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# Fish Assemblages on the Grand Bank of Newfoundland

by

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SPECIAL SESSION ON CHANGES IN FISH POPULATIONS

## Abstract

Delimitation of broad zoogeographic regions characterized by a relatively homogeneous biological composition is a reasonable initial approach to identification of natural compartments in ecosystems. A 16-year time series (1971-82, 1984-87) of data from Spring groundfish surveys conducted on the Grand Bank of Newfoundland was analysed using numerical classification techniques with this goal in mind. Six fish assemblages constituted a regular pattern on the Bank and their areal distributions were found to be strongly aligned with bottom depth and oceanographic features. Consideration of their overall biological coherence allowed a merging and reformulation of the original six assemblages into four, and analysis of catch rates in these suggested that species composition was relatively stable over time. Whether the Grand Bank assemblages correspond to groups of functionally-linked fishes remains an open question of considerable theoretical interest. Nonetheless, the definition of areas where species broadly recur and overlap has multispecies management implications.

## Introduction

Theoretical and experimental studies suggest a possible natural organization of ecosystems into relatively simple compartments based on trophic dynamics. Whether one refers to subsystems, blocks (May, 1972; 1973), modules (Paine, 1980) or coevolved food webs (Gilbert, 1977), the underlying idea is that food webs are made up of compartments characterised by groups of species that are strongly inter-connected but interact only weakly with species belonging to any other group. The existence of such compartments as a feature of ecosystems remains an open question. Pimm and Lawton (1980) and Pimm (1982) argue against the existence of natural dynamical constraints leading to compartmentalization and therefore to the generalization of such phenomena. They do recognise, however, the existence of compartments whose boundaries are aligned with different types of habitat. Each of these would require different types of specializations that in turn would preclude strong links between species in the different habitats (Pimm, 1982).

In addition to the potential theoretical importance, the possible organization of ecosystems into compartments should be considered as well from the practical viewpoint of marine ecosystems' assessment and management. Indeed, there is a growing international concern with the limitations of a species-by-species approach in the fisheries, and increased interest in so-called "multispecies management" (FAO, 1978; Mercer, 1982; May, 1984; Mahon, 1985).

Compartment modelling is useful as a descriptive approach to the dynamic behaviour of ecosystems and as a tool for summarizing extensive ecological data (O'Neill, 1979). An example drawn from the Northwest Atlantic concerns the evaluation of possible effects of hydrocarbon exploration on the Grand Bank ecosystem. A simple box model with four compartments and their respective boundaries was designed to represent horizontal spatial variability on the Banks (Silvert, 1985). One other example and fuller discussion is found in Tyler *et al.* (1982) which makes reference to the existence of groups of fishes that interact among themselves and are unlinked to other groups even though they may overlap in geographical distribution. Tyler *et al.* present these as Assemblage Production Units (APU's), and do so in the context of defining an operational unit for the management of a multispecies fishery.

An underlying biological basis to support the APU as a management unit would be implied by the verification of a compartmented organization in the fisheries ecosystem. Dynamical constraints underlying compartments could account for the existence of more than one APU in the same habitat, whereas lack of such constraints would lead to APU's roughly congruent with main habitats in the region.

Identification of compartments in open ocean fisheries is not a simple task. It requires extensive knowledge of the species involved and often even controlled experimental manipulation. A reasonable approach to delimiting compartments solely conditioned by habitat (Pimm, 1982), is to try to identify broad geographic regions that are characterized by a relatively homogeneous biological composition. The recognition of subsystems within these compartments would then require further investigation of trophic relationships.

Identification of fish assemblages by using objective multivariate analytical tools can therefore be a first step in approaching the management of multispecies fisheries systems (Gabriel and Murawski, 1985). Such work, pioneered by Fager and Longhurst (1968) and Day and Pearcy (1968), has had the important objective of defining regions where the recurrent overlap of individual species distributions determines the existence of characteristic faunal compositions (e.g. Overholtz, 1982; Gabriel, 1983; Mahon *et al.*, 1984; Colvocoresses and Musick, 1984). These studies have shown that regions on continental shelves with a relatively homogeneous fish composition are strongly aligned with bottom depth and circulation patterns. These areas can be taken as candidate geographic compartments for modelling and/or management purposes. Once areas are defined, attention can then be directed to investigate biological variability and organisational structure within each area, as well as interactions between areas.

An important issue in the study of assemblages is the temporal scale encompassed by the analysis. There are two main reasons. The first has to do with validation of the assemblage itself. Multivariate techniques eventually involve less objective decisions, for example in the choice of clusters in a dendrogram or the number of factorial axes to be used. These decisions can influence conclusions in terms of reported assemblages and respective geographic contours. A rational way of checking for assemblage validity is to examine stability in species composition and recurrence of geographical distribution of the assemblage over a period of years.

A second and more important reason for using an adequate time frame stems from how one approaches the different stability properties (see Pimm, 1984 for a review) of such a complex system as a fish assemblage. Connell and Sousa (1983) stress that "both the minimum area and the minimum time period for which an assemblage may be judged as stable or persistent are functions of the life history characteristics of the species being considered". The minimum time period used should at least encompass one complete turnover of the assemblage. This would be close to the average life expectancy of the species having the highest value of this population parameter in the assemblage. For fishes, this is likely to be a relatively long time, with data found only in the time series available as commercial fishery statistics.

Our paper is an attempt to address some of these matters. It presents a study of data collected by Spring groundfish surveys conducted by the Northwest Atlantic Fisheries Centre (Dept. Fisheries and Oceans, St. John's, Nfld) on the Grand Bank of Newfoundland (NAFO divisions 3LNO). Its underlying philosophy derives from that discussed above. Numerical classificatory techniques were used to identify groundfish species which overlap and recur in their geographic distribution on the Grand Bank, and thereby to define assemblages. The areas covered by these fish assemblages were mapped and the respective fish composition described. A further investigation was then carried out in order to check for biological coherence of the assemblages found and to analyse temporal trends in biomass indices for the period 1971-87.

## Materials and Methods

### Data

Stratified random groundfish surveys have been conducted in NAFO Divisions 3LNO off Newfoundland since 1971. The research vessel A.T. Cameron conducted the surveys until 1984, at which time it was replaced by the Wilfred Templeman. The vessels were inter-calibrated and appropriate conversion factors applied where necessary (Gavaris and Brodie, 1984). Tows are for 30 minutes at 2.5 knots. Stratification is by latitude, longitude and depth. Sets are allocated to strata according to area, with all strata containing at least two sets. Bottom temperatures are recorded on each set. Temperatures differed from year to year as well as from site to site, but generally were in the range of -1.5 to as much as 9° C. In the analysis, biomass of all groundfish species comprising at least 0.1% of the total catch was included. Table 1 presents the list of species.

Biological data from the groundfish surveys were analyzed on an annual basis for each of the 16 Spring seasons (1971-82, 84-87) using standard classificatory techniques. Stations were first clustered using two agglomerative algorithms of Cluster Analysis. Different techniques were used to overcome problems concerning cluster validity and finally results were interpreted with the help of a polithetic divisive technique.

**Cluster Analysis**

Cluster analysis was applied as an exploratory technique. The Bray-Curtis index measured dissimilarity between hauls of each pair of stations. This index ranges from zero (identical stations) to unity (dissimilar stations) and has been used in similar analyses by other authors (Gabriel, 1983; Overholtz, 1983; Sinclair, 1985; Mahon and Sandeman, 1985). In addition to performing well in measuring overlap in simple simulated situations (Bloom, 1981), the coefficient has some appealing properties in the fisheries context, especially as regards its sensitivity to abundant species.

Observations (*i.e.* fishing stations) were clustered by two agglomerative polithetic methods. These were Group Average (Sokal and Michener, 1958) and Ward's Minimizing Error Sum of Squares (Ward, 1963). Even though Ward's method was originally developed for use with euclidian distances, there is considerable empirical and formal evidence suggesting that it performs well even with non-metric distances (cf. Batagelj, 1988) such as the Bray-Curtis. These two clustering techniques had previously been successfully applied to groundfish data by Gomes (1987).

Computations were carried out using the CLUSTAN package (Wishart, 1982) and results were assessed for validity by four different methods: (i) mapping the clusters and checking for geographical continuity of stations belonging to the same cluster (ii) visual confirmation of cluster coherence in the two-way table yielded by TWINSPAN (see below) (iii) using Jardine and Sibson's (1971) deltas, available in procedure COMPARE of CLUSTAN (iv) matrices randomly chosen were analyzed by using the relocation procedure available in procedure RELOCATE of CLUSTAN, the results being compared with those previously found by Group Average and Ward's method. Convergence of the results of RELOCATE with those of Group Average and Ward's method was taken as good evidence that a global optimum had been found (Wishart, 1982).

Group Average and Error Sum of Squares have differences in clustering 'intensity' (see Clifford and Stephenson, 1975 and Boesch, 1977 for a thorough discussion) that were explored for purposes of cluster validation. Joint use of the two methods was conducted by first identifying clusters yielded by Group Average that were geographically coherent. This method resulted in a considerable number of stations 'laid-off' by the chaining effect. These stations were often atypical, but a quick inspection of the tight clusters of Ward's dendrogram (with its few lay-offs), provided a clue to the closeness of those stations to more typical ones. Consideration of the geographical position of these stations and the results of TWINSPAN provided a basis to more comfortably accept or reject the suggestion provided by Ward's clusters.

### Interpretation of results - TWINSPAN

Hill *et al.* (1975) proposed a polithetic divisive method based on an ordination technique under the name of "Indicator Species Analysis". This method has been refined and computerized by Hill (1979) as TWINSPAN. Results are displayed in a two-way table that fulfils requirements of non-exclusivity. An ubiquitous species can therefore be associated with more than one cluster of stations by simple visual inspection. Inspection of such two-way tables allowed the recognition of biological features of each of the main station clusters previously identified by cluster analysis. Such features included not only actual differential species - i.e. species having a clear 'preference' for a given cluster - but also the absence of an otherwise widespread species in a cluster, or anomalies in cluster richness (number of species present). These features were used on a regular basis to classify stations laid off the main clusters or to ratify the classification of those ambiguous stations usually located on geographical boundaries of the areas occupied by the main station groups.

## Fish Assemblages on the Grand Bank

The classification analysis revealed that the distribution of certain groundfish species overlapped consistently within relatively well-defined broad geographical areas and over time. These species comprised the more abundant groundfish on the Bank, to judge from their catch rates, and were considered to form fish assemblages due to their recurrent co-occurrence in samples taken in each respective area during the 16-year time period. Boundaries of these characteristic areas were drawn for each year, and thereby produced a general biogeographic picture of the Grand Bank in regard to the groundfish fauna.

The main results concerning the groundfish assemblages follows. Readers should refer to figures 1 and 2 for a clearer understanding in following the text.

## Results of Classification Analysis

Four major clusters of stations recurrently appeared in the dendrograms computed for each Spring of the 16-year time-series. Geographic boundaries of three of the four major clusters approximately followed isobaths near the edge of the Bank. The three groups were deemed accordingly - Shallow Group (stations shallower than 80 m), Intermediate Group (stations between 80 m and 200 m) and Deep Group (stations deeper than 200 m). (These bathymetric limits were variable from year to year in some areas and should be merely taken as the more usual values). The fourth major cluster comprised stations just to the east of the Avalon Peninsula and was called the Avalon Group. Both the Intermediate Group and the Deep Group were further subdivided into two subgroups of stations each on the basis of apparent faunal differences. Stations in each of these subclusters were located in continuous strips encircling the Bank in a way that was more or less geographically consistent from year to year.

Figure 1 presents the main physical features of the Grand Bank and Figure 2 presents the geographical extent of each of the main clusters of stations identified. The situation portrayed is of course a somewhat 'average' stereotyped picture that does not represent any particular year.

## Groundfish Assemblages Summary

Table 2 and Figure 3 summarize the composition of the main groundfish assemblages identified on the Grand Bank. Species are ranked according to their relative abundance. This is only a rough ordering because assemblages underwent quantitative changes in their composition during the time period analyzed. A more detailed description of each group follows.

### Shallow Group

The Shallow Group occupies a major shallow area on the southeast Grand Bank. Its species composition was remarkably constant over the time period analyzed. The eastern, southern and western borders of the Shallow Group lie near the 90-m isobath. The group extends to the Whale Bank in the west and meets the Avalon Group to the north. Stations in the Shallow Group had depths ranging from 40 to 100 m, with average values around 70 m and standard deviations of 12 m or less. Bottom temperatures were usually between -1 and +2 ° C.

Four species dominate this group: yellowtail flounder, American plaice, cod and thorny skate. Yellowtail flounder was the key species used to identify stations belonging to this group. Three other species also recur in the Shallow Group, but in much lower abundance: striped wolffish, sea raven, and longhorn sculpin. Striped wolffish was usually restricted to samples taken south of 45 ° N latitude.

Avalon Group

The Avalon Group occupies the zone around the Virgin Rocks, most of the Avalon Channel, and the southern Downing Basin, with boundaries that changed position considerably from year to year. Station depths varied between 70 and 180 m with average values around 120 m and standard deviations between 25 and 40 m. Bottom temperatures were between -1.5 and 0 ° C.

The Avalon Group has two strong dominants: American plaice and cod. The third characteristic species is the Arctic eelpout, almost always present although in very low amounts. The group is remarkably poor in regard to number of species found in its stations relative to the other areas of the Bank. Stations of this group were distinguished from Shallow Group stations to the south by the disappearance of two important species - thorny skate and yellowtail flounder. These two species were not usually found north of a line between Whale Bank and Virgin Rocks. Yellowtail was often caught further north than was thorny skate, mainly in the Virgin Rocks area. The differential distribution of these two species suggested the existence of an intermittent narrow transition zone between the Avalon Group and the Shallow Group, indicated in Figure 2 with a different shadowing pattern and where typical dominants are cod, plaice and yellowtail with eelpouts in very low abundance.

The Avalon Group was distinguished from the Intermediate Group by the absence of thorny skate and the lower species richness of the former. As mentioned, boundaries between these two groups are very variable in position. They can be expected to lie between lines **a** and **a'** of Figure 2 to the east, and lines **b** and **b'** of the same figure to the west.

Intermediate Group

This group occupies a transition zone between the two shallow water groups (Shallow and Avalon) and the Deep Group. Three species dominate - American plaice, cod and thorny skate. Other species, much lower in abundance though constant in their presence, provided a basis upon which to subdivide the Intermediate Group into a NE-Intermediate Sub-Group and a SW-Intermediate Sub-Group.

NE-Intermediate Sub-Group

The NE-Intermediate Sub-Group occupies a vast deeper area comprising the Downing Basin and much of the northeast Grand Bank. Its southwest limit extends to near Carson Canyon. The deeper boundaries of this sub-group are indicated with the letter **c** in Figure 2; they lie between the 200 m and 280 m isobaths. These boundaries were relatively variable in depth from one year to another, the exact placement dependent on the upper distribution limit of redfish, the dominant species in the NES-Deep Sub-Group (see below). The shallower limits of the NE-Intermediate Sub-Group were near the 90 m isobath and with average depths around 150 m and standard deviations close to 50 m. Bottom temperatures were between -1.2 and 2.3° C.

The NE-Intermediate Group basically includes American plaice, cod and thorny skate. Other species usually present in relatively low abundance were Arctic eelpout, Greenland halibut and wolffishes (especially spotted wolffish). Arctic eelpout was usually the more abundant of these lesser species, with a distribution mainly to the north and northeast of Carson Canyon but also often found in the Hoyles and Kettle Canyon region.

SW-Intermediate Sub-Group

The SW-Intermediate Sub-Group occurs along a narrow strip on southern and western upper continental slope. Typical depths of stations belonging to this sub-group were between 90 and 200 m, with average values around 110 m. In the Whale Bank area, some included stations were shallower than 90 m. Difficulties arose for almost every year in determining the deeper boundary of this sub-group, not only due to yearly changes in the actual depth of the boundary but also because of imprecision arising from the steep slope in the area. As with the previous sub-group, the position of the deeper boundary was set dependent on the upper limits of typical species in the Deep Group (see below). There is some evidence that hakes and redfish from the W-Deep Sub-Group are more prone to move above the 150-200 m depth zone in the southwest (line **d** in Figure 2) than to the north and east of the Bank.

The SW-Intermediate Sub-Group basically comprises American plaice, thorny skate and cod. Species recurring in much smaller amounts are witch flounder and striped wolffish. Localized invasions by species from deeper waters, especially redfish and hakes, is a frequent phenomenon. The SW-Intermediate Sub-Group includes the Whale Bank and the Whale Deep to the west of the Grand Bank. This region is relatively unstable in its species composition as compared to the rest of the area occupied by the sub-group and might justify separate treatment. The core of the Whale Bank and Deep region seems to be fairly constant in regard to the dominating presence of cod, thorny skate and American plaice. Most of the area, however, is prone to invasion by species typical of other assemblages. Stations to the north often resemble typical stations from the Avalon Group in that they lack thorny skate and/or may include Arctic eelpout which has extended its distribution all along the Avalon Channel. Yellowtail flounder, a typical representative of the Shallow Group, is often found to the south in the Whale region but shallower than 90 m. Lumpfish, whose main distribution is further to the north on the St. Pierre and Green Banks, is also sometimes found in significant amounts on Whale Bank. One other species occasionally found in the Whale region as well as the rest of the SW-Intermediate Sub-Group is the witch flounder.

Deep Group

The Deep Group encircles the Grand Bank below 200 m. The upper depth limit is rather variable. Boundaries between the Deep and the Intermediate Groups tend to become shallower as one moves clockwise (south and west) along the upper continental slope. To the west of the Grand Bank the boundary frequently lies shallower than 150 m. The absence of deeper samples precludes a full assessment of the Deep Group distribution limits. The outside depth limits are expressed by a dashed line in Figure 2 drawn to include all samples taken on the upper slope by the groundfish surveys analyzed. The Deep Group is dominated by redfish, but is also distinguished in being the richer group in terms of number of different species recurrently occurring. Differences in the relative importance of species other than redfish lead to a subdivision of the group into a NES-Deep Sub-Group and a W-Deep Sub-Group.

NES-Deep Sub-Group

This sub-group occurs along the northern, eastern and southern borders of the Grand Bank. Its boundary with the W-Deep Sub-Group is in the Tail of the Bank region, lying in a relatively unstable position between Denys and Jukes Canyons. The shallow limit of the NES-Deep Sub-Group to the north and east of the Grand Bank is marked with letter **c** in Figure 2, and ranged between 180 and 280 m from year to year. These variations were mostly caused by irregular invasions of shallower waters by redfish. In some years a transition strip between the NES-Deep Sub-Group and the NE-Intermediate Sub-Group was identified, with redfish, Arctic eelpout, cod, thorny skate and plaice the important species. To the southwest, the upper limit of the NES- Deep Sub-Group becomes progressively more indeterminate, but it seems to become somewhat shallower. Stations in the NES Sub-Group had average depths around 280 m and standard deviations around 50 m. Bottom temperatures were warmer than in most other groups, ranging from 0 to 4° C.

Three species dominate the NES-Deep Sub-Group by abundance and constant presence: redfish, cod and thorny skate. Five other species and species-groups were found on a regular basis; in approximate rank order they are American plaice, wolffishes (striped, spotted and broadhead), Greenland halibut, witch flounder and roughhead grenadier. Vahl's eelpout was often present, although its abundance was always very low.

W-Deep Sub-Group

The W-Deep Sub-Group occurs along the western slope of the Grand Bank. As mentioned, its boundary with the NES-Deep Sub-Group lies between Jukes and Denys Canyons. The upper depth limit of this sub-group is marked with the letter **d** in Figure 2. This can be as shallow as 100 m, somewhat shallower than the upper limit of the NES-Deep Sub-Group. Variability in that limit is mostly due to occasional invasions of shallower waters by redfish and hakes. Average depth of stations was around 250 m and there were high annual standard deviations, ranging from 60 to 90 m. Bottom temperatures were almost always greater than 0 and could reach +9° C, the highest temperature recorded at the bottom during the surveys analyzed.

One species dominates the W-Deep Sub-Group - redfish. Haddock (since 1983), halibut (since 1978), cod, white hake and thorny skate follow in importance. Nevertheless the abundance of these species in relation to redfish is much lower than in the NES-Deep Sub-Group. Other species usually present in low abundance were American plaice, other hakes (silver and longfin) and argentine. Angler and marlin-spike were almost always present though in very low abundance.

**Oceanographic Framework**

Ocean circulation on the Grand Bank is dominated by the southward-flowing cold Labrador Current (Smith *et al.*, 1937; Lazier, 1982; Petrie and Anderson, 1983). To the south of the Bank, the warm North Atlantic Current flows offshore to the east. Most of the volume transport of the Labrador Current occurs in a high velocity offshore core (temperature +3 to 4° C, salinity around 34.9 ppt) centred over the 600-800 m isobath of the continental slope off Labrador. An inshore portion of the Current contains the greatest volume of cold water (temperature -1 to +2° C, salinity 32.5 to 33.5 ppt) and flows over the Labrador shelf or upper continental slope. Approaching the northern Grand Bank, the Labrador Current splits into three main branches - an inshore shelf stream through the Avalon Channel, a main branch along the eastern edge of the Bank and a third eastern component towards and around Flemish Cap.

There appears to be a close relationship between the major physical oceanographic features of the Grand Bank and the distribution of the groundfish assemblages we have identified (Figure 2). The Avalon Assemblage, with its low diversity, is basically under the influence of the inshore stream of the Labrador Current. All three significant species of the Avalon Assemblage (cod, plaice, Arctic eelpout) tolerate very cold water (<0° C). The NE-Intermediate Assemblage could be called the 'Labrador Current main branch assemblage' for the geographic areas covered by both roughly coincide.

The main offshore branch of the Labrador Current is generally confined between 50 and 200 m along the eastern edge of the Bank. This branch contains waters of the two different types and origins present in the entire Labrador Current, and it bounds and interacts with the shelf water on the northern and eastern parts of the Bank. Bottom temperatures in the NE-Intermediate area are usually higher and in a broader range than in the Avalon area. Thorny skate, apparently less tolerant to negative temperatures than cod and plaice, is absent in the Avalon Assemblage but present in the NE- Intermediate region. The NES-Deep Sub-Group, basically characterized by the presence of redfish, apparently occurs underneath the position of the Labrador Current main branch. Bottom temperatures are usually low but positive in that area. Observed annual variability in the position of the upper limit of this assemblage, interpreted as shallow intrusions of redfish, is suggested to depend on the depth of the Labrador Current main branch.

The warm North Atlantic Current (temperature 8-10° C, salinity 34.7-35.1 ppt) enters the Grand Bank region from the southwest, turns off the Tail of the Bank, and exits to the northeast. An oceanic front, with a wide dynamic trough of current reversal between the North Atlantic Current and the Labrador Current main branch, seems to be a permanent feature offshore to the south and west of the Tail of the Bank. Warm Atlantic waters sometimes penetrate the southern and southwestern parts of the Grand Bank. This penetration does not have the same magnitude every year and is spatially heterogeneous in relation to the bottom topography of the area. Mixed water forms over the western, southern and southeastern slopes of the Bank from the warm Atlantic water, the cold water from the Labrador Current and, particularly in the western slope, the fresh run-off from the St. Lawrence River (Forrester and Benoit, MS 1981). The SW-Intermediate Sub-Group is under the influence of this mixed water, with very heterogeneous characteristics as it goes around the Bank. Bottom temperatures in the area occupied by this assemblage occur over a broad -1.5 to 9° C range.

The W-Deep Sub-Group is clearly under the influence of warm slope water. Bottom temperatures in the W-Deep area were seldom negative and average values during surveys fell in between 3 and 8° C, with values as high as 11° C. The number of species present in hauls in the W-Deep area were usually the highest recorded in all the Bank in spite of the fact that total biomass was strongly dominated by a single species, redfish (Figure 5). Examples of species usually found only there, with temperature range preferences suggested by Scott and Scott (1988), were common angler (6-10° C), pollack (7-15° C), marlin-spike (3-4° C), Atlantic argentine (7-10° C), haddock (1-13° C), spiny dogfish (3-15° C), silver hake (6-8° C), longfin hake (3.5-6.5° C) and white hake (5-11° C).

Shelf water on the central Grand Bank, the area of the Shallow Assemblage, is a mixture of Labrador Current water and slope water plus modifications due to local seasonal heating and input of fresher water from the Gulf of St. Lawrence. There is little detailed information available on water circulation in the area. Conflicting evidence exists concerning the presence of a gyre on the central part of the Grand Bank which could be responsible for an apparent retention of water there (Smith *et al.*, 1937; Buzdalin and Elizarov, 1962; Forrester and Benoit, 1981).

## Biological Coherence of Assemblages

Multivariate techniques are useful tools for taking a first exploratory step towards defining faunal assemblages. The next step is to identify those that are biologically coherent. A biologically coherent assemblage is one in which the components (fish stocks in our case) are totally enclosed within it, as opposed, for example, to an assemblage whose area encompasses only an ontogenic phase of a given stock with the other ontogenic phases in areas of other contiguous assemblages. A coherent assemblage is most easily recognized when its species are exclusive to that assemblage.

Yellowtail flounder seems exclusive to the Shallow Assemblage of the Grand Bank. Regardless of whether it is composed of one or several stocks, the Shallow Assemblage is coherent with respect to yellowtail. The same is not so in the cases like the cod, a species that was important in all assemblages identified. If cod in the Shallow Assemblage belong to the same stock as do the cod in another contiguous assemblage, it makes little sense to consider the Shallow Assemblage as a relatively independent compartment in the Grand Bank ecosystem for purposes of modelling or management.

Where ubiquitous recurrent species are responsible for a part of the overlap between assemblages, further investigation is required to judge how coherent and natural are the assemblages yielded by the multivariate analysis. One might end up fusing areas belonging to initially separated assemblages if they share stocks comprising an important proportion of the total biomass. A brief literature review was carried out for the dominant groundfish species in order to confront the assemblages herein presented with biological information on their populations.

Atlantic cod

Based on analysis of meristics, tagging data, growth rate, parasite loads and allele frequencies (Templeman, 1962, 1974; Lear, 1985, 1986) there seems to be no support for keeping the Avalon Group distinct from a "cod's point of view". In keeping with current practice it will be assumed that this group has more association with the NE-Intermediate Group (division 3L) than with the Shallow Assemblage.

Yellowtail flounder

The Shallow Assemblage encompasses the bulk of the yellowtail distribution on the Grand Bank. This species is found in all shallow waters of 3LNO, although the majority of the commercial catch comes from 3N (Brodie and Walsh, 1988). Yellowtail was also found in small amounts on St. Pierre Bank and in inshore areas around the Avalon Peninsula (Pitt, 1970). Yellowtail is a shallow water species with relatively restricted movements as shown by tagging experiments (Lux, 1963; Walsh, 1987). Stock delimitation within the Shallow Assemblage area, if any, is not known. Yellowtail has been managed as a single stock in NAFO division 3LNO and there seems to be no good reason to join the Shallow Assemblage with any other assemblage based on this species.

American plaice

American Plaice has been managed as a single stock on the Grand Bank (NAFO divisions 3LNO). Its distribution is fairly wide on the Bank, ranging from deep water concentrations (520 m) in the northern part of our NES-Deep Assemblage to a juvenile nursery in shallow waters of the Tail of the Bank (Walsh and Brodie, 1988). The majority of the plaice biomass is in the shallow-intermediate waters (55-183 m) of 3L and 3N (Walsh and Brodie, 1987). Fish appear to move but little once settled and little intermingling is expected among adults. The strongest suggestion for merging assemblages from a "plaice's point of view" is between the Shallow and NE-Intermediate Assemblages, but existing evidence was not considered strong enough to take this action.

Redfish

There are three redfish species on the Grand Bank, the abundant beaked redfishes (*Sebastes mentella* and *Sebastes fasciatus*) and the more sporadic golden redfish (*Sebastes marinus*). Ni (1981a,b) presents evidence that *S. fasciatus* is dominant in the shallower range of redfish distribution (200-400 m in 3LN, 200-500 m in 3O) and *S. mentella* is dominant in the deeper parts, with transition zones at 400-500 m in 3LN and more than 500 m in 3O. Sampling stations during the surveys analyzed in our work seldom went deeper than 500 m and in most cases were shallower than 400 m. The redfish in our Deep Assemblage is therefore assumed to be mostly *S. fasciatus*. The usual NAFO practice of separating redfish in 3O from 3NL for management purposes will be followed in this paper.

**Merging Assemblages**

There is evidence that some of the groundfish stocks which make up an important percentage of the biomass in the Grand Bank assemblages extend their geographic distribution over more than one assemblage. This fact underlines the need for reformulating assemblages when certain sorts of ecological investigation are intended. In what follows, our main objective is to analyze groundfish biomass trends within biologically coherent areas.

The Deep Assemblage is dominated by beaked redfish, a deep-water species caught in very small amounts in all the Intermediate Assemblage area. Cod in the NES Deep Sub-Group area may belong to the northern complex while in the W-Deep Sub-Group cod biomass is relatively low. Cod does not seem to offer any good reason for merging any Deep and Intermediate sub-groups. The same is true of plaice. The Deep Sub-Groups therefore were not merged.

The Avalon and NE-Intermediate groups were merged as were the Shallow and SW-Intermediate groups. These decisions were made in keeping with current evidence and practice regarding the structure of the cod stocks, with cod taken south of 46° N latitude associated with the 3NO stock, and other cod, particularly those from the northern Grand Bank and Avalon Channel, treated separately.

Having gone through this reformulation exercise, we end up with four groups of stations that encompass areas of relative biological homogeneity on the Bank in regard to groundfish: NES-Deep, W-Deep, Avalon/NE-Intermediate, and Shallow/SW-Intermediate. Trends in biomass and species composition over time will be presented next for the entire Grand Bank as well as for each of these four areas.

## Catch Trends in Grand Bank Assemblages

Catch-per-unit-effort data from the groundfish surveys were used as an index of biomass abundance for the period 1971-82, 1983-87. Species composition of the catch was used to build up cumulative percentage graphs. Reliability of each data point in the graphs depends upon the number of stations used to derive that data point, with the values summarized in Table 3. Special care should be taken when analyzing catch rates of merged assemblages in regard to species that are present in only one of a pair of merged regions.

Following the reformulation, the new catch rates of these species have been affected by the number of stations in the region where they are not present. Catch rates of such species in years of particularly anomalous ratios between the number of stations in each merged region should be regarded with care.

*Shallow/SW-Intermediate* - Cod, plaice, yellowtail and thorny skate dominate the biomass of demersal catches in this assemblage (Figure 4) which extends over almost all the shallow Bank. The index of total abundance fluctuated around 150 Kg/tow since 1973 but rose to over 200 Kg/tow since 1984. This high results from a rising trend in the biomass of cod.

*Avalon/NE-Intermediate* - The broad area comprised by this assemblage is dominated by only two species - plaice and cod (Figure 4). Total catch-per-unit-effort has been stable at over 150 Kg/tow since 1976, but there has been a shift in relative abundance of cod and plaice in the catches since 1982. An increase in the catch rates for cod since that date has been matched by a decrease for plaice.

*NES-Deep* - Total catch rates in the area comprised by this assemblage exhibit strong fluctuations (Figure 5), reflecting the variability in the two dominant species of the assemblage - cod and redfish. Redfish attains catch rates well over 100 Kg/tow, a value that stands near the top for all species in any assemblage studied. Catch rates for cod are also rather unstable when compared with the same index in shallower assemblages. The awkward value for cod in 1984 should be regarded with caution due to the low sampling rate in this assemblage area in that year (Table 3).

*W-Deep* - Sampling rates in this assemblage are the lowest ones recorded (Table 3,) and the values for years like 1972 and 1981 are particularly unreliable. Catch rates for total biomass in the area of the Bank comprised by this assemblage exhibit strong fluctuations (Figure 5) basically caused by high variability in redfish, the dominant species in the assemblage. Some of the catch rates observed here for redfish are the highest for any species on the Bank.

*Entire Grand Bank* - The biomass of demersal groundfish catches on the Grand Bank during the time period analyzed was dominated by a small number of species (Figure 6). The index of total abundance has fluctuated around 200 Kg/tow with relatively higher values since 1984. This high is apparently due to an increasing trend in the catch rate of cod observed in all assemblages except the deep ones. Other species, like yellowtail or plaice, remained relatively stable or, like redfish, did not exhibit any pronounced trends.

A species which deserves mention is the thorny skate. Usually making up a significant proportion of the catch (Figures 4, 5, 6), thorny skate is not a target species in the fisheries. Apparently this species underwent a shift from a catch rate level of 25-30 Kg/tow in the 70's to 15-20 Kg/tow in the 80's (Figure 7). This shift closely follows trends in the Shallow/SW-Intermediate assemblage for this species.

Figure 8 compares total catch rates in each of the various assemblages considered and for the entire Grand Bank. The highest fluctuations are found in the two deep assemblages, but with no apparent match in their peaks and valleys. The other two assemblages, which occur over large areas of the Bank, are comparatively much more stable over time, and the same is true for the entire Grand Bank.

## Discussion

Classificatory analysis of 16 years of Spring groundfish survey data indicated a high degree of spatial consistency in the clustering pattern of stations and in the species that characterize each cluster. The Grand Bank could be divided into six regions defined on the basis of their fish assemblages. These were mapped, described, and reformulated for biological coherence. The assemblages maintained their species composition over the time period analyzed and also retained the major attributes of their spatial configuration.

There are common methodological problems involved in this type of analysis (Mahon, *et al.*, 1984; Gabriel and Murawski, 1985; Bock, 1988), which we will briefly address. The intrinsic variance of ecological samples may result in the misallocation of stations by the clustering procedure selected. We sought to overcome this by using a reallocation procedure, mapping the clusters, and by checking the agglomeratively built dendrograms against a divisive, and more robust, method. Even so, one cannot preclude misclassifications. Stations occurring near assemblage boundaries on the steep continental slope at the edge of the Bank are particularly prone to these.

Multivariate methods also require decisions about the scale of approach to spatially aggregated data. In the case of cluster analysis, this translates into decisions about the clustering level at which the groups are defined. Concern is whether the cluster scale chosen matches the scale of the ecological processes of interest. Determining production of species like cod or plaice, both widespread on the Bank, is likely to require a different scale of approach than that for more localized species. Our attempt to find biologically coherent assemblages solved the problem as regards the abundant commercial species, which of course are also usually the more widespread ones. As a general rule, one might first approach broad regions such as the continental shelf at high resolution (medium levels of hierarchical clustering), and then merge areas according to strong biological constraints, such as stock delimitation of abundant species and/or management practicability.

Studies of marine demersal fish assemblages have shown that the main biogeographic contours on continental shelves and slopes are aligned with depth (Haedrich and Krefft, 1978; Overholtz, 1983; Gabriel, 1983; Colvocoresses and Musick, 1984; Mahon *et al.*, 1984; Gomes, 1987). A variety of physical factors - light level, pressure, water mass characteristics, sediment properties - are associated with depth change. Local influences of some of these factors account for a variety of deviations from a simple depth- aligned biogeography. North-south differences have also been observed in studies extending over enough degrees of latitude (Gabriel, 1983; Gomes, 1987).

It is usually possible to recognize without much trouble a characteristic group of species that dominates the shallow portion of the continental shelf within a restricted depth range. Easily recognizable also is a group of deep dwellers dominating portions of the continental slope, and which tends to have a much broader depth range than the shallow shelf group. Groups falling intermediate between these two extremes have been identified, but are usually more difficult to characterize. They are sometimes no more than a mix of species from the shallow and deep groups with no abundant or distinctive species of their own.

The fish assemblages identified by us on the Grand Bank fit well into this general picture. The contours of Figure 2 are strongly aligned with depth and the general oceanographic circulation of the area. Yellowtail and redfish are the typical abundant representatives from the shallow and deep areas respectively, while cod, plaice and thorny skate are abundant and widespread enough over the whole area to raise problems when attempting to completely compartmentalize the Bank.

Overlap in the species distributions that form the bases of our assemblage definitions does not necessarily imply significant strength of interaction among the species. Multivariate techniques in and of themselves bring little insight to the question of the influence of abiotic factors versus species interactions in determining the observed distribution patterns. Further investigation concerning trophic ecology of the species involved is required to clarify connectance within assemblages and support the 'energy usage groups' concept of Tyler *et al.* (1982).

There is an interesting parallel between Tyler *et al.*'s (1982) APU concept and the blocks, or compartments, that May (1972, 1973) argues are a possible requirement for local stability in ecosystem structure. Pimm (1982) predicts that compartment boundaries in nature, when present, should basically fit boundaries between different habitats and exist for biological reasons, rather than responding to dynamical constraints of the type developed in studies of model ecosystems. The oceanographic setting for the Newfoundland banks suggests that the assemblage areas portrayed in Figure 2 might indeed correspond to different habitats, at least as these would be perceived by wide-ranging species. However, as just mentioned, it still remains to clarify species connectance and interaction strength *within* any Grand Bank assemblage.

APU's are suggested to be useful management units, especially if they do indeed reveal emergent properties such as resilience and persistence (*e.g.* Pimm and Hyman, 1989). This would have major importance for determining multispecies production. Tyler *et al.*

(1982) admit the possible existence of more than one APU within the same assemblage area, which suggests at least two explanations. The strength of functional links may decline over distance in a large assemblage area, as suggested by Tyler *et al.* (1982), as the opportunity for biological interactions decreases. On the other hand, there may exist actual dynamical constraints in marine ecosystems of the type discussed on theoretical grounds by May (1973) and Pimm (1982).

Regardless of the actual balance between biotic and abiotic factors in determining the observed patterns of Figure 2, the simple definition of relatively homogeneous areas in terms of species composition has relevance to multispecies management. Mahon *et al.* (1984) make the same point. Mixed catches within the area of a given assemblage offer a certain redundancy in terms of species composition and relative abundances. Such information can be of value in dealing with bycatch and providing general guidelines for overall rational planning and management.

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TABLE 1. List of common and scientific names of species used in the analysis and refered to in the text.

| Common name | Scientific name |
|---|---|
| American plaice | *Hippoglossoides platessoides* |
| Angler, Common | *Lophius americanus* |
| Argentine, Atlantic | *Argentina silus* |
| Capelin | *Mallotus villosus* |
| Cod, Atlantic | *Gadus morhua* |
| Eelpouts | *Lycodes spp.* |
| Eelpout, Vahl's | *Lycodes vahlii* |
| Eelpout, Artic | *Lycodes reticulatus* |
| Greenland halibut | *Reinhardtius hippoglossoides* |
| Haddock | *Melanogrammus aeglefinus* |
| Hake, Longfin | *Urophycis chesteri* |
| Hake, Silver | *Merluccius bilinearis* |
| Hake, White | *Urophycis tenuis* |
| Halibut | *Hippoglossus hippoglossus* |
| Longhorn sculpin | *Myoxocephalus octodecemspinosus* |
| Lumpfish, Common | *Cyclopterus lumpus* |
| Marlin-spike | *Nezumia bairdi* |
| Pollack | *Pollachius virens* |
| Redfish | *Sebastes spp.* |
| Roughhead grenadier | *Macrourus berglax* |
| Sea raven | *Hemitripterus americanus* |
| Shorthorn sculpin | *Myoxocephalus scorpius* |
| Smooth skate | *Raja senta* |
| Spiny dogfish | *Squalus acanthias.* |
| Thorny skate | *Raja radiata* |
| Witch flounder | *Glyptocephalus cynoglossus* |
| Wolffish, Broadhead | *Anarhichas denticulatus* |
| Wolffish, Spotted | *Anarhichas minor* |
| Wolfish, Striped | *Anarhichas lupus* |
| Yellowtail flounder | *Limanda ferruginea* |

TABLE 2. Groundfish Assemblages in the Grand Bank. Horizontal lines separate sets of species with decreasing order of magnitude as expressed by kg/tow in hauls. Within each order of magnitude, species were ranked by approximate decreasing order of abundance. Species without asterisks were found present in most or all of the area of the correspondent assemblage at least 13 out of 16 years.
(*) Showed up at least 13 out of 16 times, though in more or less restricted regions within the group area.
(**) Showed up between 7 and 12 years out of 16.

| |
|---|
| **Shallow Group** |
| Plaice, cod, yellowtail fl., thorny skate |
| Stripped wolffish (*), sea raven, longhorn sculpin |
| **Avalon Group** |
| Plaice, cod |
| Artic eelpout |
| **Intermediate Group** |
| NE-Intermdt. Sub-Group |
| Plaice, cod, thorny skate |
| Artic eelpout, greenland halibut, spotted wolffish |
| SW-Intermdt Sub-Group |
| Plaice, cod, thorny skate |
| Witch fl., striped wolffish, artic eelpout (*) |
| **Deep Group** |
| NES-Deep Sub-Group |
| Redfish, cod, thorny skate, plaice |
| Greenland halibut, roughhead grenadier, witch fl., striped wolffish, |
| Vahl's eelpout(**), spotted wolffish(**), broadhead wolffish(**), |
| W-Deep Sub-Group |
| Redfish, haddock(**) |
| White hake, cod, halibut, thorny skate, plaice |
| Witch fl., silver hake, longfin hake, argentine, angler, marlin spike |

TABLE 3. Number of stations in each assemblage area used to calculate abundance indices and species proportions. Spring trawl surveys of period 1971-82 1984-87.

| | Years | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 84 | 85 | 86 | 87 |
| Shallow | 32 | 30 | 39 | 23 | 42 | 46 | 58 | 57 | 131 | 87 | 39 | 76 | 74 | 108 | 151 | 124 |
| SW-Intermd | 17 | 3 | 26 | 14 | 8 | 17 | 10 | 18 | 33 | 36 | 23 | 53 | 27 | 50 | 48 | 89 |
| Shallow+SW Intermd. | 49 | 33 | 65 | 37 | 50 | 63 | 68 | 75 | 164 | 123 | 62 | 129 | 101 | 158 | 199 | 173 |
| NE-Intermd | 19 | 24 | 13 | 54 | 33 | 40 | 42 | 47 | 60 | 56 | 49 | 52 | 17 | 104 | 96 | 84 |
| Avalon | 8 | 8 | 7 | 11 | 10 | 12 | 41 | 28 | 29 | 28 | 3 | 23 | 15 | 50 | 62 | 59 |
| Avalon+NE-Intermd | 27 | 32 | 20 | 65 | 43 | 52 | 83 | 75 | 89 | 84 | 52 | 75 | 32 | 154 | 158 | 143 |
| NES-Deep | 34 | 11 | 13 | 15 | 10 | 17 | 31 | 23 | 50 | 41 | 41 | 28 | 5 | 52 | 40 | 55 |
| W-Deep | 12 | 4 | 12 | 8 | 8 | 14 | 10 | 14 | 26 | 16 | 7 | 19 | 18 | 13 | 17 | 22 |

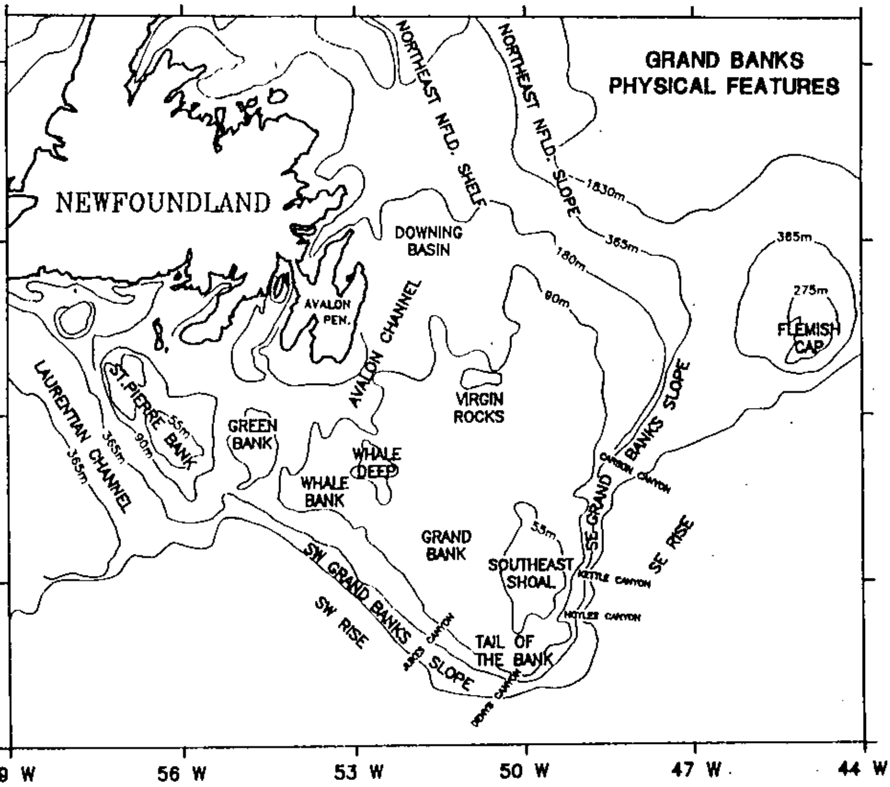


Fig. 1. Isobathymetrics and other physical features of the Grand Banks region.

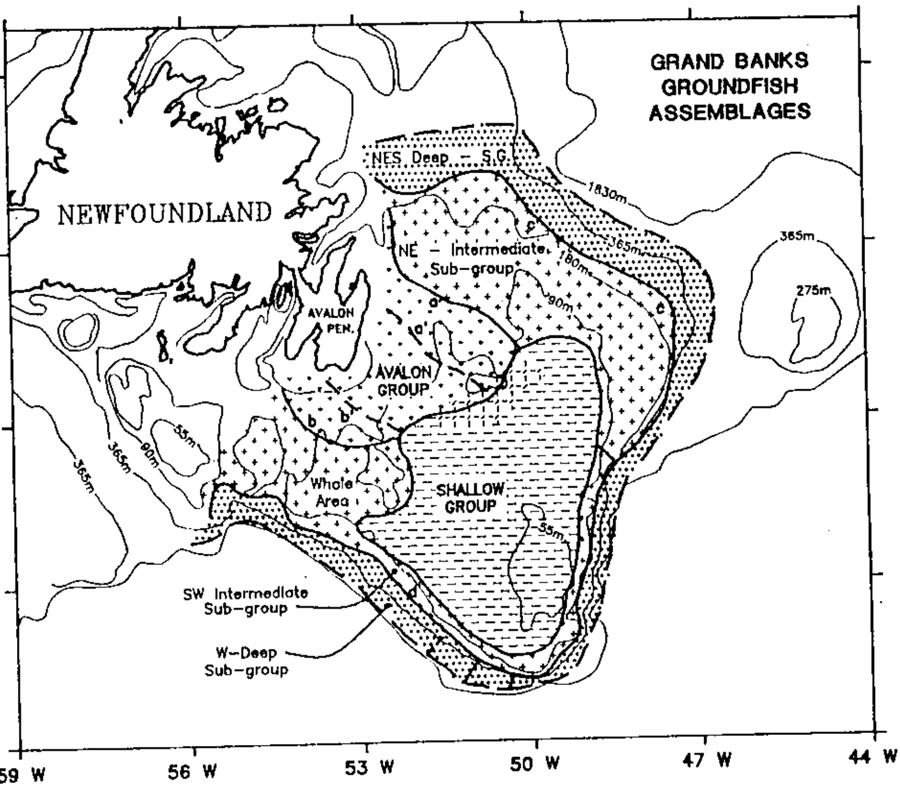


Fig. 2. Geographic position of cluster groups on the Grand Bank. The contours presented were pooled out of 16 spring situations analysed. They do not represent any year in particular but rather the more typical situation found. Different patterns cover areas with different fish assemblages. The Deep and Intermediate areas are subdivided in two sub-groups each (see text).

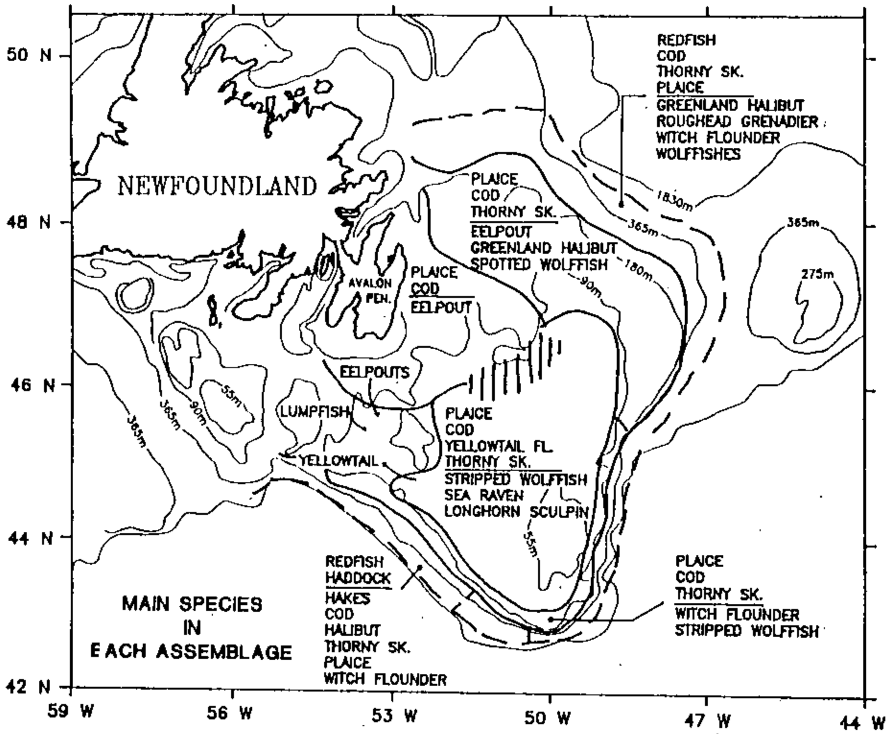


Fig. 3. Main species in each of the six fish assemblages considered. Species are ranked by approximate decreasing order of abundance in the hauls. Straight horizontal lines separate groups of species having different order of magnitude in the catches.

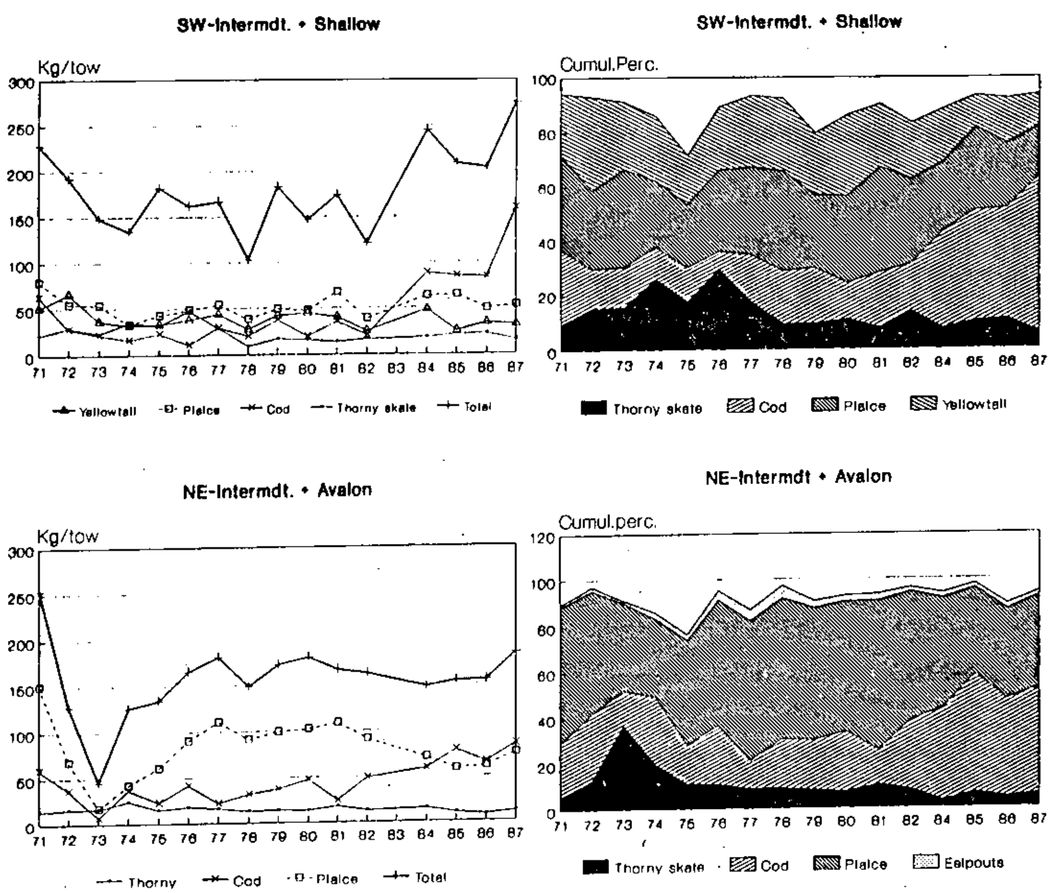


Fig. 4. Trends in SW-Intermediate + Shallow and NE-Intermediate + Avalon combined assemblages during period 1971-82 1984-87. Line graphs present trends in catch per unit effort (Kg/tow) of spring trawl surveys and shadowed graphs present relative proportion (cumulative percentage) of main species in hauls.

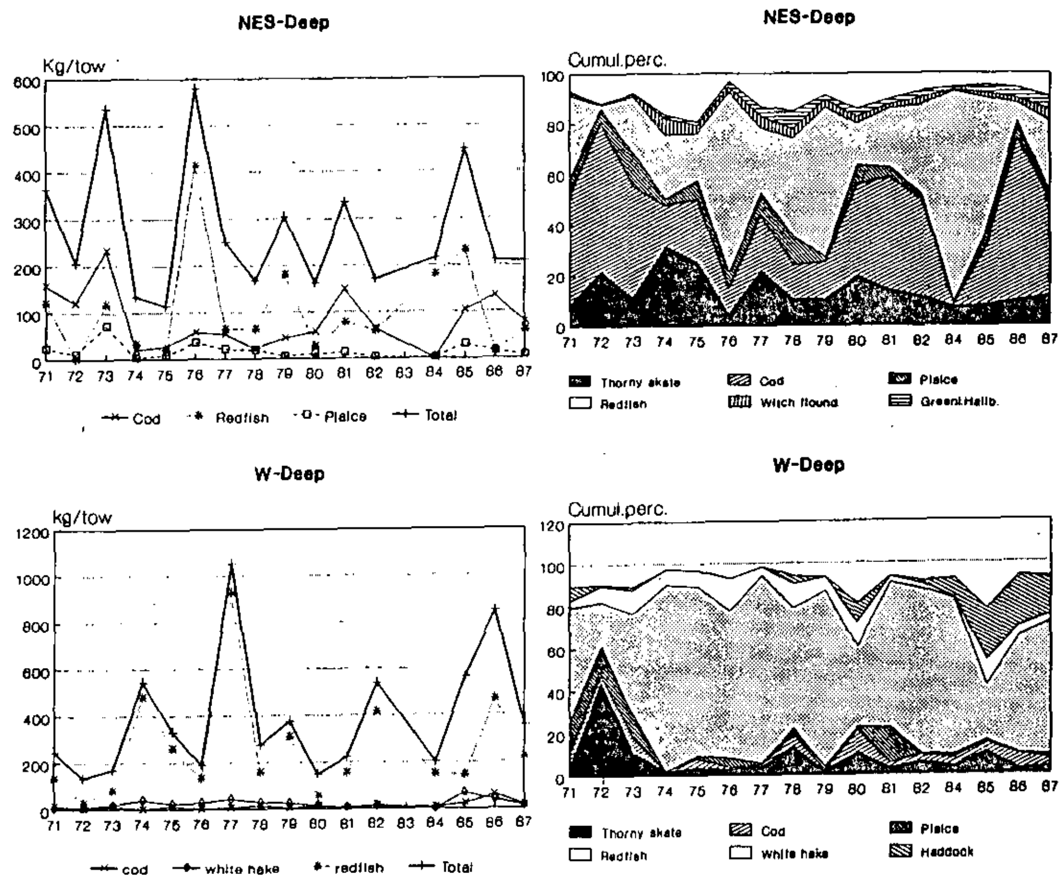


Fig. 5. Trends in NES-Deep and W-Deep assemblages during period 1971-82, 1984-87. Line graphs present trends in catch per unit effort (Kg/tow) of spring trawl surveys and shadowed graphs present relative proportion (cumulative percentage) of main species in hauls.

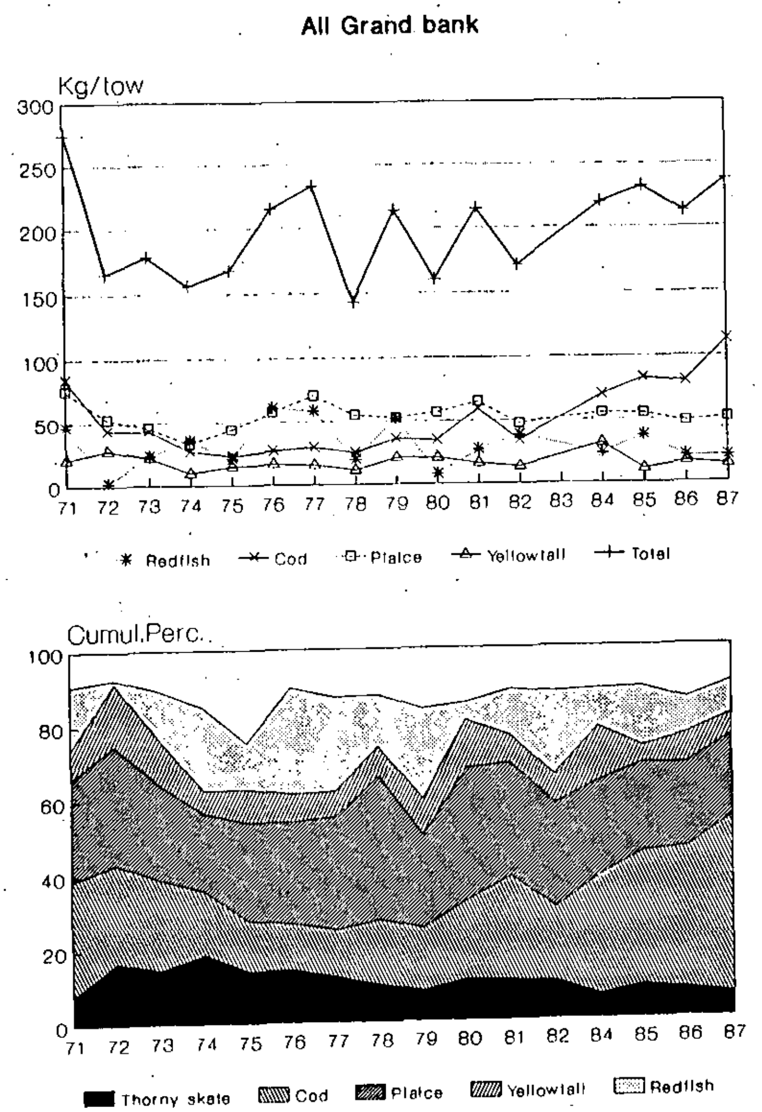


Fig. 6. Trends in the Grand Bank (all assemblages combined) during period 1971-82 1984-87. Line graph presents trends in catch per unit effort (Kg/tow) of spring trawl surveys and shadowed graph presents relative proportion (cumulative percentage) of main species in hauls.

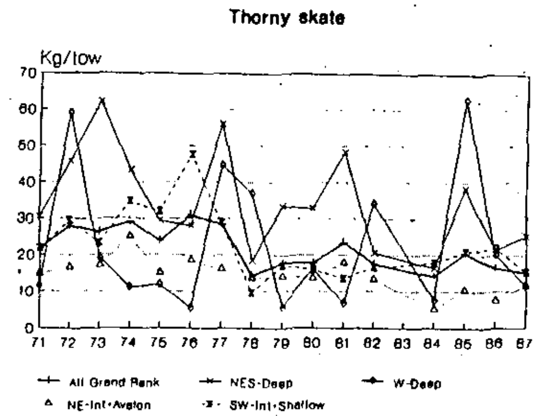


Fig. 7. Trends in catch per unit (Kg/tow) of thorny skate in various assemblage areas and in all Grand Bank. Spring trawl surveys carried out during period 1971-82 1984-87.

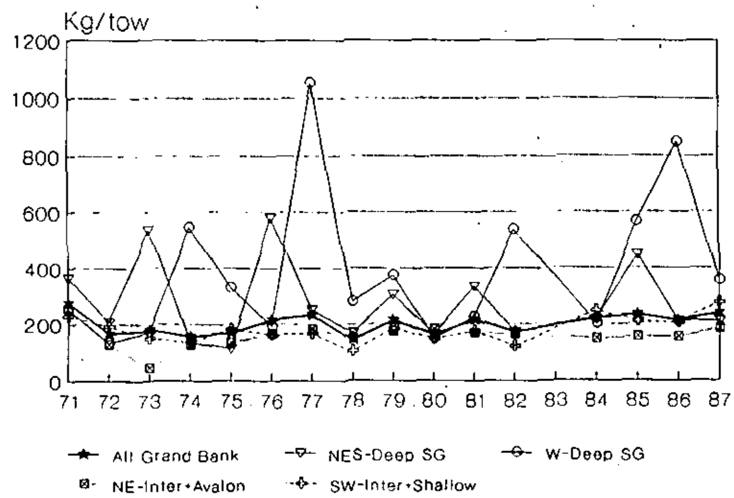


Fig. 8. Trends in catch per unit effort (Kg/tow) of all species in various assemblage areas and in all Grand Bank. Spring trawl surveys carried out during period 1971-82 1984-87.