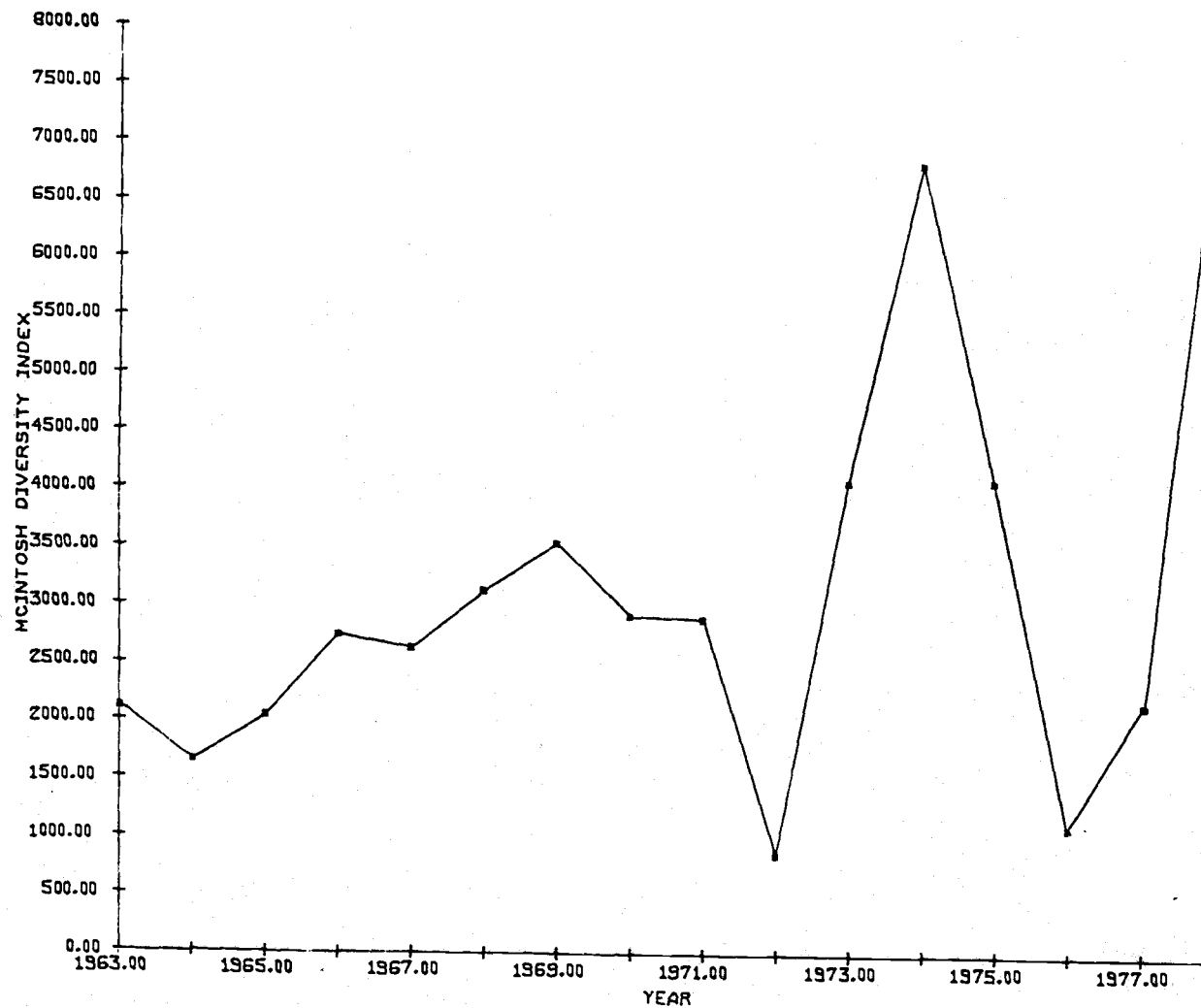
Figure 47. Slope and Canyon assemblage McIntosh diversity trends, Fall 1963-1978.



silver hake were dominant , but only 15% as abundant as in 1963 (Fig 31; Table 7). The smaller peak of 1971 was caused by an increase in numbers to 778 fish and a return to 23 species, while the decline and 4 year low trend from 1973 to 1976 occurred when numbers again dropped to a low of 148 in 1976 with only 7 species being taken. (Fig 29) shows that although silver hake were still dominant in 1971, red hake again had a major share of the relative abundance. However, although the relative abundance ratios of blackbelly rosefish, gulfstream flounder, red hake, and silver hake were more nearly similar in 1976, the low numbers of fish and species caused a decline in diversity (Table 4). The rapid rise in diversity in 1978 resulted because numbers recovered to 1135 fish and the number of species recorded increased to 24. Relative abundance at this time reached a high degree of parity, but species dominance had shifted substantially from the early 1960's, red hake and blackbelly rosefish were codominant with silver hake 3rd in abundance (Fig 31; Table 4,7).

Shallow assemblage diversity showed a much different directional trajectory than the Slope and Canyon assemblage. Diversity in this assemblage peaked at 3538 in 1969 after experiencing a period of slow increase in the early 1960's. This peak was followed by a steep decline to 867 in 1972, followed by rather large oscillations that resulted in peaks of 6842 and 7170 in 1974 and 1978 respectively (Fig 48; Table 5). These fluctuations in diversity from 1963-1978 were caused primarily by changes in numerical abundance of haddock and silver hake and to a lesser extent windowpane flounder, longhorn sculpin, yellowtail flounder,

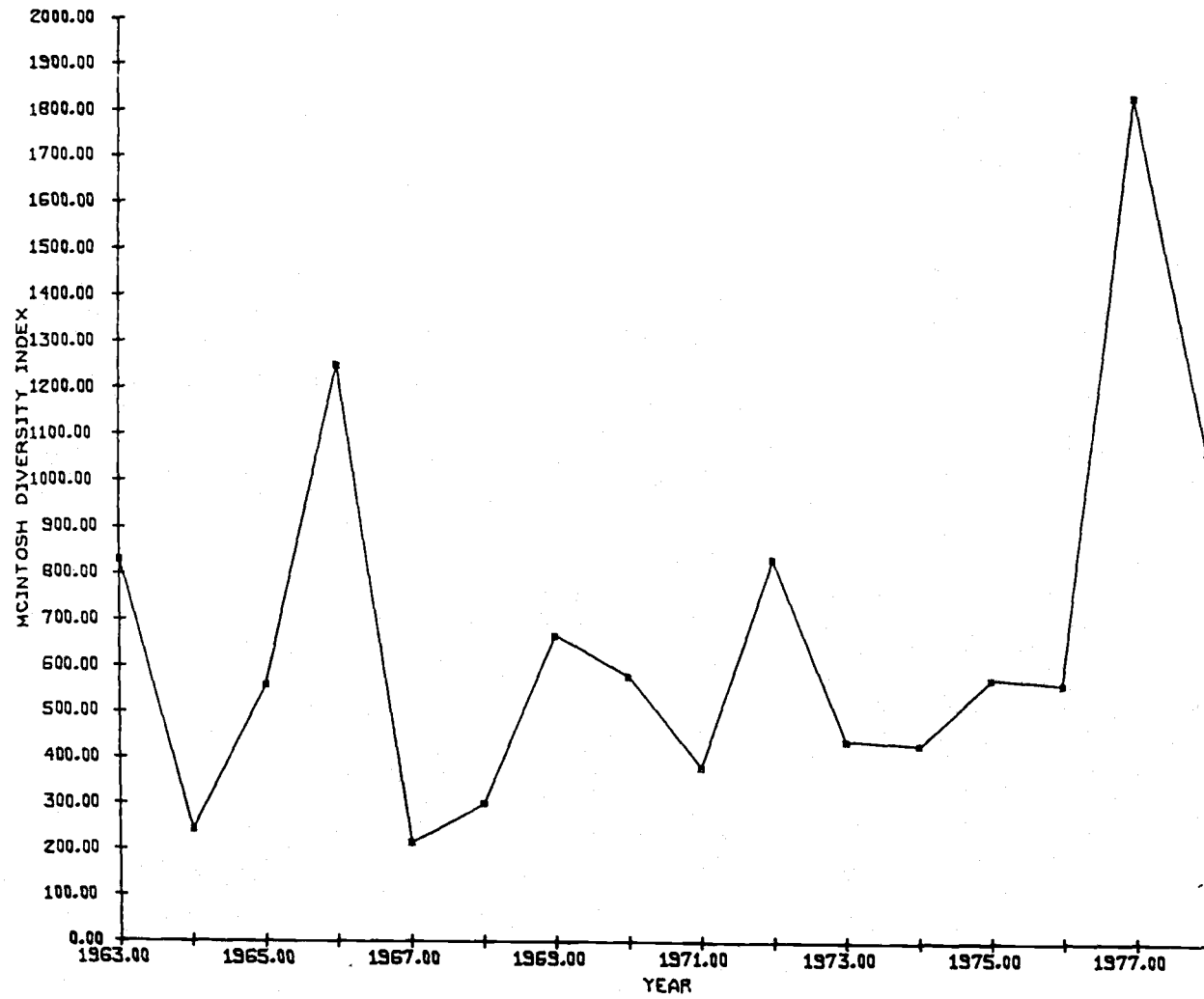
Figure 48. Shallow assemblage McIntosh diversity , Fall 1963-1978



and little skate, with relative abundance changes and species shifts playing a more minor role (Fig 38; Table 5,8). Haddock dominated the assemblage in the early 1960's and diversity increased steadily as the percentage of haddock declined. The low diversity value of 1971 reflects a drop in both total catch/tow and numbers (Fig 33; Table 5,8). Species composition through this period had changed dramatically from total domination by haddock to a state of equivalence where many species were represented (Fig 38; Table 5). The rapid increases and decreases in diversity that occurred in the mid to late 1970's were caused by changes in the catch of silver hake, windowpane flounder, and little skate (Fig 48). By 1978 not only had the species percent composition changed substantially, but density appeared to be much more variable than it had been in the earlier years of the time series.

Long-term diversity in the Northeast Peak assemblage was characterized by rapid changes without prominent trends, although a gradual increase occurred from 1967 onward (Fig 49). This assemblage was also dominated by haddock from 1963-1965 and the 1966 peak in diversity occurred because haddock declined, total numbers increased and relative abundance ratios for the other important species were more nearly similar (Tables 6,9). From 1967 to 1974 the assemblage diversity ranged from 215 to 832 and species composition, although dominated at times by mailed sculpin, was characterized by fairly even distribution of several species (Table 6,9). This tendency began to change in 1975 and by 1976 the assemblage was again dominated by haddock. Mean catch/tow in numbers for haddock had increased to well above the early 1960's

Figure 49. Northeast Peak assemblage McIntosh diversity , Fall
1963-1978



levels and the relative proportion of the total species composition for this species had returned to former levels (Table 6,9). Diversity in 1976 remained low because of a decrease in species number as well as the above mentioned haddock dominance. The large increases in diversity that occurred in 1977 and 1978 relative to the former period, were caused by continued high values in mean catch/tow for cod and haddock, but also because relative abundance and species richness showed an upward movement (Table 6,9).

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 location, physical and chemical data set used in the fall 1976 canonical correlation analysis accounted for about 26% of the variation in species distribution for 33 species of interest. The variables included in the analysis were latitude, longitude, depth, bottom temperature, bottom salinity, and bottom oxygen. The first 3 canonical axes accounted for 73.9% of this total, a cumulative redundancy of 19.0% (Table 10). 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

Table 10. Canonical Variable 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		
		Canonical V1	CV2	CV3	CV1	CV2	CV3	CV1	CV2	CV3
Species	15	-.509	.149	.232				-.089	.105	.111
	22	.101	.091	-.046						
	23	-.263	.342	-.244				-.176	-.377	.058
	26	-.428	.113	-.163				-.015	-.437	.142
	27	.552	-.117	-.144				.333	.210	-.204
	28	.387	.017	.063				.534	.416	.188
	32	.003	.081	.053				.084	-.147	.068
	33	-.023	.097	.161				.433	.086	.104
	69	.456	-.408	-.100	-.147	.613	.284			
	72	.285	.203	.536	.607	.332	.027	-.237	.637	-.328
	73	.059	.544	.195	.600	-.263	.048	.262	-.534	.177
	74	.370	.525	.131	.647	-.069	-.235	.383	-.300	.072
	75	.337	.158	.199	.439	.274	.167	.425	.209	.015
	76	.564	-.022	.341	.447	.614	.083	-.030	.527	.055
	77	-.109	-.109	.034	-.220	-.043	-.460	.303	.616	.057
	102	.281	.048	.362	.395	.365	.141	.409	-.035	-.026
	103	-.245	-.124	-.102	-.246	-.111	.126	-.427	.309	.303
	104	-.235	-.265	.210	-.326	.051	-.588	-.417	.418	.366
	105	-.158	.324	-.083	.115	-.419	-.095	.080	-.442	.144
	106	-.145	.364	.078	.295	-.324	.114	.109	-.301	.040
	107	.179	-.267	.140	-.107	.407	-.187	.368	.138	-.225
	108	-.326	.165	-.351	-.087	-.439	.504	-.527	.041	.251
	131	-.379	-.415	.405						
	156	.359	-.544	.050				-.295	.529	-.199
	163	-.078	.432	-.136				.101	.478	.063
	164	-.034	.432	-.092				-.500	.034	.194
	176	-.082	.198	.023						
	181	-.134	.043	-.079				.130	-.125	.224
	192	.011	.240	.106				.233	.073	.353
	193	-.043	.265	.122				-.133	-.316	.034
	197	.145	-.073	.184				-.261	.414	-.039
	502	.249	.284	.303				-.275	.169	.072
	503	-.471	-.239	-.379				-.256	.399	-.077
Variables										
Latitude		.306	.922	.074	.904	-.333	.066	.873	.012	-.131
Longitude		-.458	-.164	.597	-.004	.064	.113	.240	-.032	.474
Depth		.885	-.432	.049	.030	.849	-.071	-.107	.792	-.448
Bottom Temp.		-.179	-.696	-.233	-.590	.258	.366	-.252	.720	-.465
Bot. salinity		.463	-.547	.422	-.107	.753	-.586	-.374	.909	-.133
Bot. oxygen		-.316	.450	-.581	.041	-.613	.407	.199	-.908	.144
RC		.975	.961	.874	.871	.841	.750	.979	.968	.943
% variation		8.2	7.2	3.6	11.1	9.1	4.3	9.2	11.8	2.8
Total										
variation		25.7			28.3		32.6			
Significance		p<.001	p<.001	p<.05	p<.001	p<.001	p<.05	p<.001	p<.001	p<.001

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, I decided to use them in another analysis, excluding the other species. The right hand or x data set explained 28.3% of the total variation in distribution for this selected set of 14 species (Table 10). Again 3 canonical axes were important, accounting for 86.6% of the total explained variation. The first canonical variable had a high correlation with latitude ($r=.904$) and the gadoids as a group were highly positively correlated with this canonical variable (Table 10). It appears that although Georges Bank spans only about 2 degrees in total north-south latitudinal variation, this variable is useful for defining centers of gadoid biomass. CV2 expresses a depth and bottom salinity gradient as did CV1 in the first analysis, with correlations of .849 and .753 respectively. Here again the gadoids generally showed a positive loading, while the shallow water flounders expressed a negative correlation, suggesting the difference between these shelf break and shallow species respectively (Table 10).

The third analysis did not reveal any new trends, accounting for 32.6% of the variation in species distribution and defining 3 important canonical axes that explained 73% of this total. Canonical variable 1 again expressed a latitudinal gradient and CV2 showed a positive relationship with depth, bottom temperature and bottom salinity.

In general, then, although significant orthogonal canonical axes were defined in each of three data sets, the amount of variation that was actually explained by these canonical variables was 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

Important questions in marine community ecology remain unanswered and uninvestigated. Questions of community persistence and stability are meaningful not only for general understanding and knowledge, but also 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 responses. For example, the application of single species assessment technologies to assemblages of fishes may result in simplification of the community such that less productive fish populations 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 short term reaction to a potential problem.

Declines in total finfish abundance on the continental shelf of the northeastern USA reached unprecedented levels over the period 1961-1972. Not only had total effort on this complex of species increased six times, but biomass had declined to 55% of

former levels (Brown et al 1976). During this same 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 Autumn 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 to be very helpful for defining demersal fish assemblages from the Georges Bank region. This multivariate method has been shown to be generally useful for defining species complexes from contageously distributed demersal fish data (Gabriel and Tyler 1980; Tyler et al 1982). Multivariate analysis of variance results also confirmed the discrete nature of the cluster groups and 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 period 1963-1978 in the fall and 1968-1978 in the spring, but they also appear to have retained their spatial configuration 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. The Slope and Canyon assemblage appears to be seasonally invariant in spatial area while the Shallow and Intermediate grow and subside slightly on a seasonal basis. The Northeast Peak and Gulf of Maine Deep assemblage appear to exchange depth zones, resulting in elongated spring groups.

The reasons for the seasonal changes in area that occur in all the assemblages except the Slope and Canyon are not known. Gradient analyses accounted for only a portion of the variability in species distribution, but the nature of the data used in the analyses and other potential bias may have precluded the resolution of this issue. Encroachment on the Shallow assemblage by the the Intermediate and Northeast Peak assemblages probably occurs because of localized migration of resident fishes triggered by warming trends in the late spring. Tyler (1971) concluded that temperature was the most influential forcing factor in this region and therefore it is a logical choice for explaining these small-scale migrations.

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 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. In terms of distribution this ecosystem appears to have species with several strategies for exploiting the various habitats. Species such as goosefish, sea raven, and ocean pout are distributed rather uniformly over the whole of the region and adult as well as juvenile fish do not appear to be segregated by size. In contrast to this, several species such as silver hake have concentrations of adults or juveniles in specific assemblages (Almeida pers comm 1982). This strategy for silver hake is not surprising since they are known to be cannibalistic and many of the other species that utilize the strategy are also (Langton and Bowman 1980). There are also several species such as blackbelly rosefish, witch flounder and yellowtail flounder that occur in only one or two assemblages. These species show no life history separation and for the most part are invertebrate feeders (Langton and Bowman 1980).

Seasonal migrations of adult resident demersal fish and recruitment of juveniles to adult stocks may also account for some of the seasonal variation that occurs in several of the Georges Bank assemblages. The final group of fish, the periodics, such as mackerel and bluefish, become important during the warmer months of the year and their seasonal and long-term temporal pictures are correlated with spring warming and general warming trends respec-

tively (Anderson 1979; Davis 1977). Research CPUE for bluefish and long finned squid on Georges Bank increased in the mid 1970's, a period of time when a general warming trend was peaking on Georges Bank (Davis 1977). This seasonal component was not included in any of the analyses because the species are pelagic and the goal of this analysis was to ascertain the dynamics of the resident demersal community. Only they are conducive to these types of assemblage definition procedures. Once the demersal fish groups are constructed, the contribution of the various pelagic components and their assemblage dynamics can be investigated relative to the assemblage of interest.

The energy budget of Georges Bank serves as another plausible explanation for the particular species distributions I found. Georges Bank is a very 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 observed in many other marine environments, the region is characterized by high primary productivity over the period from April to November. Yearly primary production levels are as high as $450\text{gC/m}^2/\text{yr}$ in the shallow (less than 100 meters) zone of Georges Bank (Cohen et al 1982). This shallow mixed zone encompasses the same area as the Shallow and Intermediate assemblages delineated in my cluster analysis results. The area contains fish assemblages comprised of invertebrate predators as the dominant

component of the demersal fish biomass, many of them juveniles and subadults (Langton and Bowman 1981). Primary prey items for these species include euphausiids, copepods, mysids, amphipods and other invertebrates. This part of the ecosystem is fairly closely tied to primary production. The other assemblages that I 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 in nature (Langton and Bowman 1981).

Another interesting aspect to these distributional hypotheses involves a more general examination of these resident assemblage species, coupled with known trophic ecology. The Shallow and Intermediate assemblages appear to have the highest potential for competition to occur because they contain species with similar food habitats and a high degree of dietary overlap (Langton and Bowman 1980; Bowman 1980; Langton 1981). The deeper assemblages on the other hand contain species that effectively partition their food resources such that little if any overlap occurs (Langton and Bowman 1980).

The Shallow assemblage in contrast to the others, underwent profound changes in mean weight and number /tow as well as species composition and relative abundance. The assemblage was transformed from one dominated by commercially important species, yellowtail flounder and haddock (largely subadults) in the early 1960's, to a

complex of species that included winter skate, little skate and windowpane flounder (Fig 34). Total assemblage catch/tow in weight had recovered considerably by the late 1970's, but the species complex became dominated by elasmobranchs and fish of little economic importance (Figs 33,34). Haddock dominated all Georges Bank assemblages, except the Slope and Canyon, in the early 60's due primarily to the 1962 and 1963 year classes that were several times larger than any that were previously observed (Clark et al 1982).

Stability theory as discussed in Holling (1973); and Sutherland (1980) is valuable for describing the assemblages responses that I observed. The Northeast peak, Slope and Canyon, and Shallow assemblages all responded differently to perturbations from fishing fleet activity. These responses can be decomposed for better understanding. The Northeast Peak assemblage was apparently fairly resilient to system changes, although one species, haddock, was responsible for most of the fluctuation. The Slope and Canyon assemblage was also resilient, but did experience some slight changes in species composition. The Shallow complex experienced dramatic changes in species composition and relative abundance and also declines in density. This assemblage appears to be unable to maintain stability under the influence of exogeneous and endogenous perturbations. All three assemblages were exposed to potential type III perturbations from the fleet (Sutherland 1980), but only one, the Shallow assemblage, experienced pronounced changes in system state. The Northeast Peak assemblage remained within its domain of attraction (Holling 1973) or permissible

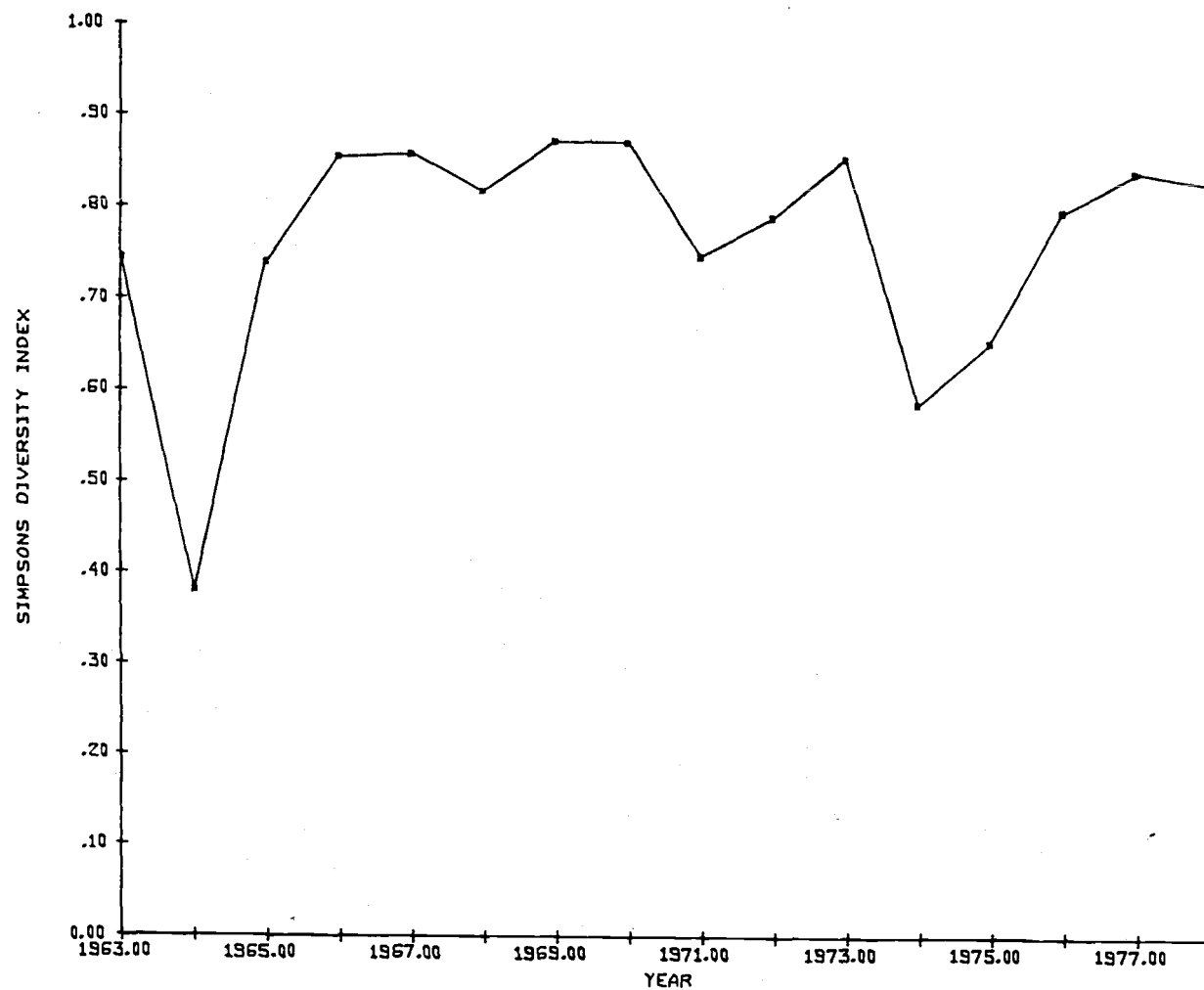
region (Overton pers comm. 1980) as did the Slope and Canyon assemblage. The Shallow assemblage on the other hand was displaced from its domain of attraction and this community was transformed into a system state that was far less desirable than the original. These stability responses can be coupled directly to the preceding trophic dynamics discussion. I hypothesize that the Shallow assemblage is inherently unstable due to the trophic linkages of its component taxa, and it would be expected to respond with changes in species composition and relative abundance if perturbed. The peripheral assemblages conversely are more resilient to perturbations because of their uncoupled trophic dynamics.

McIntosh diversity indices were generally useful for following trends in density, species richness and relative abundance for Georges Bank assemblages. Most applications of diversity center on site specific indices or alpha diversities (Whittaker 1967), but this study focused on a higher order concept or beta diversity that represented an intra-community measure of species response in spatially stable zones. The long-term temporal aspect of this study also allowed yearly comparisons of diversity within assemblages. Although the index is sensitive to the three previously mentioned variables, it appears that species richness was the least important directional determinant in this study. Some species simply disappeared for short periods of time from particular assemblages, but on a more regional scale none actually vanished from the Georges Bank area. Distributional shifts, sampling inadequacies, and catchability changes may have contributed to the paucity of species that was observed at times in particular

assemblages. Changes in numerical density and relative abundance appeared to account for most of the changes that occurred. The Shallow assemblage for instance maintained high species richness throughout the time period, but nevertheless experienced large fluctuations in diversity in the late 1970's. This trend was caused by fluctuations in the numerical density of silver hake, little skate and windowpane flounder. I purposely chose an index that was sensitive to density because this measurement is particularly useful to monitor in exploited fish stocks. Simpson heterogeneity measures on the same data from the Shallow assemblage were not nearly as informative because they tracked only species richness and relative abundance. This index indicated that diversity changed only in 1964 and 1974, when haddock and silver hake were dominant respectively (Fig 50).

The gradient analysis I performed using canonical correlation on selected spring and fall data sets accounted for only about 25% of the total variation in species biomass distribution. This result was surprising at first since I felt that the variables I used would explain much more of the variation than this. There were several factors that may have influenced the outcome of this analysis. Although the bottom salinity and oxygen data were accurate, the information was not collected at exactly the same time as the data on species abundance. Local variation may have been greater than I expected. The coarse spatial nature of the bottom salinity and oxygen data may have precluded an efficient analysis. Also the local nature of the information, ie. Georges Bank only, may have deemphasized the gradients because ranges in the

Figure 50. Shallow assemblage Simpson diversity trends, Fall
1963-1978



variables were rather narrow. An analysis that included the whole east coast for instance would probably have accounted 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 (Whittaker 1967; McIntire 1973). Either the actual gradients were not strong enough to explain more than a small percentage of the species distribution or further data collection and analysis is necessary.

The questions of persistence and stability of demersal fish assemblages that were defined and investigated in this study have direct implications to the management of Georges Bank. Not only were stable zones with specific resident fishes delineated, but they were present over the long-term temporal record. Seasonal spatial changes were small and could be accounted for in any management plan. 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 stability or resilience (Holling 1973) that a particular assemblage might have. Peripheral assemblages might be less susceptible to severe species composition changes because their component species are less trophically linked. The Shallow assemblage appears to be particularly vulnerable to perturbations both inside and outside the area and therefore management decisions could be tailored accordingly. This

study provides a useful conceptual framework for managing many of the demersal fish stocks on Georges Bank. Some particular applications of these ideas are presented in the ensuing chapters.

Chapter 2: Linear programming as a Potential Management Methodology for Multispecies Otter Trawl Fisheries.

Introduction

Many of the management problems associated with multispecies fisheries fall into the two major categories, technological and biological interactions. Technological interactions involve fisheries where the harvest of one species may cause an incidental catch of another species to occur (FAO 1977). Those fisheries that use otter trawls as their primary gear serve as particularly salient examples of this type of interplay. Biological interactions on the other hand are simply interspecific dynamic responses that result in shifts in abundance of two or more species (FAO 1977). Examples of this mechanism include competition, predation, and trophic feedback networks such as occurred in the Great Lakes with the introduction of the alewife (Smith 1970). A fishery in this situation could impact different stocks because of trophic interactions. These problems are extremely difficult to address and at the present time no standardized assessment procedures for calculating yields from multispecies complexes are available. A firm paradigm or at least some viable working hypotheses for multispecies management would be helpful.

Most multispecies yield studies have necessarily concentrated on the interaction question by redefining the domain of standard single species models and then directing them toward multispecies complexes. Paulik (1967) used this approach to explore exploita-

tion rates and maximum sustainable yields in Pacific salmon where several stocks were subject to a common fishery. His study showed that exploitation rates that extracted high yields from a productive race of salmon might cause a coincident extinction of another less productive race that was present in the same system. Other studies (Brown 1976; Halliday and Doubleday 1976; Pinhorn 1976; and Pope 1976; 1979) applied surplus production models to multispecies communities. These applications assume that composite biomass responds to effort in a much more uniform manner than does each individual stock or that total effort data gives a better indication of total biomass fluctuations than would effort for any one species of the group (FAO 1977). Broad spectrum approaches such as these are valuable, but as previously mentioned they often are inapplicable in situations where fluctuating species compositions occur, and they are normally applied without considering trophic or spatial linkages.

Another likely approach and one that has been investigated by several authors is to use optimal control theory to manage multispecies fisheries. Brown et al (1973) used linear programming to describe the multispecies otter trawl fishery of the Northeastern coast of the United States. They showed that management based on single species quotas was unrealistic when by-catch occurred in directed fisheries. The total summed multispecies quota was unobtainable in these situations. Hilborn (1976) used dynamic programming to explore the salmon mixed stock question in relation to escapement policies. His analysis showed that fixed escapement for the two stock case was only optimal under very limited circum-

stances. Other studies have focused on the problem by dealing with economic considerations and parameter uncertainty in models by using optimal control policies (Huppert 1979; Palm 1975).

In order to apply any of these methods with a goal of ecological integrity and meaning, one must consider the spatial and trophic aspects of the fish community of interest. The assemblage concepts and analyses described in the previous chapter are a possible conceptual framework for the solution to this problem. They provide a good protocol for coupling the spatial and interspecific dynamics of fish communities. The assemblages that I defined are in general agreement with studies of Georges Bank commercial landings data and are therefore appropriate for yield investigation experiments (Murawski et al 1981).

I used the Georges Bank assemblages in linear programming exercises designed to investigate the yield potentials of the various groups. The method was useful for describing the dynamics of assemblages as related to quota based fisheries and is applicable even under conditions of fluctuating species composition. Using data from the spring and fall of 1978 and the five cluster groups defined in the previous chapter, I allocated proportions of the Georges Bank quota for a selected group of species, to the various assemblages.

Methods

The fishing year was simplified by dividing the interval into two, 6-month periods, representing the species distributions and compositions that existed in the assemblages defined by the spring and fall analyses. Quota estimates were obtained from Northeast Fisheries Center (NEFC) assessment documents for species that are currently being investigated. In the case of species that are presently assessed as composite categories, such as other finfish, or that have no ongoing analytical study, the actual 1978 catch was assumed to represent the quota. The assemblage quotas (AQ) for each species were obtained from the following expression and are summarized in (Table 11).

$$AQ_i = \frac{AC_i}{TC_i} (GBi)$$

where:

AC_i= assemblage CPUE for each species

TC_i= total research CPUE for each species

GB_i= overall Georges Bank quota in metric tons for each species

i= species of interest

By-catch ratios used in this study were obtained from three sources, ICNAF statistical bulletins, Northeast Fisheries Center groundfish surveys and NEFC sea sampling cruises. The 1978 by-catch ratios from the ICNAF statistical bulletin were obtained from table 5, which lists main species sought and accompanying

Table 11: Georges Bank assemblage quotas (000's mt) and proportion of quota from survey CPUE estimates, for Fall and Spring, Shallow (Sh), Intermediate (Inter), Slope and Canyon (S&C), Gulf of Maine Deep (GM-De) and Northeast Peak (NP)

Fall:

	Sh	mt	Inter	mt	S&C	mt	GM-De	mt	NP	mt
Silver hake			.095	2.85	.072	2.16	.833	24.99		
Red hake			.337	2.70	.080	0.64	.583	4.66		
White hake			.032	0.01	.023	0.01	.045	0.28		
Yellowtail flounder	.134	0.29	.866	1.91						
Haddock	.008	0.08								
Atlantic cod	.175	1.93					.119	1.19	.873	6.73
Winter flounder	.942	2.87	.029	0.09			.300	3.30	.523	5.75
Windowpane flounder	.976	0.83	.024	0.02					.029	0.09
Witch flounder			.043	0.02	.008	.004	.949	.047		
American plaice			.009	0.01	.003	.003	.988	1.14		
Pollock	.113	0.57					.504	2.52	.383	1.92

Spring:

Silver hake										
Red hake					.976	29.28	.006	.160	.018	.540
White hake					.272	2.18	.339	2.71	.389	3.11
Yellowtail flounder	.693	1.52	.186	0.41	.547	.164	.453	.136		
Haddock	.219	2.19	.008	0.08					.121	0.27
Atlantic cod	.155	1.71	.165	1.82			.063	0.63	.710	7.10
Winter flounder	.808	2.46					.044	0.48	.636	7.00
Windowpane flounder	.952	0.81	.048	0.04					.192	0.59
Witch flounder			.229	0.11	.130	0.07	.397	.199	.244	.122
American plaice							.768	0.88	.232	0.27
Pollock	.015	0.08					.051	0.26	.934	4.67

by-catches (ICNAF 1980). Mean by-catch ratios for the two 6-month periods were calculated and are summarized in Table 12. Research by-catch ratios were obtained directly from the fall and spring surveys by using research CPUE. Sea sampling information was obtained from a cruise upon which I participated during the summer of 1979, on a commercial fishing vessel from Gloucester, Ma. Tow by tow records of species, catches, length frequencies, and discard were obtained on this cruise and were applicable only to the Gulf of Maine Deep and Shallow assemblages because the vessel utilized only these areas during the trip.

The aforementioned estimates of assemblage quotas and accompanying by-catch ratios, were used in a series of linear programs with catch maximization objective functions. Two types of linear programs were utilized, one with constraints that represented directed fisheries for all the species involved and the other with directed fisheries for at least two species, with accompanying species that were only harvested through incidental catch by the directed fishery. A directed fishery is one in which effort is applied toward the particular species of interest, ie. the species sought by the fleet. The Intermediate assemblage was not investigated nor were the spring periods from the Northeast Peak Interior and Northeast Peak-Gulf of Maine Deep assemblages. The linear programs were implemented and solved on the Multi-Purpose Optimization System (MPOS), a system available on the Oregon State University computer system. The MPOS package used the simplex method, a standard linear program solution technique, to solve the assemblage linear programs (Hillier and Lieberman 1980).

Table 12: Mean bycatch ratios for selected Georges Bank species from ICNAF Table 5, 1978.

Fall:

	Atlantic Cod	Haddock	Pollock	American Plaice	Witch Flounder	Yellowtail Flounder	Red Hake	Silver Hake	White Hake	Windowpane Flounder
Atlantic cod	1.000	.384	.183	.055	.024	.073	.008	.020		
Haddock	.227	1.000	.083	.025	.008	.032	.002	.037		
Pollock	.176	.190	1.000	.030	.011	.012	.007	.011		
American plaice	.209	.063	.093	1.000	.154	.095				
Witch flounder				.500	1.000					
Yellowtail flounder	.094	.019	.007	.022	.033	1.000				
Red hake							1.000			
Silver hake	.051	.037	.023	.012	.003	.009	.011	1.000		
White hake									1.000	
Windowpane flounder										1.000

Spring:

	Atlantic Cod	Haddock	Pollock	American Plaice	Witch Flounder	Yellowtail Flounder	Red Hake	Silver Hake	White Hake	Windowpane Flounder
Atlantic cod	1.000	.385	.133	.056	.018	.110	.003	.006		
Haddock	.284	1.000	.125	.020	.009	.048		.003		
Pollock	.282	.151	1.000	.031	.060	.015		.004		
American plaice	.185	.122	.064	1.000	.191					
Witch flounder					1.000					
Yellowtail flounder	.124	.036	.032	.012	.027	1.000		.004		
Red hake							1.000			
Silver hake								1.000		
White hake									1.000	
Windowpane flounder										1.000

Results

A fishery in the Slope and Canyon assemblage during the spring could catch about 96% of the total projected assemblage quota, amounting to 100% of the silver hake quota, 40% of the red hake and 87% of the white hake allotment (Table 13:I). The only directed effort would be on red hake and the catch of the other species would result strictly from incidental catch in this fishery. The fall scenario in this assemblage is quite different due to distribution changes by silver hake. During this season a maximum of only 89 mt is possible given the intraspecific quota constraints shown in (Table 13:II). In this case the optimal policy would be to apply all fishery effort toward catching silver hake, but even this solution would only harvest 1.1% of the potential silver hake quota because the smaller red and white hake allotments constrain the total possible catch. For example after catching 24 mt of silver hake, 100% of the white hake quota for the assemblage (10mt) would have been caught. Only 8.6% of the red hake potential harvest could be taken (Table 13:II). Table 13:III represents another scenario in the Slope and Canyon assemblage where American plaice and witch flounder are found in small quantities. In this case with potential directed fisheries on the silver hake and red hake stocks, the optimal policy to follow is a directed fishery on red hake. This species composition and quota distribution results in a total catch of only 76.6 mt or 2.7% of the maximum possible catch (Table 13:III).

Under the option of directed fisheries for cod, haddock and

Table 13. Linear programming results for the Slope and Canyon Assemblage, 1978.

1. Spring: survey ratios directed fishery for silver hake, red hake, by catch of white hake.

X_1 = silver hake
 X_2 = red hake

Objective function:
 $1.029 X_1 + 34.920 X_2$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Silver hake	1. $1.000 X_1 + 33.920 X_2$	LE 29,280	0.00	29,280	100.00
Red hake	2. $0.029 X_1 + 1.000 X_2$	LE 2,180	863.20	863	39.60
White hake	3. $0.005 X_1 + 0.161 X_2$	LE 160	--		86.90
	Maximum Catch	30282			
	Maximum Possible Catch	31548			
	% of maximum	95.99			

II. Fall: survey ratios, directed fishery for silver hake, red hake, white hake

X_1 = silver hake
 X_2 = red hake
 X_3 = white hake

Objective function:
 $3.688 X_1 + 1.819 X_2 + 7.575 X_3$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Silver hake	1. $1.000 X_1 + 0.579 X_2 + 2.411 X_3$	LE 2,160	24.00	24	1.10
Red hake	2. $2.273 X_1 + 1.000 X_2 + 4.164 X_3$	LE 640	0.00	55	8.60
White hake	3. $0.415 X_1 + 0.240 X_2 + 1.000 X_3$	LE 10	0.00	10	100.00
	Maximum Catch	89			
	Maximum Possible Catch	2180			
	% of maximum	3.20			

III. Fall: survey ratios, directed fishery for silver hake, red hake, by catch of white hake, American plaice, witch flounder.

X_1 = silver hake
 X_2 = red hake

Objective function:
 $2.727 X_1 + 1.579 X_2$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Silver hake	1. $1.000 X_1 + 0.579 X_2$	LE 2,160	0.00	24	1.11
Red hake	2. $1.727 X_1 + 1.000 X_2$	LE 640	42.00	42	6.60
White hake	3. $0.415 X_1 + 0.240 X_2$	LE 10	--	10	100.00
American plaice	4. $0.011 X_1 + 0.007 X_2$	LE 3	--	.3	10.00
White flounder	5. $0.011 X_1 + 0.007 X_2$	LE 8	--	.3	3.80
	Maximum Catch	76.6			
	Maximum Possible Catch	2321			
	% of maximum	2.7			

pollock in the Northeast Peak assemblage, 100% of the total assemblage quota could be harvested (Table 14:I). In this situation the optimal policy is to direct effort toward all three of these species. A linear program based on directed fisheries on cod and haddock with incidental catches of pollock results in an optimal strategy that exploits both of the former species. This fishery could harvest, 96.5% of the total assemblage quota and only the pollock harvest, at 70.7% and 1350 mt, would be less than the 100% possible for the other two species (Table 14:II). Under an alternative where directed fisheries for cod and haddock and by-catches of pollock and winter flounder are the possible options, 96% of the total assemblage maximum possible catch could be harvested. As with the two previous fall fisheries in this assemblage a directed fishery on cod and haddock is the optimal policy to pursue (Table 14:III). The addition of winter flounder to this particular experiment has no effect on possible catches of the other three species, but results in only 26.7% of the assemblage quota or 24 mt of winter flounder harvested (Table 14:III). The low by-catch ratios of winter flounder in the two directed fisheries did not constrain catches in the other three fisheries. When bottom trawl survey by-catch ratios were utilized in a linear program that simulated possible directed fisheries on cod, haddock and pollock, an option similar to (Table 14:I), the directed catch outcome as well as the total possible harvest were much different. The best choice under the survey constraints is a directed fishery on haddock, with only by-catch of the other two species. A directed fishery on haddock would harvest 100% of this species, while tak-

Table 14. Linear programming results for the Northeast Peak Assemblage, 1978, with ICNAF by-catch ratios.

I. Fall: directed fisheries for atlantic cod, haddock, and pollock.

x_1 = atlantic cod
 x_2 = haddock
 x_3 = pollock

Objective function:
 $1.567 x_1 + 1.310 x_2 + 1.366 x_3$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 x_1 + 0.227 x_2 + 0.176 x_3$	LE 5,750	4042.00	5,750	100.00
Haddock	2. $0.384 x_1 + 1.000 x_2 + 0.190 x_3$	LE 8,730	7065.00	8,730	100.00
Pollock	3. $0.183 x_1 + 0.083 x_2 + 1.000 x_3$	LE 1,920	594.00	1,920	100.00
	Maximum Catch	16400			
	Maximum Possible Catch	16400			
	% of maximum	100.00			

II. Fall: directed fisheries for cod and haddock, by catch of pollock.

x_1 = cod
 x_2 = haddock

Objective function:
 $1.384 x_1 + 1.227 x_2$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 x_1 + 0.227 x_2$	LE 5,750	4128.00	5,750	100.00
Haddock	2. $0.384 x_1 + 1.000 x_2$	LE 8,730	7145.00	8,730	100.00
Pollock	3. $0.183 x_1 + 0.083 x_2$	LE 1,920	--	1,348	70.20
	Maximum Catch	15828			
	Maximum Possible Catch	16400			
	% of maximum	96.5			

III. Fall: directed fisheries for cod, haddock, by catch of pollock and winter flounder.

x_1 = cod
 x_2 = haddock

Objective function:
 $1.384 x_1 + 1.227 x_2$

Constraints:

		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 x_1 + 0.227 x_2$	LE 5,750	4128.00	5,750	100.00
Haddock	2. $0.384 x_1 + 1.000 x_2$	LE 8,730	7145.00	8,730	100.00
Pollock	3. $0.183 x_1 + 0.083 x_2$	LE 1,920	--	1,350	70.30
Winter flounder*	4. $0.004 x_1 + 0.001 x_2$	LE 90	--	24	26.70
	Maximum Catch	15854			
	Maximum Possible Catch	16490			
	% of maximum	96.1			

ing 32.6% of the cod and 19.1% of the pollock quota. The total maximum catch would amount to 10,973.6 mt, representing 66.9% of the total maximum possible catch (Table 15:I). It appears that the survey by-catch ratios are much more constraining than the ICNAF ratios, a brief examination of (Table 14:I;15:I) shows the difference in the magnitudes of the various ratios.

The Gulf of Maine Deep assemblage provided some interesting linear programming results because of its species composition and disparity in relative abundance. Tables 16 and 17 show results from linear programming simulations that utilized data from the Gulf of Maine Deep assemblage on Georges Bank. In option I (Table 16), directed fisheries for cod, haddock, pollock, American plaice, witch flounder, and silver hake are examined. This assumes that a directed fishery for all these species is possible and that by-catch for the other species would result. The optimal strategy for this set of criteria is a directed fishery on pollock, American plaice, witch flounder, and silver hake (Table 16 and 17). This results in 92.9% of the maximum possible catch being harvested, a total of 31225 mt (Table 16:I). However, cod, an important commercial species would only be harvested at about 50% of its assemblage quota, resulting in a actual catch of 1620 mt for this species. If this scenario were changed slightly so that fisheries for cod, haddock, and American plaice were the possible directed components, a much larger proportion of the cod and pollock assemblage quotas could be taken (Table 16:II). In this case a directed fishery for cod and American plaice is the optimal design to pursue. This policy would result in a much smaller per-

Table 15. Linear programming results for the Northeast Peak Assemblage, 1978, with survey by-catch ratios.

.1. Fall: directed fisheries for cod, haddock, and pollock.

X_1 = cod
 X_2 = haddock
 X_3 = pollock

Objective function:
 $5.855 X_1 + 1.257 X_2 + 29.777 X_3$

Constraints:

			Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1.	$1.000 X_1 + 0.215 X_2 + 5.086 X_3$	LE 5,750	0.00	1,877	32.60
Haddock	2.	$4.659 X_1 + 1.000 X_2 + 23.691 X_3$	LE 8,730	8730.00	8,730	100.00
Pollock	3.	$6.197 X_1 + 0.042 X_2 + 1.000 X_3$	LE 1,920	0.00	367	91.10
		Maximum Catch	10973.6			
		Maximum Possible Catch	16400			
		% of maximum	66.91			

Table 16. Linear programming results for the GM-Deep Assemblage, 1978, with ICNAF by-catch ratios.

I. Fall: directed fisheries for cod, haddock, pollock, American plaice, witch flounder, and silver hake					
x_1 = cod x_2 = haddock x_3 = pollock x_4 = American plaice x_5 = silver hake x_6 = witch flounder					
Objective function: $1.666x_1 + 1.460x_2 + 1.418x_3 + 1.519x_4 + 1.126x_5 + 1.500x_6$					
Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000x_1 + 0.227x_2 + 0.176x_3 + 0.709x_4 + 0.051x_5$	LE 3300	0	1620	49.09
Haddock	2. $0.324x_1 + 1.000x_2 + 0.190x_3 + 0.063x_4 + 0.057x_5$	LE 1190	0	1190	100.00
Pollock	3. $0.183x_1 + 0.083x_2 + 1.000x_3 + 0.093x_4 + 0.023x_5$	LE 2520	1179	1815	72.02
American plaice	4. $0.055x_1 + 0.025x_2 + 0.030x_3 + 1.000x_4 + 0.012x_5 + 0.500x_6$	LE 1140	665	1140	100.00
Witch flounder	5. $0.024x_1 + 0.008x_2 + 0.011x_3 + 0.154x_4 + 0.003x_5 + 1.000x_6$	LE 470	280	470	100.00
Silver hake	6. $0.020x_1 + 0.037x_2 + 0.011x_3 + 1.000x_5$	LE 24990	24997	24990	100.00
	Maximum catch			31275	
	Maximum possible catch			33610	
	% of maximum			92.9	
II. Fall: directed fisheries for cod, haddock, American plaice, by catch of pollock, witch flounder, and silver hake.					
x_1 = cod x_2 = haddock x_3 = American plaice					
Objective function: $1.439x_1 + 1.252x_2 + 1.272x_3$					
Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000x_1 + 0.227x_2 + 0.209x_3$	LE 3300	2938	3142	95.2
Haddock	2. $0.384x_1 + 1.000x_2 + 0.063x_3$	LE 1190	0	1190	100.0
American plaice	3. $0.055x_1 + 0.025x_2 + 1.000x_3$	LE 1140	973	1140	100.0
Pollock	4. $0.133x_1 + 0.033x_2 + 0.093x_3$	LE 2520	--	629	25.0
Witch flounder	5. $0.024x_1 + 0.008x_2 + 0.154x_3$	LE 470	--	221	47.0
Silver hake	6. $0.020x_1 + 0.037x_2$	LE 24990	--	59	0.2
	Maximum catch			6381	
	Maximum possible catch			33610	
	% of maximum			19.0	

centage of the pollock and witch flounder quota being harvested, 25% vs 72% and 47% vs 100% respectively (Table 16:I and II). Silver hake is also under harvested using this strategy, but this occurs because the by-catch of this species in the cod fishery is small and none occurs in the American plaice fishery, the two species designated for directed catch under this option (Table 16:II). Using this option only 19% of the maximum possible catch could be harvested without exceeding the haddock and American plaice assemblage quotas. This would change dramatically if another linear program that included a directed fishery for silver hake was included because the total assemblage quota for this species could be harvested as in (Table 16:I) and approximately 93% of the maximum possible catch could be taken.

Table 17 outlines the results from a sea sampling cruise aboard a large commercial side trawler. In this particular case only a directed fishery for cod and American plaice, the two species that this vessel directed its effort toward during this cruise, were examined using linear programming. The optimal solution here included directed fisheries on both species. The constraints in this run however, resulted in a harvest of 3113 mt or 48.8% of the maximum possible catch (Table 17). Haddock and white hake were harvested at 100% of the total assemblage catch and this constrained catches on the other species. A low percentage of the directed species of interest, cod and American plaice, were harvested under this plan.

A fairly extensive set of seasonal linear programming options

Table 17. Linear programming results for the Gulf of Maine-Deep Assemblage, 1978, with sea sampling by-catch ratios.

I. Fall: directed fishery cod and American plaice, by catch of haddock, with flounder and white hake.

X_1 = cod

X_2 = American plaice

Objective function:

$$1.148X_1 + 1.643X_2$$

Constraints:

				Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
cod	1.	$1.000X_1 + 0.643X_2$	LE	3300	940	1055	32.0
American plaice	2.	$0.148X_1 + 1.000X_2$	LE	1140	178	314	27.5
Haddock	3.	$1.182X_1 + 0.440X_2$	LE	1190	--	1190	100.0
Witch flounder	4.	$0.178X_1 + 0.597X_2$	LE	470	--	274	58.3
White hake	5.	$0.148X_1 + 0.790X_2$	LE	280		280	100.0
Maximum catch				3113			
Maximum possible catch				6380			
% of maximum				48.8			

were investigated using information from the Shallow assemblage. A spring fishery with possible directed catches on a subset of the Shallow assemblage species, cod, haddock, and yellowtail flounder, resulted in 100% of the maximum possible catch being harvestable, with directed fisheries on the three aforementioned species being the optimal policy (Table 18:I). A further analysis based on a more realistic set of spring Shallow assemblage species resulted in a somewhat different catch. Cod, haddock, and yellowtail directed fisheries yielded 5265 mt or 60.6% of the maximum possible catch. The fishery was constrained by the cod, haddock and the windowpane flounder catches which would all reach 100% of their respective assemblage quotas under this particular allocation example (Table 18:II). The assemblage quotas for yellowtail and winter flounder would amount to only 15.7 and 12.7% of their possible assemblage quotas respectively (Table 18:II).

Table 19 shows the results of several linear programming experiments using ICNAF by-catch ratios and information from the fall bottom trawl survey. In this trial the assemblage quotas for the species of interest vary considerably (Table 17:I). Potential directed fisheries for cod, haddock, pollock, and yellowtail flounder and accompanying by-catch constraints result in an optimal directed catch policy of pollock, and yellowtail flounder exploitation. The resulting maximum catch, 859 mt, was only 29.9% of the maximum possible catch, with cod catches comprising only about 5% of it's possible assemblage quota (Table 19:I). The total quota for this species complex was constrained by the haddock and yellowtail catches and the small cod catch resulted because of

Table 18. Linear programming results for the Shallow Assemblage, 1978, with ICNAF by-catch ratios.

I. Spring: directed catch for cod, haddock and yellowtail flounder.						
X_1 = cod X_2 = haddock X_3 = yellowtail Objective function: $1.495X_1 + 1.332X_2 + 1.160X_3$						
Constraints:						
			Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000X_1 + 0.284X_2 + 0.124X_3$	LE	1710	1053	1710	100.0
Haddock	2. $0.385X_1 + 1.000X_2 + 0.036X_3$	LE	2190	1737	2190	100.0
Yellowtail	3. $0.110X_1 + 0.048X_2 + 1.000X_3$	LE	1520	1321	1520	100.0
Maximum catch			5420			
Maximum possible catch			5420			
% of maximum			100.00			
II. Spring: directed catch for cod, haddock, yellowtail, by catch of winter flounder and windowpane flounder.						
X_1 = cod X_2 = haddock X_3 = yellowtail Objective function: $1.495X_1 + 1.332X_2 + 1.160X_3$						
Constraints:						
			Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000X_1 + 0.284X_2 + 0.124X_3$	LE	1710	1219	1719	100.0
Haddock	2. $0.385X_1 + 1.000X_2 + 0.036X_3$	LE	2190	1720	2190	100.0
Yellowtail	3. $0.110X_1 + 0.048X_2 + 1.000X_3$	LE	1520	21	238	15.7
Winter fl.	4. $0.200X_1 + 0.227X_2 + 2.993X_3$	LE	2460	--	308	12.5
Windowpane	5. $0.231X_1 + 0.264X_2 + 3.470X_3$	LE	810	--	810	100.0
Maximum catch			5265			
Maximum possible catch			8690			
% of maximum			60.6			

Table 19. Linear programming results for the Shallow Assemblage, 1978, with ICNAF by-catch ratios.

I. Fall: directed catch for cod, haddock, pollock, yellowtail

X_1 = cod
 X_2 = haddock
 X_3 = pollock
 X_4 = yellowtail flounder

Objective function:
 $1.640 X_1 + 1.342 X_2 + 1.378 X_3 + 1.120 X_4$

	Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 X_1 + 0.227 X_2 + 0.176 X_3 + 0.094 X_4$	LE	1,930	0	96	5.0
Haddock	2. $0.334 X_1 + 1.000 X_2 + 0.190 X_3 + 0.019 X_4$	LE	80	0	80	100.00
Pollock	3. $0.103 X_1 + 0.083 X_2 + 1.000 X_3 + 0.007 X_4$	LE	570	393	393	69.0
Yellowtail	4. $0.073 X_1 + 0.032 X_2 + 0.012 X_3 + 1.000 X_4$	LE	290	285	290	100.00
	Maximum catch				859	
	Maximum possible catch				2,870	
	% of maximum				29.9	

II. Fall: directed fishery for cod, yellowtail, by catch of pollock and haddock

X_1 = cod
 X_2 = yellowtail

Objective function:
 $1.073 X_1 + 1.094 X_2$

	Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 X_1 + 0.094 X_2$	LE	1,930	195	221	11.5
Yellowtail	2. $0.073 X_1 + 1.000 X_2$	LE	290	276	290	100.0
Haddock	3. $0.384 X_1 + 0.019 X_2$	LE	80	--	80	100.0
Pollock	4. $0.183 X_1 + 0.007 X_2$	LE	570	--	38	6.7
	Maximum catch				629	
	Maximum possible catch				2,870	
	% of maximum				21.9	

III. Fall: directed catch for cod, yellowtail, bycatch of haddock, pollock, winter fld., windowpane fld.

X_1 = cod
 X_2 = yellowtail

Objective function:
 $1.073 X_1 + 1.094 X_2$

	Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species
Cod	1. $1.000 X_1 + 0.094 X_2$	LE	1,930	199	216	11.2
Yellowtail	2. $0.073 X_1 + 1.000 X_2$	LE	290	181	196	67.6
Haddock	3. $0.384 X_1 + 0.019 X_2$	LE	80	--	80	100.0
Pollock	4. $0.183 X_1 + 0.007 X_2$	LE	570	--	38	6.7
Winter fld.	5. $0.406 X_1 + 4.250 X_2^*$	LE	2,870	--	851	29.7
Windowpane fld.	6. $0.400 X_1 + 4.150 X_2^*$	LE	830	--	830	100.0
	Maximum catch				2211	
	Maximum possible catch				6570	
	% of maximum				33.7	

From survey by catch ratios

this. If the plan were changed slightly so that cod and yellowtail flounder were the species receiving directed effort, with haddock and pollock only harvested as incidental catch in these two fisheries, an even lower catch incurred. In this case 629 mt or 21.9% of the maximum catch was possible and of this total the cod and pollock catches again were low, 11.5% and 6.7% respectively (Table 19:II). A third scenario involves possible cod and yellowtail directed fisheries along with by-catch of haddock, pollock, winter flounder, and windowpane flounder. The addition of these other species probably makes this species complex more realistic in terms of the species that would actually be harvested in a fishery that exploited this assemblage. The total catch of 33.7% changes little from the previous examples, but one of the constraining species changes from yellowtail to windowpane flounder. This results in a lowered amount of yellowtail flounder being harvested, a continued low portion of the cod quota being taken and only 29.7% of the winter flounder quota possible, the species with the largest potential assemblage quota (Table 19:II). 2211 mt out of a possible 6570 mt would result from this strategy primarily because such a low percentage of the cod and winter flounder quotas could be taken (Table 19:III).

By-catch ratios from the autumn survey appear to produce about the same results as in the directed cod, haddock, pollock, and yellowtail flounder fishery that was studied using ICNAF ratios (Table 19:I;20:I). In this situation a directed fishery for only yellowtail flounder is the optimal catch policy, and the resulting catch of 801 mt is 27.9% of the maximum possible catch. This

Table 20. Linear programming results for the Shallow Assemblage,
1978, with survey by-catch ratios.

Fall: directed fishery for cod, haddock, pollock, yellowtail

X_1 = cod
 X_2 = haddock
 X_3 = pollock
 X_4 = yellowtail

Objective function:

$$1.246X_1 + 10.000X_2 + 50.000X_3 + 12.962X_4$$

Constraints:

Constraints:		Assemblage Quota	Directed Catch	Total Actual Catch	% by Species	
1.	$1.000X_1 + 8.629X_2 + 40.143X_3 + 10.407X_4$	LE	1930	0	643	33.3
2.	$0.125X_1 + 1.000X_2 + 5.000X_3 + 1.296X_4$	LE	80	0	80	100.0
3.	$0.025X_1 + 0.200X_2 + 1.000X_3 + 0.259X_4$	LE	570	0	16	2.8
4.	$0.076X_1 + 0.771X_2 + 3.857X_3 + 1.000X_4$	LE	290	62	62	21.4
	Maximum catch				801	
	Maximum possible catch				2870	
	% of maximum				27.9	

fishery would be constrained by the low available haddock biomass in this assemblage, a very low percentage of the assemblage quotas could be harvested (Table 20). The two species with the largest assemblage quotas, cod and pollock, would be greatly underharvested (Table 20). The percentage of the cod quota harvested would increase compared to the same fishery based on ICNAF by-catch ratios (table 19:I).

Discussion

Linear programming, one optimization technique in a general set of decision making procedures known as operations research methods, deals with the problem of allocating limited resources among competing activities in the best possible or optimal manner (Hillier and Lieberman 1980). This method has been generally useful in scientific and industrial applications that required decisions on particular problems of the type associated with many variables and possible outcomes. It provides optimal or unique solutions based on reference to the objective function employed in the model (Hillier and Lieberman 1980). Linear programming, as well as some of the other operations research methods, offer possible solutions to the complexities of managing a multispecies fishery.

This particular application of linear programming addressed the problem of how to maximize the total catch of several species, within an assemblage, when quotas, relative abundance levels, and by-catch rates were different for each species in the group. This application dealt strictly with the technological interaction aspects of multispecies otter trawl fisheries that operated on particular Georges Bank assemblage groups. The assemblages defined in the previous chapter were helpful as an organizational tool that addressed the spatial and temporal distribution problem of the various assemblage component species. It also provided a procedure for estimating intra-assemblage quota levels based on research vessel CPUE within particular assemblages. Many of the

aforementioned studies that dealt with this type of technical interaction problem lacked this type of organization and were in many cases out of spatial and temporal phase with the species they addressed.

As a method for the assessment of multispecies trawl fisheries, this linear programming procedure shows promise, but not without the associated problems that accompany any analytical fisheries procedure. By-catch ratios, obtained from commercial catch information and sea sampling data, appear to be the best type of data to use for this particular analysis. Incidental catch ratios developed from this source should represent the species composition that is actually vulnerable to the trawl fishery operating on the particular species complex in question. Bottom trawl surveys tend to be much more conservative since the gear utilized, catches a much larger proportion of small fish than would a corresponding commercial trawl. (Azarovitz et al 1981). The resulting inflated by-catch ratios tend to constrain the catch much more quickly, thus less of the assemblage quota for certain species is harvestable. Research vessel data can be made more useful however, by filtering it with commercial length frequency information and catch ogive analysis (Mayo et al 1981). The conservative nature of research survey information may be used to good advantage if a goal of assemblage maintenance of a total species complex is the desired outcome. The usefulness of intra-assemblage quotas determined from research CPUE should also be scrutinized carefully because catchabilities of different species may change with gear type. Fortunately for this study, CPUE from this

research survey has been shown to be useful for following commercial trends (Clark 1979). Patterns from cluster analysis match up quite nicely with those developed from commercial catch information (Murawski 1981). Research catch in a particular assemblage therefore, was a useful criterion for determining the percent of the total Georges Bank quota that should be allotted to each group.

Another problem of interest that this analysis addressed was the seasonal effect of species relative abundance levels on the maximum harvestable total catch in the various assemblages. It appears from comparing cluster results for the four seasons that a biannual fishing year is an appropriate temporal scale of resolution for this problem. Winter species distribution is reflected nicely by the spring survey while summer distributions are echoed by the patterns observed in the autumn. Although I concentrated on linear programs representing the warmer months of the year, the shifts in abundance that occur in the other part of the year, represented by the spring survey ratios, need to be addressed in this management scheme. The Slope and Canyon assemblage illustrates this point because migration of particular assemblage species changes the maximum catch as well as the assemblage quotas. Silver hake concentrate in this assemblage during the winter and spring and are more dispersed in the fall (Table 13:I,II). This allows 96% of the total assemblage quota to be harvested in the spring, but only 3% in the fall (Table 13:I,II,III). The fact that only research vessel by-catch ratios, subject to problems noted previously, were available, may have influenced this outcome, but the point that seasonal differences must be

addressed has been sufficiently illustrated. This pattern is also shown in the Shallow assemblage where increased availability of haddock and yellowtail due to migration and concentration, produces a similar spring increase in total maximum catch (Table 18;19). To successfully manage a particular assemblage using this method, the seasonal species distribution patterns involved must be examined and incorporated into the management scheme.

An interesting outcome of this study was the discovery of the different propensities of particular assemblages for harvesting the maximum possible catches. In general the catch potential for the Shallow assemblage appears low while the opposite trend occurs in the Northeast Peak and Gulf of Maine Deep assemblages. This effective ability to harvest close to the maximum is related directly to the relative abundance of the species as well as the relative magnitude of the assemblage quotas. Assemblages with simple species compositions or low by-catch rates tend to allow a larger percentage of the maximum possible catch to be harvested while assemblages having numerous species represented in the commercial catch as well as high by-catch and disparity in assemblage quotas, tend to produce lower possible catches. The Northeast Peak assemblage for instance has a rather simple species composition and the relative magnitudes of quotas for cod, haddock and pollock are similar. By-catch rates of pollock and winter flounder are low in the cod and haddock directed fisheries, resulting in 96% of the maximum possible catch being harvestable (Table 14:III). The low winter flounder quota does not constrain the catch because by-catch rates for this species in the directed fisheries are very

low (Table 14:III).

The Shallow assemblage illustrates how complex species composition, unequal relative abundance and assemblage quotas that vary by orders of magnitude, at least for the fall period, can depress the catch potential of a multispecies complex. A fishery in this assemblage could harvest only 22% of the maximum inter-specific quota in a cod and yellowtail flounder directed fishery (Table 19:II).

The potential for harvesting multispecies complexes of demersal fish is clearly related to species composition, relative abundance and magnitude of quotas of the various species. Linear programming with catch maximization objective functions is useful for assessing the potentials of commercial fisheries with single species based quota objectives or management schemes. Species with low assemblage quotas and high by-catch in directed fisheries tend to constrain maximum possible catches. By-catch ratios from commercial fisheries appear to be the most useful source of information, but research vessel data may also be used and can be corrected for catchability bias. Other applications of this method with different objective functions might also be useful in assessing multispecies potentials. In cases where low quotas of certain species constrain total catches of other more commercially important species, the restraining species may be deemed unimportant and excluded from the analysis. If other objectives such as assemblage maintenance (Tyler et al 1982) were desired, then perhaps more conservative strategies based directly on research vessel

results would be necessary. This analysis showed that even in species complexes that meet the above criteria for maximum harvest, the potential for obtaining the total summed interspecific assemblage quota is low. This analysis addressed only the system state that occurred in 1978 on Georges Bank, therefore yearly updates of relative abundance and quota estimates would be necessary. The recruitment of a large haddock year class for instance could change the overall picture dramatically. Fortunately linear programming is extremely flexible, allowing changing conditions to be easily incorporated into an analysis.

Chapter 3: Trophic Dynamics and Shallow Assemblage Multispecies Model.

Introduction

The importance of interspecific interactions to multispecies fisheries problems and investigations cannot be stressed enough, yet little quantitative information is actually available to formulate hypotheses and promulgate judgements on the effects of these species interplays in the marine environment. Much speculation and intuitive thought about ecological linkages has occurred, but it has been difficult to prove or even postulate how observed community phenomenon were induced. The ecological mechanisms of community interactions are not well understood, especially in marine offshore communities. The difficulty is compounded by a fluctuating environment, which can in any given year decimate year classes of even the most dominant fish in a community. Competition and predation are thought to be powerful community organizational mechanisms in limnetic, terrestrial and intertidal communities, but their effect on offshore marine assemblages is only speculated or based on weak evidence. At present there is a paucity of marine community or ecosystem models because species couplings are not well understood and mechanistic theory is lacking. Researchers are also unable to conduct field experiments in the marine offshore environment, a further impediment to understanding important species linkages. Perhaps the solution lies in extrapolation of results from more easily studied environments to the marine case and hypothesis investigation by constructing system dynamics models with proposed mechanisms in place. Adaptive management ex-

periments in which fishing effort is arranged over assemblages so that new insight is gained could also be helpful (Tyler et al 1982). These models may help us to understand why or how important fluctuations occur and have possible implications in the management of marine fish populations.

Most community or ecosystem modeling exercises have concentrated on predation as the principal ecological mechanism of interspecific interaction because this phenomenon is readily observable from food chain investigation studies. Mortality, the dynamic result of predation, is easily modeled, while more subtle mechanisms such as competition are not as clearly understood nor are the associated feedback structures that actually cause population change. It would be valuable to couple these mechanisms with population homeostatic responses in communities of interacting species. To do this correctly it is necessary to account for spatial and temporal zoogeographical patterns of the species of interest so that the populations are in phase with the proposed mechanisms.

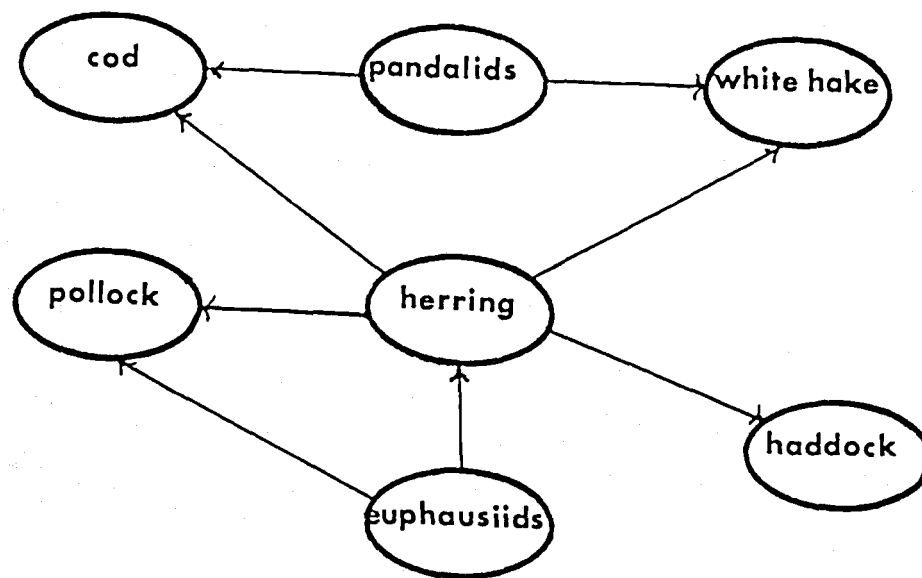
Georges Bank assemblages, as defined by hierarchical cluster analysis, were useful as an organizational framework for constructing food web diagrams and system level conceptual models. This conceptual framework, along with several hypotheses of long-term system change, was used to construct a multispecies fisheries model of the Shallow assemblage. Simulations from this model were used to attempt to explain observed historic trends in this assemblage by using the simple ecological mechanisms noted above.

Main Component Food Web

Marine food webs can be so complex that resolution of important linkages is of prime importance if progress in understanding system behavior is to be made. Atlantic cod, for instance, consume over 300 separate food items during their maturation from juvenile to adult fish (Bowman pers. comm. 1982). The Sea raven is similarly bonded to a host of prey populations during their life history (Tyler et al 1982). To understand system behavior it is necessary to investigate interspecific interactions on a coarse level (Overton pers comm. Dept. of Stat., OSU 1980, Silvert 1982). This approach preserves relevant dynamic behavior and eliminates unnecessary complexity that results from a literal interpretation of food habits information (Tyler pers comm. Dept. of Fish. and Wild., OSU 1981). Coarse assemblage food diagrams were constructed for the Northeast Peak, Slope and Canyon and Shallow assemblages. These schematic representations account for important predator prey linkages that affect top level fish predators in each assemblage group. They were assembled by using NEFC food habits studies that were available for the important species of each community (Maurer and Bowman 1975, Langton and Bowman 1980; Bowman 1981; Langton 1981) and do not include zooplankton.

The Northeast Peak assemblage, represented in (Fig 51), is rather simple if only important species interactions are included. Most of the species in this group are in some way or another tied into the Georges Bank herring stock. Even haddock, a rather strict invertebrate predator, preyed extensively on herring eggs during

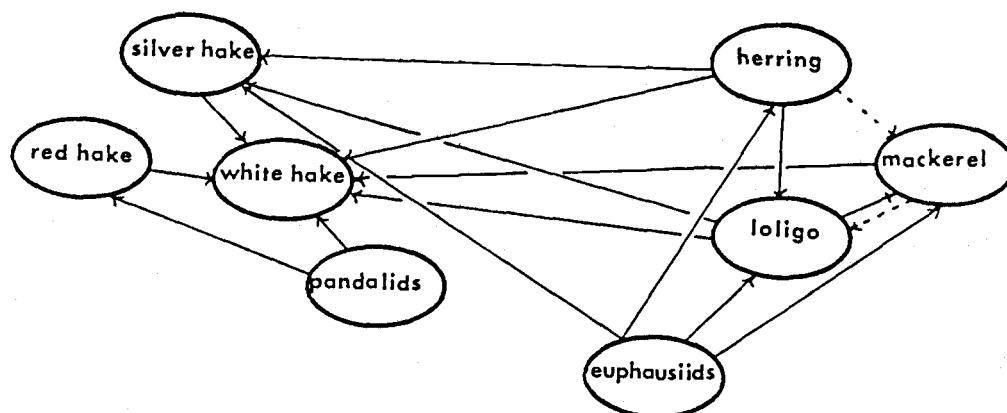
Figure 51. Coarse food web structure for the Northeast Peak assemblage



fall spawning seasons (Langton and Bowman 1980). The effect of declining herring biomass on this assemblage predator prey network is unknown, but the American sand lance, a species that recently reached unprecedented levels of abundance, may have served as a substitute prey item for these resident predators (Sherman et al 1981). Atlantic cod are known to prey heavily on sand lance (Overholtz and Nicolas 1977).

The species complex in the Slope and Canyon assemblage was slightly more intricate than the Northeast Peak with several more seasonal migrants assuming a prominent role in community dynamics (Fig 52). Mackerel, herring, and long-finned squid all migrate through this assemblage on a seasonal basis and appear to be important links in the assemblage trophic hierarchy. They also constitute a feeding triangle that operates during different life history and distributional stages of each stock. Adult mackerel feed on larval herring during the spring while young mackerel may serve as a major prey item for long-finned squid during the summer months. Long-finned squid adults consume adult herring and young long-finned squid are eaten by adult mackerel during the summer (Langton and Bowman 1980). These species as well as euphausiids are linked to the silver and white hake stocks of this assemblage (Fig 52). Black belly rosefish, a species of importance in this group, are not included because it was not routinely sampled for food habits information. Available information indicates that this species feeds heavily on crustacean prey, euphausiids are probably particularly important (Maurer and Bowman 1975). As in the Northeast Peak assemblage, the effect of declining herring biomass

Figure 52. Coarse food web structure for the Gulf of Maine assemblage.



on the Slope and Canyon assemblage is unknown, but it probably is less significant since this species is present in the assemblage for only a short time during the summer months.

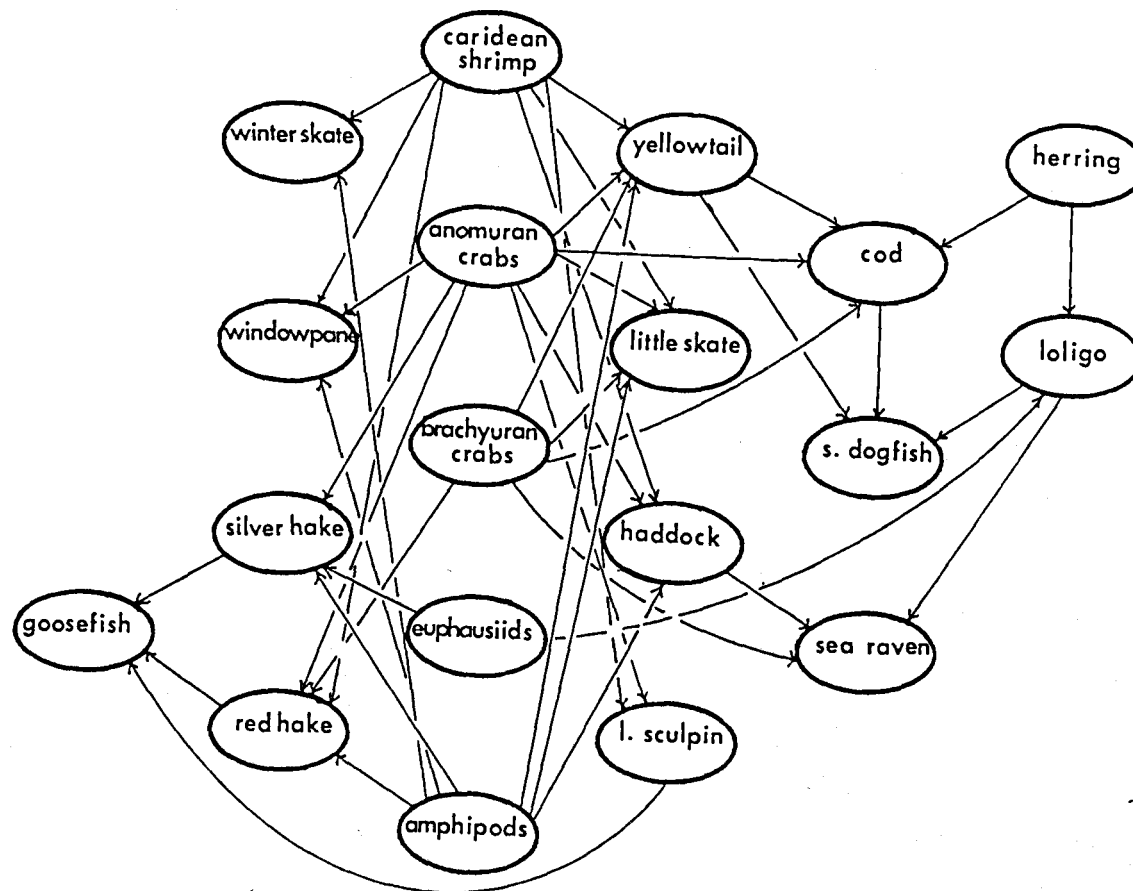
The Shallow assemblage appears to be one of the more complex of the Georges Bank groups due to the number of species and the intricate nature of its invertebrate-based food web (Fig 53). The resident predatory species such as cod, goosefish, and sea raven are supplemented during the summer months by intermittent levels of spiny dogfish and long-finned squid. Eight species of invertebrate predators comprise the bulk of the biomass in this assemblage, utilizing a common invertebrate prey pool shown in Fig 53.

As noted previously the haddock, silver hake and red hake present in this assemblage are generally the juvenile stages of these three species, the adult stocks being present in other assemblages. These juvenile fish as well as the juveniles of the other stocks present and to some extent the adults share several common prey items (Langton and Bowman 1981; Bowman 1980).

Model Background

As noted in Chapter 1, there were three distinct periods of species composition change in the Shallow assemblage from 1963-1978. These periods were 1963-1967, 1968-1972 and 1973-1978. The species complex in this assemblage moved from one dominated by haddock to a yellowtail flounder-longhorn sculpin intermediate group to a final state where winter skate, little skate, and windowpane flounder were the major species. What had caused this

Figure 53. Coarse food web structure for the Shallow assemblage



directional movement of the species composition and relative abundance? The assemblage had been dominated by commercially important species, but the resultant system state was one controlled by species of little economic importance.

What mechanisms were responsible for the changes that were observed in the Shallow assemblage? Were these trends the result of the intense fishery that operated on Georges Bank at this time, had the environment changed or did interspecific interactions transform the community state? It is difficult to separate the effects of these three global influences, but for the purposes of model building and hypothesis investigation it is necessary and relevant to decompose their influences. This allows one to isolate suspected driving variables and mechanisms in models such that their propensity for generating changes in system states might be studied.

In the case of the Shallow assemblage the pertinent ecological question is could simple interspecific interactive mechanisms in part have initiated the assemblage responses that were observed from 1963-1978? This question is interesting because of the implications it would have on multispecies management and also since important inferences concerning this type of marine trophic food web would be gained. To address these questions it is necessary to remove the effects of the environment that would confound any results one might obtain in a simulation exercise. The model then would be used to attempt to explain part of the variability observed over the long-term, acknowledging that important environmental

influences were not included.

Trajectory Hypotheses

In the early 60's the Georges Bank haddock stock experienced two successive years of outstanding recruitment such that there was nearly a three-fold increase in stock weight and a four-fold increase in stock numbers. Juvenile and subadult haddock dominated the Shallow assemblage during this period. An intense haddock fishery developed on Georges Bank when foreign distant water fleets were attracted to the large numbers of 2-3 year-old fish that were present in 1965 and 1966 (Clark et al 1982). This caused a drastic decline in the adult stock and corresponding low recruitment (Clark et al 1982). This decline in recruitment caused the number of haddock in the Shallow assemblage to decrease rapidly. The likely competitive release, triggered by removing haddock biomass, allowed the other regular components of this assemblage to increase their numbers and biomass. This change in species composition did not occur at once, but progressed through a series of gradual changes due to time lags in population dynamic processes and fishing pressure.

Several scenarios can serve as plausible explanations for the system state changes that were observed. Competitive interactions between juveniles and subadults of yellowtail flounder, windowpane flounder, longhorn sculpin, little skate, and winter skate may have accounted for the eventual skate-windowpane dominated system. Yellowtail flounder and longhorn sculpin may have responded more quickly to the haddock demise due to faster growth and recruitment

responses than the other three species. This would account for the period between 1968 and 1972 where these two species showed increases in biomass and numbers (Figs 36,37). The skates and windowpane flounder however, were potentially superior competitors, but with slower growth responses and recruitment capabilities. It therefore took a longer span of time for these three species to show the increasing trends that were observed. Concomitant to this proposed explanation, fishing effort on yellowtail flounder had been increasing, resulting in downward trends in this stock (Fig 54), (Parrack 1976). Therefore, the mechanisms of competition coupled with fishing pressure on the assemblage may have been responsible for the observed trends. Long-term prey responses may also have been an influential factor.

Another possible process that may have contributed to the directional changes that occurred in this assemblage was predation pressure on the juvenile stages of these stocks. During the mid years of this time series, the catch/tow of several predators increased dramatically in this assemblage. Cpuce from research cruises showed increasing trends during the 70's for long-finned squid, spiny dogfish, and bluefish (Figs 19,55,56). These predators were only present during several of the warmer months, possibly acting as an intense source of predation in addition to resident predators such as cod and goosefish. Predation, through predator selection, density dependence, or some other response, may have operated alone or in conjunction with competition to initiate the responses that occurred. Juvenile skates and windowpane flounder are potentially less desirable as prey items due to dif-

Figure 54. Yellowtail flounder commercial catch index, (tons per standard day fished) from (Clark et al 1981)

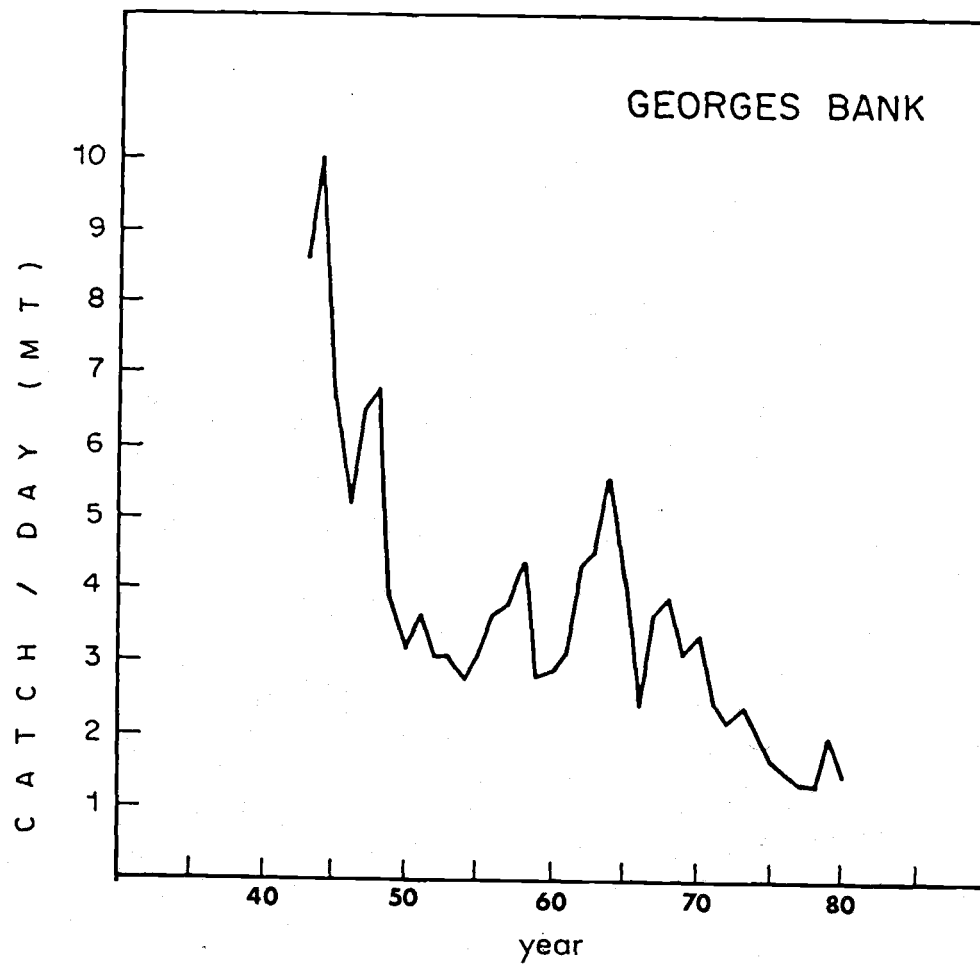


Figure 55. Spiny dogfish research catch/tow (kg), Fall 1963-1978

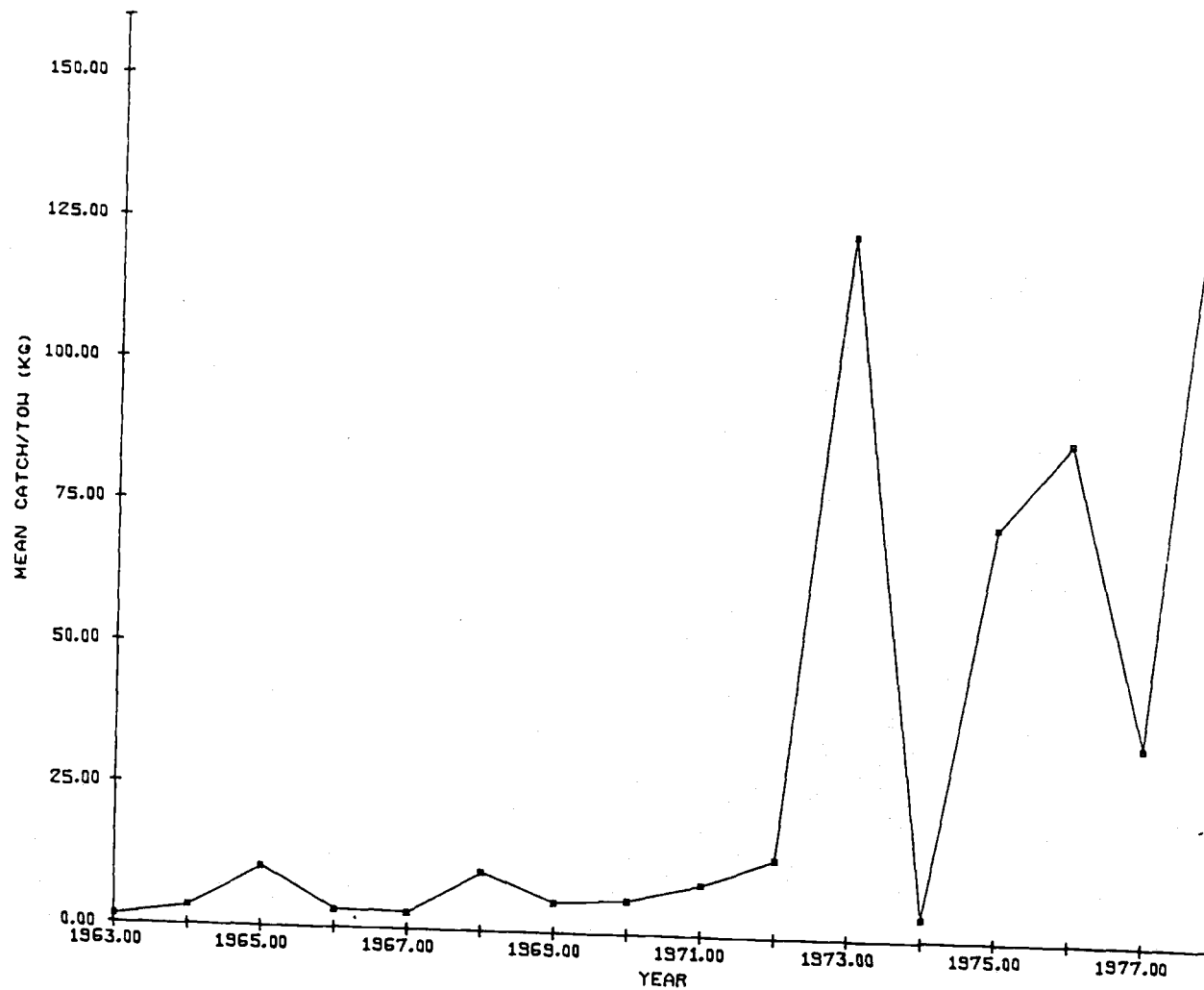
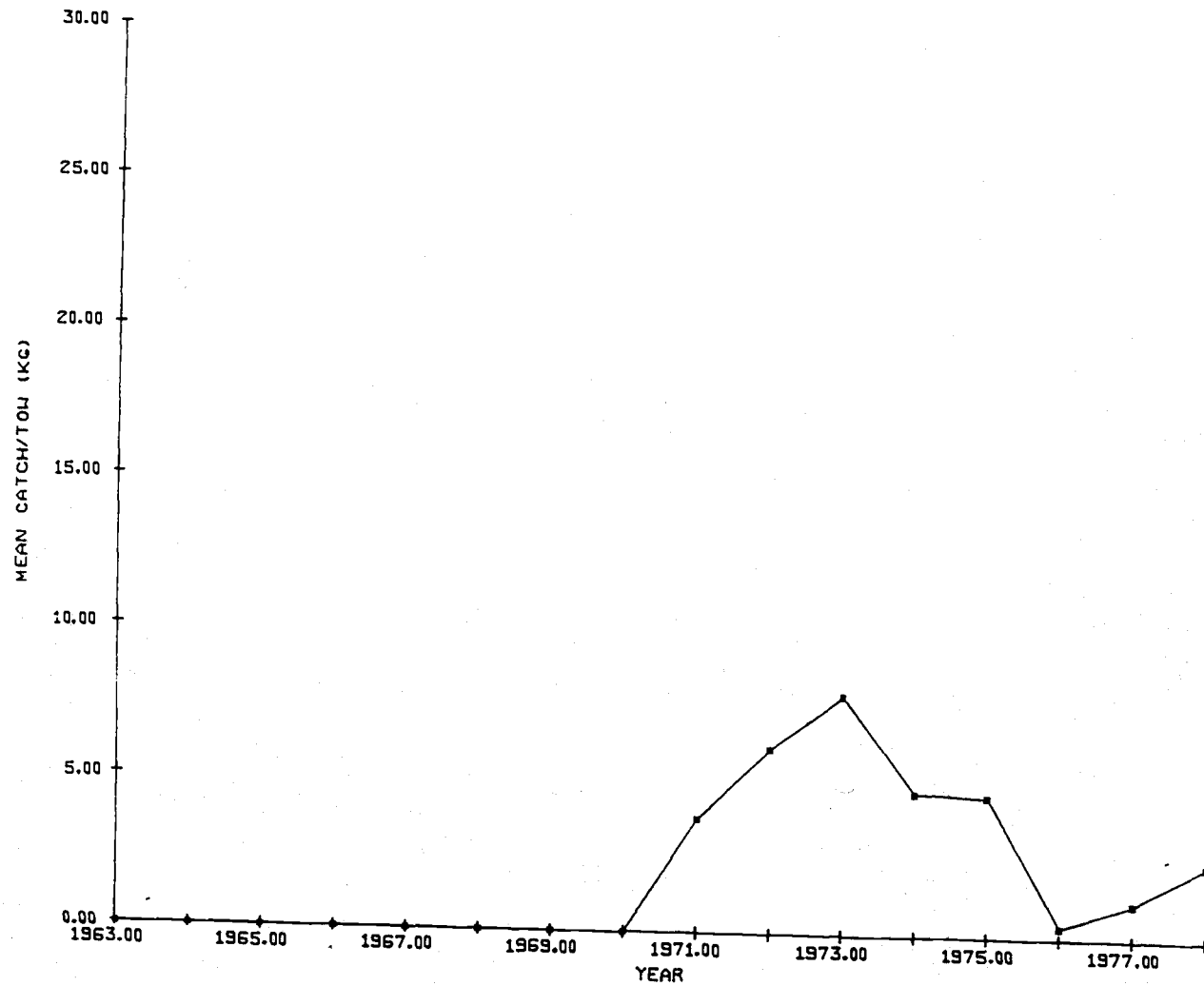


Figure 56. Bluefish research catch/tow (kg), Fall 1963-1978



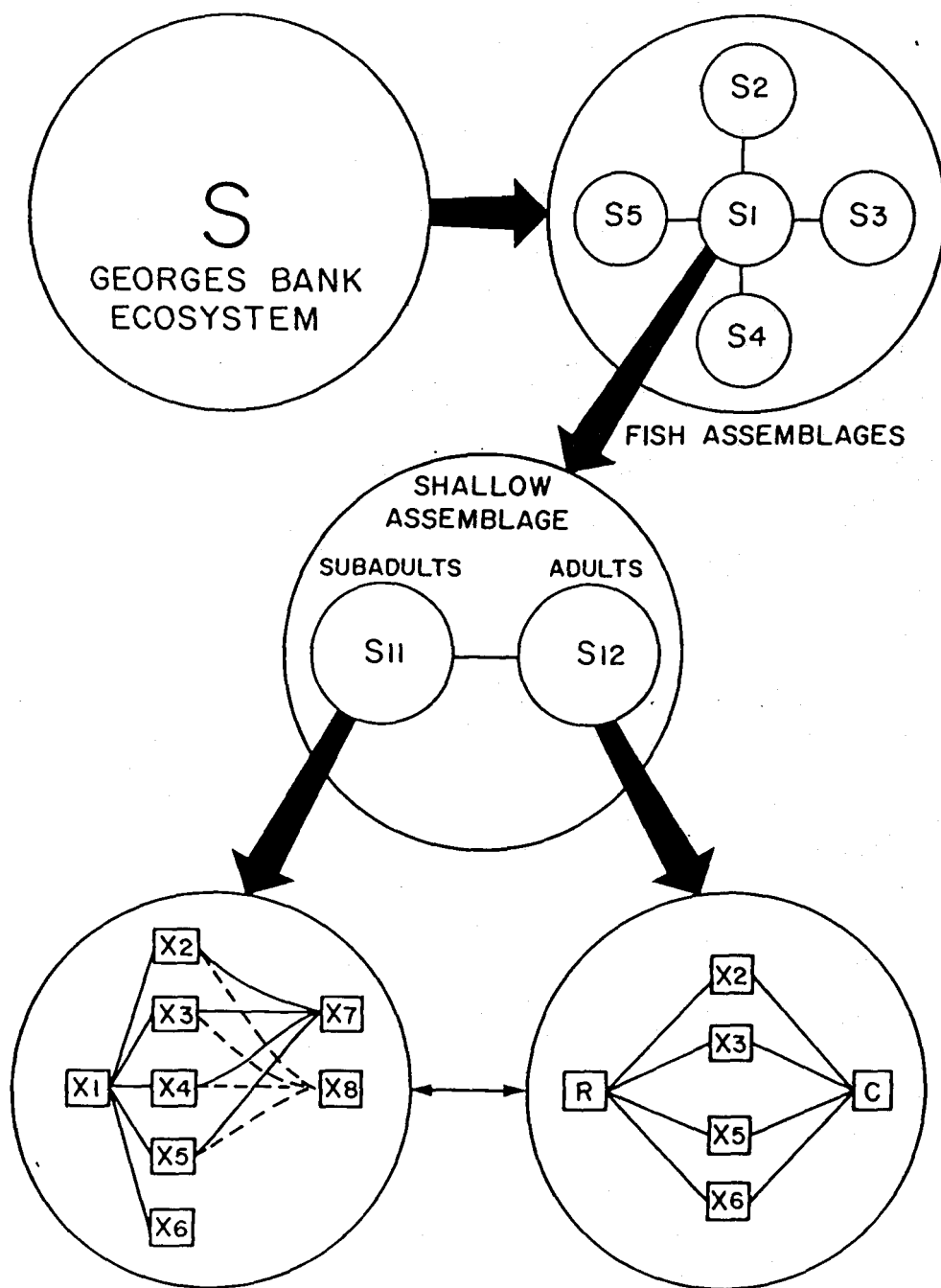
ferences in behavior, accessibility or palatability, while longhorn sculpin, although perhaps not a desirable prey species as an adult, is more accessible and of a correct size and body configuration when it is a juvenile and subadult. Yellowtail flounder are preyed upon by cod, goosefish, spiny dogfish, and a host of other predators (Langton and Bowman 1981).

Overall System Perspectives

Part of general systems theory involves the decomposition of the system of interest into its' component subsystems to allow for practical management of the modeling process (Overton 1977). A subsystem of particular interest can easily be isolated then for model construction, validation or other purposes, within this overall structure. This method of hierarchical organization is extremely useful for dealing with the complex problems encountered in conceptualizing, constructing, and implementing a large system model (Overton 1977)

The target system is addressed within this overall system organization viewpoint, giving a clearer understanding of the actual position that the particular subsystem occupies (Overton 1977). Fig 57 represents a hierarchical schematic viewpoint of the Georges Bank ecosystem as defined by numerical classification methods. White and Overton (1977) use these diagrams to illustrate the hierarchical nature of systems. The Georges Bank system in this case is composed of the five assemblages, S1...S5, represented in Fig 57. The Shallow assemblage, or S1, is of particular interest here as a focus for a multispecies model. Two

Figure 57. Georges Bank system hierarchy, with Shallow assemblage subsystems



particular subsystems, S11 and S12 the subadult and adult sections of the model, will be approached separately, but ultimately coupled as shown in Fig 57.

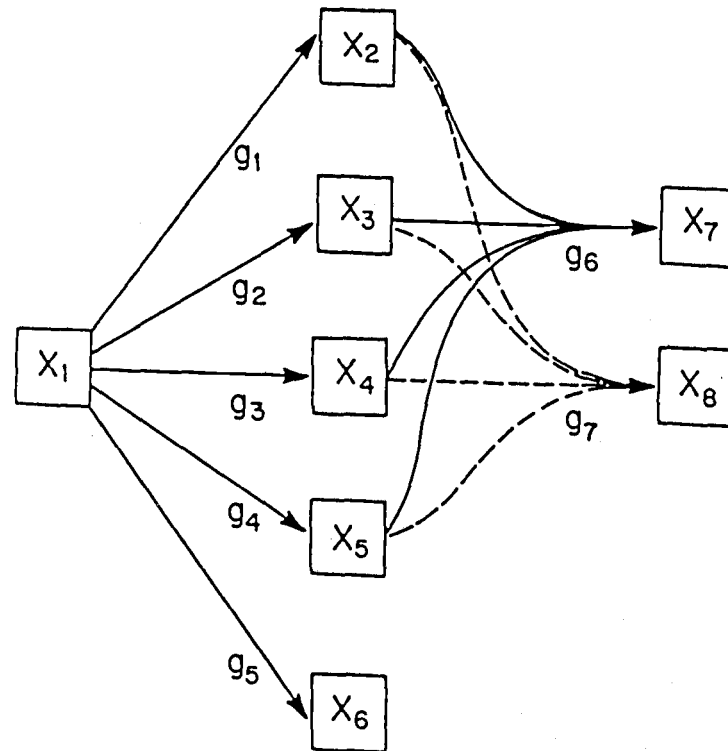
Subsystem Organization

Following Overton (1977) and White and Overton (1977), state variables or X's were used to model particular system states at given time intervals. Input variables or Z's are used to model system driving variables, update functions, g's are used to model system processes and b's are system parameters.

Subadult Subsystem

Fig 58 shows the basic structure of the subadult subsystem of the Shallow assemblage that was modeled using this convention. Five different fishes, X2...X6, compete for the prey items available in X1. The competitors were prioritized such that the feeding order was haddock, skates, windowpane, yellowtail flounder, and longhorn sculpin. Little skate and winter skate were lumped together because of similarities in population dynamics and to facilitate model construction. The flow of biomass from X1 to X2...X6 was modeled by using g functions, g1...g5, to update biomass for each competitor on a yearly interval. The g functions are of a general type of analytical modeling formulation with stable properties known as donor-recipient controlled functions (Hall and Day 1977). (Fig 59) shows that this particular equation is one of a family of asymptotic relationships that serve as potential vehicles for modeling interspecific interactions. The g

Figure 58. Basic subadult subsystem structure from the Shallow assemblage model



X_1 3 Prey Species

X_2 Yellowtail Flounder

X_3 Longhorn Sculpin

X_4 Haddock

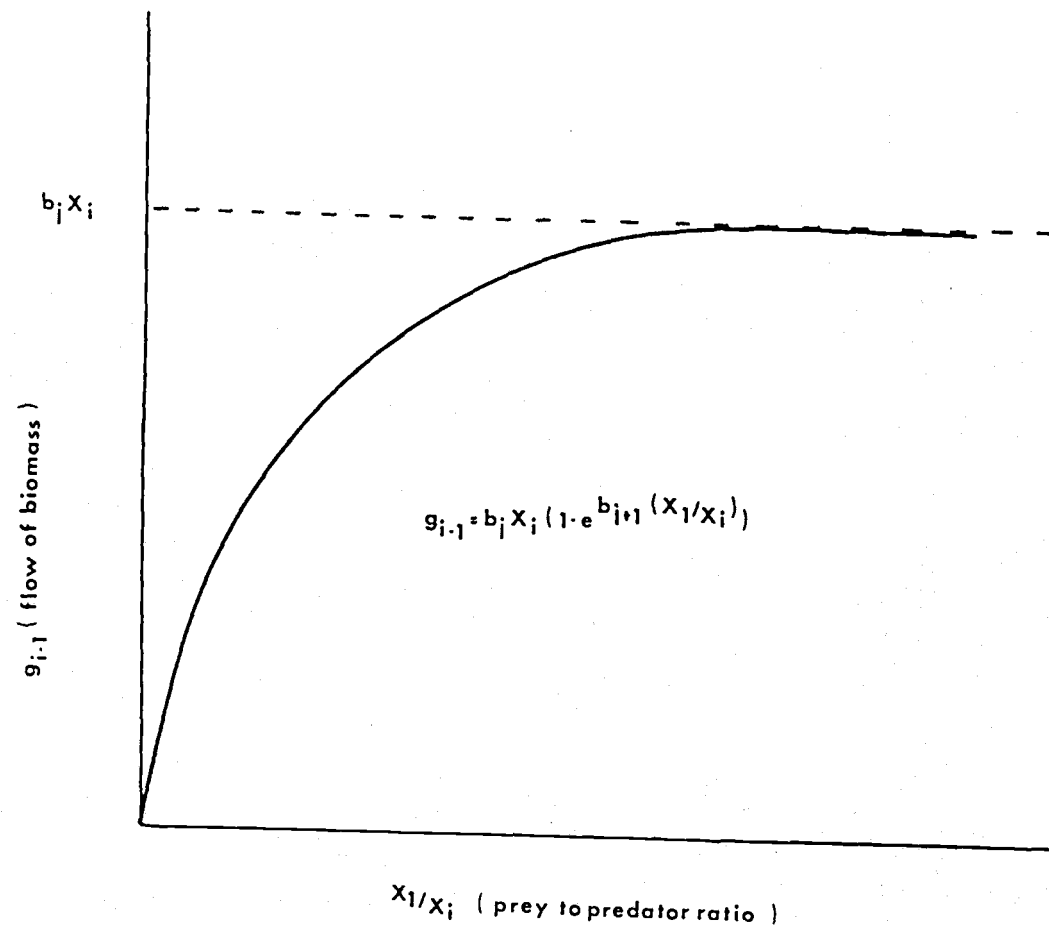
X_5 Windowpane Flounder

X_6 Skates

X_7 Spiny Dogfish

X_8 Loligo sp.

Figure 59. Response curve for typical donor-recipient g equations



functions for the competitive species are characterized generally by

$$(1) \quad g_{i-1} = b_j x_i (1 - e^{b_{j+1} x_1 / x_i})$$

where:

g_{i-1} = flow of biomass from X_1 to X_i

X_1 = prey biomass available for predation by X_i

X_i 's = biomass of particular competitor of interest

b_j 's = g age specific parameters

The competing species, $X_2 \dots X_6$, are subject to potential predation by spiny dogfish, X_7 , and long-finned squid, X_8 . Another system simplification allowed the exclusion of X_6 , the skate biomass from predation by the previously mentioned predators (Fig 58). The g functions for the predators were also used to update the biomass of competing species over the yearly interval. These relationships are given by the following general equation.

$$(2) \quad g_{i-1} = b_j x_i (1 - e^{b_{j+1} (b_{j+2} x_2 + b_{j+3} x_3 + b_{j+4} x_4 + b_{j+5} x_5 / x_i)})$$

where:

g_{i-1} = flow of biomass from $X_2 \dots X_5$ to X_i

X_i = biomass of particular predator

$X_2 \dots X_5$ = biomass of prey species

b_j 's = g age specific parameters

$i = 6, 7$

The g functions utilized in this model are density dependent relationships that are easily adapted to numerous conditions of

competition and predation. Competition, nonselective predation and predator preference are just a few of the possible mechanisms that can be adapted to this strategy.

X4, haddock biomass and dynamics, was not modeled explicitly in this exercise, but input on a yearly basis as a value from an age specific Z or forcing function trajectory (Fig 60). This idea comes from the hypotheses that were developed concerning the assemblage responses that were triggered by the decline of haddock. Neither were the predator dynamics modeled explicitly, but were treated as system inputs via driving variable trajectories (Figs 61,62), which influenced the dynamics of the five competing species .

A formal age structure was maintained in the subadult portion of the Shallow assemblage model because it was felt that most of the relevant dynamic behavior of many marine fish populations occurs in the juvenile and subadult stages of their life history. The propensity for competition, mass mortality, and predation influences is greatest during the early life history stages of fish. This idea is in agreement with other studies that have observed that there are distinct separations between the life history processes of adult and juvenile animal populations (Deriso 1978, Deriso 1980).

For the simplified purposes of this model, yellowtail flounder, longhorn sculpin, haddock, and windowpane flounder matured and recruited to the adult population at age 3. This agrees with studies on the population dynamics of these species

Figure 60. Haddock biomass (mt) used as an input trajectory for the Georges Bank Shallow assemblage model

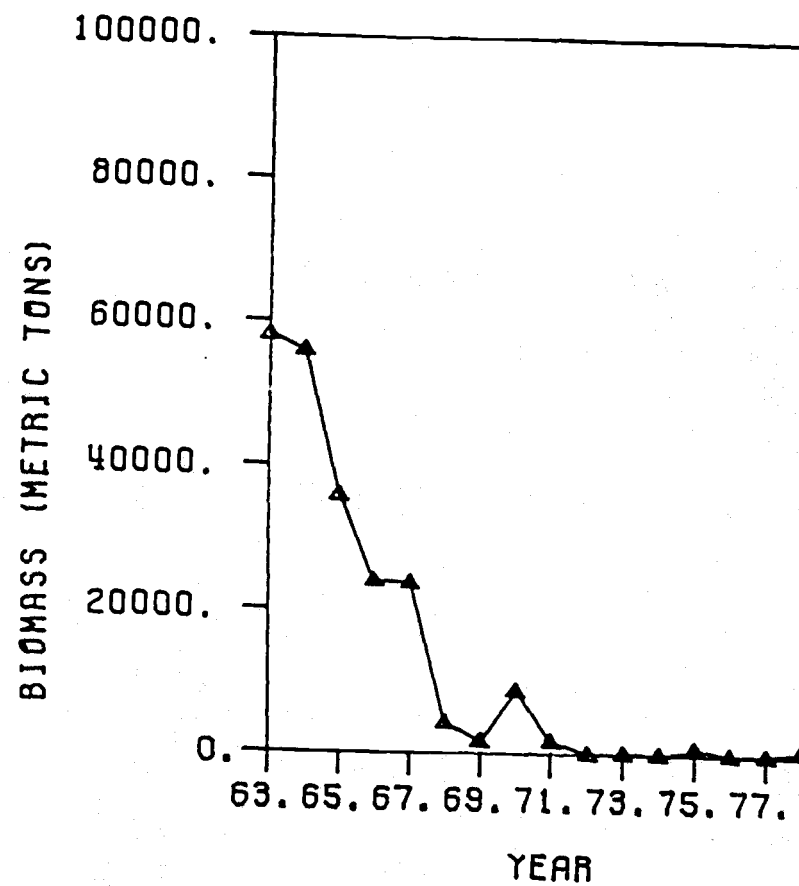


Figure 61. Spiny dogfish biomass (mt) used as an input trajectory for the Georges Bank Shallow assemblage model

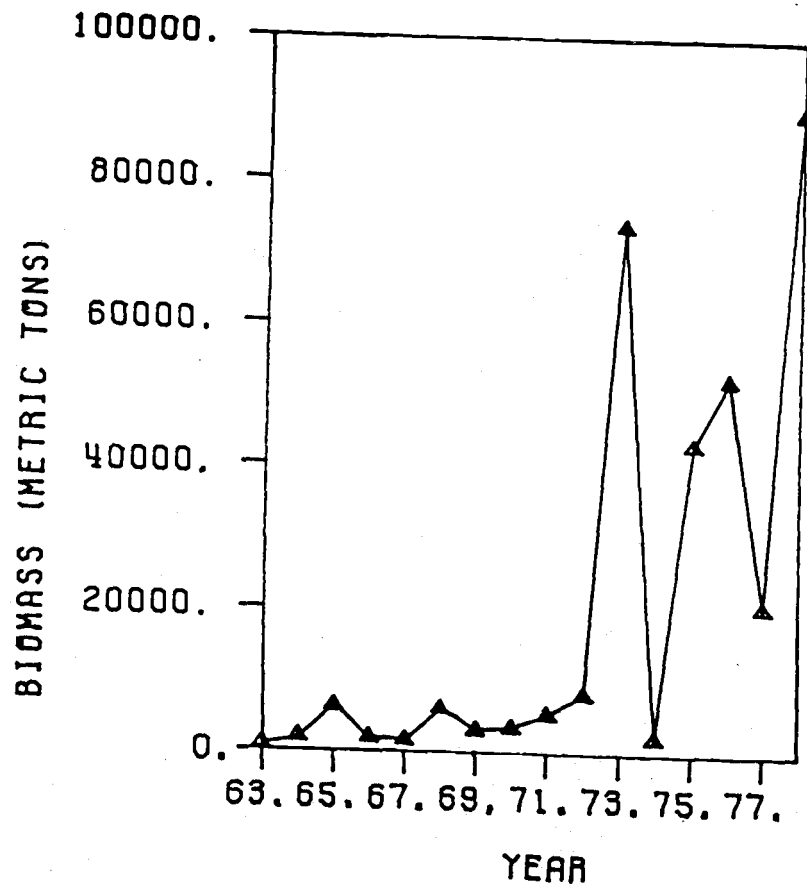
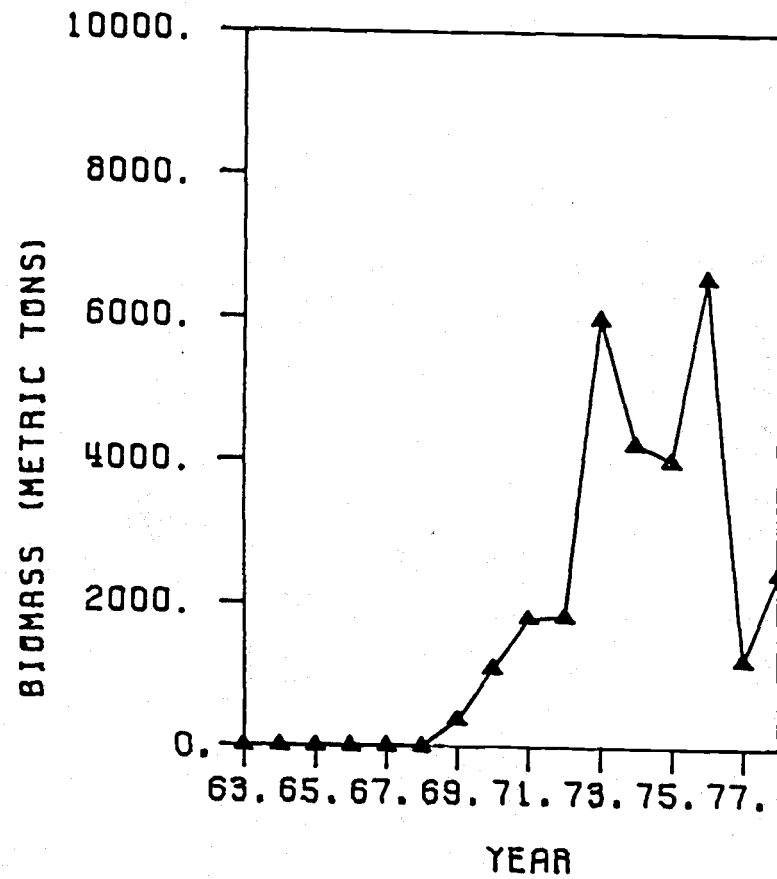


Figure 62. Loligo biomass (mt) used as an input trajectory for the Georges Bank Shallow assemblage model



(Parrak 1976; Morrow 1951; Clark et al 1982; Dery and Livingstone 1982) respectively. Skates on the other hand were presumed to mature at age 5 in accordance with Holden (1973) and Waring (1980). The subadult section of the model dealt with these young age groups, all competitive and predatory mechanisms were instituted at this level. No larval fish dynamics were addressed in this model, fish larvae were produced from species-specific, stock-larval recruitment relationships. Death occurred from constant natural mortality rates, updated numbers of juvenile fish were calculated and entered into the first age group of each species.

Mortality of Subadults

Mortality on the early life history stages of yellowtail flounder, longhorn sculpin, windowpane flounder, and skates originated from two sources, a constant level of natural background mortality that occurred over the whole year, and pulsed predation that occurred over a much shorter time interval. The constant source of natural mortality can be thought of as emanating from resident ubiquitous predators such as cod, goosfish, and sea raven, as well as any diseases or natural events that might serve as mortality agents. Pulse predation as previously mentioned is initiated from input driving variable trajectories of spiny dogfish and long-finned squid biomass. Two types of predatory mechanisms are available in the model: a strictly density dependent predator response, and a response that is sensitive to prey density as well as type. In the former mode the predators

ration is determined by the prey density, while for prey preference, a ration is removed differentially from the possible prey reservoir. These mechanisms are evoked by changing the parameters, $b_{j+2} \dots b_{j+5}$, in equation (2), depending on the particular response that is being investigated. For instance the b_j 's are all equal to unity when the predatory behavior is based strictly on a compensatory relationship. This potential predatory mechanism operates during the productive seven month period, May through November, that the dynamic portion of the subadult model focuses on. Values for parameters, $b_j \dots b_{j+i}$, in equation (2) were obtained by using 16-year mean values of biomass from the X2...X5 species, a 16-year mean value for spiny dogfish and a ten year mean of long-finned squid biomass. This information was obtained from minimum biomass estimates from the Shallow assemblage. CPUE from the shallow assemblage for all the species was corrected for day-night differences in catchability over the entire 1963-1978 time series (Sissenwine and Bowman 1978). Minimum biomass estimates from these corrected mean catch/tow values were calculated as

$$(3) \quad B_i = \frac{W_i A}{a}$$

where:

B_i = minimum biomass of species i

W_i = mean catch/tow of species i

A = area of the shallow assemblage (20373 km**2)

a = area swept by the survey trawl (.03419 km**2)

Tyler and Dunn (1976) found that adult marine groundfish typically consume between 1 and 2% of their body weight per day. A ration estimate of 2%/body wt/day was utilized to calculate an upper limit to total prey biomass consumed by a particular predator over a 60 day period. These estimates along with the total prey biomass were used to determine the g6 and g7 relationships based on the premise that a predator is seldom satiated. Two predatory scenarios were parameterized; moderate and intense predation cases where 25% and 75% respectively of the predators ration was obtained from the early life history stages of the X2...X5 complex over a 60 day period. It was felt that for the purposes of model parameterization, these predation levels represent an interesting range for investigation.

Total instantaneous natural mortality during the seven month period was calculated from conditional mortality rates (Ricker 1975, pp11) as

$$(4) \quad bN_{ij} = n1_{ij} + n2_{ij} - n1_{ij}n2_{ij}$$

where:

N_{ij} = Species and age-specific seasonal mortality for 7 months

$n1_{ij}$ = Species and age-specific mortality from predation

$n2_{ij}$ = Species and age specific background natural mortality from resident predators and other sources

This was converted to an instantaneous rate by

$$(5) \quad bM_{ij} = -\ln(1 - N_{ij})$$

No source of fishing mortality operated on the young fish in the subadult model. Additional mortality occurs during the five unproductive months of the year from natural causes such as resident predators.

Growth of Subadults

A change in growth, induced through exploitation of common prey resources by, $X_2 \dots X_6$, was the primary mechanism where by the effect of competition was expressed in this model. Dynamic feedback on growth resulted in two possible pathways for population response to occur. Increased growth through a competitive release of prey biomass could result in a larger mean size of fish of the particular species and a complimentary increase in stock biomass. This would be particularly true for species that have fast growth and mature at an early age. The other feedback mechanism that could be triggered by competition is a change in recruitment. The adult spawning stock biomass could increase through increase in size-at-age, causing a corresponding rise in age-specific fecundity and recruitment. This would occur if the spawning stock biomass were at a level that allowed for such increases as in the case of most exploited populations.

To estimate growth correctly within the framework of the competitive g equations, it is necessary to work with average age-specific stock size, the arithmetic mean of the initial and final biomass for each age group (Ricker 1975). This value is given by the following expression found in (Ricker 1975, pp239).

$$(6) \quad XB_{ij} = \frac{(X_{ij}(1 + e^{(bG_{ij} - bM_{ij})})}{2}$$

where:

XB_{ij} =age specific mean biomass for the seven month productive season

X_{ij} =biomass at the start of the interval

bG_{ij} =age specific potential instantaneous growth rate

bM_{ij} =age specific natural mortality rate

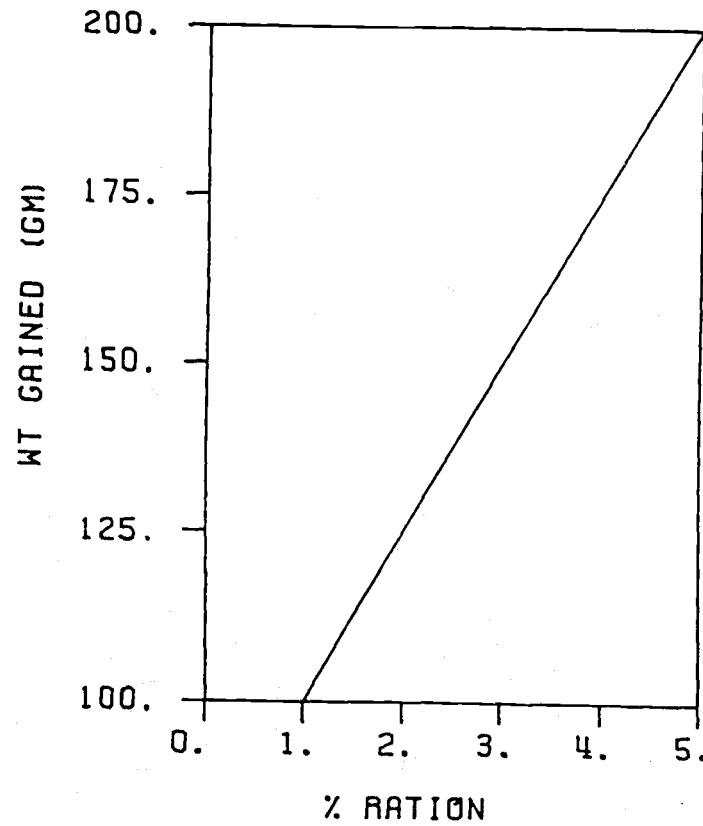
i =species

j =age group

These average biomass estimates were used in a system of equations similar to equation (1), except modified to account for sequentialized feeding effects (Overton pers comm. Dept. of Stat., OSU 1980). The conceptual ideas discussed in the trajectory hypothesis section were used to establish a feeding hierarchy for the 5 competing species. This meant that available food resources were funnelled through a species based on its position in this schedule. Haddock had first priority followed by skates, windowpane flounder, yellowtail flounder, and longhorn sculpin. The total flow of prey biomass to a particular competitor was determined in this relationship through density dependent effects. These sequentialized dynamic flow equations were parameterized in much the same manner as the predation equations, except that a 5%/body wt/day upper limit ration was chosen because smaller fish with larger food intakes on a body weight basis were involved. This estimate of total prey consumed was used to calculate age specific rations based on a 210 day productive season.

Ration determined the age-specific weight gain through the type of functional relationship represented in Fig 63. These

Figure 63. Hypothetical ration-growth functional relationship for age specific weight gain.



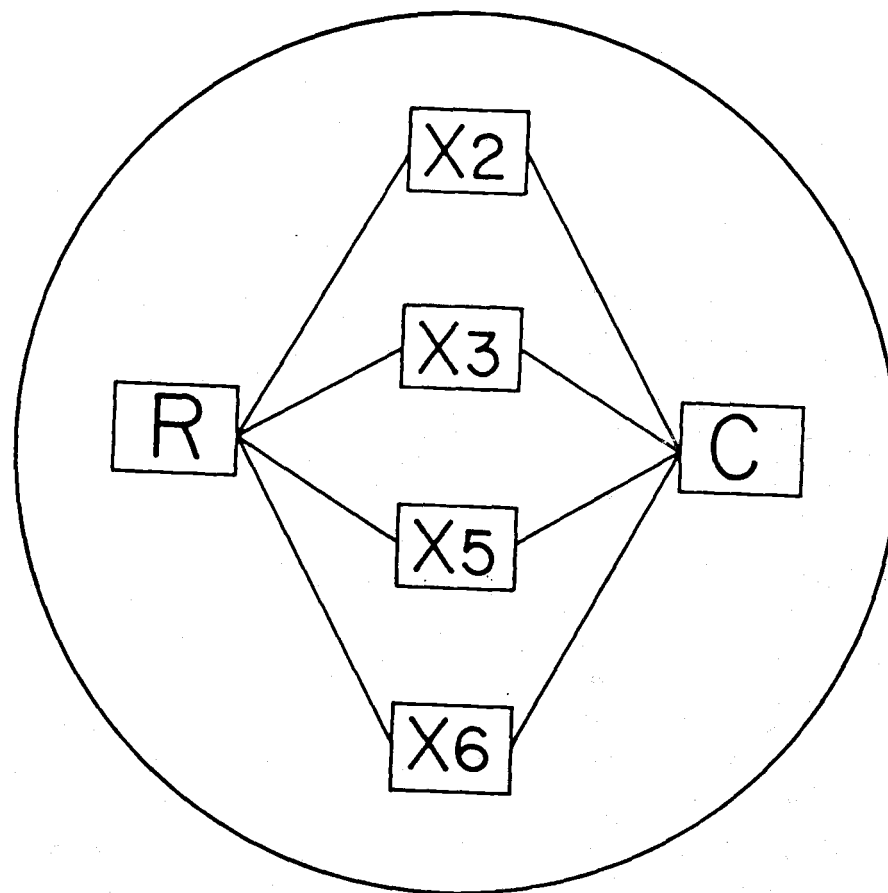
relationships were formulated to relate a continuum of rations to the corresponding growth that would result at age for each species. Percent ration ranged from 1-5%, 1% representing the case where a species received little food due to intense competition, while a 5% ration represented the converse. These weight gain relationships were consistent with growth trends from aforementioned assessment documents and studies reported in the literature.

Adult Subsystem

A schematic representation of the adult subsystem can be found in Fig 64. Yellowtail flounder, longhorn sculpin, windowpane flounder, and skate biomass was modeled with a modified adult life history approach as discussed in Deriso 1980. This approach approximates the behavior of a full age structured model without the associated burdens of model size and complexity (Deriso 1980). This is especially important when building a large system model. Several general observations from population demographic studies indicate the validity of this method. A paucity of individuals in older age groups in species with protracted age structures is a common pattern in populations (Deriso 1978). Many adult populations appear to share common mortality trends over most of their age distribution and mortality agents are quite different during the 'juvenile and adult stages of a species' life history (Deriso 1978). These trends serve as useful simplifications for dealing with population dynamics of iteroparous species.

The equation that served as the basis for the life history

Figure 64. Adult subsystem schematic, from Fig 57, where adult stocks (X's) produce catch (C) and recruits (R)



stage model is found in (Deriso 1980). Equation 4 from his study was modified slightly to accomodate yearly changes in fishing mortality. This yielded as equation that accounted for stock biomass changes, calculated generally as

$$(7) \quad XA_{i+1} = (1+bk_i)(1-bA_i)(XEA_i) - (bk_i)(1-bA_i)^2(XEA_i/XA_i)(XEA_i-1) + XR_i$$

where:

XA_i 's=adult biomass of species i

bki 's=species specific Ford growth coefficient

bAi 's=species specific annual total mortality rate

XEA_i =surviving fraction of the catchable stock

XR_i 's=species specific recruitment biomass from graduating subadult age groups

In this submodel the adult stocks of the four previously mentioned species are subject to a fishery and their biomass determines recruitment from species specific stock recruit relationships. The fishery is initiated by using an input trajectory that approximates actual yearly instantaneous fishing mortality rates that occurred from 1963-1978. These rates were obtained from NEFC assessment documents or by inference from observed trends in other species (Parrak 1976; Waring 1980; Clark et al 1982). Natural mortality was assumed constant ($M=0.2$) for the adult stocks, a level consistent with values used routinely to assess dynamic processes of Georges Bank fish stocks (Parrak 1976; Clark et al 1982). No attempt was made to model adult haddock dynamics because few adults actually inhabit this assemblage dur-

ing the productive season. Recruitment of juvenile haddock to the Shallow assemblage for the most part occurred through transport of larvae from spawning grounds located in other assemblages, particularly the Northeast Peak assemblage.

Mortality of Adults

To maintain continuity and incorporate instantaneous rates from the species-specific vectors into equation (7), which describes a fishery in which actual total mortality operates, it was necessary to convert to actual mortality rates. Figs 65,66 show mortality vectors for yellowtail flounder and skates respectively. Yearly catch from each adult stock was found by utilizing actual rates calculated as

$$(8) \quad bu_i = \frac{bF_i bA_i}{bZ_i}$$

$$(9) \quad Xc_i = bu_i XA_i$$

where:

Xc_i =species specific catch in tonnes (t).

bF_i, bM_i, bZ_i, bA_i = various mortality rates

Growth of Adults

Ford growth coefficients were obtained for yellowtail flounder, longhorn sculpin, windowpane flounder, and skates by using a combination of Walford graphs and iterations using the Brody growth model (Ricker 1975; Deriso 1980). Mean weights at age used in the Walford graphs were obtained from available literature (Parrak 1976; Morrow 1951; Dery and Livingstone 1982; Waring 1980) respectively. Estimated values of k were obtained by using equation 1 from (Deriso 1980), given as equation 10 here.

$$(10) \quad W_{i,t} = W_{k,t-(t-k)} \left(\frac{1-p^{1+(i-k)}}{1-p} \right)$$

Figure 65. Yellowtail flounder instantaneous fishing mortality trajectory 1963-1978

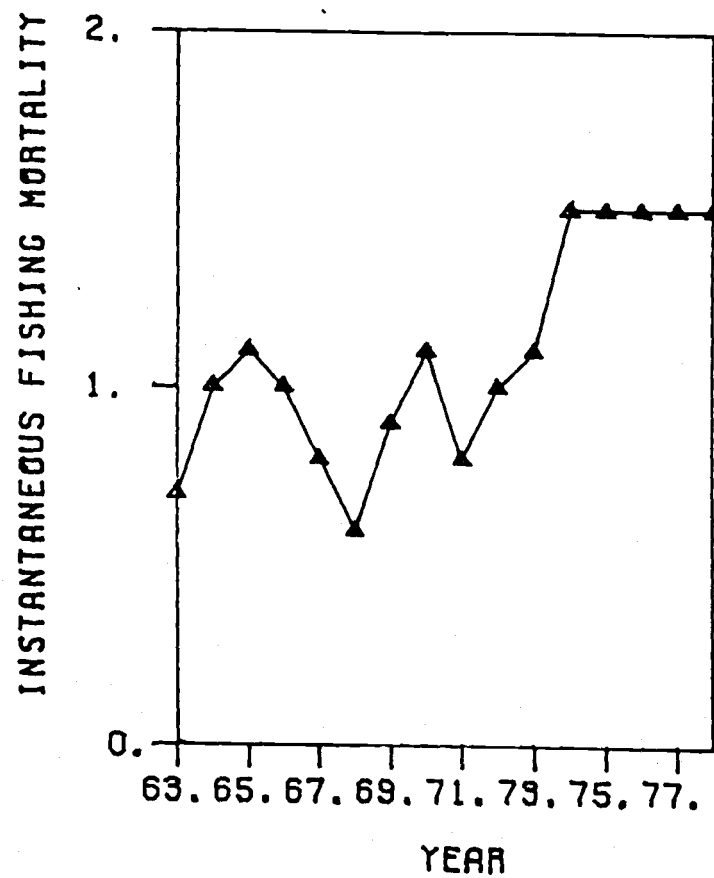
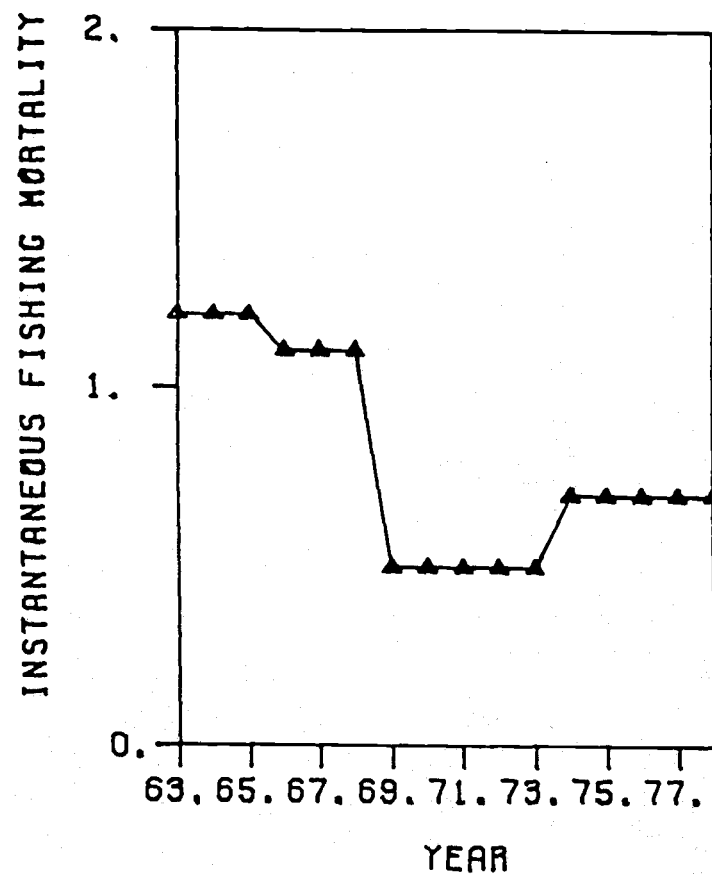


Figure 66. Skate instantaneous fishing mortality trajectory
1963-1978



where:

$W_{i,t}$ = average wt of catchable adult (i years old) during year t.

p = Ford growth coefficient

k = age of recruitment

Trial values of k were substituted into this equation until the best estimate of mean weight at age was obtained by comparison with the published results.

Recruitment

Species specific recruitment functions were developed for the adult stocks by inference from life history information available in the literature. By utilizing information on fecundity, maturity, stock size from minimum stock biomass estimates, sex ratios and mean weight at age of fish in the population, stock recruit functions were produced. Egg mortality was implicit in the adult relationships because the functions were parameterized to produce subadults in the correct order of magnitude relative to observed stock trends. A constant mortality was applied such that the resultant product of the relationships was the number of juvenile fish just prior to entering the model age structure. A similar method was used in Walters et al (1980). Survival was set at 50%, a compromise from studies of larval and egg mortality on several species (Saville 1956; Graham et al 1972; Harding and Talbot 1973)

A Beverton and Holt stock-recruit function was chosen to model yellowtail and windowpane flounder dynamics. This asymptotic curve is routinely applied to flatfish stock recruitment problems (Cushing 1973; Ricker 1975). Longhorn sculpin larval output was modeled with a Ricker function (Ricker 1975). This function was utilized because of the relatively low fecundity of the species, the relatively large size of its eggs, their demersal nature, and its relatively short life history (Morrow 1951; Bigelow and Schroeder 1953). Skates on the other hand, as most elasmobranchs, have a much different early life history phase than most teleost fishes. The genus *Raja*, of which both winter and little skate are members, has eggs that are fertilized internally (Waring 1980). Elasmobranch fecundity is extremely low in general due to internal development or embryonic protective structures which are limited by internal size. Little skate fecundity was estimated by (Holden 1974) to be only 33 eggs/year/female, slightly lower than several other species with fecundities that ranged between 60 and 150 eggs per year. (Holden 1971; Waring 1980). These differences coupled with general slow growth and maturity suggest that a direct linear, stock-recruit relationship exists in elasmobranch populations and in this genus in particular (Holden 1973; Holden 1977; Waring 1980). Parameters and equations for these four juvenile stock-recruit functions are shown in (Table 21).

Prey Population Dynamics

The X1 biomass represents three different prey types that are the available food sources for the five competing fishes (Fig 56). This submodel does not address prey population dynamics

Table 21: Equations and parameters for stock-larval recruitment functions utilized in the Shallow assemblage model.

1. Yellowtail flounder: Beverton & Holt
 $XL(2) = (1.0 / (b(63) + (b(64) / XA(2))))$

2. Longhorn sculpin: Ricker
 $XL(3) = b(65) * XA(3) * (\exp(b(66) * XA(3)))$

3. Windowpane flounder: Beverton & Holt
 $XL(5) = (1.0 / (b(67) + b(68) / XA(5))))$

4. Skates: Direct
 $XL(6) = b(69) * XA(6)$

where:

$$b(63) = 3.385E-09$$

$$b(64) = 4.730E-05$$

$$b(65) = 2.01E04$$

$$b(66) = -1.10E-04$$

$$b(67) = 1.6EE-08$$

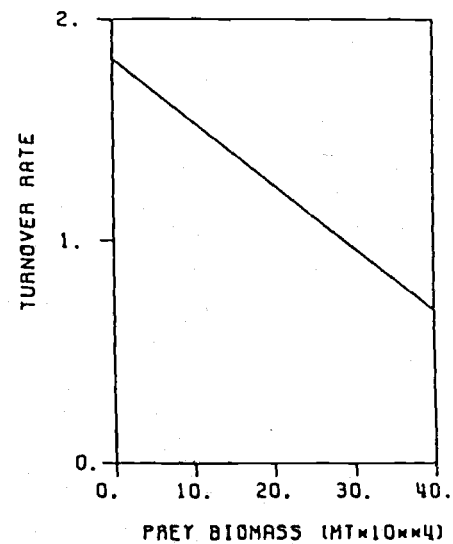
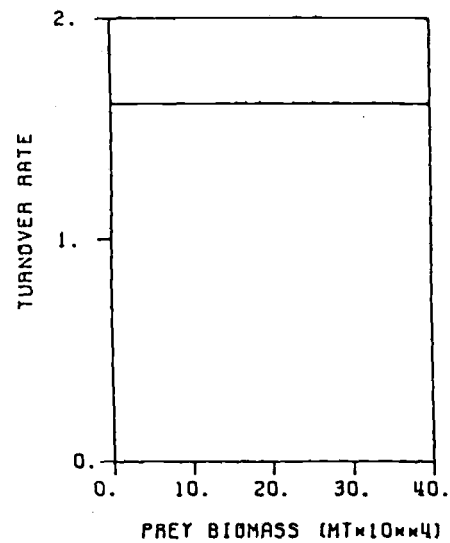
$$b(68) = 3.741E-05$$

$$b(69) = 6.9667E03$$

specifically, but utilizes two potential turnover rate mechanisms to update yearly estimates of prey biomass. The three general prey sources can be thought of as representing (a) amphipods, (b) polychaetes, and (c) a small shrimp, such as Crangon sp., Mysids or euphausiids. Annual turnover rates for (a), (b), and (c) were estimated to be 5.0, 2.0, and 1.5 respectively. These were converted to instantaneous rates and used to update prey biomass on a yearly basis by using equation (6). These turnover rates can be thought of as compromise values that were obtained by consulting the general macrobenthic literature (Sanders 1956; Cohen 1979; Warwick 1980). Benthic biomass for this simplified system was estimated using standing crop values from (Wigley and McIntire 1964). This analysis yielded an estimate of approximately 1.0×10^6 mt of available prey biomass of which the percentage breakdown was 40%, 40%, and 20% respectively.

A prey biomass submodel then was constructed based on these turnover rates and within this order of magnitude for the three standing crops. Turnover rates were either constant or density dependent and are illustrated for (a), the amphipod component, in (Fig 67). The appropriate turnover rate as well as an estimate of prey specific mortality over the seven month productive season was used in equation (7), except the age structure factor was removed. Yearly changes in prey biomass were therefore based on average values of prey and competitor biomass updated through equation (7) with a constant mortality applied to the prey over the remaining portion of the year.

Figure 67. Amphipod prey turnover rates under constant and density dependent conditions



Overall Model Organization

The basic logical structure of the Georges Bank Shallow assemblage model is displayed in Fig 68. In this schematic diagram the submodel structure as previously discussed is coupled through dynamic processes that are in operation over the yearly interval. The model was programmed to simulate assemblage events on a yearly basis. It was designed so that the various combinations of competition, predation, predator preference and prey turnover rates could be investigated with simulation experiments. The model was interfaced with SIMCON, a multipurpose simulation model processor, that was originally developed at the University of British Columbia by Hilborn et al. (1973). Fig 69 shows a simplified flow diagram that generally traces model events that occur over a year. Combinations of mechanisms were set at the beginning of each simulation and evoked in the various submodels as shown in the figure. A typical run with predation would involve taking the first left branch in Fig 69. A choice of density dependent or predator selection is made and predation mortality is calculated and added to the other sources of natural mortality. The model branches back to the subadult submodel, updates the age structure of each species based on growth and mortality and proceeds to the adult submodel (Fig 69). Adult biomass is updated through new recruitment, and total mortality is applied and species are updated for the year. Prey biomass is then updated based on 1 of 2 annual turnover rates (Fig 69). This completes a year and the model cycles back to the beginning of the next period (Fig 69).

Figure 68. Georges Bank Shallow assemblage logical structure diagram

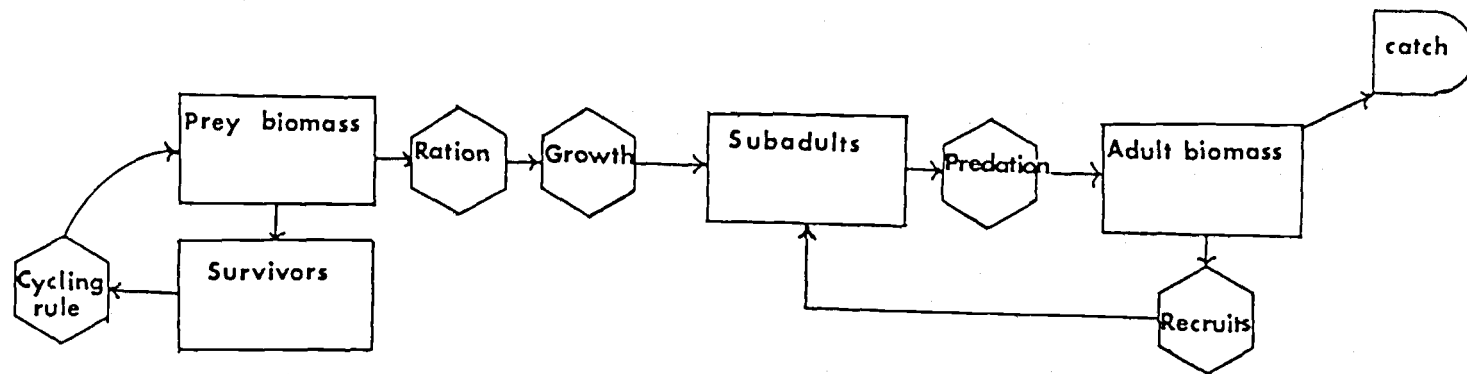
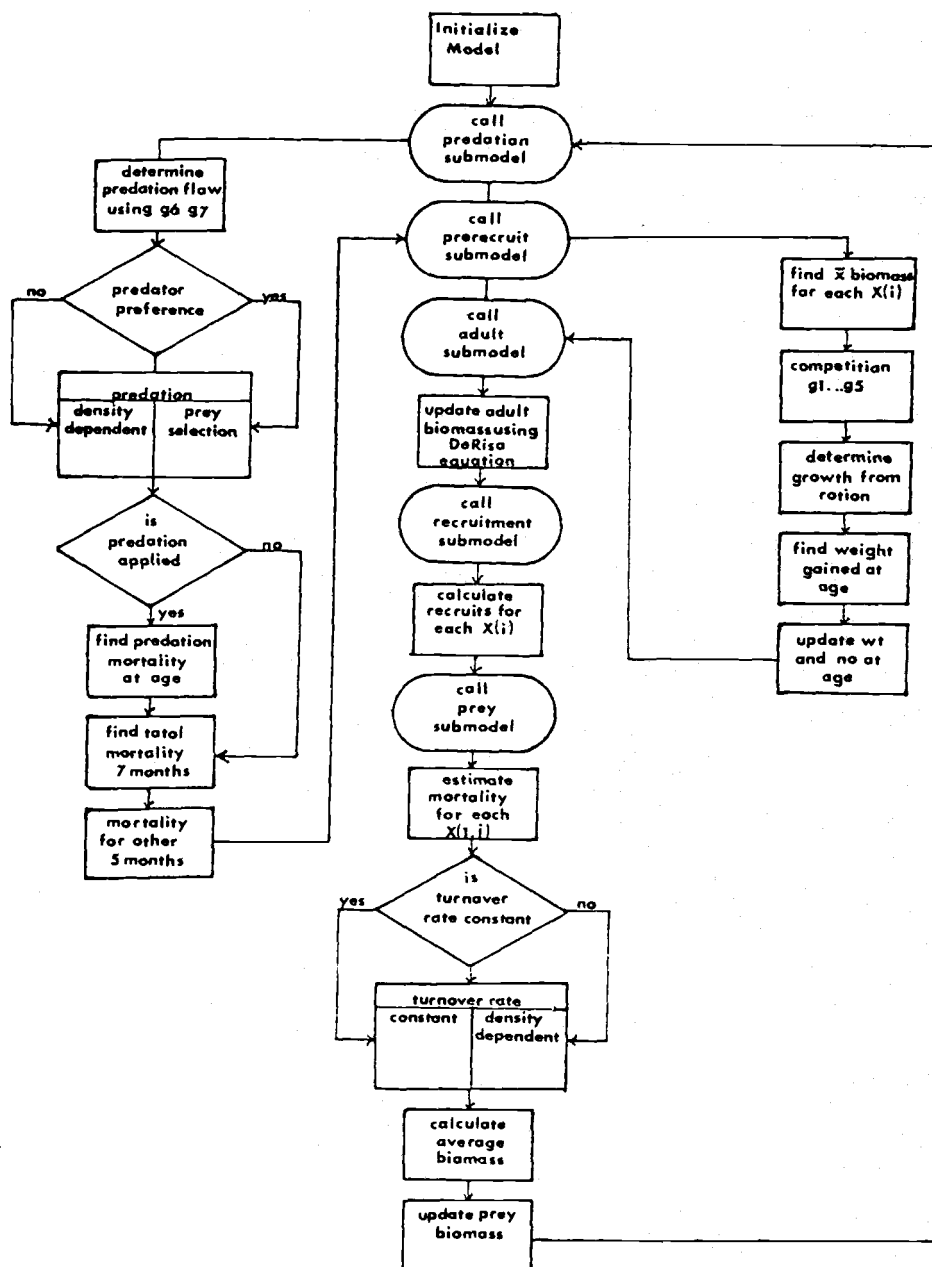


Figure 69. Georges Bank Shallow assemblage model flow diagram



Simulation Results

The Georges Bank shallow assemblage model was used to investigate several different interspecific response scenarios with the idea of explaining trends that were observed over the interval 1963-1978. The model design, based on previously noted conceptual hypotheses, was such that it was only necessary and desirable to investigate a small subset of the 210 possible combinations of 2 competition, 3 predation and 2 prey turnover rates. The competitive network shown in Fig 58 between the five species, yellowtail flounder...skates, was an invariant feature of the model. Since competition was a formal part of the model structure, the simulation experiments were performed first with competition only, then the other mechanisms were switched on and added to the experiments. Under these circumstances it was possible to exclude many of the potential combinations of mechanisms. Fourteen simulations were deemed enough to investigate relevant model response boundaries.

Simulation experiments with this model provided some interesting insights into possible interspecific interactions that occurred in the shallow assemblage. Table 22 lists the various experiments and results of the 14 simulations that were employed to examine the effects of different combinations of interspecific interactive mechanisms. The predicted time trends of each of the four species, yellowtail flounder, longhorn sculpin, windowpane flounder, and skates were correlated with observed trends that are 3-year moving averages of minimum biomass estimates from the research vessel surveys 1963-1978. The r^2 values shown in Table 22 provide a coarse measure of how much variation in the inter-

specific trend was explained by the model. Rigorous statistical treatment and hypothesis testing is impossible with this type of model because the underlying probability distributions associated with model parameters are unknown. Consequently only rough measures of model goodness of fit are possible. The total r^{*2} column in Table 22 represents a measure of overall model performance based on total variation explained by the four species fits under a specific set of mechanisms. For a simulation experiment that had the moderate competition mechanism in place the r^{*2} values for yellowtail flounder and longhorn sculpin were very low, while those for windowpane flounder and skates were moderately high to high respectively (Fig 70). These results contrast to a simulation including predation (Fig 71) that explained a much larger percentage of the total variation for the former two species. This trial confirms what was shown in other experiments (Table 22), that when predation is coupled with competition a much better overall fit results. Most of the cases where some combination of competition and predation was involved resulted in the best overall model fits (Fig 72). The exception occurred in three cases under constant prey turnover rate conditions where the r^{*2} value for skates was extremely low and one case under density dependent prey turnover conditions where the total r^{*2} value was 0.04 less than the mean value (Fig 72).

Growth

Growth, the principal dynamic feedback pathway for competition and to a lesser extent predation, showed species specific changes

Figure 70. Observed vs predicted trajectories for species Yellowtail flounder, Longhorn sculpin, Windowpane flounder, and Skates, for a simulation under moderate competition (C1) and density dependent P/B conditions.

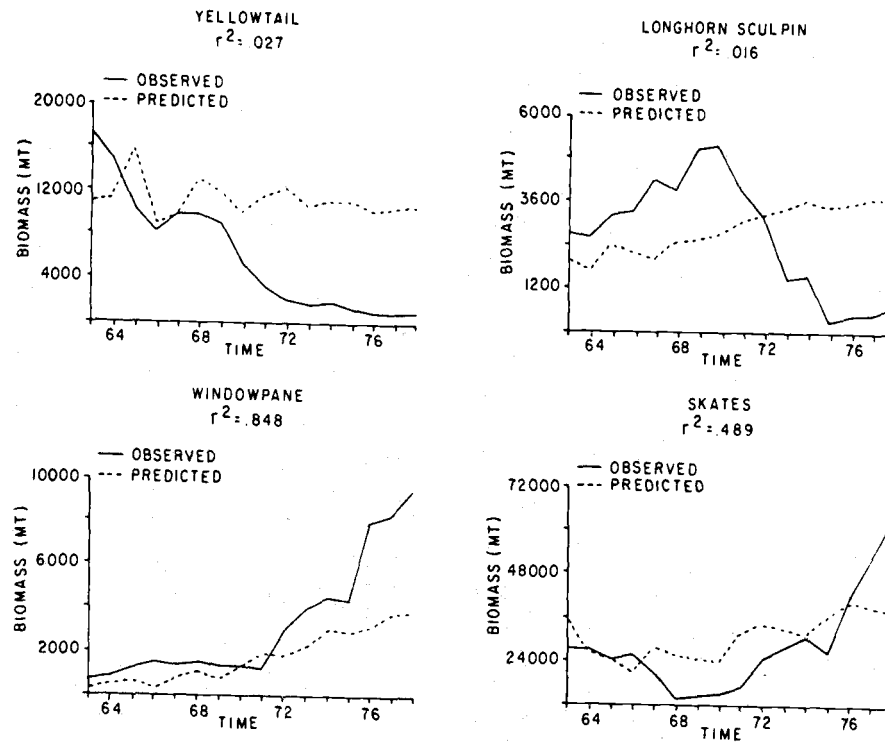


Figure 71. Observed vs predicted trajectories for Yellowtail flounder, Longhorn sculpin, Windowpane flounder, and Skates, for a simulation under moderate competition-intense predation (C1P2) and density dependent P/B conditions

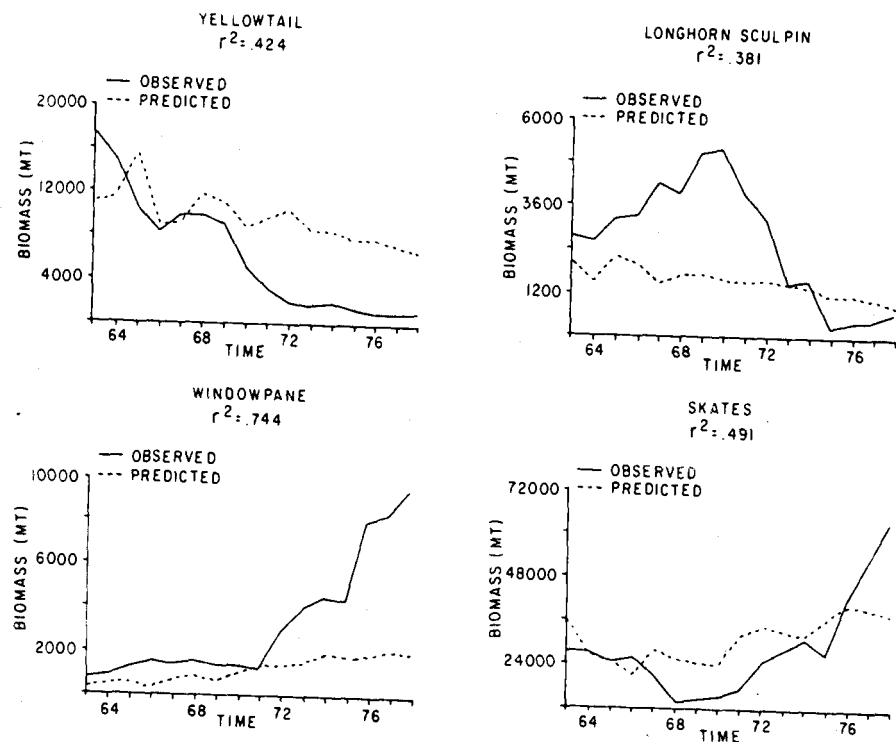


Table 22: Coefficients of variation (r^2) for various simulation experiments using Georges Bank shallow assemblage model. Observed minimum intraspecific biomass (3 year moving average) correlated with predicted intraspecific biomass.

Competition*		Constant Prey Turnover Rate	Density Dependent Prey Turnover Rate	Predation*		Predator Preference	Yellowtail Flounder	Longhorn Sculpin	Windowpane Flounder	Skates	** Total (R^2)
1	2			1	2						
x		x					.265	.017	.812	.300	1.394
	x	x					.434	.268	.719	.071	1.492
x		x		x			.431	.205	.792	.346	1.774
x		x			x		.576	.346	.743	.408	2.073
	x	x		x			.563	.311	.636	.066	1.576
	x	x			x		.667	.327	.521	.049	1.564
	x	x			x	x	.679	.316	.368	.050	1.413
x			x				.027	.016	.848	.489	1.380
	x		x				.150	.003	.839	.445	1.437
x			x	x			.199	.236	.815	.491	1.741
x			x		x		.424	.381	.744	.491	2.040
	x		x	x			.359	.158	.808	.452	1.777
	x		x		x		.541	.297	.745	.458	2.042
	x		x		x	x	.567	.243	.789	.458	2.057

* 1 moderate
2 intense

** Across column sum of (r^2 's) for a particular experiment, a coarse measure of best model fit.

Figure 72. Georges Bank Shallow assemblage simulation summary

Constant P/B^*

		Predation			
		0	low	high	
Competition	low	—	+	+	$\bar{X} = 1.61$
	high	—	—	—	

Density dependent P/B^*

		Predation			
		0	low	high	
Competition	low	—	—	+	$\bar{X} = 1.78$
	high	—	+	++	

* + \geq mean r^2 value

- < mean r^2 value

where \bar{X} = mean of the r^2 columns in Table 23.

over the simulation time series. Fig 73 shows the different basic responses of the 5 species, yellowtail flounder...skates , with age 3 simulated weight presented for comparative purposes . Haddock and yellowtail flounder showed the greatest range in mean weight change, followed by longhorn sculpin, skates and windowpane flounder (Fig 73). Windowpane showed strong increases and decreases in growth while skates showed a fairly steady increasing trend (Fig 73). Growth trajectories for haddock and yellowtail showed similar rapid declines in the early 1960's, but yellowtail weights at age 3 remained low throughout the decade, then showed a general increasing trend (Fig 73). Longhorn sculpin and windowpane experienced very rapid increases in weight during the early 1960's, but windowpane growth peaked much earlier than longhorn sculpin (Fig 73).

Growth, under competition, showed dynamic responses, dependent on the particular experiment. Fig 74 compares simulated growth trends for yellowtail flounder...skates under conditions of moderate and intense competition with prey biomass responding via constant turnover rates. Under moderate competition the four species show increased size at age with time, but windowpane growth did begin to decline slightly after reaching a maximum in the period 1965-1970 (Fig 74). A decline in Haddock biomass coupled with increasing prey resources initiated the increases in size at age for the four species. Under intense competition, prey resources declined and growth patterns for the competing species changed markedly. Yellowtail weights declined to minimum values and skate growth showed a steady downward trend (Fig 74). After slight in-

Figure 73. Growth responses for Yellowtail...Skates under moderate competition (C1) and constant P/B conditions

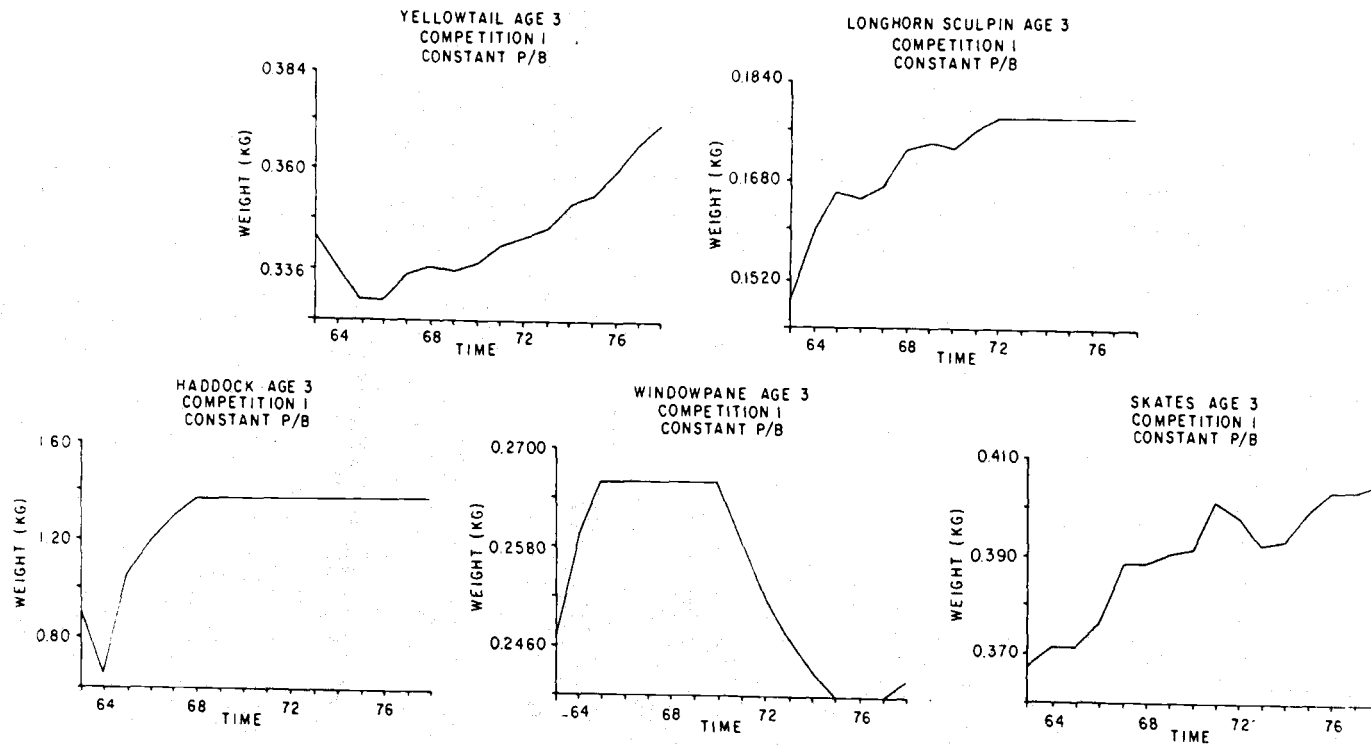
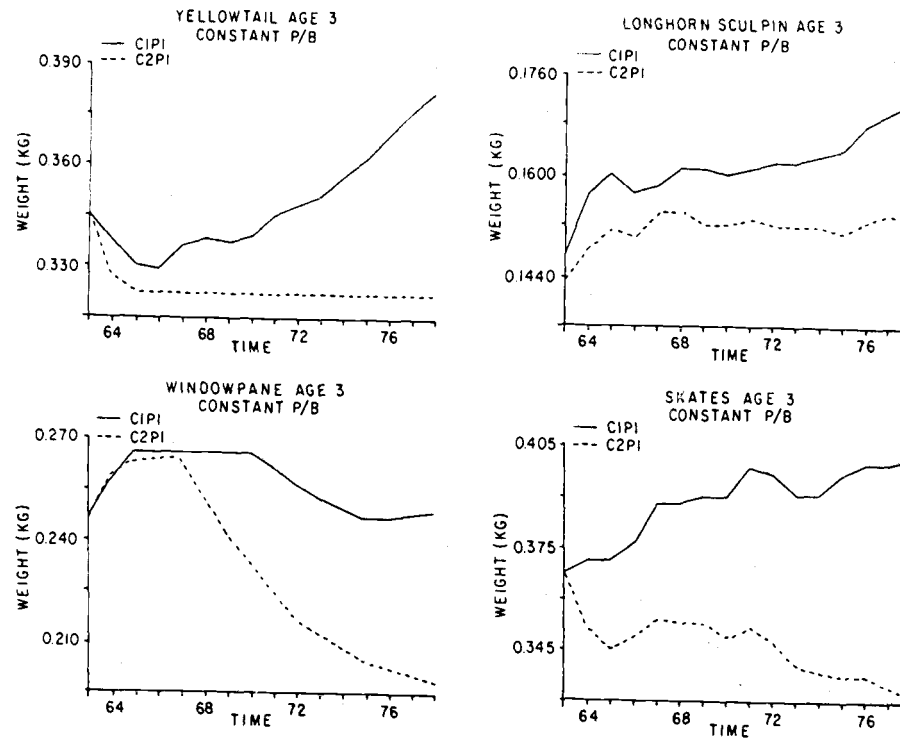


Figure 74. Growth responses for species X2,X3X5,X6, under moderate competition (C1P1) and intense competition (C2P1) both with moderate predation (P1) as well as constant P/B conditions



creases in mean weight at age, growth of windowpane flounder declined steadily and longhorn sculpin size at age stabilized (Fig 74). This figure shows the effect of declining food resources, (Fig 85), under intense competition, on the growth responses of the four species.

Adding predation to the model caused growth changes especially in the later years of the time series. Fig 75 traces divergent growth responses for yellowtail flounder under states of moderate competition and two levels of predation. The addition of predation to the model caused increased growth in age 3 fish by reducing intraspecific competition, or more directly by increasing the % ration that the age 3 yellowtail biomass obtained. Trends in yellowtail flounder growth (Fig 75) can be compared to skate growth trajectories found in Fig 76. As the figures show, yellowtail growth responses occurred earlier in the time series and were of a larger magnitude (Figs 74,75). Both species showed similar directional changes (increases) in growth when predation was included in the simulation (Fig 75, 76)

Growth trajectories were somewhat different for simulations that utilized density dependent prey turnover rates. Yellowtail flounder growth under moderate competition showed the same pattern of increased growth with increasing predatory intensity (Fig 74; 76). Additional runs with competition at a more intense level resulted in a more pronounced decline in growth during the early 1960's, with a slower recovery period that lasted for the rest of the decade, followed by an increase that converged with the mode-

figure 75. Yellowtail flounder age 3 growth responses under moderate competition (C1) (C1) and moderate predation (C1P1), intense predation (C1P2) conditions with constant P/B

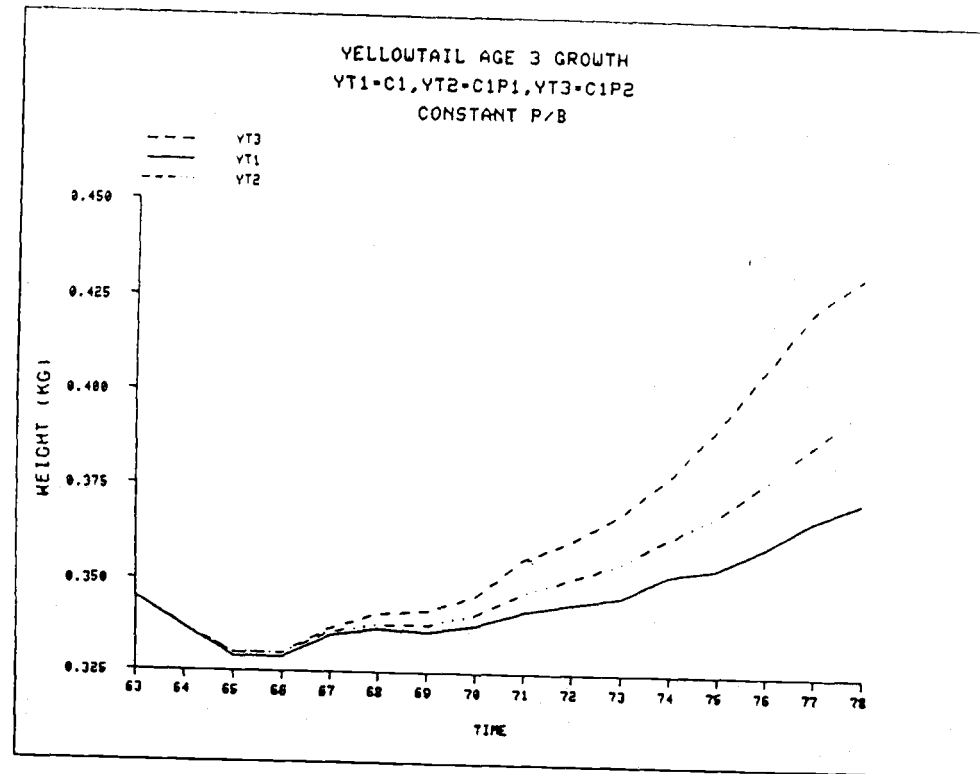
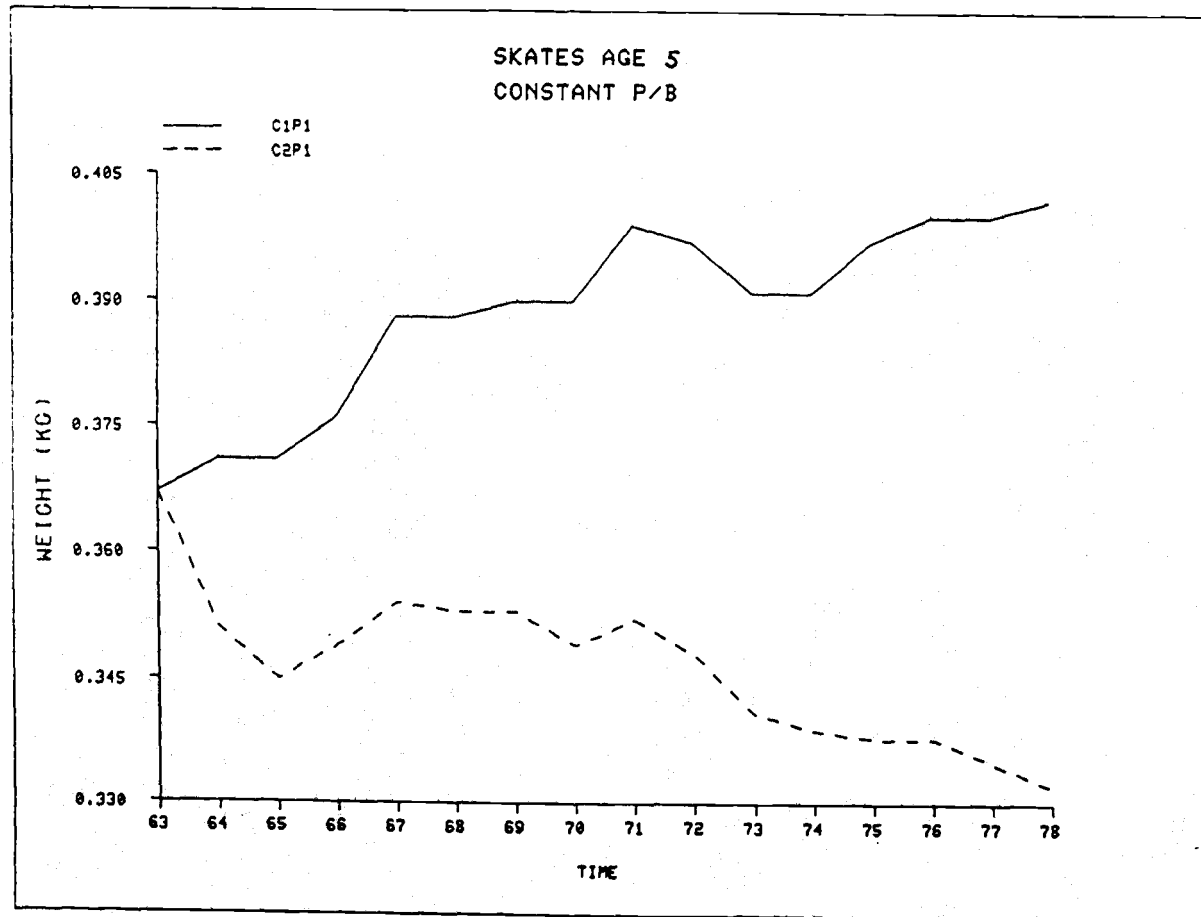


Figure 76. Skate age 5 growth responses under moderate competition and moderate predation (C1P1) and intense predation (C1P2) conditions with constant P/B



rate competition trends in the late 70's (Fig 77). Windowpane flounder showed consistent trends between runs and little range in growth except that intense competition produced a slight downward trend in the 70's (Fig 78). These responses are only slightly different than that shown in (Fig 74) for windowpane in terms of range, but do differ sharply from the precipitous drop that was experienced in the late 70's. Longhorn sculpin growth maintained the same general pattern shown in (Fig 74), but the rate of increase for both levels of competition was much steeper (Fig 79). Differences between moderate competition and intense competition were expressed in the 60's, with the former competitive level producing the largest increases in growth. Both levels converged to maximum values during the 1970's (Fig 79). Trends in skate growth were somewhat different from the gradually increasing trend in (Fig 74), a more asymptotic response was observed (Fig 80). Intense competition resulted in a substantial drop in growth during the early 1960's and continued low levels until the late 70's while moderate competition simulations showed a sharply increasing trend through the 60's with growth reaching a maximum in the decade of the 1970's (Fig 79).

Growth studies typically deal with the intraspecific effects of population density, oceanographic factors, or environmental perturbations (Jones 1979; Clark et al. 1982; Kreuz et al. 1982). Simulations from this model suggest that interspecific interactions may also have some dynamic effects on growth rates of competing demersal fishes. Predation too seems to have potential for growth modification through reductions in density that release

Figure 77. Yellowtail flounder age 3 growth under several competition and predation conditions with density dependent P/B

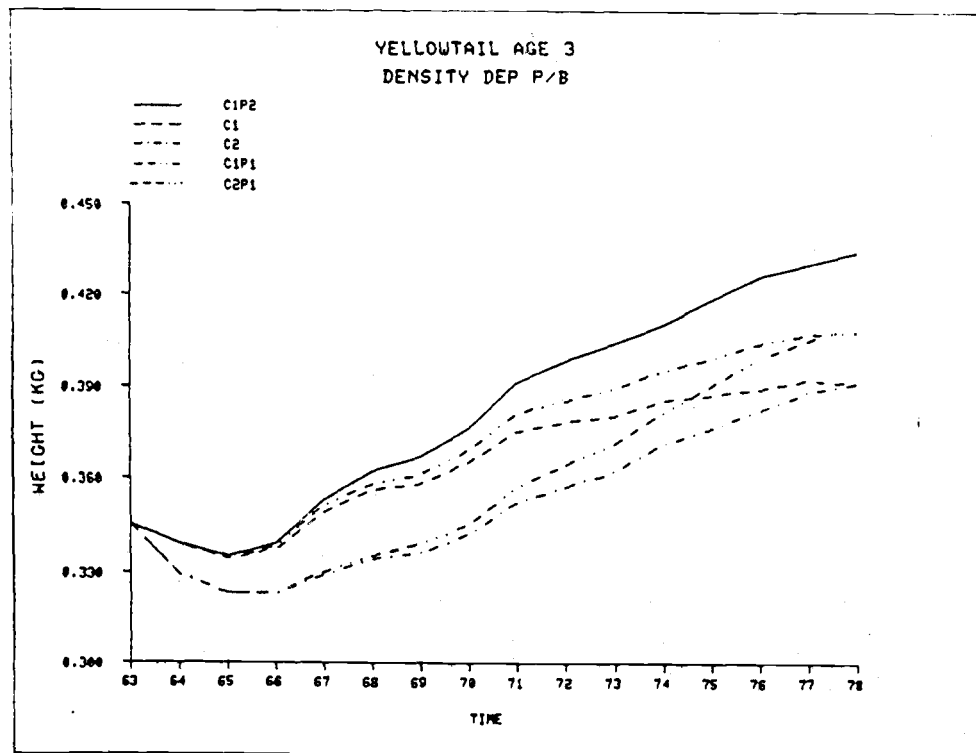


Figure 78. Windowpane flounder age 3 growth responses under moderate competition (C1), intense competition (C2) and moderate predation (C1P1) conditions with density dependent P/B

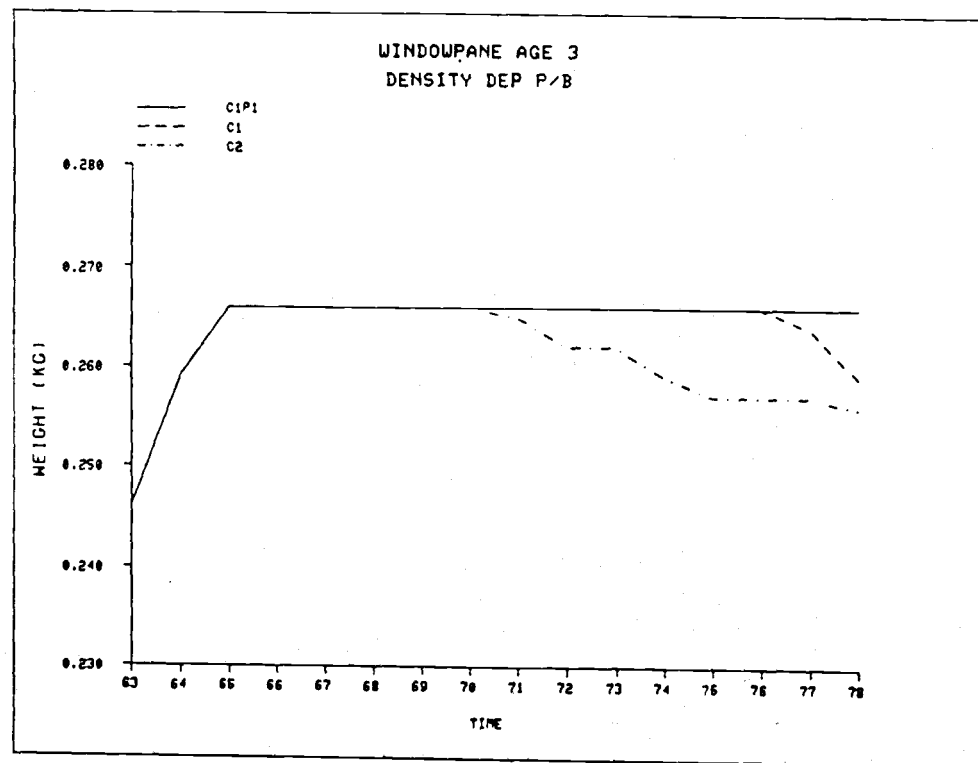


Figure 79. Longhorn sculpin age 3 growth responses under moderate competi-
 tion (C1),intense competition (C2) conditions with density
 dependent P/B

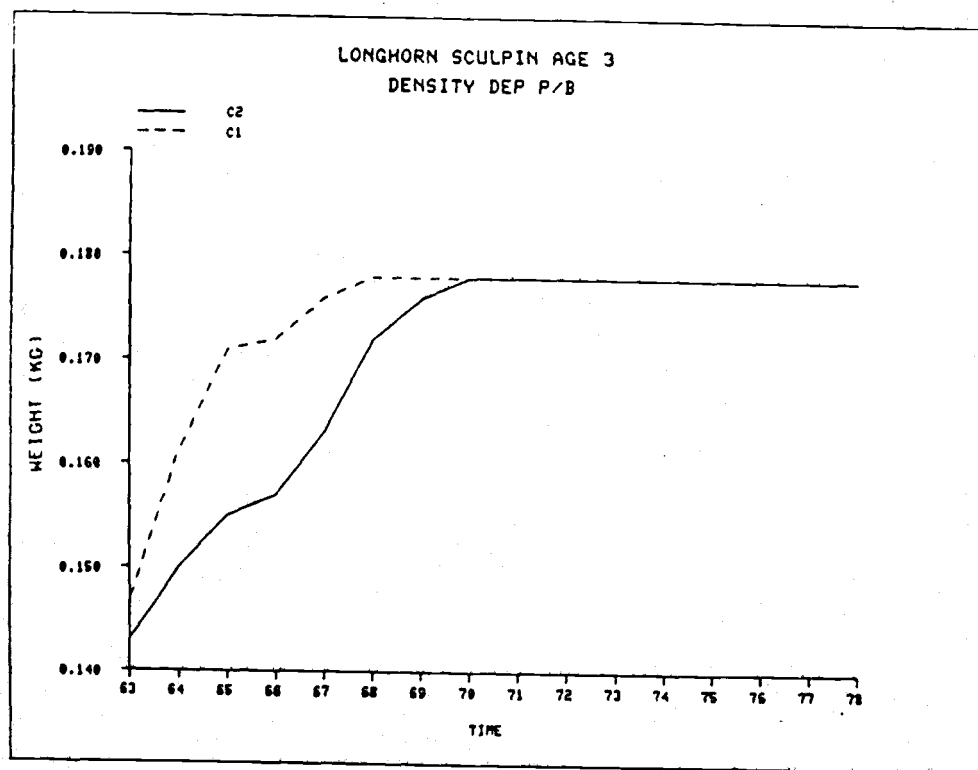
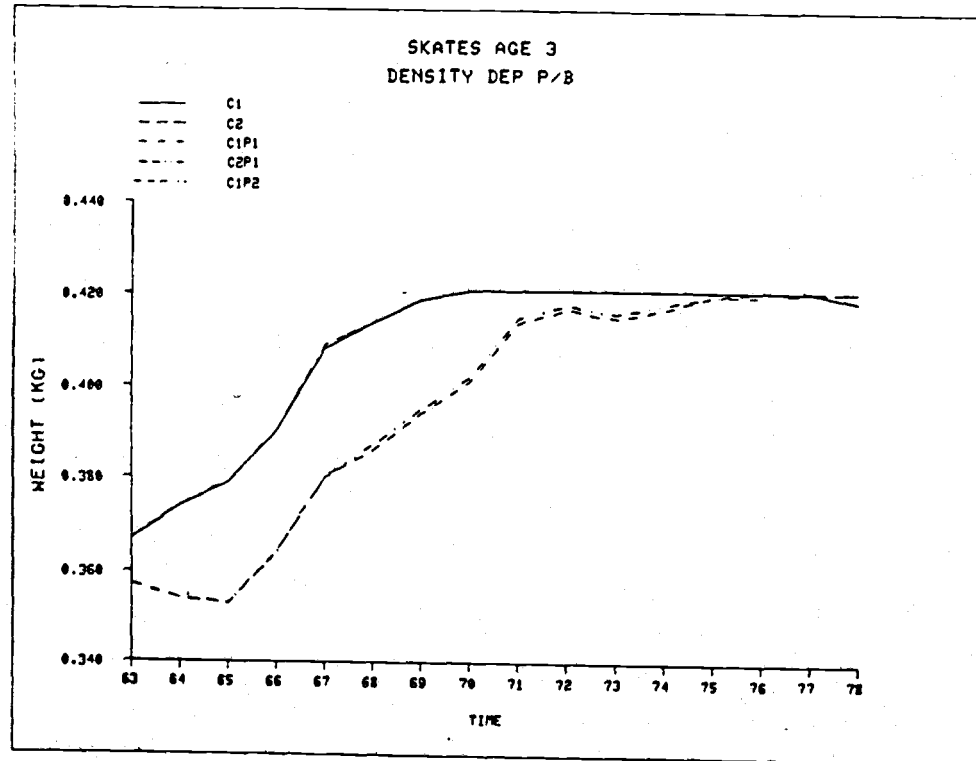


Figure 80. Skates age 5 growth responses under several competition and predation conditions with density dependent P/B



available prey resources, resulting in increased rations for survivors. Specific responses seem to depend on the growth plasticity of the particular species in question. Tyler (1976) showed that fish, for example winter flounder, have strategies of growth and reproduction that are coupled directly with ration levels. Simulations from this shallow assemblage model link interspecific interactions, growth responses and corresponding reproductive capabilities.

Recruitment

Fig 81 shows simulated recruitment time tracks that were produced with the shallow assemblage model for the four species. With the exception of longhorn sculpin, it appears that recruitment trends under constant P/B rates were fairly consistent regardless of the competitive intensity. Yellowtail flounder recruitment changed little with increasing competition while windowpane flounder showed a diverging response during the 70's. Of these species, skates showed the largest response when competition intensity was varied (Fig 81). This is reflected in the r^2 values of (Table 22). Patterns of recruitment for longhorn sculpin showed almost reversed trends depending on competitive state, the intense competition mechanism producing a pronounced and steady decline (Fig 81). The recruitment trajectories for the three aforementioned species necessarily match patterns for total stock biomass shown in (Fig 71).

Simulated recruitment trends, under several competition and predation hypotheses, are displayed in Fig 82. All species tended

Figure 81. Recruitment responses for Yellowtail flounder, Longhorn sculpin, Windowpane flounder, and Skates under moderate competition (C1P1), intense competition (C2P1) and moderate predation conditions with constant P/B.

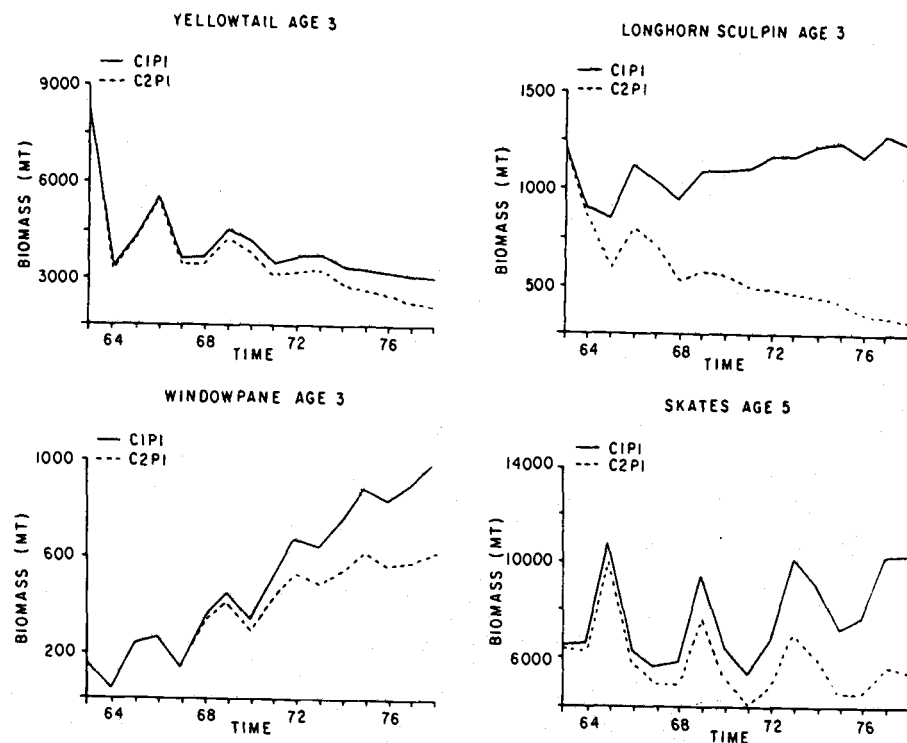
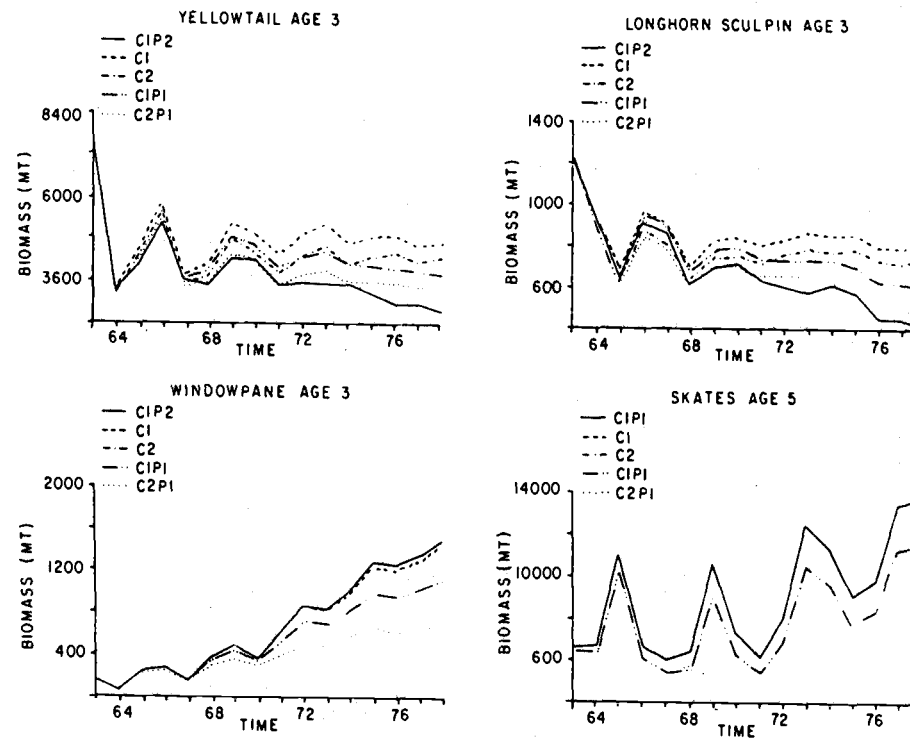


Figure 82. Recruitment responses for Yellowtail flounder, Longhorn sculpin, Windowpane flounder, and Skates, under several competition and predation conditions with density dependent P/B



to show divergent ranges of response with time, but these trends were highly species dependent. Yellowtail flounder recruitment showed a variety of responses to competition and predation intensity, with moderate competition and moderate competition-intense predation acting as a bound on this particular set of experiments (Fig 82). It appears that intense competition and predation acted to dampen oscillations in recruitment in the late 60's and throughout the 1970's. Longhorn sculpin shows similar changes in trends with increasing time and intensity of competition and predation such that almost a 400 mt difference in recruitment biomass resulted depending on the experiment (Fig 82). Responses in recruitment for windowpane flounder were such that only differences in scale resulted from the experiments. Trends remained similar although somewhat damped by intense competition and both levels of predation (Fig 82). Recruit biomass at age 3 varied by almost 800 mt at the end of the time series under this set of experiments for this species. Skate recruitment also showed no changes in trends under the various experiments, but did show some scale changes (Fig 82). Moderate competition, moderate competition and predation, and moderate competition-intense predation produced the higher magnitude trajectory while intense competition and intense competition-moderate predation the lower.

Predation by dogfish and squid

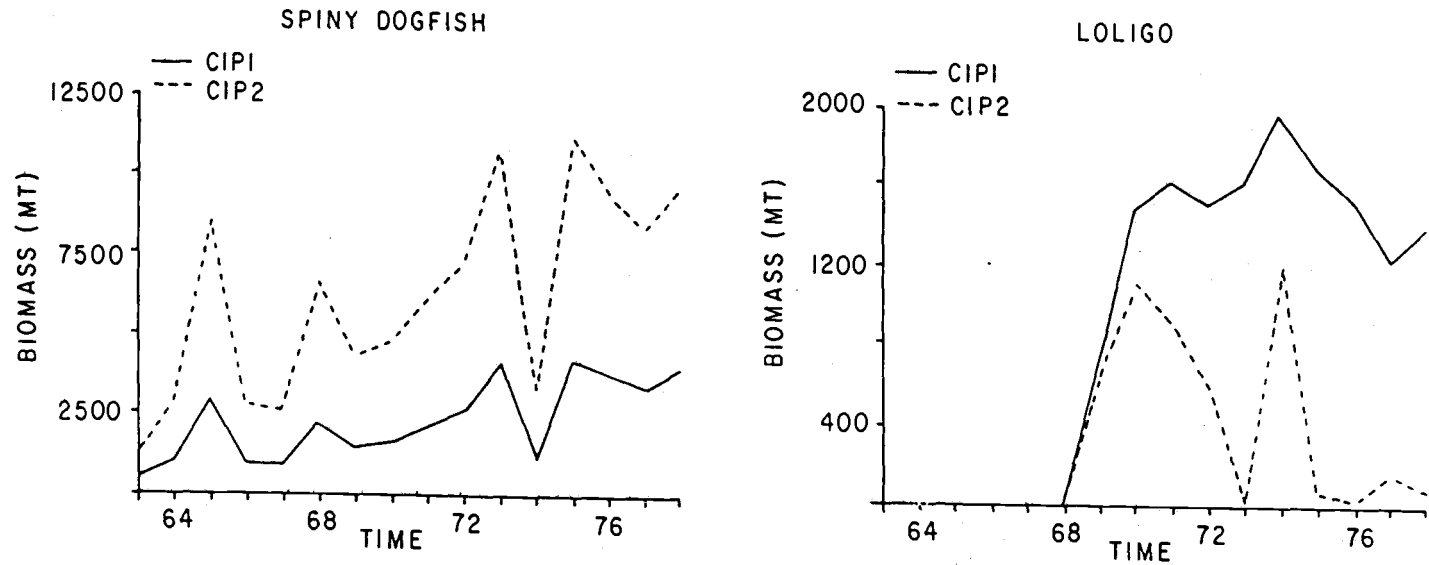
Driving variable trajectories of spiny dogfish and squid biomass were used to simulate the effects of predation on the early life history stages of the 5 competing species. The

responses generated by these predation trends are shown in Fig 83. Constant and density dependent P/B rates produced similar results, but only the constant case is covered graphically. Trends for moderate and intense predation were similar for spiny dogfish, but intense predation produced biomass flows of a higher magnitude, about two times as large (Fig 83). Spiny dogfish consumption responses reflect the increasing abundance of this species in the shallow assemblage during the 70's.

The biomass of long-finned squid also increased dramatically in this assemblage during the late 60's and remained high throughout the 1970's. Simulated consumption by this species, therefore, also followed predictable trends, at least for the moderate predation cases (Fig 83). Since consumption by spiny dogfish and squid was sequentialized with equation (3), the flow of biomass from the five competing species into squid via function $g(7)$, was tied directly to skate intake.

The mechanism of predation acted to modify the simulated demersal fish community in several ways. As previously mentioned growth rates increased in response to decreased density when predation was initiated. More importantly predation influenced recruitment levels in the 1970's by affecting the survival rate of the early life history stages of yellowtail flounder, longhorn sculpin, windowpane flounder, and skates. Fig 82 stresses the point that recruitment biomass varied inversely with predation intensity, thus decreased survival of recruits determined stock trends for yellowtail flounder, longhorn sculpin, and windowpane

Figure 83. Spiny dogfish and long finned squid consumption under moderate predation (C1P1) and intense predation (C1P2) conditions with constant P/B

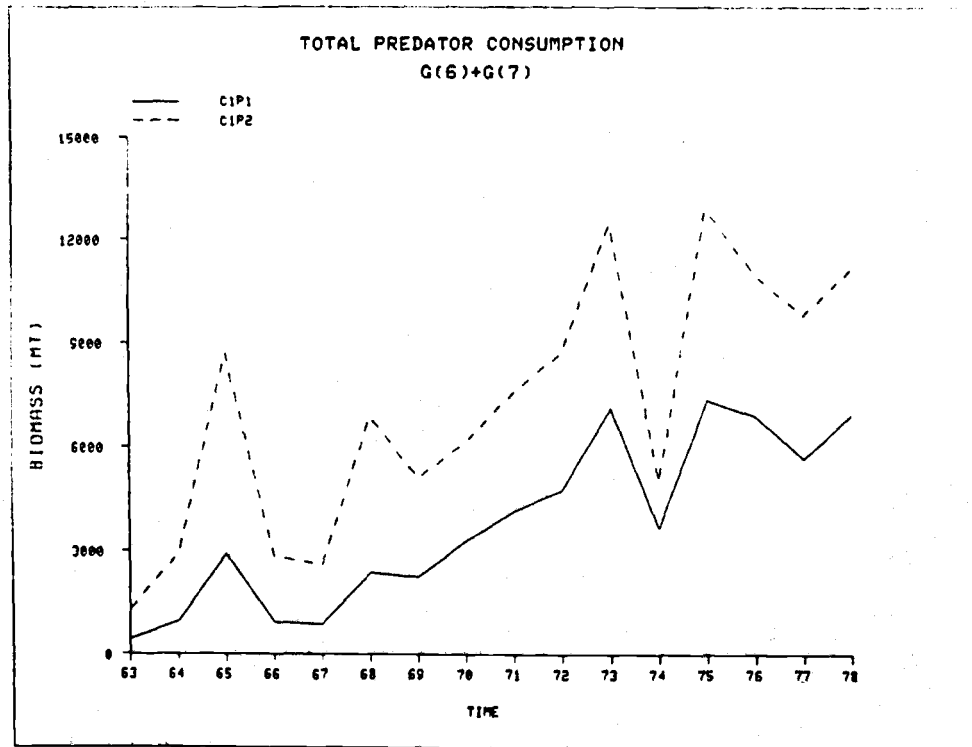


flounder and influenced skates indirectly through feedback on growth. Fig 83 shows that as prey consumption reached higher levels under intense predation circumstances, intake by squid varied inversely with spiny dogfish ingestion. This in effect represents competition between the two predators for a scarce resource with spiny dogfish being the better competitor through model design. Since predator dynamics were not explicitly modeled, predator responses are not the important issue here. Fig 84 shows total predator consumption, 1963-1978, for both predation intensities. An increase in total predation intensity resulted in a corresponding increase in total consumption by the two simulated species (Fig 84). This was accomplished by changing model parameters, which ultimately resulted in the two predators obtaining a higher percentage of their ration from the yellowtail flounder...skates species complex.

Evaluation of Model Behavior

To gauge whether this model produced meaningful results it was necessary to investigate the behavioral properties of the various interactive mechanisms and driving variables. It is useful to study model responses under several conditions so that a description of general model performance and behavior is available (Overton 1977). Systematic approaches such as factorial designs, Yates Algorithm's and other incremental change methods are available to study model trends, but often the required number of runs to establish model directions is uneconomical or unnecessary, especially in larger models (Overton 1977; Box et al 1978). This

Figure 84. Total predator consumption under moderate predation (C1P1) and intense predation (C1P2) conditions with constant P/B



model was evaluated under several different assumptions and changes in competition, fishing mortality trajectories and haddock and predator biomass. The effects of these changes in system forcing vectors and mechanisms were appraised by observing trends in the competing species with correlation analysis. This provided a qualitative method for determining how sensitive the various species were to change in these potentially important factors. It was impossible to attribute the amount of variation explained to the particular mechanism or forcing function of interest, since the effects were not strictly additive.

In any model behavior experiments with complex analytical, mechanistic models, it is difficult to design and judge the outcomes. Only qualitative methods are useful for evaluation purposes because model mechanisms tend to be synergistic and unseparable. The whole process of model evaluation is highly model specific.

Yellowtail flounder was perhaps the most responsive species in the shallow assemblage model. It appears that the competitive hierarchy as well as the haddock and fishing mortality trajectories were all important in determining trends for this species. Poor correlations resulted in all cases where competition or the haddock trajectory were eliminated or neutralized, and the same outcome occurred when several trajectories of constant fishing mortality were implemented. Also, poor correlations resulted when all but one mechanism or driver was nullified. The best fit was obtained when the haddock trajectory, competition and fishing mortality were all present in the model.

Longhorn sculpin was also responsive to all the drivers and competitive mechanisms, but a combination of competition and the haddock trajectory yielded the best overall results. The two other cases of one neutral component resulted in positive correlations, but the former accounted for much more variation. Experiments that tested the sensitivity of the one factor cases suggested that no one driver or mechanism was overly important in determining longhorn sculpin directions.

Windowpane flounder appear to have been only slightly influenced by trends in driving variables and competition. The best correlations were obtained under conditions where only competition or the haddock trajectory were in effect, but these differed only slightly from the case where several constant fishing mortality trajectories were implemented.

Skate biomass was influenced by the haddock and fishing mortality trajectories and competition variables, but the fishing mortality trajectory seems to have been most influential. Competition and the haddock trajectory, though, also appeared to influence trends in the skate dynamics. In cases where all components except one were neutralized the r^2 values were similar albeit slightly higher for the fishing mortality trajectory. Cases where pairs of factors were evaluated also yielded similar positive trends.

Skate trends were definitely responsive to the different prey turnover rate scenarios utilized in the model. Under intense competition and constant prey turnover the r^2 for skates dropped

precipitously due to declining prey resources and increased had-dock competition (Table 22; Fig 85). Yellowtail flounder trends were sensitive to prey turnover rate. Longhorn sculpin did not appear to be quite as sensitive to prey turnover rate as yellow-tail flounder. Windowpane flounder also appears to be less sensitive to prey turnover rate, but distinct decreases in r^2 did result under prey limiting conditions.

Predator trajectories appear to have been important influences on the trends of the four species yellowtail flounder, longhorn sculpin, windowpane flounder, and skates. Sensitivity analysis suggested that the time sequence of these trajectories was important for determining species responses. For instance if the time trend in predator biomass is reversed, a poor model fit results. The donor-recipient equations damped the effect of high intensity predation because parameter changes in these equations are not strictly multiplicative (Fig 84). For example a 3-fold increase in b_j in equation (2) would not necessarily result in a 3-fold increase in biomass consumed. The effects of intense predation are diminished somewhat by the asymptotic nature of these equations (Fig 59). This means that the effect of depensatory predation in the 70's was somewhat diminished, the large predator biomass did not have quite the expected high impact.

The responses of the particular species under moderate competition, without predation, occurred for different reasons. Windowpane flounder correlations remained high under both prey turnover hypotheses because this species consistently obtained en-

ough food resources to maintain an increasing trend over the time series. This occurred primarily because of its place in the competitive hierarchy which insured this increasing trend. Skate trends on the other hand were very closely tied into prey dynamics suggesting a more direct link to prey density. Skate biomass showed a slower tendency to respond to changes induced by interspecific competition, due to limited ability to respond via growth and its prolonged recruitment time lag. Yellowtail flounder and longhorn sculpin responded similarly in that poor r^2 values resulted because of increasing trends in stock biomass in the latter years of the simulated time span. The modeled food resource was expanding rapidly, which resulted in increasing trends for these two species that were opposite to the actual observed phenomenon.

Under intense competition without predation, prey resources were unable to maintain sufficient density under the constant P/B state. This prey decline caused a poorer model fit for windowpane flounder and skates and a better trend for yellowtail flounder and longhorn sculpin. The opposite occurred under the density dependent prey turnover rate hypothesis (Table 22).

The addition of predation to the basic model results in more variation being explained and stable trends in all the species (Table 22). This mechanism acts primarily on the latter years of the series by dampening biomass increases in yellowtail flounder and longhorn sculpin with the resulting effect of slightly increasing r^2 for windowpane and skates. Predation in this model

has a slight effect on growth rates of the four species, but more importantly results in a positive feedback on windowpane and skate stock biomass and negative feedback on yellowtail and longhorn biomass. These biomass responses ultimately cause time-lagged changes in recruitment of the four species. Predation on the yellowtail flounder...skates species complex caused a positive feedback on prey biomass in the latter years of the series. With increasing predation intensity, prey biomass shows a corresponding increase, causing slight increase in skate biomass due to increased prey availability that occurred because of declines in haddock, yellowtail and longhorn sculpins. This mechanism then when coupled with the competitive effects induced by large year classes of haddock in the early years of the time series, yields more realistic simulated trends. Better model fits are obtained under both prey turnover rate hypotheses when predation is added to the model (Table 22). In all four cases where only predation intensity is varied, a fairly robust model fit results, the best being under intense predatory conditions (Table 22). Intense competition, when coupled with predation under constant P/B results in parallel, but sharper, system states changes than produced by intense competition only. The same scenario under density dependent P/B results in model fits similar to the above moderate competition and predation and intense predation cases. These better fits were obtained because yellowtail flounder trends fit observed behavior much more closely. The best yellowtail fits are obtained under conditions of predator preference irrespective of turnover rates.

The influx of squid into this assemblage may be related to general warming trends as well as stock increases (Davis 1977; Lange et al 1980). The reasons for substantial increases in indices of spiny dogfish catch/tow in the shallow assemblage are not obvious, but probably relate to distributional shifts, since net increases in biomass of this species requires considerable time periods (Wood et al. 1979). One possible explanation might involve the general warming trend noted above as well as declines in primary food resources of this species in other locations. This highly migratory species depended heavily on herring stocks which were depleted in the late 60's and early 70's (Anthony and Waring 1978).

Model Implications

Studies of community structure in the general ecological literature typically address the subject of interspecific interaction by studying the effects of competition and predation on species coexistence and density (Caswell 1976; Hastings 1977; Caswell 1978). These investigations necessarily center on questions of evolutionary time and hence do not contribute much to our understanding of perspectives in the short-term or ecological time scale. Of interest in the shorter term is the influence of predation and competition on species density. Although field studies have examined the incidence of these two mechanisms in the natural setting, (Paine 1974; Hairston 1980; Larson 1980), they have not focused on how system homeostasis occurs nor on dynamic change within the studied populations. It is of great interest to fishery

ecologists and managers to know how fishery systems will respond when perturbed by fishing and environmental change and what interspecific interactions will result. Up to now we have observational evidence to support the hypothesis that interspecific mechanisms can serve as organizers of community structure for exploited marine fishes (Dann 1980).

Competition has long been recognized as an important interspecific regulatory mechanism in freshwater environments. Limnologists and fishery biologists have observed over many years that competitive interactions may cause profound changes in mortality and growth of fishes. Salmonid communities in particular show the effects of competition for space and food. (Borgeson 1966) stated unequivocally that "the factor that most profoundly effects trout survival and growth is competition". Other studies have affirmed the importance of competition in determining spatial segregation and affecting growth rates of freshwater fishes (Smith 1970; Bennett 1971; Connell 1975; Svardson 1976 and Stewart et al 1981).

Terrestrial competitive relationships in floral and faunal communities have been investigated in numerous locations. Competition appears to be an important controlling agent in successional stages of plant and animal communities (Connell 1977). Most field experiments have necessarily centered on vegetation or small vertebrates because of the difficulty in manipulating large mobile vertebrate populations (Connell 1975). One such study on salamanders of the genus (Plethodon) spanned several years, show-

ing that competition on an altitude gradient in several mountain ranges was an important determinate of interspecific distribution (Hairston 1980). Studies of competition in the marine environment have focused on the intertidal and subtidal zones of several oceans. Barnacle competition was observed by (Connell 1961), the subordinate species being excluded from areas of mutual preference. A controlled field experiment confirmed that competition for food occurred between two starfish (Menge 1972). Paine (1974) showed that populations of mussels and barnacles were competing for space in the intertidal. One very interesting recent study dealt with interference competition between two fishes of the genus Sebastes. This controlled field experiment demonstrated that interspecific territoriality was responsible for the separation of two rockfish with a high degree of dietary overlap (Larson 1980). The competitive dominant excluded its congener from the shallow productive region. Potential marine fish competitive interactions were reviewed by (Dann 1981), but all the proposed stock interactions were based strictly on observational evidence. Circumstantial evidence suggests that competitive interactions may be responsible for major biomass oscillations in pelagic and demersal fish populations off the California coast, New England and in the North sea (Riffenburgh 1969; Sherman et al 1981 and Hempel 1978) respectively.

Predation as a community homeostatic mechanism has been investigated in both theoretical and field experiments. It is recognized that predation effects may range from simple removals of available prey by opportunistic predators to near extinctions

induced by large populations of selective predators. Many studies have centered on the predator mediated coexistence theme with predators acting as a stabilizing element between competing species ((Hastings 1977; Caswell 1978; Hairston 1980). Zooplankton communities in freshwater lakes are strongly influenced by the addition of planktivorous fish, which quickly drive the larger dominant species to low levels (Hall et al. 1970; Caswell 1976). Intertidal invertebrate predators can greatly influence their prey populations and piscivorous fish can control or even deplete their forage base (Dayton 1971; Paine 1974; Stewart 1981). Size specific predation serves as the mechanistic infrastructure for an ecosystem model of the North Sea (Anderson and Ursin 1977).

The Georges Bank shallow assemblage model suggests that at least part of the observed change in interspecific biomass in this assemblage from 1963-1978 may be explained by interspecific interactions. These simulations provide only circumstantial evidence and hence should be interpreted cautiously, because other plausible explanations or hypotheses may also have utility and be equally useful in explaining the observed change. It appears, however, that some inferences may be drawn from the results of these experiments.

Table 22 suggests that competition alone cannot, for the most part, explain much of the long-term fluctuations observed in this assemblage. This is to be expected since the biomass responses of the yellowtail flounder...skates complex are tied directly into the X1 prey source. Regardless of prey turnover rate, after had-

dock were reduced in the assemblage, prey biomass responded by showing upward trends. Essentially no effective competition was occurring in the latter years of the time series because the dominant competitor, haddock, was no longer exerting much influence on the assemblage. The dynamic responses of yellowtail flounder, longhorn sculpin, windowpane flounder and skates during the early years suggest that competition did effectively reduce the growth and reproductive capabilities of the four demersal fishes, and intense predation by the five fish competitive network caused a short term reduction in benthic invertebrate prey resources. Although no time series of quantitative benthic data exists for the region, the prey responses, with the exception of intense competition under constant P/B conditions, seem reasonable under the regime that existed in the early 60's. Since haddock biomass was high prior to 1963 (Clark et al 1982), the downward trend in prey biomass that the model predicts seem plausible. Prey biomass responses, at least under density dependent turnover, appear consistent with findings that suggest that demersal fish may cause only short term declines in benthic prey populations (Arntz 1980). Competition could not serve as a plausible mechanism for explaining the total long-term changes in species abundance that occurred in this assemblage, but it may have served as a catalyst that allowed subsequent assemblage transformations to occur. The suggestion here is that competition has little influence unless large year classes of demersal fish competitors are present. If so intra and interspecific competitive effects may help initiate directional changes in growth, stock biomass and recruitment of com-

petitors.

To explain the maximum amount of variation with this model design, competition must occur in the early years of the time series and short term seasonal predation in the latter. Observed trends in haddock biomass suggest that competition between this species, and the other demersal fish modeled, occurred in the early 60's. Several authors have implicated competition as a possible source of change of haddock and yellowtail flounder density (Royce et al. 1959; Pitt 1970). This may explain the short term increase in yellowtail flounder catch/tow indices that occurred in the mid to late 60's.

Subsequent release of prey resources, coupled with a fairly intense fishery on yellowtail flounder and seasonal predation, allowed species such as windowpane flounder and skates to experience steady increases in biomass in the late 70's. Seasonal predation acted as a compensatory mortality source which had a direct impact on yellowtail flounder and longhorn sculpins, and indirect feedback on windowpane flounder and skates. This is the same type of predatory effect observed in simulations of salmonid predators on their alewife prey resource in Lake Michigan. Predation intensity was independent of prey density resulting in large potential changes in prey biomass (Stewart 1981).

Results from this model suggest that competition between haddock and the other demersal fish in this assemblage occurred in the early 60's. Release of prey resources after haddock declined, coupled with a fairly intense fishery on yellowtail flounder and

seasonal predation, allowed species such as windowpane flounder, little skate, and winter skate to experience steady increases in biomass in the early 1970's. I think that investigating these types of hypotheses could be an important link in resolving multispecies and ecosystem issues.

Literature cited

- Almeida, F.P., and E.D. Anderson. 1982. Status of the Silver hake resource off the Northeast coast of the United States- 1981. National Marine Fisheries Service. Northeast Fisheries Center. WoodsHole Laboratory Reference Document. 81-36. 78pp.
- American Fisheries Society. 1980. A list of common and scientific names of fishes from the United States and Canada. Special publication No. 12. 174pp.
- Anderson, K.P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser FRA Danmarks Fiskeri-Og Havundersogelser. N.S. 7: 319-435.
- Anderson, E.D. 1979. Assessment of the northwest Atlantic mackerel, Scomber scombrus, stock. National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service. SSRF-732. 13pp.
- Anthony, V.C., and G. Waring. 1978. The assessment and management of the Georges Bank herring fishery. Pages 72-111 in A. Saville editor. The assessment and management of pelagic fish stocks. Rapports et Proces-Verbaux des Reunions. No. 177. 517pp.
- Arntz, W.E. 1980. Predation by demersal fish and its impact on the dynamics of macrobenthos. Pages 121-149 in K.R. Tenore and B.C. Coull editors. Marine Benthic Dynamics. University of South Carolina Press.
- Azarovitz, T.R. 1981. A brief historical review of the Wood-Hole laboratory trawl survey time series. Canadian Special Publication of Fisheries and Aquatic Sciences. 58: 62-67.
- Barney, R.O. 1981. Fisheries projections. In pages 105-115 G.O. Barney editor. The global 2000 report to the president of the U.S.: entering the 21st century Volume II: the technical report. Pergamon Press. USA.
- Bennett, G.W. 1971. Management of lakes and ponds. Van Nostrand Reinhold Company. New York, N.Y. USA.
- Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. United Kingdom Ministry of Agriculture, Fisheries. Fisheries Investigations. 19: 533pp.
- Bigelow, H.B., and W.C. Schroeder. 1953. Fishes of the Gulf of Maine. Fishery Bulletin of the Fish and Wildlife Service. No. 74.
- Bloom, S.A. 1981. Similarity indices in community studies: potential pitfalls. Marine Ecology. 5: 125-128.

Boesch, D.F., and R.C. Swartz. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environmental Protection Agency Ecological Research Series. EPA-600/3-77-033. March 1977. 115pp.

Borgeson, D.P. 1966. Trout lake management. Pages 168-178 in A. Calhoun editor. Inland Fisheries Management. Department of Fish and Game. California. 546pp.

Bowman, R.E. 1980. Food of 10 species of northwest Atlantic juvenile groundfish. Fishery Bulletin. 79: 200-206.

Box, G.E.D., W.G. Hunter and J.S. Hunter. 1978. Statistics for experimenters: An introduction to design, data analysis and model building. John Wiley and Sons. USA.

Brown, B.E., J.A. Brennan, E.G. Heyerdahl, and R.C. Hennemuth. 1973. Effect of by-catch on the management of mixed species fisheries in Subarea 5 and statistical area 6. International Commission for the Northwest Atlantic Fisheries Research Document. 99: 217-231.

Brown, B.E., J.A. Brennan, M.D. Grosslein, E.G. Heyerdahl, and R.C. Hennemuth. 1976. The effect of fishing on the marine finfish biomass in the N.W. Atlantic from the Gulf of Maine to Cape Hatteras. International Commission for the Northwest Atlantic Fisheries Research Bulletin. 12: 49-68.

Caswell, H. 1976. Community structure: a neutral model analysis. Ecological Monographs. 46: 327-354.

... 1978. Predator-mediated coexistence: a nonequilibrium model. The American Naturalist. 112: 127-154.

Clark, S.H. 1979. Application of bottom trawl survey data to fish stock assessment. Fisheries. 4(3) 9-15.

..., W.J. Overholtz, and R.C. Hennemuth. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. Journal of Northwest Atlantic Fishery Science. 3: 1-27.

..., L.O'Brien, and R.K. Mayo. 1981. Yellowtail flounder stock status-1981. Laboratory Reference Document No. 81-10. National Marine Fisheries Service. Northeast Fisheries Center. Woods Hole, Ma. 02543. 47pp.

Clifford, H.T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press. New York. USA.

Cohen, E.B., M.D. Grosslein, M.P. Sissenwine, and F. Steimle. 1982. Energy budget of Georges Bank. Pages 95-107 in M.C. Mercer editor. Multispecies approaches to fishery management advice. Canadian Special Publication Fisheries Aquatic Sciences. No. 59. 169pp.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*. 42: 710-723.

... 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M.L.Cody and J.M.Diamond editors. *Ecology and Evolution of Communities*. Belknap Press of Harvard. Cambridge, Ma. USA.

... 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*. 111: 1119-1144.

Cushing, D.H. 1970. The idea of a unit stock. In *Fisheries Biology: a study in population dynamics*. The University of Wisconsin Press. Madison. USA. pp 39-60.

... 1973. Recruitment and parent stock in fishes. University of Washington Press. WSG-73-1. July 1973. 197pp.

Dann, N. 1981. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. Symposium on the biological basis of Pelagic Fish Stock Management. International Council for the Exploration of the Seas. No 24.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*. 41:481-484.

Davis, C.W. 1979. Bottom water temperature trends in the middle Atlantic bight during spring and autumn, 1964-1976. National Oceanic and Atmospheric Administration Technical Report. National Marine Fisheries Service. SSRF-739. 13pp.

Deriso, R.B. 1978. Non-linear age structured models for seasonally breeding populations. PhD. thesis. University of Washington. 159pp.

Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age structured model. *Canadian Journal of Fisheries and Aquatic Sciences*. 37: 268-282.

Dery, L., and R.L.Livingstone. 1982. Windowpane flounder *Scophthalmus aquosus*. In pages 199-203 M.D.Grosslein and T.R.Azarovitz editors. *Fish Distribution. MESA New York Bight Atlas Monograph 15*. New York Sea Grant Institute.

Dix, M.L. 1957. Sugar maple in forest succession at Washington D.C. *Ecology*. 38: 663-665.

Elliot, J.M. 1971. Statistical analysis of samples of benthic invertebrates. Freshwater Biological Association. Scientific Publication No. 25. 148pp.

FAO. 1977. Some scientific problems of multispecies fisheries. Report of the Expert Consultation on Management of Multispecies Fisheries. Fisheries Technical Paper No. 181. Rome, 20-23 Sept. 42pp.

Fox, W.W. 1974. Fitting the generalized stock production model by least squares and equilibrium approximation. Fishery Bulletin. 73: 23-36.

Gabriel, W.L., and A.V. Tyler. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. Marine Fisheries Review. 42:83-88..

Graham, J.J., S.B. Chenoweth, and C.W. Davis. 1972. Abundance, distribution, movements and lengths of larval herring along the western coast of the Gulf of Maine. Fishery Bulletin. 70:307-321.

Graham, M. 1935. Modern theory of exploiting a fishery, and application to North sea trawling. Journal du Conseil. 10: 264-274.

Grosslein, M.D. 1969. Groundfish survey program of BCF Wood-Hole. Commercial Fisheries Review. 31(8-9):22-35.

Grosslein, M.D., R.W. Langton, and M.P. Sissenwine. 1978. Recent fluctuations in pelagic fish stocks in the Northwest Atlantic, Georges Bank region, in relation to species interactions. In pages 374-404 A. Saville editor. The assessment and management of pelagic fish stocks. Rapports et Proces-Verbaux des Reunions. Vol 177. 517pp.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report (meeting in Hamburg, January 1965). International Council for the Exploration of the Seas., C.M. Doc. No.3.

... 1978. Fishery management: new strategies for new conditions. Transactions of the American Fisheries Society. 107: 1-11.

Hairston, N.G. 1980. Species packing in the salamander genus Desmognathus: what are the interspecific interactions involved. The American Naturalist. 115: 354-366.

... 1980. Evolution under interspecific competition: field experiments on terrestrial salamanders. Evolution. 34: 409-420.

Hall, D.J., W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography. 15: 839-928.

Hall, C.S. and J.W. Day. 1977. Systems and models: Terms and basic principles. Pages 1-36 in C.S. Hall and J.W. Day editors. Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories. John Wiley and Sons. USA.

Hastings, A., 1978. Spatial heterogeneity and the stability of predator prey systems: predator mediated coexistence. *Journal of Theoretical Population Biology*. 14:380-395. .

Halliday, R.G., and W.G. Doubleday. 1976. Catch and effort trends for the finfish resources of the Scotian shelf and an estimate of the maximum sustainable yield of groundfish. *International Commission for the Northwest Atlantic Fisheries. Selected Papers*. 1: 117-128.

Hempel, G. 1978. Symposium on the changes in the North Sea fish stocks and their causes. *Rapports et Proces-Verbaux des Reunions*. Vol. 172. 449pp.

Harding, D., and J.W. Talbot. 1973. Recent studies on the eggs and larvae of the plaice (*Pleuronectes platessa* L.) in the southern bight. Pages 261-269 in B.B. Parrish editor. *Fish Stocks and Recruitment. Rapports et Proces-Verbaux des Reunions*. No. 164. 372pp.

Hilborn, R., J. Stander, and W. Webb. 1973. A control system for FORTRAN simulation programming. *Simulation*. 20:172-175.

... 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. *Journal of the Fisheries Research Board of Canada*. 33:1-5.

Hillier, F.S., and G.J. Lieberman. 1980. *Introduction to operations research*. Holden-Day Inc. San Francisco, Ca. USA.

Hoff, J.G., and R.M. Ibara. 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. *Estuarine and Coastal Marine Science*. 5: 665-678.

Holden, M.J. 1977. *Elasmobranchs*. Pages 187-215. In J.A. Gulland editor. *Fish Population Dynamics*. John Wiley and Sons. New York. USA.

... 1973. Are long term sustainable fisheries for elasmobranchs possible? *Rapports Proces-Verbaux des Reunions*. 164:360-367.

Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review Ecological Systems*. 4: 1-23.

Huppert, D.D. 1979. Implications of multipurpose fleets and mixed stocks for control policies. *Journal of the Fisheries Research Board of Canada*. 36:845-854.

Inglesias, J. 1981. Spatial and temporal changes in the demersal fish community of the Ria de Arosa (NW Spain). *Marine Biology* 65: 199-208.

International Commission for the Northwest Atlantic Fisheries. 1975. Standing Committee on Research and Statistics. Redbook 1975. Dartmouth. Canada.

International Commission for the Northwest Atlantic Fisheries. 1980. International Commission for the Northwest Atlantic Fisheries Statistical Bulletin. 28.

Jones, R. 1979. Relationships between mean length and year class strength in North sea haddock. International Council for the Exploration of the Seas. C.M. 1979-G:45. mimeo. 16pp.

Karentz, D., and C.D. McIntire. 1977. Distribution of diatoms in the plankton of Yaquina estuary, Oregon. Journal of Phycology. 13:379-388.

Keniston, J.A. 1978. Program cluster: an aid to numerical classification using the CDC cyber computer. Pleuronectid project technical report no. 2. Oregon State University Sea Grant. OSU Marine Science Center. Newport, Oregon. January 1978.

Knight, W., and A.V. 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. Fisheries Research Board of Canada Technical Report. No. 402. 15pp.

Krebs, C.J. 1978. Ecology: The Experimental Analysis of Distribution and Abundance. Harper and Row. New York, N.Y. USA.

Kreuz, K.F., A.V. Tyler and G.H. Kruse. 1982. Variation in growth of Dover soles and English soles as related to upwelling. Transactions of the American Fisheries Society. 111: 180-192.

Lange, .M.T., and M.P. Sissenwine. 1980. Biological considerations relevant to the management of squid (Loligo pealei and Illex illecebrosus) of the northwest Atlantic. Marine Fisheries Review. 42:23-37.

Lane, P.A., G.H. Lauff and R. Levins. 1975. The feasibility of using a holistic approach in ecosystem analysis. In pages 111-128 S.A. Levin editor. Ecosystem analysis and prediction. Proceedings of a SIAM-SIMS conference held at Alta, Utah. July 1-5. 1974. 337pp.

Langton, R.H., and R.A. Bowman. 1981. Food of eight Northwest Atlantic pleuronectiform fishes. National Oceanic and Atmospheric Administration. Technical Report NMFS. SSRF-749. 16pp.

..., and R.E. Bowman. 1980. Food of fifteen northwest Atlantic gadiform fishes. National Oceanic and Atmospheric Administration Technical Report NMFS. SSRF-740. 23pp.

... 1981. Diet overlap of some northwest Atlantic finfish. International Council for the Exploration of the Seas.C.M. 1981-G:50.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. Transactions of the American Fisheries Society. 106: 1-11.

Larson, R.J. 1980. Competition, habitat selection , and the bathymetric segregation of two rockfish (Sebastes) species. Ecological Monographs. 50: 221-239.

Lett, P.F., and A.C.Kohler. 1976. Recruitment: a problem of multispecies interaction and environmental perturbation, with special reference to Gulf of St. Lawrence Atlantic herring (Clupea harengus harengus). Journal of the Fisheries Research Board of Canada. 33: 1353-1371.

Majkowski, J. 1981. Application of a multispecies approach for assessing the population abundance and the age structure of fish stocks. Canadian Journal of Fisheries and Aquatic Sciences. 38: 424-431.

Maurer, R.O., and R.E.Bowman. 1975. Food habits of marine fishes of the northwest Atlantic-- data report. Northeast Fisheries Center. WoodsHole Laboratory Reference. 75-3. 90pp.

May, R.M., J.R.Beddington, C.C.Clark, S.J.Holt, and R.M.Laws. 1979. Management of multispecies fisheries. Science. 205: 267-277.

Mayo,R.K., A.M.Lange, S.A.Murawski, M.P.Sissenwine, and B.R.Brown. 1981. A procedure for estimating rates of escapement and discard, based on research vessel bottom trawl survey catches. International Council for the Exploration of the Seas. C.M. G:62.

McIntire, C.D. 1978. The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estuarine and Coastal Marine Sciences. 6: 447-457.

McIntosh,R.P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology. 48: 392-404.

Mech, D.L. 1962. Ecology of the timber wolf (Canis lupus) in Isle Royale National Park. Purdue University. PhD Thesis.

Menge, B.A. 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology. 53: 635-644.

Moore, E. 1947. The sand flounder, Lophopsetta aquosa (Mitchill); a general study of the species with special emphasis on age determination by means of scales and otoliths. Bulletin Bingham Oceanographic Collection. 11:(3) 1-79.

Morrow, J.E. 1951. The biology of the longhorn sculpin, Myoxocephalus octodecemspinosus Mitchill, with discussion of the southern New England "trash" fishery. Bulletin Bingham Oceanographic Collection. 13(2): 1-89.

Mills, E.L. 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities. Journal of the Fisheries Research Board of Canada. 26: 1415-1428.

... 1980. The structure and dynamics of shelf slope ecosystems off the northeast coast of north america. Pages 25-47 in K.R.Tenore and B.C.Coull editors. Marine Benthic Dynamics. University of South Carolina Press.

Murawski, S.A., A.M.Lange, M.P.Sissenwine, and R.K.Mayo. 1981. Definition and analysis of otter trawl fisheries off the northeast coast of the United States based on multi-species similarity of landings. International Council for the Exploration of the Seas. C.M. G: 63.

Odum, H.T., and E.C.Odum. 1976. Energy basis for man and nature. McGraw-Hill book Co. USA.

Overholtz, W.J., and J.R.Nicolas. 1977. Apparent feeding by the fin whale (Balaenoptera physalus) and the humpback whale (Megaptera novaengliae), on the American sandlance, (Ammodytes Americanus), in the northwest Atlantic. Fishery Bulletin. 77:285-287.

Overton, W.S. 1975. The ecosystem modeling approach in the Coniferous Forest Biome. Pages 117-138 in B.Patten editor. Systems Analysis and Simulation in Ecology. Vol.3. New York. USA.

Overton, W.S. 1977. A strategy of model construction. Pages 50-73 in C.A.S.Hall and J.W.Day editors. Ecosystem modeling in theory and practice: an introduction with case histories. John Wiley and Sons. New York. USA.

Oviatt, C.A., and S.W.Nixon. 1973. The demersal fish of Narragansett bay: an analysis of community structure, distribution and abundance. Estuarine and Coastal Marine Science. 1:361-378.

Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia. 15: 93-120.

Palm, W.J. 1975. Fishery regulation via optimal control theory. Fishery Bulletin. 73:830-837.

Parrack, M.L. 1976. A catch analysis of the Georges Bank yellowtail flounder stock. National Marine Fisheries Service. Woods Hole, Ma. Unpublished MS. 15pp.

Paulik, G.J., A.S.Hourston, and P.A.Larkin. 1967. Exploitation of multiple stocks by a common fishery. Journal of the Fisheries Research Board of Canada. 24: 2527-2537.

Pella, J.J., and P.K.Tomlinson. 1969. A generalized stock production model. Inter-American Tropical Tuna Commission Bulletin. 13: 419-496.

Pennington, M.R., and M.D.Grosslein. 1978. Accuracy of abundance indices based on stratified random trawl surveys. International Commission for the Northwest Atlantic Fisheries. Research Document. 78-4-77. Serial No. 5264.

Pimentel, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Kendal Hunt Publishing Company. Dubuque, Iowa. USA.

Pinhorn, A.T. 1976. Catch and effort relationships of the groundfish resource in subarea 2 and 3. International Commission for the Northwest Atlantic Fisheries. Selected Papers. 1:107-115.

Pitt, T.K. 1970. Distribution, abundance, and spawning of yellowtail flounder, Limanda ferruginea, in the Newfoundland area of the northwest Atlantic. Journal of the Fisheries Research Board of Canada. 27:2261-1171.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. International Commission for the Northwest Atlantic Fisheries Research Bulletin. 9:65-74.

... 1976. The effect of biological interactions on the theory of mixed fisheries. International Commission for the Northwest Atlantic Fisheries Selected Papers. 1:157-162.

... 1976. The application of mixed fisheries theory to the cod and redfish stocks of subarea 2 and division 3K. International Commission for the Northwest Atlantic Fisheries Selected Papers. 1:163-170.

... 1979. The South China sea fisheries: stock assessment in multispecies fisheries. Food and Agriculture Organization of the United Nations. SCS/DEV/79/19. 106pp.

... 1979. A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels. International Council for the Exploration of the Seas C.M. 1979/H:16.

Richards, J., D.W.Armstrong, J.R.G.Hislop, A.S.Jermyn, and M.D.Nicholson. 1978. Trends in Scottish research vessel catches of various fish species in the North sea, 1922-1971. Pages 211-224 in G.Hempel editor. North Sea Fish Stocks-Recent changes and their causes. Rapports et Proces Verbaux des Reunions. No. 172. 449pp.

Ricker, W.E., and R.E.Foerster. 1948. Computation of fish production. Bulletin Bingham Oceanographic Collection. Yale University. 11(4):173-211.

... 1975. Computation and interpretation of biological statistics for fish populations. Bulletin of the Fisheries Research Board of Canada. 191. 382pp.

Riffenburgh, R.H. 1969. A stochastic model of interpopulation dynamics in marine ecology. Journal of the Fisheries Research Board of Canada. 26:2843-2880.

Rowe, V.L., H.B.N.Hynes and A.V.Tyler. 1975. Reproductive timing by the polychaetes Clymenella torquata and Praxillella praetermissa in Passamaquoddy Bay, New Brunswick. Canadian Journal of Zoology. 53:293-296.

Royce, W.F., R.J.Buller, and E.D.Premetz. 1959. Decline of the yellowtail flounder (Limanda ferruginea) off New England. Fishery Bulletin. Vol 146:1-98.

Sanders, H. 1956. The biology of marine bottom communities. Bulletin of the Bingham Oceanographic Collection. Yale University. 15:344-414.

Saville, A. 1965. Factors controlling dispersal of the pelagic stages of fish and their influence on survival. Special Publication ICNAF No.6 335-348.

Shaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-American Tropical Tuna Commission Bulletin. 1:25-56.

Sherman, K., C.Jones, L.Sullivan, W.Smith, P.Berrigen, and L.Epymont. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature. 291:486-489.

Sissenwine, M.P., and E.W.Bowman. 1978. An analysis of some factors affecting the catchability of fish by bottom trawls. International Commission for the Northwest Atlantic Fisheries Selected Papers. 13:81-87.

... 1978. Is MSY an adequate foundation for optimum yield? Fisheries. 3(6):22-24.

Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. Transactions of the American Fisheries Society. 99:754-765.

... 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. Journal of the Fisheries Research Board of Canada. 29:717-730.

Soutar, A., and J.D.Issacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. California Cooperative Oceanic Fisheries Investigations Reports. 13:63-70.

Sparre, P. 1980. A goal function of fisheries (legion analysis). International Council for the Exploration of the Seas. C.M. G:40.

Stephenson, W., and M.C.L.Dredge. 1976. Numerical analysis of fish catches from Serpentine creek. Proceedings Royal Society Queensland. 87:33-43.

Stewart, D.J., J.F.Kitchell, and L.B.Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society. 110:751-763.

Sutcliffe, W.H.Jr., R.H.Loucks., and K.F.Drinkwater. 1976. Coastal circulation and physical oceanography of the Scotian shelf and the Gulf of Maine. Journal of the Fisheries Research Board of Canada. 33:98-115.

Sutherland, J.P. 1980. The fouling community at Beaufort, North Carolina: a study in stability. MS. Duke University Marine Laboratory. Beaufort, North Carolina.

Svardson, G. 1976. Interspecific population dominance in fish communities of Scandinavian Lakes. Institute of Freshwater Research. Drottningholm. 55:144-171.

Taylor, C.C. 1953. Nature of variability in trawl catches. Fishery Bulletin. 54:145-166.

Tyler, A.V. 1971. Periodic and resident components in communities of Atlantic fishes. Journal of the Fisheries Research Board of Canada. 28:935-946.

... 1972. Food resource division among northern marine demersal fishes. Journal of the Fisheries Research Board of Canada. 29:997-1003.

... 1973. Caloric values of some North Atlantic invertebrates. Marine Biology. 19:258-261.

... 1974. Community analysis. Pages 65-85 in R.O.Brinkhurst editor. Benthos of Lakes. MacMillan. USA.

..., and R.S.Dunn. 1976. Ration, growth and measures of somatic and organ condition in relation to meal frequency in winter flounder (Pseudopleuronectes americanus), with hypotheses regarding population homeostasis. Journal of the Fisheries research Board of Canada. 33:63-75.

..., W.L.Gabriel and W.J.Overholtz. 1982. Adaptive management based on structure of fish assemblages of northern continental shelves. Pages 149-156 in M.C.Mercer editor. Multispecies approaches to fishery management advice. Canadian special publication Fisheries and Aquatic Sciences. No. 59. 169pp.

Walter, G.G. 1971. Mathematical models for estimating changes in fish populations with applications to Green bay. Proceedings of the 14th conference on Great Lakes research. International Association Great Lakes Research. 1971:170-184.

Walters, C.J. 1972. Systems analysis in the Marion lake IBP project. *Oecologia*. 11:33-44.

..., G.Steer, and G.Spangler. 1980. Responses of lake trout (Salvelinus namaycush) to harvesting, stocking and lamprey reduction. Canadian Journal of Fisheries and Aquatic Science. 37:2133-2145.

Waring, G.T. 1980. A preliminary stock assessment of the little skate (Raja erinacea) in the northwest Atlantic. Masters thesis. Bridgewater State College. Massachusetts. 122pp.

Warwick, R.M. 1980. Population dynamics and secondary production of benthos. Pages 1-24 in K.R.Tenore and B.C.Coull editors. Marine Benthic Dynamics. University of South Carolina Press. USA.

White, C., and W.S.Overton. 1977. Users manuals for Flex2 and Flex3 model processors for the Flex modeling paradigm. Forest Research Laboratory. School of Forestry. Oregon State University. 119pp.

Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biological Review*. 42:207-264.

Wigley, R.L., and A.D.McIntyre. 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. *Limnology and Oceanography*. 9:485-493.

Winters, G.H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence Atlantic herring (Clupea harengus harengus). *Journal of the Fisheries Research Board of Canada*. 33:1751-1763.

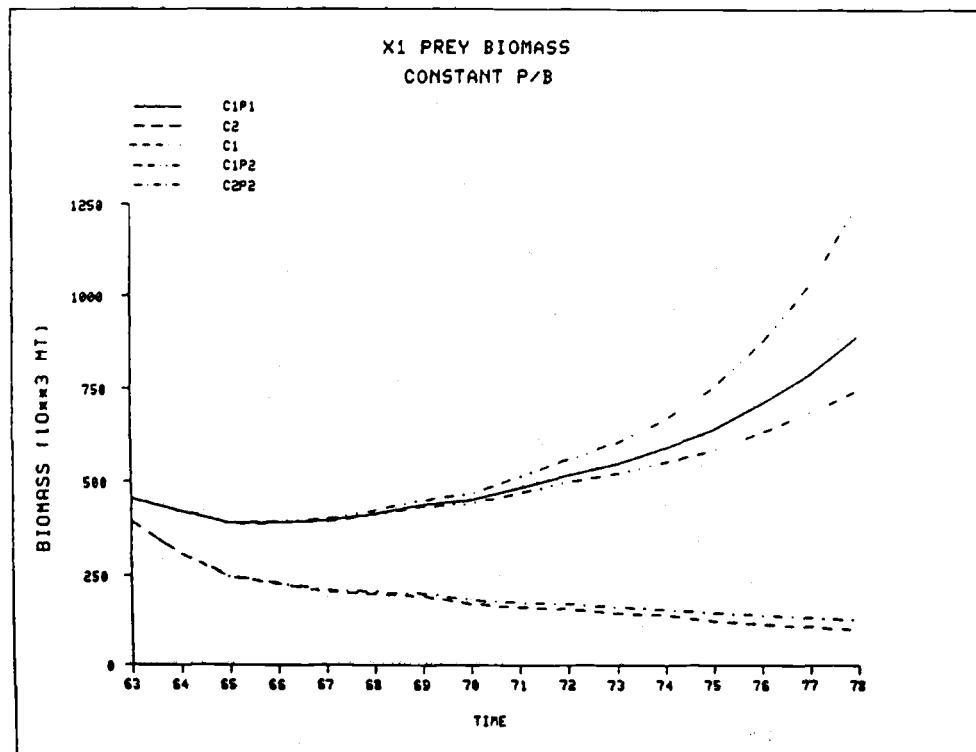
Wood, C.C., K.S.Ketchen, and R.J.Beamish. 1979. Population dynamics of spiny dogfish (Squalus acanthias) in British Columbia waters. *Journal of the Fisheries Research Board of Canada*. 36:647-656.

Appendix

Prey Biomass

The food resource or prey of the five competing yellowtail flounder...skates showed several different biomass responses depending on the prey turnover rate and the combinations of competition and predation that were used in a particular simulation. Under constant prey turnover rate conditions prey biomass experienced a steadily declining trend when intense competition was simulated (Fig 85). This downward progression was not ameliorated even with the addition of intense predation on the Yellowtail...Skate complex, the two trajectories being only slightly different (Fig 85). Under the same prey turnover provisions, prey biomass showed an increasing exponential tendency when competition was moderate (Fig 85). When moderate competition alone or moderate and intense predation were coupled with this mechanism, prey biomass increased (Fig 85). In the latter years of these three trajectories a disparity in biomass results through release of prey biomass that occurs through predation effects on the yellowtail flounder...skates complex (Fig 85). This allows prey biomass to increase proportionately faster with intensifying predation (Fig 85). Both of these prey responses seem to indicate somewhat aberrant trends since the former leads to extinction while the latter represents unchecked growth (Fig 85). General benthic macrofaunal studies suggest that both of these responses may be uncharacteristic of small benthic invertebrates who not only maintain stable numerical densities under predation, but also show population growth limits when densities are at a maximum (Rowe et al 1975; Warwick 1980). Other studies conclude that although

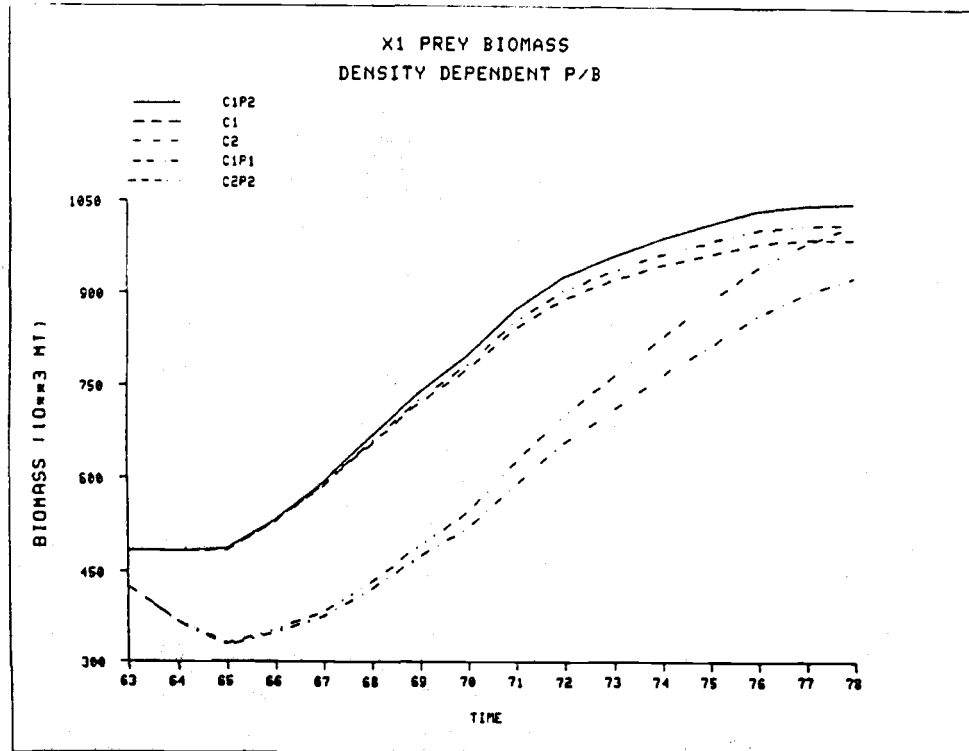
Figure 85. X1,prey biomass, trajectories under several competition and predation conditions and constant P/B



macrobenthic invertebrate prey biomass may be reduced on a short term basis by predation from demersal fish population trends did not appear to be influenced by demersal fish density (Arntz 1980).

Simulation responses suggest that the prey biomass model simulated a logistic growth function under the density dependent turnover rate hypothesis (Fig 86). Figure 86 shows invertebrate prey responses that occurred under conditions of density dependent prey turnover rate. As in the previous examples trajectories for intense and moderate competition showed different trends, but in this case the biomass levels converged at the end of the time series. Intense competition did not result in near extinction of prey biomass as occurred under a constant prey turnover rate (Fig 86). Prey biomass declined steadily in the first several years of the time series under the intense competition situation represented by intense competition and intense competition and predation in Fig 86. This period of decline was followed by a rapid increase in biomass and unlike the constant P/B case, predation pressure under intense competition and predation allowed a steeper rate of increase to occur (Fig 86). The three experiments that simulated moderate competition resulted in fairly similar trends with a small amount of divergence as time increased in the simulations (Fig 86). These runs produced a classic logistic response curve within the 16 year time span of the simulation. (Arntz 1980) discussed several response hypotheses that could be utilized for explaining observed trends in marine benthic populations that result from interspecific interactions with demersal fishes. The curves generated by using a density dependent prey model appear to

Figure 86. X1, prey biomass, trajectories under several competition and predation conditions and density dependent P/B

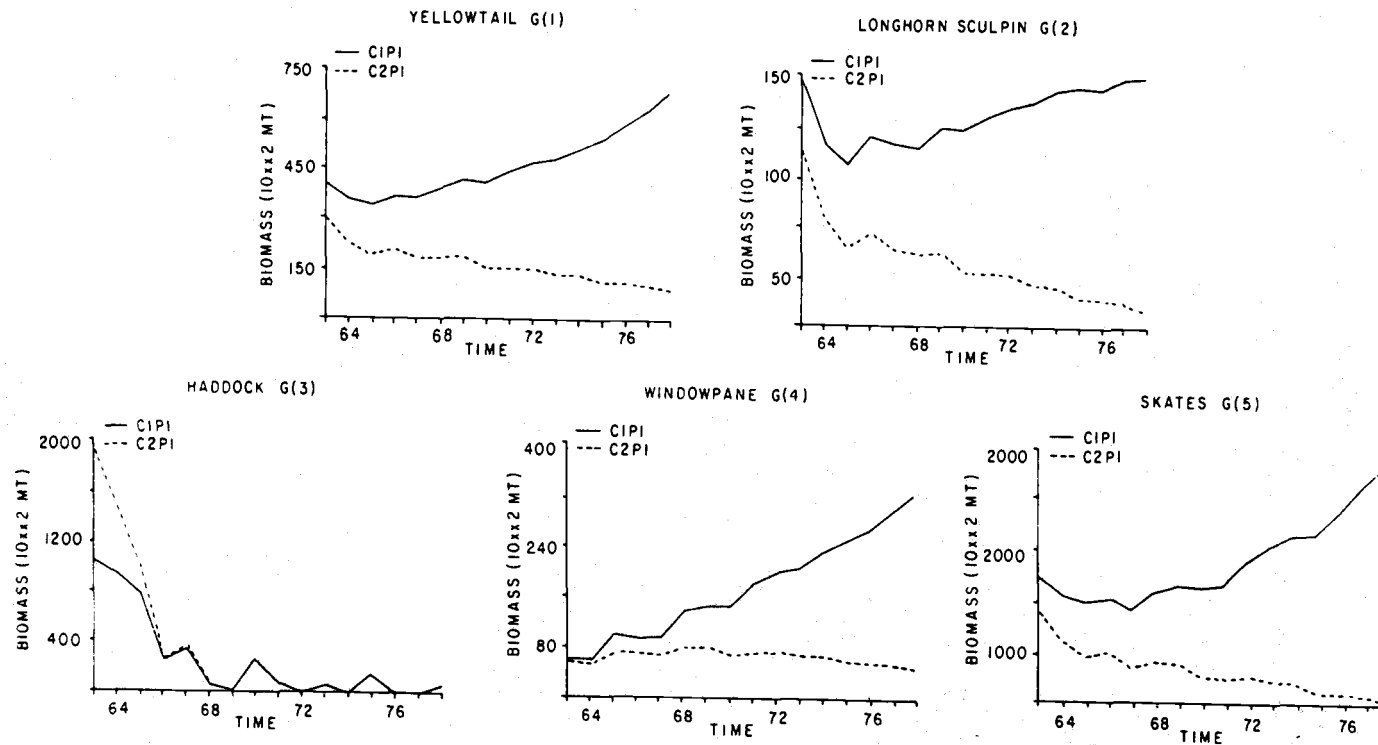


be more useful for describing prey responses to the 5 competing species.

X1 Prey Biomass Flow

In this model of the shallow assemblage demersal fish system the flow of biomass from the invertebrate prey food resource, X1, ultimately determines the daily ration of the 5 competing species. This is accomplished through the g functions which link density changes to consumption by the competitors. This primary channel then couples available food resources to growth of the competing fish and partially determines the direction of recruitment and stock biomass. Fig 87 tracks the various intraspecific g -function responses under constant prey turnover rate circumstances and is representative of simulated behavior under moderate competition and intense competition and all predation choices. Under intense competition the declining prey biomass situation, all species with the exception of windowpane flounder, showed a steadily declining trend in metric tons of intake of the prey resource. This can be explained by observing the haddock trajectory, $g(3)$, which shows the degree of difference of biomass utilization that results by varying competition intensity. Under intense competition more prey biomass is funnelled into haddock prerecruits, in the early 60's, resulting in decreased flow to the other species (Fig 87). This intense drain on prey resources in the initial years of the series could not be compensated for under a constant prey turnover rate (Fig 85), thus under intense competition (C2P1), prey intake declined with time (Figs 87).

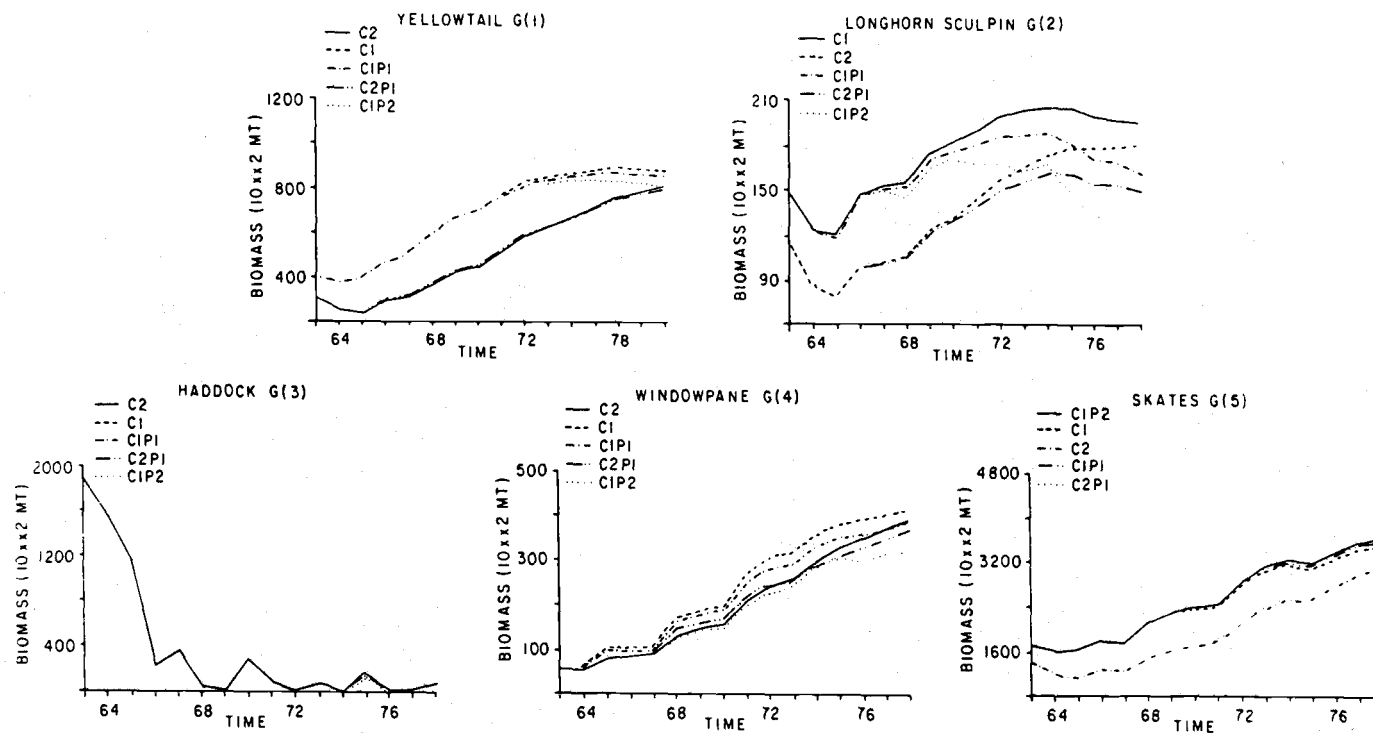
Figure 87. g responses under moderate competition (C1P1) and intense competition (C2P1) conditions with constant P/B.



Simulations that investigated moderate competitive effects produced g-function responses with increasing trajectories corresponding somewhat to prey biomass increases produced under this competition scenario (Figs 72; 87). Haddock, $g(3)$, was the exception, but predictably so since the dynamics of this species were controlled by inputting yearly estimates of numbers at age. Yellowtail flounder, Longhorn sculpin, and Skates showed initial declines in prey intake due to competition with haddock for prey resources. Yellowtail and longhorn sculpin increased intake slowly, after this initial period, while skate consumption continued to decline and then hovered at 1963 levels until 1971 when prey intake began to increase (Fig 87). Windowpane consumption remained constant from 1963-1964 and steadily increased over the remaining years of the simulation.

Density dependent prey turnover rates caused significant scaling changes in competitor consumption and slight modifications in trends for yellowtail flounder and longhorn sculpin in the 1970's (Fig 88). Considerable differences in prey consumption resulted for Yellowtail flounder, Longhorn sculpin, and Skates, when intense competition was simulated and the magnitude of the decrease was much more pronounced (Fig 88). These responses are echoed in Fig 88, which shows the rapid initial decline in prey biomass that occurred via intense competition in the early years of the time series. Trends for both the moderate competition and intense competition cases were actually very similar to the moderate competition case in Fig 87, except that the latter years reflected the homeostatic effects of density dependent prey turnover rate for

Figure 88. g responses under several competition and predation conditions with density dependent P/B



Yellowtail flounder and Longhorn sculpin (Figs 86; 88). Prey biomass consumption by the 5 competitors showed declines for all species during the early 60's under both moderate competition and intense competition conditions. Windowpane flounder showed the most rapid recovery followed by longhorn sculpin, yellowtail flounder, and skates. Yellowtail consumption reached similar levels in the late 70's under both competitive hypotheses, but differential responses occurred for longhorn sculpin and skates during the same period (Figs 88).

```

C ***** MODEL MSPECIES *****
C CONCEPTUAL FRAMEWORK AND MODEL BY BILL OVERHOLTZ AND AL TYLER
C PROGRAM BY BILL OVERHOLTZ
C A REPRESENTATION OF A MULTISPECIES DEMERSAL COMMUNITY FROM
C THE SHALLOW ASSEMBLAGE ON GEORGES BANK
C THIS MODEL CONTAINS SEVERAL SWITCHES THAT ARE USED TO EVOKE VARIOUS
C COMBINATIONS OF COMPETITION, PREDATION, PREDATOR PREFERENCE AND
C PREY TURNOVER RATES.
C
C
C SUBROUTINE UNODEL (IT)
C ZZXX
COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BMR(10)
COMMON BMA(10),BM2(10,10),BNI(10,10),BN2(10,10),BSR(10,10),BV(10)
COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPREDY(10)
COMMON XR(10,10),XT(10),XTMP(10),XTM1(10),XU(10,10),XUBAR(10)
COMMON XUG(10,10),XUTH1(10,10),XU0(10),TEMP1(16),TEMP2(16)
COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
K=NOD(IT-1963,16)+1
CALL PRED
CALL SUBADLT
CALL ADULT
CALL RECRUIT
CALL PREY
RETURN
END

C
C
C THIS SUBROUTINE CALCULATES M1(PREDATION MORTALITY) AND M2
C (NATURAL BACKGROUND MORTALITY). THE PREDATORS X7,X8 ACT AS A PULSE,GENERATING
C ALL M1 MORTALITY OVER A SHORT TIME INTERVAL. M2 IS GENERATED BY RESIDENT
C PREDATORS SUCH AS COD,GOOSEFISH AND SEA RAVENS AND APPLIED AS A CONSTANT
C RATE OVER THE YEARLY INTERVAL. NO PREDATION MORTALITY (M1) OCCURS ON X6-SKATES.
C
C
C SUBROUTINE PRED
C ZZXX
COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BMR(10)
COMMON BMA(10),BM2(10,10),BNI(10,10),BN2(10,10),BSR(10,10),BV(10)
COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPREDY(10)
COMMON XR(10,10),XT(10),XTMP(10),XTM1(10),XU(10,10),XUBAR(10)
COMMON XUG(10,10),XUTH1(10,10),XU0(10),TEMP1(16),TEMP2(16)
COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
XN(4,1)=TEMP7(K,1)
XN(4,2)=TEMP7(K,2)
XN(4,3)=TEMP7(K,3)
XP(7)=TEMP1(K)
XP(8)=TEMP2(K)

C
C
C TOTAL BIOMASS FOR EACH SPECIES IN METRIC TONS
C
C DO I=2,5
C XT(I)=(XN(I,1)+XU(I,1)+XN(I,2)+XU(I,2)+XN(I,3)+XU(I,3))/1000.0
C 1 CONTINUE
C
C
C BIOMASS FLOW FROM PREDATION, THE PARAMETERS B(53-56,59-62) ACT AS
C SWITCHES THAT EVOKE PREDATOR PREY PREFERENCE RESPONSES.
C
C
C G(6)=B(51)*XP(7)*(1-EXP1(B(52)*((B(53)*XT(2))+B(54)*XT(3))+
C 1(B(55)*XT(4))+B(56)*XT(5))/XP(7)))
C G(7)=B(57)*XP(8)*(1-EXP1(B(58)*((B(59)*XT(2))+B(60)*XT(3))+
C 1(B(61)*XT(4))+B(62)*XT(5))-G(6))/XP(8)))
C XTOTAL(1)=B(53)*XT(2)+B(54)*XT(3)+B(55)*XT(4)+B(56)*XT(5)
C 1+B(59)*XT(2)+B(60)*XT(3)+B(61)*XT(4)+B(62)*XT(5)

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```

C
C
C   TOTAL FLOW IN MT FOR EACH SPECIES
C
C   XFLOW(2)=(B(53)*XT(2)+G(6)+B(59)*XT(2)+G(7))/XTOTAL(1)
C   XFLOW(3)=(B(54)*XT(3)+G(6)+B(60)*XT(3)+G(7))/XTOTAL(1)
C   XFLOW(4)=(B(55)*XT(4)+G(6)+B(61)*XT(4)+G(7))/XTOTAL(1)
C   XFLOW(5)=(B(56)*XT(5)+G(6)+B(62)*XT(5)+G(7))/XTOTAL(1)
C
C   PERCENT BIOMASS AT AGE
C
C   DO 2 I=2,5
C   DO 3 J=1,3
C   XPER(I,J)=((XN(I,J)*XW(I,J))/1000.0)/XT(I)
3   CONTINUE
2   CONTINUE
C
C
C   PERCENT KILLED AT AGE AND PREDATION MORTALITY AT AGE
C   B(87)=A PREDATION SWITCH  0.0 NO,1.0 YES
C
C   DO 4 I=2,5
C   DO 5 J=1,3
C   XPERB(I,J)=(XFLOW(I)*XPER(I,J))/XT(I)
C   BN1(I,J)=((XN(I,J)*XPERB(I,J))/XN(I,J))+B(87)
5   CONTINUE
4   CONTINUE
C
C   TOTAL INSTANTANEOUS MORTALITY DURING 7 PRODUCTIVE MONTHS
C   CALCULATED FROM CONDITIONAL MORTALITY RATES.
C
C   DO 6 I=2,5
C   DO 7 J=1,3
C   BM2(I,J)=(BMR(I)/12.0)*7.0
C   BN2(I,J)=(1-EXP(-BM2(I,J)))
C   BAR(I,J)=(BN1(I,J)+BN2(I,J))-(BN1(I,J)*BN2(I,J))
C   BSR(I,J)=1-BAR(I,J)
C   BZR7(I,J)=-ALOG(BSR(I,J))
7   CONTINUE
6   CONTINUE
C
C   FIND TOTAL INSTANTANEOUS MORTALITY RATE FOR X6
C
C   DO 8 I=1,5
C   BM2(6,I)=(BMR(6)/12.0)*7.0
C   BZR7(6,I)=BM2(6,I)
8   CONTINUE
C
C   INSTANTANEOUS TOTAL MORTALITY FOR 5 UNPRODUCTIVE MONTHS
C   SPECIES X2,...X5
C
C   DO 9 I=2,5
C   DO 10 J=1,3
C   BZR5(I,J)=(BMR(I)/12.0)*5.0
10  CONTINUE
9   CONTINUE
C
C   INSTANTANEOUS TOTAL MORTALITY RATE FOR 5 UNPRODUCTIVE
C   MONTHS SPECIES X6
C
C   DO 11 I=1,5
C   BZR5(6,I)=(BMR(6)/12.0)*5.0
11  CONTINUE
C   RETURN
C   END
C
C
C   THIS SUBROUTINE CALCULATES AVERAGE BIOMASS AND USES IT IN
C   SEVERAL SEQUENTIALIZED COMPETITIVE RECIPIANT CONTROLLED DYNAMIC
C   FLOW EQUATIONS TO OBTAIN A YEARLY RATION FOR EACH SPECIES.  THIS
C   THEN IS CONVERTED TO GROWTH AND USED TO UPDATE BIOMASS DURING
C   A 210 DAY PRODUCTIVE SEASON(MAY-NOV).
C

```

```

C      SUBROUTINE SUBADLT
C      ZYX
C      COMMON R(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BNR(10)
C      COMMON BMA(10),BM2(10,10),BNI(10,10),BN2(10,10),BSR(10,10),BV(10)
C      COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
C      COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
C      COMMON XFLOU(10),XL(10),XN(10,10),XF(10),XPR(10,10),XPRESY(10)
C      COMMON XR(10,10),XT(10),XTEMP(10),XTH1(10),XW(10,10),XUBAR(10)
C      COMMON XUG(10,10),XUTH1(10,10),XUO(10),TEMP1(16),TEMP2(16)
C      COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
C      COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
C      DO 1 I=2,6
C      DO 2 J=1,5
C      XBAR(I,J)=0.0
C      XBART(I)=0.0
C      XR(I,J)=0.0
C      XUG(I,J)=0.0
C      XPR(I,J)=0.0
C 2 CONTINUE
C 1 CONTINUE

C
C      CALCULATE MEAN BIOMASS AT AGE, USING RICKER 1975 PP231
C      X(4,1) MUST BE RECALCULATED BECAUSE IT MUST AGREE WITH
C      THE XN(4,1) DRIVING VARIABLE
C
C      DO 25 I=2,3
C      X(4,1)=(XN(4,1)*XW(4,1))/1000.0
C 25 CONTINUE
C      DO 21 I=2,6
C      X(1,1)=(XN(1,1)*XUO(1,1))/1000.0
C 21 CONTINUE
C      DO 3 I=2,6
C      DO 4 J=1,3
C      XBAR(I,J)=(X(1,J)*(1+EXP(BG(I,J)-BZR7(1,J))))/2.0
C 4 CONTINUE
C 3 CONTINUE
C      DO 26 I=4,5
C      XBAR(6,I)=(X(6,I)*(1+EXP(BG(6,I)-BZR7(6,I))))/2.0
C 26 CONTINUE

C
C      CALCULATE TOTAL BIOMASS FOR EACH SPECIES
C
C      DO 5 I=2,6
C      XBART(I)=XBAR(I,1)+XBAR(I,2)+XBAR(I,3)+XBAR(I,4)+XBAR(I,5)
C 5 CONTINUE

C
C      SEQUENTIALIZED DYNAMIC FLOW EQUATIONS
C
C      G(3)=B(11)*XBART(4)*(1-EXP1(B(12)*(XBART(1)/XBART(4))))
C      G(5)=B(13)*XBART(6)*(1-EXP1(B(14)*((XBART(1)-G(3))/XBART(6))))
C      G(4)=B(15)*XBART(5)*(1-EXP1(B(16)*((XBART(1)-G(3)-G(5))/
C      1XBART(5))))
C      G(1)=B(7)*XBART(2)*(1-EXP1(B(8)*((XBART(1)-G(3)-G(4)-G(5))/
C      1XBART(2))))
C      G(2)=B(9)*XBART(3)*(1-EXP1(B(10)*((XBART(1)-G(3)-G(4)-G(5)-
C      1G(1))/XBART(3))))

C
C      CALCULATE RATION AND PERCENT RATION TO DETERMINE GROWTH
C
C      DO 8 I=2,6
C      DO 9 J=1,3
C      XR(I,J)=(G(I-1)*(XBAR(I,J)/XBART(I)))/210.0
C      XPR(I,J)=XR(I,J)/XBAR(I,J)
C      IF(XPR(I,J) .LE. .01) XPR(I,J)=.01
C      IF(XPR(I,J) .GE. .05) XPR(I,J)=.05
C 9 CONTINUE
C 8 CONTINUE
C      DO 22 I=4,5
C      XR(6,I)=(G(5)*(XBAR(6,I)/XBART(6)))/210.0
C      XPR(6,I)=XR(6,I)/XBAR(6,I)
C 22 CONTINUE
C      DO 24 I=4,5
C      IF(XPR(6,I) .LE. .01) XPR(6,I)=.01
C      IF(XPR(6,I) .GE. .05) XPR(6,I)=.05
C 24 CONTINUE

```

```

C
C FIND WEIGHT GAINED AND UPDATE WEIGHT AT AGE
C
      COUNT=17
      DO 10 I=2,6
      DO 11 J=1,3
      XWG(I,J)=B(COUNT)+B(COUNT+1)*(XPR(I,J))
      COUNT=COUNT+2
11 CONTINUE
10 CONTINUE
      XWG(6,4)=B(47)+(B(48)*XPR(6,4))
      XWG(6,5)=B(49)+(B(50)*XPR(6,5))
      DO 12 I=2,6
      XU(I,1)=XW0(I)+XWG(I,1)
12 CONTINUE
      DO 13 I=2,6
      DO 14 J=2,3
      XU(I,J)=XUTM1(I,J-1)+XWG(I,J)
14 CONTINUE
13 CONTINUE
      XU(6,5)=XUTM1(6,4)+XWG(6,5)
      XU(6,4)=XUTM1(6,3)+XWG(6,4)
C
C UPDATE NUMBER AT AGE
C
      DO 15 I=2,6
      DO 16 J=1,3
      XN(I,J)=(XN(I,J)*EXP(-BZR7(I,J)))
      XUTM1(I,J)=XU(I,J)
16 CONTINUE
15 CONTINUE
      DO 23 I=4,5
      XN(6,I)=(XN(6,I)*EXP(-BZR7(6,I)))
      XUTM1(6,I)=XU(6,I)
23 CONTINUE
C
C THIS ENDS THE PRODUCTIVE PART OF THE YEAR, BUT MORTALITY
C STILL OCCURS DURING THE REMAINING 5 MONTHS, UPDATE NUMBERS AT AGE
C
      DO 17 I=2,6
      DO 18 J=1,3
      L=5-J
      XN(I,L)=XN(I,L-1)*EXP(-BZR5(I,L-1))
18 CONTINUE
17 CONTINUE
      XN(6,6)=XN(6,5)*EXP(-BZR5(6,5))
      XN(6,5)=XN(6,4)*EXP(-BZR5(6,4))
C
C UPDATE BIOMASS AT AGE
C
      DO 19 I=2,6
      DO 20 J=1,3
      L=5-J
      X(I,L)=XN(I,L-1)*XU(I,L-1)/1000.0
20 CONTINUE
19 CONTINUE
      X(6,6)=XN(6,5)*XU(6,5)/1000.0
      X(6,5)=XN(6,4)*XU(6,4)/1000.0
C
C FIND TOTAL SPECIES SPECIFIC BIOMASS
C
      DO 27 I=2,5
      XTOTAL(I)=X(I,1)+X(I,2)+X(I,3)+XA(I)
27 CONTINUE
      XTOTAL(6)=X(6,1)+X(6,2)+X(6,3)+X(6,4)+X(6,5)+XA(6)
      RETURN
      END

```



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C
C
C THIS SUBROUTINE USES EQUATION 4 FROM DERISO,CJFAS 1980,#37,PP248
C TO MODEL THE BIOMASS OF EACH ADULT STOCK.
C
C START OF THE MODEL YEAR FOR X2,X3.  CALCULATE Z,A,U,V,CATCH,ESCAPEMENT
C
C SUBROUTINE ADULT
C
C ZZXX
C COMMON B4(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BMR(10)
C COMMON BMA(10),BM2(10,10),BN1(10,10),BN2(10,10),BSR(10,10),BZ(10)
C COMMON BU(10),BZA(10),BZR1(10),BZR3(10,10),BZR7(10,10),G(10)
C COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
C COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPRTY(10)
C COMMON XR(10,10),XT(10),XTMP(10),XTM1(10),XU(10,10),XUBAR(10)
C COMMON XUG(10,10),XUTH1(10,10),XUO(10),TEMP1(16),TEMP2(16)
C COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
C COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
C BFA(2)=TEMP3(K)
C BFA(3)=TEMP4(K)
C BFA(5)=TEMP5(K)
C BFA(6)=TEMP6(K)
C DO 1 I=2,3
C   BZA(I)=BFA(I)+BMA(I)
C   BAA(I)=(1-EXP(-BZA(I)))
C   BU(I)=(BFA(I)+BAA(I))/BZA(I)
C   BV(I)=(BMA(I)+BAA(I))/BZA(I)
C   XC(I)=BU(I)+XA(I)
C   XEA(I)=XA(I)-XC(I)
C 1 CONTINUE
C
C UPDATE X2,X3 BIOMASS BASED ON DERISO EQUATION
C
C DO 2 I=2,3
C   XA(I)=((1+BK(I))*((1-(BU(I)+BV(I)))*XEA(I)))-
C 1(BK(I))*((1-(BU(I)+BV(I))*2))*((XEA(I)/XA(I))*XTM1(I))+
C 1XREC(I)
C 2 CONTINUE
C
C START OF MODEL YEAR FOR X5,X6.  CALCULATE Z,A,U,V,CATCH,ESCAPEMENT
C
C DO 3 I=5,6
C   BZA(I)=BFA(I)+BMA(I)
C   BAA(I)=(1-EXP(-BZA(I)))
C   BU(I)=(BFA(I)+BAA(I))/BZA(I)
C   BV(I)=(BMA(I)+BAA(I))/BZA(I)
C   XC(I)=BU(I)+XA(I)
C   XEA(I)=XA(I)-XC(I)
C 3 CONTINUE
C
C UPDATE X5 BIOMASS BASED ON DERISO EQUATION
C
C   XA(5)=((1+BK(5))*((1-(BU(5)+BV(5)))*XEA(5)))-
C 1(BK(5))*((1-(BU(5)+BV(5))*2))*((XEA(5)/XA(5))*XTM1(5))+
C 1XREC(5)
C
C UPDATE X6 BIOMASS BASED ON DERISO EQUATION
C
C   XA(6)=((1+BK(6))*((1-(BU(6)+BV(6)))*XEA(6)))-
C 1(BK(6))*((1-(BU(6)+BV(6))*2))*((XEA(6)/XA(6))*XTM1(6))+
C 1XREC(6)
C
C REINDEX ESCAPEMENT AND RECRUITMENT AT T-1(XTM1(I)) FOR NEXT YEARS RUN
C
C DO 5 I=2,3
C   XTM1(I)=XEA(I)
C 5 CONTINUE
C DO 6 I=5,6
C   XTM1(I)=XEA(I)
C 6 CONTINUE
C XREC(2)=X(2,4)
C XREC(3)=X(3,4)
C XREC(5)=X(5,4)
C XREC(6)=X(6,6)
C RETURN
C END
C
C THIS SUBROUTINE CALCULATES LARVAL RECRUITMENT FOR X2,X3,X5,X6
C BASED ON ADULT STOCK SIZE AND A SPECIES SPECIFIC STOCK RECRUIT
C RELATIONSHIP.
C

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C      SUBROUTINE RECRUIT
C      ZZXX
COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BMR(10)
COMMON BMA(10),BN2(10,10),BN1(10,10),BN2(10,10),BSR(10,10),BV(10)
COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPREDY(10)
COMMON XR(10,10),XT(10),XTENP(10),XTN1(10),XU(10,10),XUBAR(10)
COMMON XUG(10,10),XUTH1(10,10),XUO(10),TEMP1(16),TEMP2(16)
COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
C      BEVERTON AND HOLT FUNCTION FOR YT FLD
C
      XL(2)=(1.0/(B(63)+(B(64)/XA(2))))
      IF(XA(2) .GE. 28000.0) XL(2)=2.00E08
      XN(2,1)=XL(2)*.50
C
C      RICKER FUNCTION FOR LONGHORNED SCULPIN
C
      XL(3)=B(65)*XA(3)*(EXP(B(66)*XA(3)))
      XN(3,1)=XL(3)*.50
C
C      BEVERTON AND HOLT FUNCTION FOR WINDOWPANE FLD
C
      XL(5)=(1.0/(B(67)+(B(68)/XA(5))))
      IF(XA(5) .GE. 8000.0) XL(5)=4.84E07
      XN(5,1)=XL(5)*.50
C
C      DIRECT FUNCTION FOR SKATES
C
      XL(6)=B(69)*XA(6)
      IF(XA(6) .GE. 30000.0) XL(6)=2.07E08
      XN(6,1)=XL(6)*.50
      RETURN
      END
C
C
C
C      THIS SUBROUTINE UPDATES PREY BIONASS (X1) AFTER FEEDING BY
C      THE 5 COMPETITORS (X2,...X6). 3 GROUP SPECIFIC G'S
C      (INSTANTANEOUS POTENTIAL TURNOVER RATES) ARE USED TO CONVERT
C      BIONASS AT (T) TO THE NEW BIONASS AT (T+1). G'S ARE EITHER
C      CONSTANT OR DENSITY DEPENDENT.
C
C
C      SUBROUTINE PREY
C      ZZXX
COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BMR(10)
COMMON BMA(10),BN2(10,10),BN1(10,10),BN2(10,10),BSR(10,10),BV(10)
COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPREDY(10)
COMMON XR(10,10),XT(10),XTENP(10),XTN1(10),XU(10,10),XUBAR(10)
COMMON XUG(10,10),XUTH1(10,10),XUO(10),TEMP1(16),TEMP2(16)
COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
CT=70
DO 1 I=1,3
  XPREDY(I)=XBART(I)*B(CT)
  CT=CT+1
1 CONTINUE
  XFLOW(1)=G(1)+G(2)+G(3)+G(4)+G(5)
  XBIO1=XBART(1)-XFLOW(1)
  CT1=70
  DO 2 I=1,3
    XTENP(I)=XBIO1*B(CT1)
    CT1=CT1+1
2 CONTINUE
  IF(XTENP(1) .GT. 5.0E05) XTENP(1)=5.0E05
  IF(XTENP(2) .GT. 5.0E05) XTENP(2)=5.0E05
  IF(XTENP(3) .GT. 2.5E05) XTENP(3)=2.5E05
C      ESTIMATE OF MORTALITY BY GROUP
C
      DO 3 I=1,3
        BZR1(I)=-ALOG(XTENP(I)/XPREDY(I))
3 CONTINUE

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C
C CALCULATE INSTANTANEOUS TURNOVER RATES
C B(73,74,77,78,81,82) ARE SWITCHES USED TO OPERATE VARIOUS TURNOVER RATES.
C
  BG(1,1)=(B(73)+1.61)+(B(74)+(B(75)+B(76)*XTMP(1)))
  BG(1,2)=(B(77)+0.69)+(B(78)+(B(79)+B(80)*XTMP(2)))
  BG(1,3)=(B(81)+0.41)+(B(82)+(B(83)+B(84)*XTMP(3)))
C
C AVERAGE BIOMASS FOR EACH GROUP
C
  DO 4 I=1,3
    XBAR(1,I)=(XPREY(I)*(1+EXP(BG(1,I)-BZR1(I)))/2.0
  4 CONTINUE
C
C UPDATE PREY BIOMASS (X1) AND APPLY MORTALITY FOR REST OF THE YEAR
C
  XBART(1)=XBAR(1,1)+XBAR(1,2)+XBAR(1,3)
  XBART(1)=XBART(1)*.90
  RETURN
  END
C
C THIS SUBROUTINE INITIALIZES THE PARAMETERS AND STATE
C VARIABLES FOR THE GEORGES BANK SHALLOW ASSEMBLAGE MODEL.
C
  SUBROUTINE UINIT
  ZZXX
  COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BHR(10)
  COMMON BMA(10),BN2(10,10),BN1(10,10),BN2(10,10),BSR(10,10),BV(10)
  COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
  COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
  COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPREY(10)
  COMMON XR(10,10),XT(10),XTMP(10),XTM1(10),XU(10,10),XUBAR(10)
  COMMON XUG(10,10),XUTH1(10,10),XUO(10),TEMP1(16),TEMP2(16)
  COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
  COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
  REWIND 44
  READ(44,*)(B(I),I=1,87)
  BK(2)=.600
  BK(3)=.500
  BK(5)=.400
  BK(6)=.500
  BMA(2)=.200
  BMA(3)=.200
  BMA(5)=.200
  BMA(6)=.200
  BHR(2)=.600
  BHR(3)=.400
  BHR(4)=.600
  BHR(5)=.400
  BHR(6)=.400
  XA(2)=6928.8
  XA(3)=1322.1
  XA(5)=207.1
  XA(6)=18587.0
  XTM1(2)=7000.0
  XTM1(3)=1184.0
  XTM1(5)=181.0
  XTM1(6)=8530.0
  XUO(2)=.002
  XUO(3)=.002
  XUO(4)=.002
  XUO(5)=.002
  XUO(6)=.004
  XUBAR(1)=6.31E-03
  XUBAR(2)=2.28E-02
  XUBAR(3)=5.00E-02
  XREC(2)=5000.0
  XREC(3)=753.9
  XREC(5)=115.7
  XREC(6)=6514.7
C
C DRIVING VARIABLES,XTMP1=XP(7),XTMP2=XP(8),TEMP3=BFA(2),TEMP4=BFA(3)
C TEMP5=BFA(5),TEMP6=BFA(6),TEMP7=XN(4,J)

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C      READ(44,*)(TEMP1(I),I=1,16)
      READ(44,*)(TEMP2(I),I=1,16)
      READ(44,*)(TEMP3(I),I=1,16)
      READ(44,*)(TEMP4(I),I=1,16)
      READ(44,*)(TEMP5(I),I=1,16)
      READ(44,*)(TEMP6(I),I=1,16)
      DO 1 I=1,16
      READ(44,*)(TEMP7(I,J),J=1,3)
1 CONTINUE

C
C      TWO DIMENSIONAL STATE ARRAYS
C
      DO 2 I=2,3
      READ(44,*)(XN(I,J),J=1,5)
2 CONTINUE
      DO 3 I=5,6
      READ(44,*)(XN(I,J),J=1,5)
3 CONTINUE
      DO 4 I=2,6
      READ(44,*)(BG(I,J),J=1,5)
4 CONTINUE
      DO 6 I=2,6
      READ(44,*)(X(I,J),J=1,5)
6 CONTINUE
      DO 8 I=2,6
      READ(44,*)(XU(I,J),J=1,5)
8 CONTINUE
      DO 10 I=2,6
      READ(44,*)(XUTM1(I,J),J=1,5)
10 CONTINUE
      XBART(1)=5.0E05
      RETURN
      END

      SUBROUTINE CCON
      COMMON B(100),BAA(10),BAR(10,10),BFA(10),BG(10,10),BK(10),BNR(10)
      COMMON BMA(10),BM2(10,10),BNI(10,10),BN2(10,10),BSR(10,10),BV(10)
      COMMON BU(10),BZA(10),BZR1(10),BZR5(10,10),BZR7(10,10),G(10)
      COMMON X(10,10),XA(10),XBAR(10,10),XBART(10),XC(10),XEA(10)
      COMMON XFLOW(10),XL(10),XN(10,10),XP(10),XPR(10,10),XPRED(10)
      COMMON XR(10,10),XT(10),XTMP(10),XTM1(10),XU(10,10),XUBAR(10)
      COMMON XUG(10,10),XUTM1(10,10),XUO(10),TEMP1(16),TEMP2(16)
      COMMON TEMP3(16),TEMP4(16),TEMP5(16),TEMP6(16),TEMP7(16,3)
      COMMON XPER(10,10),XPERB(10,10),K,XREC(10),XTOTAL(10)
      RETURN
      END

C
C      FUNCTION EXP1(A)
C
C      EXP OF -9.2=.0001, A SUFFICIENTLY SMALL NUMBER
C
      EXP1=0.0
      IF(A .LT. -9.2) RETURN
      EXP1=EXP(A)
      RETURN
      END

```